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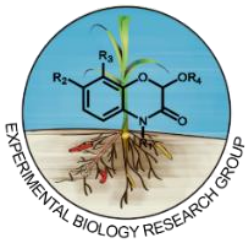

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SOIL LEGACY EFFECTS OF *PHOTORHABDUS* BACTERIA METABOLITES ON PLANT PERFORMANCE AND RESISTANCE

A THESIS SUBMITTED TO THE FACULTY OF SCIENCE, UNIVERSITY OF NEUCHÂTEL IN FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY (PhD) IN BIOLOGY

BY

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Declaration

I, Jaspher Ewany, declare that this thesis is my original work and has not been presented for the award of a degree in any other University.

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List of abbreviations

ANOVA	Analysis of Variance
BGC	Biosynthetic Gene Clusters
Bt	*Bacillus thuringiensis*
BXD	Benzoxazinoid
C	Carbon
CABI	Centre for Agriculture and Bioscience International
CN	Organic carbon – Nitrogen ratio
DDA	Data-Dependent Acquisition
DNA	Deoxyribonucleic acid
EPNs	Entomopathogenic nematodes
FAO	Food and Agriculture Organisation of the United Nations
FAW	Fall Armyworm
FBMN	Feature-Based Molecular Networking
GNPs	Global Natural Products
IPM	Integrated Pest Management
LB	Lysogeny Broth agar
LOI	Loss of Ignition
MIR	Microbe-Induced Resistance
MK	Mechanically Killed
MS	Mass spectrometry
N	Organic Nitrogen
Pbio	Bioavailable phosphorus
PCA	Principal Component Analysis
PCoA	Principal Coordinates Analysis
PCR	Polymerase Chain Reaction
PERMANOVA	Permutational Analysis of Variance
PLS-DA	Partial Least-Squares Discriminant Analysis
RH	Relative Humidity
RPM	Revolutions Per Minute
SEM	Standard Error of the Mean
SOM	Soil Organic Matter
UGTs	UDP-glycosyltransferases
UHPLC-QTOFMS	Ultra-High-Performance Liquid Chromatography-Quadrupole Time-of-Flight Mass Spectrometry

General abstract

Photorhabdus bacteria are potent insect-killing microbes offering a prime opportunity for environmentally benign pest control. However, applying *Photorhabdus* bacteria by foliar sprays or soil drenching without its entomopathogenic nematode vector introduces bacterial cells and toxins into the soil. Yet, the soil legacy effects of *Photorhabdus* bacteria and their metabolites on plants and other organisms are unknown.

In this study, I investigated the soil legacy effects of *Photorhabdus* metabolites on soil microbial community, plant physiology, performance and resistance against insect attack. To achieve this, I conditioned soils with: i) *Photorhabdus*-infected insect cadavers or mechanically killed (MK) larvae, ii) water extracts of toxins derived from *Photorhabdus*-infected insect cadavers, or from MK larvae, iii) cell-free *Photorhabdus* culture supernatants, iv) autoclaved soil complemented with 10% of live soil previously conditioned with *Photorhabdus*-infected insect cadavers or MK, and used non-conditioned soil as the control. I then measured plant growth traits and biomass accumulation in plants grown on the different soil conditioning treatments. Next, I employed amplicon sequencing to determine how soil conditioning affected the bacterial, nematode, and fungal communities. Finally, I evaluated the performance of *Diabrotica balteata* and *Spodoptera frugiperda* larvae feeding on plants grown on conditioned soil, and I used metabolomics to profile plant responses at the metabolic level.

I showed that all soil conditioning treatments significantly improved plant growth by 10 – 26% compared to controls. However, there were no significant differences in the height, leaf length and width, and number of crown roots of experimental plants compared to controls. Similar plant growth effects were observed in plants grown on complemented soil, underscoring the role of soil microorganisms in these results. Upon analysing the soil microbial community, soil conditioning with *Photorhabdus*-infected insect cadavers or MK significantly altered the bacterial and nematode communities, while the fungal community remained stable. Notably, beneficial bacteria and nematode species were more abundant in conditioned than in control soil, likely explaining the improved plant growth in conditioned soil. I also showed that plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers significantly suppressed the feeding of insect larvae in a strain-specific manner. Specifically, *D. balteata* and *S. frugiperda* larval weights were reduced by 10 – 20% and 10 – 59% respectively, less than the control. Moreover, resistant plants accumulated twelve and eight distinct root and leaf metabolites, respectively, with known biological effects against insects and pathogens.

Based on these findings, I conclude that soil conditioning with *Photorhabdus* metabolites improves plant growth, modulates the microbial community towards a structure that benefits plant growth and conditioning with selected *Photorhabdus* strains triggers plant systemic responses against root and leaf-feeding herbivores.

Keywords: *Photorhabdus*, soil conditioning, plant growth, microbial community, resistance, *Diabrotica balteata,* and *Spodoptera frugiperda*

Résumé général (French version)

Les bactéries Photorhabdus sont des microbes puissants qui tuent les insectes et offrent une excellente opportunité pour lutter contre les ravageurs de manière écologique. Cependant, l'application de bactéries *Photorhabdus* par pulvérisation foliaire ou arrosage du sol sans leur vecteur nématode entomopathogène introduit des cellules bactériennes et des toxines dans le sol. Or, les effets à long terme des bactéries *Photorhabdus* et de leurs métabolites sur les plantes et autres organismes sont inconnus.

Dans cette étude, j'ai examiné les effets résiduels des métabolites de *Photorhabdus* sur la communauté microbienne du sol, la physiologie des plantes, leur performance et leur résistance aux attaques d'insectes. Pour ce faire, j'ai conditionné les sols avec : i) des cadavres d'insectes infectés par *Photorhabdus* ou des larves tuées mécaniquement (MK), ii) des extraits aqueux de toxines provenant de cadavres d'insectes infectés par *Photorhabdus* ou de larves MK, iii) des surnageants de culture de *Photorhabdus* sans cellules, iv) du sol autoclavé complété avec 10 % de sol vivant préalablement conditionné avec des cadavres d'insectes infectés par Photorhabdus ou des larves MK, et j'ai utilisé du sol non conditionné comme témoin. J'ai ensuite mesuré les caractéristiques de croissance des plantes et l'accumulation de biomasse chez les plantes cultivées sur les différents traitements de conditionnement du sol. Ensuite, j'ai utilisé le séquençage d'amplicons pour déterminer comment le conditionnement du sol affectait les communautés bactériennes, nématodes et fongiques. Enfin, j'ai évalué les performances des larves de *Diabrotica balteata* et *Spodoptera frugiperda* se nourrissant de plantes cultivées sur un sol conditionné, et j'ai utilisé la métabolomique pour établir le profil des réponses des plantes au niveau métabolique.

J'ai démontré que tous les traitements d'amendement du sol amélioraient considérablement la croissance des plantes, de 10 à 26 % par rapport aux plantes témoins. Cependant, aucune différence significative n'a été observée en termes de hauteur, de longueur et de largeur des feuilles, ni de nombre de racines pivotantes entre les plantes expérimentales et les plantes témoins. Des effets similaires sur la croissance des plantes ont été observés chez les plantes cultivées sur un sol amendé, soulignant le rôle des micro-organismes du sol dans ces résultats. Après analyse de la communauté microbienne du sol, l'amendement du sol avec des cadavres d'insectes infectés par *Photorhabdus* ou MK a considérablement modifié les communautés bactériennes et nématodes, tandis que la communauté fongique est restée stable. Il est à noter que les bactéries bénéfiques et les espèces nématodes étaient plus abondantes dans le sol amendé que dans le sol témoin, ce qui explique probablement l'amélioration de la croissance des plantes dans le sol amendé. J'ai également montré que les plantes cultivées sur des sols amendés avec des cadavres d'insectes infectés par *Photorhabdus* ont considérablement réduit l'alimentation des larves d'insectes d'une manière spécifique à chaque souche. Plus précisément, le poids des larves de *D. balteata* et *S. frugiperda* a été réduit respectivement de 10 à 20 % et de 10 à 59 %, soit moins que dans le

sol témoin. De plus, les plantes résistantes ont accumulé respectivement douze et huit métabolites distincts dans leurs racines et leurs feuilles, dont les effets biologiques contre les insectes et les agents pathogènes sont connus.
Sur la base de ces résultats, je conclus que l'amendement du sol avec des métabolites de *Photorhabdus* améliore la croissance des plantes, module la communauté microbienne vers une structure favorable à la croissance des plantes et que l'amendement avec des souches sélectionnées de *Photorhabdus* déclenche des réponses systémiques chez les plantes contre les herbivores qui se nourrissent des racines et des feuilles.

Mots clés : *Photorhabdus*, amendement du sol, croissance des plantes, communauté microbienne, résistance, *Diabrotica balteata* et *Spodoptera frugiperda*

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General introduction

Maize (*Zea mays* L.)

Maize (*Zea mays* L.) is a native crop of the Americas that was first domesticated in southern Mexico about 9,000 years ago (Kennett et al., 2020). Maize cultivation has since spread widely and become one of the most cultivated crops in both developing and developed economies, including 165 countries in Africa, Europe, the Americas, and Asia (FAOStat, 2021). Being a C4 plant, maize has one of the best photosynthetic efficiencies and can adapt to environmental conditions ranging from the tropics to temperate zones, making it easier to cultivate worldwide (Mekonnen and Gerbens-Leenes, 2020). The global land area under maize cultivation is estimated to be over 197 M ha, with sub-Saharan Africa, Asia and Latin America dedicating significantly more land than other regions in the world (FAOStat, 2021).

Today, maize is considered to be a global staple cereal, with annual production exceeding 1 billion metric tons (García-Lara and Serna-Saldivar, 2019). In Sub-Saharan Africa, it is a staple food cultivated by over 300 million people, particularly smallholders, who produce the majority (~70–90%) of the region's maize on small plots of less than 0.5 hectares Mathenge et al., 2014 (Mathenge et al., 2014; Daly et al., 2016; Epule et al., 2021). Households consume maize in various forms such as fermented dough, roasted maize, corn porridge, corn oil, and corn beer (Ranum et al., 2014; Adiaha et al., 2016; Ekpa et al., 2019). Beyond household consumption, maize is traded as animal feed, and many farmers sell their surplus produce to millers to earn income to finance household needs (Adiaha et al., 2016). Maize cultivation is therefore crucial in reducing rural poverty and food insecurity (Epule and Bryant, 2015; Manda et al., 2018), making it one of the crops of significant importance that requires research attention.

As the global population escalates, maize cultivation and demand in developing countries are expected to double between 2020-2050 to sustain an estimated 9.3 billion people by 2050 (Bahar et al., 2020). However, farmers are challenged with increasing production amidst various biotic and abiotic stressors that reduce yield and quality. In many recent studies, insect pests such as the fall armyworm and pathogens have been well documented as the major cause of yield reduction and quality in maize (James and Zikankuba, 2018; Savary et al., 2019; Kansiime et al., 2023; Benjamin et al., 2024). With the high volume of chemical pesticides used against pests and their undesirable off-target effects, it's been suggested that sustainable management strategies are required while increasing yields to meet global food demands (Mulungu et al., 2024).

Fall armyworm (*Spodoptera frugiperda*)

Fall Armyworm (FAW), *Spodoptera frugiperda*, is one of the most devastating crop pests in Africa, destroying staple crops such as maize and sorghum (Day et al., 2017; Bateman et al., 2018). The major damages are caused at the larval stage of the pest life cycle, and specifically, in sub-Saharan Africa, it's been estimated that annual losses to FAW in maize, rice, sorghum,

and sugarcane could be up to 13 billion USD (Abrahams et al., 2017). In maize alone, yield losses due to FAW are predicted to be around 40-45% (Bateman et al., 2018), posing threats to food security and livelihoods of millions of smallholders in the African continent.

In Africa, FAW was first detected in 2016 in Nigeria and because of its migratory nature, reports of spread were recorded in over 45 African countries in a short period (Goergen et al., 2016; Abrahams et al., 2017), including in the Islands such as Madagascar, Seychelles and Cabo Verde (Day et al., 2017; FAO, 2018a). Asian countries are the recent regions of FAW invasion (Sharanabasappa et al., 2018; Sun et al., 2021; Qi et al., 2021; Ge et al., 2022). *Spodoptera frugiperda* is an indigenous pest of the Americas that feeds on over 350 plant species worldwide, making it easier for the pest to establish in new areas (Montezano et al., 2018). It has been reported that the persistence of FAW in new areas is facilitated by the availability of many host plants, and the favourable conditions such as the tropical and subtropical climates, which have been found suitable for their constant reproduction (Goergen et al., 2016; Midega et al., 2018; Montezano et al., 2018). Several other African countries such as Gabon, Equatorial Guinea, Uganda, Rwanda, Burundi, Tanzania, Ethiopia, Kenya, Zimbabwe, Zambia, Angola, Democratic Republic of Congo, and Madagascar have climate conditions that favour FAW survival and establishment (Early et al., 2018; Paudel Timilsena et al., 2022). Thus, these countries could become potential origins of future FAW outbreaks (Day et al., 2017; Paudel Timilsena et al., 2022).

Since the detection of FAW in Africa, synthetic pesticides have been widely used to control this pest (Day et al., 2017). It's been reported that more than 60% of farmers applied pesticides against FAW in Ghana and Zambia (Abrahams et al., 2017), whereas over 48% of farmers applied the chemical method in Ethiopia and Kenya (Kumela et al., 2018). It's been reported that many governments of African countries procured and distributed synthetic chemical pesticides to farmers, mainly the cheapest options, such as methomyl, methyl parathion, endosulfan, and lindane. These are classified under highly hazardous pesticides (FAO, 2018a). Moreover, farmers usually used these toxic products without suitable personal protective equipment, which increases the risks associated with their use (Bateman et al., 2018). The indiscriminate use of chemicals has made control against FAW difficult due to the development of resistance to several groups of pesticides namely, carbamates, organophosphates, pyrethroids and new chemistries (Al-Sarar *et al.,* 2006; Carvalho *et al.,* 2013; Sparks and Nauen, 2015; Zhu *et al.,* 2015; Bolzan *et al.,* 2019; Gutiérrez-Moreno *et al.,* 2019; Kumela *et al.,* 2019; Lira *et al.,* 2020; Boaventura *et al.,* 2021; Garlet *et al.,* 2021; Muraro *et al.,* 2021). Field resistances to *Bacillus thuringiensis* (Bt) based products applied against the pest have also been reported (Storer e*t al.,* 2010; Zhu *et al.,* 2015; Chandrasena *et al.,* 2018; Yang *et al.,* 2018; Boaventura *et al.,* 2021). With this high level of reliance on chemical pesticides and the development of pest resistance to control agents used against FAW, it has

been recognized that a sustainable Integrated Pest Management (IPM) system is required (FAO and CABI, 2019).

Banded cucumber beetle (*Diabrotica balteata* LeConte)

Another important pest that is problematic to maize production is the banded cucumber beetle (*Diabrotica balteata* LeConte), which belongs to the genus *Diabrotica Chevrolat* (Coleoptera: Chrysomelidae). The genus comprises over 400 *Diabrotica* species (Derunkov and Konstantinov, 2013)**,** with several polyphagous members that feed on a wide range of globally cultivated crops (Saba, 1970; Hirsh and Barbercheck, 1996; Moeser and Vidal, 2004; Derunkov and Konstantinov, 2013; Alouw and Miller, 2015). Specifically, *D. balteata* adults and larvae are known to feed on the leaves and roots respectively, of many plant species, including cabbages, okra, lettuce, onion, beet, pea, sweet potato, soybean, bean, squash, cucumber, and maize (Saba, 1970; Cardona et al., 1982; Banda at al., 2004; Clark et al., 2004; Walsh et al., 2020). The ability of *D. balteata* to spread and cause severe economic losses beyond the native regions has been documented (Johnson et al., 2016; Marchioro and Krechemer, 2018). The wide availability of host plants has been cited among the factors facilitating the rapid spread and establishment of insect pests in new regions (Seebens et al., 2015)**.** Moreover, on a global scale, the annual losses caused by invasive pest species were estimated to be US$77 billion (Bradshaw et al., 2016).

As a root-feeding insect, the main strategies to control *D. balteata* are based on seed treatments, in-furrow spraying, and the application of granular pesticide (Walsh et al., 2020). However, the cryptic behaviour of *D. balteata* makes it difficult to target with pesticide sprays, and also, the adult and larvae often defend themselves from natural enemies by sequestering cucurbitacin compounds (Ferguson and Metcalf, 1985; Eben and Barbercheck, 1996; Tallamy et al., 1998; Gámez-Virués and Eben, 2005; Robert et al., 2017; Zhang et al., 2019a)**.** Cucurbitacin is considered to be the bitterest compound obtained from plant tissues by adult *D. balteata* and is transferable into the eggs and larvae through females (Ferguson and Metcalf, 1985; Bruno et al., 2022). *D. balteata* is among the insect pests that are well adapted to cucurbitacin compounds and prefer to feed on plants with a high cucurbitacin content (Jaccard et al., 2021; Bruno et al., 2022). Although the cucurbitacin sequestered by *D. balteata* does not impact some natural enemies, it has an antibiotic activity against the entomopathogenic fungus, *Metarhizium anisopliae* (Tallamy et al., 1998; Bruno et al., 2022). Thus, making it difficult to achieve control with certain biocontrol methods. To date, pesticides belonging to organophosphates, phenylpyrazole and neonicotinoids are reported to be widely used against *D. balteata* (Salles, 2000; Viana and Marochi, 2002; Walsh et al., 2020). The frequent use of these pesticide-based controls has rendered them ineffective against *D. balteata* due to pest resistance (Walsh et al., 2020), suggesting that sustainable pest

management strategies are required to combat this pest. Generally, pest resistance leads to the misuse of pesticides where farmers increase rates and application frequency in an attempt to get rid of pests in crop fields (Kumela et al., 2018; Sisay et al., 2019). This exacerbates risks to expose farm workers, contaminate the final harvested produce with pesticide residues, and the environment (Pouokam et al., 2017). These problems have prompted the need to develop more environmentally safe methods with more efficacy against the two pests, FAW and *D. balteata*.

Entomopathogenic nematodes

Entomopathogenic nematodes (EPNs) are tiny, obligate soil-dwelling worms that are lethal to a wide range of insects and have been used as biological control agents against agricultural pests (Poinar, 1979; Lacey et al., 2015; Klein, 2018; Shapiro-Ilan and Lewis, 2024). EPNs widely used as pest control agents are mainly from the genera *Steinernema* and *Heterorhabditis*, which are obligate lethal pathogens of insects (Lacey et al., 2001; Georgis et al., 2006; Kaya et al., 2006; Shapiro-Ilan et al., 2014). *Steinernema* and *Heterorhabditis* establish mutualistic relationships with bacteria of the genera *Xenorhabdus* and *Photorhabdus*, respectively. The nematodes carry the symbionts inside their intestines and release them immediately after penetrating the body of a suitable insect host via the insect cuticle or openings such as the mouth, the anus and the spiracles (Brivio et al., 2004; Elesftherianos et al., 2010; Castillo et al., 2011; Lewis and Clarke, 2012; Toubarro et al., 2013). The bacteria produce toxins and digestive enzymes that kill and pre-digest the infected insect, and antibiotics and repulsive toxins that protect the insect from competing microorganisms, predators, and scavengers (Webster et al., 2002; Ffrench-Constant et al., 2003; Sicard et al., 2006; Bode, 2009; Singh et al., 2014; Gerdes et al., 2015; Singh and Forst, 2016). Nematode-infected insect host usually dies between 24 – 48 hours, then nematodes and bacteria proliferate in the insect cadaver until all resources are depleted. Nematodes and bacteria re-establish symbiosis and abandon the insect cadaver to search for new hosts (Ffrench-Constant et al., 2007; Bode, 2009; Gerdes et al., 2015).

Among the biological methods applied globally, EPNs have proven to contribute an important part in sustainable Integrated Pest Management (IPM) programs, with several positive attributes, including safety to humans, beneficial organisms, and the environment (Akhurst and Smith, 2002; Ehlers, 2005; Shapiro-Ilan and Grewal, 2008). EPNs have been used against several problematic soil-dwelling and root-boring pests (Grewal et al., 2005; Ehlers et al., 2008; Lacey et al., 2015; Jaffuel et al., 2020). However, the use of EPNs has been limited by their varying efficacy in field applications due to their sensitivity to adverse environmental conditions (Lacey et al., 2015). To overcome these, developments have been made to improve the application and efficacy of EPNs, not only belowground but also in non-soil habitats. Examples

include the application of EPNs in liquid, powder, or solid streams into the soil against the western corn rootworm (*Diabrotica virgifera virgifera*) or EPNs encapsulated in alginate beads against *D. balteata* larvae, which effectively improved control of these pests in the field and greenhouse conditions (Ehlers et al., 2008; Kim et al., 2015; Jaffuel et al., 2020). Moreover, healthy *D. balteata* larvae are attracted to EPN-infected cadavers, which increases the chances of infectivity as EPN-infected cadavers become aggregation sites (Zhang et al., 2019b). The application of EPNs has also been enhanced with sprayable gel formulations and protectants to target aboveground pests (Acharya et al., 2020). Notably, foliar sprays of EPNs aboveground have been successful in controlling *Bemisia tabaci, Plutella xylostella, Synanthedon pictipes* and *Spodoptera frugiperda* (Schroer and Ehlers, 2005; Schroer et al., 2005; Cuthbertson et al., 2007; Shapiro-Ilan et al., 2010; Fallet et al., 2022).

Entomopathogenic nematode symbiotic bacteria for pest control

EPN symbiont bacteria *Photorhabdus* and *Xenorhabdus* applied alone without the EPN vector are potent biological control agents against many agricultural pests, plant pathogens, and human parasites (Ahantarig et al., 2009; Orozco et al., 2016; Shawer et al., 2018; Vitta et al., 2018; Vicente-Díez et al., 2021; 2023). When ingested or contacted by insects, *Photorhabdus* and *Xenorhabdus* bacteria operate by producing several toxic compounds and metabolites that have antibacterial, insecticidal, cytotoxic, antimicrobial, antifungal, acaricidal and antiparasitic properties (Waterfield et al., 2005; Eleftherianos et al., 2007; Ffrench-Constant et al., 2007; Furgani et al., 2008; Bode, 2009; Grundmann et al., 2014; Tobias et al., 2016; Muangpat et al., 2017; Antonello et al., 2018; Vitta et al., 2018; Eroglu et al., 2019; Cevizci et al., 2020). This arsenal of toxins and metabolites usually kill insects within 24 – 48 hours (Adams and Nguyen, 2002; Ffrench-Constant et al., 2003; 2007; Bode, 2009; Gerdes et al., 2015). The *Xenorhabdus* and *Photorhabdus* metabolites and toxins also protect the insect cadaver against competitors that reside in the soil, for example, predators and pathogens, including the necrotrophic ones (Nealson et al., 1990; Webster et al., 2002; Sicard et al., 2006; Park et al., 2009; Singh et al., 2014; Singh and Forst, 2016). Notably, *Photorhabdus*-killed insects were found to be repellent to foraging ants (Baur et al., 1998; Zhou et al., 2002; Gulcu et al., 2018; Muller et al., 2024) and also to crickets, wasps and calliphorid flies (Gulcu et al., 2012). These toxic protectants play an important role in enabling EPNs to complete their life cycles, and specifically in *Steinernema*, the absence of defensive compounds has negative effects, ranging from poor development of infective juveniles to interruption of the entire lifecycle (Tobias et al., 2017).

Due to their high oral and contact toxicity against insect pests, EPN symbiont bacteria have been researched for sole application, as EPNs have shown unreliably varying results against many target pests (Denno et al., 2008; Lacey and Shapiro-Ilan, 2008; Toepfer et al., 2010;

Campos-Herrera et al., 2012). Therefore, the symbiont bacteria have often been isolated and applied by foliar spraying or soil drenching (Abdel-Razek, 2003; Mohan et al., 2003; Vyas et al., 2008; Shahina et al., 2011; Aatif et al., 2014; Kakade et al., 2023; Abdisa et al., 2024). To date, many *Photorhabdus* and *Xenorhabdus* strains have been explored for effectiveness against pests. For example, Salazar-Gutiérrez *et al.* (2017) showed that *P. akhurstii* subsp. *akhurstii* SL0708 was highly effective against the larvae of *G. mellonella* and *S. frugiperda*, causing death between 48 – 72 h. In their study, *Spodoptera frugiperda* was the most susceptible, exhibiting a loss of movement, inability to feed, and diarrhoea before death (Salazar-Gutiérrez et al., 2017). The species, *Xenorhabdus nematophila* (X1) and *P. laumondii* subsp. *laumondii* (GPS12) were tested against the female mushroom mite, *L. perniciosus* and *S. exigua* larvae, and over 85% mortality was achieved (Park and Kim, 2000; Bussaman et al., 2006; 2009). Additionally, many tested *Photorhabdus* and *Xenorhabdus* strains have been recommended to control mosquitoes (da Silva et al., 2013; Fukruksa et al., 2017; Vitta et al., 2018; Da Silva et al., 2020).

Over the past few decades, efforts have been put in place to enhance the application of *Xenorhabdus* and *Photorhabdus* bacteria by exploring their cell-free supernatants in pest control. These supernatants have been tested and shown to have lethal effects on many insects and mites (Brillard et al., 2002; Cabral et al., 2004; Dhanasekaran and Thangaraj, 2014; Sadekuzzaman et al., 2017; Eroglu et al., 2019). Studies have demonstrated that oral ingestion of *Photorhabdus* supernatant caused high mortality in adults of the sweet potato whitefly and Colorado potato beetles (Blackburn et al., 2005; Shrestha and Lee, 2012). Additionally, supernatants of *Xenorhabdus* strains *X. szentirmaii* and *X. nematophila* caused over 90% mortality when applied to the mobile stages of *T. urticae*, (Eroglu et al., 2019). Because of their control efficacy, it is suggested that only supernatants of these symbionts could potentially serve as alternatives to synthetic pesticides in pest control (Cevizci et al., 2020).

Soil legacy effects of *Photorhabdus* metabolites on plant performance and resistance

Soil legacy effects refer to the lasting impact of previous changes in soil conditions on the soil's current ability to perform ecosystem functions (Nannipieri et al., 2023). Soil legacy formation involves changes in soil microbial communities, nutrient dynamics, organic matter composition, and chemical signalling, creating a conditioning that persists and affects the ecosystem performance (van der Putten et al., 2013). These changes can be driven by a myriad of biotic and abiotic factors (Wurst and Ohgushi, 2015; Bennett and Klironomos, 2019; Canarini et al., 2021; Adekanmbi et al., 2022). However, the main drivers of soil legacies in agricultural systems have been attributed to plant and microbial-mediated mechanisms. Plants can impact their growth environments by altering the soil microbiome via rhizodeposition, litter inputs, and symbiotic associations (Kulmatiski et al., 2008; van der Putten et al., 2013). Plant litter inputs

drive nutrient cycling and can leave behind physical, chemical, and biotic legacies that impact soil functioning and plant growth (Elgersma et al., 2012; Bonanomi et al., 2021, 2023). Moreover, plant secondary metabolites and sugars released as root exudates can affect the microbial community by either attracting or repelling certain soil organisms, thus creating a plant-specific microbial signature that can persist and strongly influence plant growth (Philippot et al., 2013; Haichar et al., 2014; Gfeller et al., 2023).

On the other hand, microorganisms such as fungi and bacteria applied as inoculants in agriculture can have a carryover legacy effect that affects the soil microbial communities (Deng et al., 2019; Jiménez et al., 2020), the growth of succeeding plants and plant-insect interactions (Pineda et al., 2020; Carvalheiro et al., 2021; Davis et al., 2023). The direct effect of some beneficial microbes on the soil microbial communities has been shown (Deng et al., 2019; Jiménez et al., 2020). Additionally, it has been found that microbial inoculum applied by foliar spraying can modulate plant metabolism (De Kesel et al., 2021; Martínez-Medina et al., 2024). When these metabolites are released via root exudates, they can significantly impact the soil microbial communities without direct contact with the microbial inoculum (Bais et al., 2006; Philippot et al., 2013; Rasool et al., 2025). These plant and microbial-mediated soil conditioning legacies by previous plants may influence the microbial community that the current plant encounters or interacts with, consequently impacting plant growth and performance (Philippot et al., 2013). The resultant changes in soil microbial communities can positively affect crop production through the recruitment of beneficial microorganisms that support plant growth or negatively via the accumulation of plant pathogens that reduce plant growth (Dudenhöffer et al., 2018; Santoyo et al., 2021; Zhang et al., 2022; Gul et al., 2023). While the impacts of plant secondary metabolites and some microbial inoculants as mediators of plant-soil feedbacks is generally well understood, the soil legacy effects of *Photorhabdus* bacteria and their metabolites are still unknown.

Photorhabdus bacteria are used to control *Spodoptera frugiperda* and *Diabrotica balteata* because of their proven control efficacy against a wide range of pests, pathogens and parasites (Ahantarig et al., 2009; Orozco et al., 2016; Shawer et al., 2018; Vitta et al., 2018; Vicente-Díez et al., 2021; 2023). The bacteria have been isolated and often applied by foliar spraying or soil drenching to target belowground and aboveground pests (Abdel-Razek, 2003; Mohan et al., 2003; Vyas et al., 2008; Shahina et al., 2011; Aatif et al., 2014; Kakade et al., 2023; Abdisa et al., 2024). However, massive densities of bacteria are introduced into the soil by the application methods (drenching) or by decomposing *Photorhabdus*-infected insect cadavers. Yet, their soil legacy effects are unknown (Grewal et al., 2001; Regaiolo et al., 2020).

Objectives of this PhD thesis

The overall objective of this study was to investigate the soil legacy effects of *Photorhabdus* bacteria on plant physiology, performance and resistance to insect attack. To this end, I measured:

i) Plant performance in a greenhouse environment
ii) Plant metabolite levels and resistance against *D. balteata* and *S. frugiperda* – belowground and above-ground insect herbivores, respectively.
iii) Soil microbial communities and their effects on plant growth

In Chapter 1, I investigated the impact of conditioning soils with *Photorhabdus*-infected insect cadavers on plant growth and biomass accumulation. I hypothesised that *Photorhabdus*-derived toxins and metabolites released from decomposing insect cadavers or cell-free *Photorhabdus* culture supernatants impact plant growth and biomass accumulation via microbial community changes. To test this hypothesis, I conducted a series of plant growth and plant biomass measurements of plants grown in soils conditioned with: i) *Photorhabdus*-infected insect cadavers, ii) water extracts of toxins derived from *Photorhabdus*-infected insect cadavers, or iii) cell-free *Photorhabdus* culture supernatants. To mechanistically link the potential changes in soil microbial communities caused by *Photorhabdus* metabolites to plant growth, I conducted soil sterilisation and complementation experiments and measured plant growth and biomass accumulation.

In Chapter 2, I assessed the performance of the root-feeding herbivore, *D. balteata* and the leaf-feeding herbivore, *S. frugiperda* larvae, on maize plants grown in soils conditioned with *Photorhabdus*-infected insect cadavers. I hypothesised that conditioning the soil with *Photorhabdus*-infected insect cadavers alters the secondary metabolite production in plants and that these changes, in turn, affect the performance of both root- and leaf-feeding herbivores. To test this hypothesis, I fed *D. balteata* and *S. frugiperda* larvae *ad libitum* on fresh roots and leaves, respectively, of plants grown on soils conditioned with *Photorhabdus*-killed insect cadavers or with mechanically killed insect larvae, or on control, non-conditioned soils. Then, I measured the performance of *D. balteata* and *S. frugiperda* larvae by weighing larvae and calculating the percentage mortality whilst feeding on plants grown on the different soil conditioning treatments. To evaluate plant responses to soil conditioning at the metabolic level, I analysed small molecular weight metabolites in the roots and leaves of plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers, mechanically killed insect larvae or non-conditioned soil as the control.

In Chapter 3, I examined the effect of soil conditioning with *Photorhabdus*-infected insect cadavers on soil microbial communities. I hypothesised that *Photorhabdus*-derived toxins and metabolites, released from decomposing insect cadavers, affect the soil microbial community.

To test this hypothesis, soil conditioning experiments were set up in a greenhouse environment, and I collected samples of three soil treatments: i) non-conditioned control soil, ii) soil conditioned with *Photorhabdus*-infected insect cadavers, and iii) soil conditioned with mechanically killed insect larvae. Amplicon sequencing was used to examine the composition and diversity of bacterial, nematode, and fungal species in the different experimental soil treatments.

Graphical Abstract:

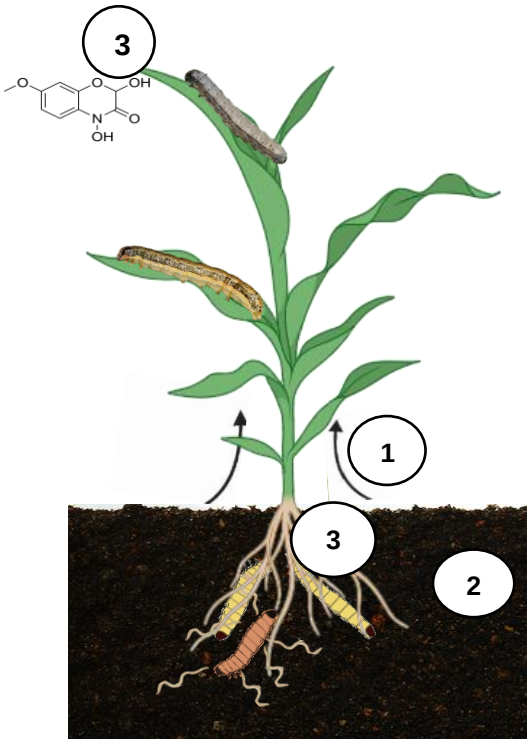

Figure 1. (1) Soil conditioning with *Photorhabdus*-infected insect cadavers can create a soil legacy effect that can impact plant growth. (2) Soil conditioning may also impact the resident microbial communities' composition and diversity in the rhizosphere of plants. (3) These changes in the rhizosphere can modulate the systemic plant defense in plant roots and leaves, and impact root and leaf-feeding herbivores.

Chapter 1

Soil legacy effects of *Photorhabdus* metabolites on plant performance

Abstract

Photorhabdus bacteria are lethal insect pathogens, offering a prime opportunity for environmentally benign pest control. Due to their high oral and contact toxicity, the bacteria can be applied directly without the vectoring nematode host by foliar spraying or soil drenching. This results in massive amounts of bacterial cells, toxins and metabolites in the soil. While the direct effects of *Photorhabdus* bacteria and their metabolites on target insect pests are known, their indirect effects on plant performance are unknown.

In the present study, I investigated the soil legacy effects of *Photorhabdus* bacteria and their toxins on the performance of maize plants. To achieve this, I measured plant growth traits and biomass accumulation in plants grown on soils conditioned with: i) *Photorhabdus*-infected insect cadavers or mechanically killed (MK) larvae, ii) water extracts of toxins derived from *Photorhabdus*-infected insect cadavers, or from MK larvae, iii) cell-free *Photorhabdus* culture supernatants and compared them with plants grown on non-conditioned control soil. To mechanistically link the potential changes in soil microbial communities caused by *Photorhabdus* metabolites to plant growth, I conducted soil sterilisation and complementation experiments and measured plant growth and biomass accumulation.

I showed that soil conditioning significantly improved plant total biomass by: 10 – 20% in soil conditioned with *Photorhabdus*-infected insect cadavers or MK larvae, 11 – 20% in soil conditioned with cell-free *Photorhabdus* culture supernatants, and by 10 – 26% in soil conditioned with water-extracts of toxins derived from macerated *Photorhabdus*-infected insect cadavers. Similar plant growth-promoting effects were observed in plants grown on complemented soil, highlighting the role of soil microorganisms in this context. However, no significant differences were observed in the heights, leaf length and width of plants grown on the different soil conditioning treatments compared to control plants. In the experiments with water extracts of toxins, the total biomass of plants grown on soil conditioned with water extracts of macerated MK larvae was insignificant across three independent experiments, indicating *Photorhabdus*-specific effects. Taken together, the results of MK larvae in all experiments indicate: i) *Photorhabdus*-independent effects in soils conditioned with *Photorhabdus-infected* insect cadavers because introducing insect biomass (independently of being killed by *Photorhabdus*) impacts plant growth, and ii) *Photorhabdus*-specific effects because introducing *Photorhabdus* cell-free supernatants, or water extracts of *Photorhabdus*-killed larvae, but not of MK-killed insects, improves plant growth.

Introduction

Insect pests are a significant constraint to global food production (Savary et al., 2019; IPPC, 2021). The annual crop losses caused by insect pest damage are estimated to range between 20 – 40% (FAO, 2020). From a financial perspective, it is estimated that pests cause economic losses of about $70 billion and that the total food consumed by pests can feed more than 1 billion people (Birch et al., 2011; Savary et al., 2019; FAO, 2020).

The Fall Armyworm (FAW), *Spodoptera frugiperda,* and the banded cucumber beetle (*Diabrotica balteata* LeConte) are serious pests, causing severe economic losses in maize (Saba, 1970; Banda et al., 2004; Clark et al., 2004; Johnson et al., 2016; Day et al., 2017; Bateman et al., 2018; Marchioro and Krechemer, 2018; Walsh et al., 2020). On a global scale, the annual losses to invasive pest species, including *S. frugiperda* and *D. balteata* were estimated to be US$77 billion and yield losses due to FAW infestation in maize alone are predicted to be around 40-45% (Bradshaw et al., 2016; Abrahams et al., 2017; Bateman et al., 2018). FAW pose threats to the food security and livelihoods of millions of smallholders in many countries, particularly in Africa and Asia (Day et al., 2017; FAO, 2018b; Sharanabasappa et al., 2018; Sun et al., 2021; Qi et al., 2021; Ge et al., 2022).

The management of *S. frugiperda* and *D. balteata* has traditionally relied on synthetic pesticides, which have become ineffective as these insects are resistant to chemicals (Salles, 2000; Day et al., 2017; Kumela et al., 2018; Lira et al., 2020; Walsh et al., 2020; Boaventura et al., 2021; Garlet et al., 2021; Muraro et al., 2021). Moreover, most pesticides applied against these pests are classified as highly hazardous, and their continuous use in pest control poses environmental and human health risks (FAO, 2018a). With the high level of reliance on chemical pesticides and the development of pest resistance, it has been recognized that a sustainable Integrated Pest Management (IPM) system is required (FAO and CABI, 2019). In addition, the increasing consumer demand for organic food with no pesticide residues and the strict regulations on food safety and quality in the international market point towards a need for sustainable control strategies in food production systems whilst minimizing the environmental impacts of pest control (Kiers et al., 2008; Gomiero et al., 2011; Ribeiro et al., 2012; Ray et al., 2013; Damalas and Koutroubas, 2018; Willer et al., 2023).

One of the promising alternatives to synthetic pesticides is entomopathogenic nematodes (EPNs) and their symbionts to control agricultural pests. EPNs from the genera *Steinernema* and *Heterorhabditis* are the commonly used EPNs to control root herbivores, and recent developments have enabled their usage against leaf herbivores (Acharya et al., 2020; Fallet., 2022a; 2022b). *Steinernema* and *Heterorhabditis* are obligate lethal pathogens of insects with mutualistic relationships with bacteria of the genera *Xenorhabdus* and *Photorhabdus*, respectively. The nematodes carry the symbionts in their guts and release them immediately after penetrating a suitable insect host (Ffrench-Constant et al., 2003; Bode, 2009). The

bacteria produce toxins and digestive enzymes that kill and pre-digest the infected insect, and antibiotics and repulsive toxins that protect the insect from competing microorganisms, predators, and scavengers (Webster et al., 2002; Ffrench-Constant et al., 2003; Sicard et al., 2006; Bode, 2009; Singh et al., 2014; Gerdes et al., 2015; Singh and Forst, 2016). Then, nematodes and bacteria proliferate in the insect cadaver until all resources are depleted. Nematodes and bacteria re-establish symbiosis and abandon the insect cadaver in search of a new host, leaving behind insect remains with all the different toxic and non-toxic metabolites produced by the bacteria. The effects of nematode-killed insect remains on the next generation of plants are not well understood.

In agricultural settings, EPNs and their symbionts are used to control insect pests in two main manners: 1) direct application of the EPNs in the soil, rhizosphere, or aerial parts of the plant, and 2) due to the high oral and contact toxicity, the bacteria are also often isolated and applied without the vectoring EPN host by foliar spraying or soil drenching (Abdel-Razek, 2003; Mohan et al., 2003; Vyas et al., 2008; Shahina et al., 2011; Aatif et al., 2014; Kakade et al., 2023; Abdisa et al., 2024). As a result, massive amounts of bacterial cells and metabolites, which have insecticidal, antimicrobial, acaricidal, cytotoxic and antiparasitic properties, are introduced into the soil (Waterfield et al., 2005; Eleftherianos et al., 2007; Ffrench-Constant et al., 2007; Bode, 2009; Tobias et al., 2016; Muangpat et al., 2017; Antonello et al., 2018; Vitta et al., 2018; Eroglu et al., 2019). While the direct effects of *Photorhabdus* cells and metabolites in the target insect pest are generally well understood, their indirect effects on the next generation of plants are not well understood (Grewal et al., 2001; Regaiolo et al., 2020).

In the present study, I investigated the impact of conditioning soil with *Photorhabdus*-infected insect cadavers on plant growth and biomass accumulation. I hypothesised that *Photorhabdus*-derived toxins and metabolites released from decomposing insect cadavers impact plant growth and biomass accumulation. To test this hypothesis, I conducted a series of plant growth and plant biomass measurements in plants grown in soils conditioned with: i) *Photorhabdus*-infected insect cadavers, ii) water extracts of toxins from *Photorhabdus*-infected larvae, or iii) cell-free *Photorhabdus* culture supernatants. To mechanistically link the potential changes in soil microbial communities caused by *Photorhabdus* metabolites to plant growth, I conducted soil sterilisation and complementation experiments and measured plant growth traits and biomass accumulation. This study demonstrated that both *Photorhabdus* toxins delivered in soil by the methods explained above, and the microbial community created by soil conditioning with *Photorhabdus*-killed larvae, improved plant growth. This work significantly advances the utilisation of *Photorhabdus* bacteria in IPM programs and will allow growers to exploit *Photorhabdus* strains in many different ways to support sustainable agriculture.

Materials and Methods

Insect rearing

Spodoptera frugiperda larvae were fed on an artificial diet (in g/Kg: soy milk 31.7, wheat germ 90, sugar 36.56, dried yeast 17.81, cholesterol 0.5, methylparaben 1, sorbic acid 2.3, ascorbic acid 2.46, vitamin B complex 0.184, chloramphenicol 0.269 and agar 27.5). The adults were kept in insect-rearing cages with a constant supply of pure water and a 10% sucrose solution. Eggs were collected twice a week. Insect rearing was maintained under a controlled temperature (25 ± 2°C). Larvae at 4-6th instar were used for all the experiments.

Soil Material

The soil used in this study was collected from the Agroscope farm in Changins, Nyon, Switzerland (46°23'55.9"N 6°13'58.9"E). Several sub-samples were collected at different locations in an area of about 4,000m^2. All the sub-samples were then thoroughly mixed and transferred to 120-litre weather-resistant plastic containers for storage. The containers were stored outdoors at the Institute of Biology, University of Neuchâtel.

Bacterial strains

The *Photorhabdus* bacterial strains used in this study are listed in Table 1. We selected a genetically diverse set of *Photorhabdus* strains belonging to five species in the phylogenetic tree of *Photorhabdus* bacteria, all of which have shown the highest control efficacy against insect larvae in our mortality tests. Bacterial strains were cultured in lysogeny broth (LB) agar plates at 28°C. Bacterial strains were re-plated monthly, and the cultures were refreshed from glycerol stocks every six months.

Table 1: *Photorhabdus* bacteria strains used in the study

Species	Strain
P. bodei	ID81
	ID83
P. cinerea	ID158
	ID163
P. khanii subsp*. khanii*	ID316
	ID317
P. laumondii subsp*. laumondii*	ID22
	ID25
	ID79
P. tasmaniensis	ID138
	ID139
	ID323

Insect infection assays

Spodoptera frugiperda larvae were infected with the different *Photorhabdus* strains by directly injecting bacterial cultures into their bodies. To this end, ten microliters (10 µL) of bacterial suspensions were injected at the back, neck or behind the last pair of false legs using the Hamilton syringe. To prepare the bacterial suspensions, 25 ml of LB broth medium was inoculated with a single colony of *Photorhabdus* bacteria and incubated overnight at 28 °C and 180 rpm of constant agitation for 14-16 hours. Before injecting the larvae, the overnight liquid culture optical density (OD_{600}) was measured and adjusted to OD_{600}=1. The injections were performed using a Hamilton syringe, and the injected larvae were kept at room temperature in plastic trays. Insect mortalities were recorded at regular intervals for 96h, and *Photorhabdus*-infected insect cadavers were used for soil conditioning experiments as described below.

Soil conditioning with *Photorhabdus*-infected *S. frugiperda* cadavers

To condition soil with *Photorhabdus*-infected insect larvae, field soil was mixed with sand (0-4mm) at a 1 to 1 ratio (hereafter referred to as experimental soil). Then, desired amounts of soil-sand mixture were transferred to plastic containers, and *Photorhabdus*-infected larvae or mechanically killed (MK) larvae were buried equidistantly from each other (Fig. 1). Five *Photorhabdus*-infected cadavers or MK insect larvae per 365g of soil (equivalent to soil filled in 0.5l square plastic pots) were used. The conditioned soil was left under greenhouse conditions and moistened regularly for seven days. Control soil was treated similarly, but no insect cadavers were buried. After this time period, the conditioned soil was homogenized and transferred to 0.5l square plastic pots and used to plant maize (var. Delprim). Plant growth and biomass accumulation were evaluated regularly as described in the plant growth measurements section below. The experiment was repeated seven times. Soil sub-samples of treatments, *Photorhabdus*-infected cadavers, MK insect larvae and the control were collected from each experiment and stored at -20°C for soil microbial composition analyses.

Soil physicochemical properties

Soil physicochemical properties were analysed at the Laboratory of Functional Ecology, Institute of Biology, University of Neuchâtel, Switzerland. Soil samples were oven-dried at 35 – 40 °C for 48 hours and sieved to <2 mm to exclude large stones and plant material. Subsamples of approximately 2.5 – 2.55g of the 2 mm soil were used for the bioavailable phosphorus. The sieved samples were ground into fine powder, and 10-15mg of the sample was used for the CHN analyses. The soil physicochemical parameters measured included 1) Bioavailable phosphorus (P) estimated by extraction with sodium bicarbonate, Olsen method, 2) relative humidity (RH), achieved by weighing samples desiccated at 105 °C, 3) Soil organic matter content (SOM), measured by heating the samples at 450 °C for 4 hours, using the loss of ignition (LOI) method and 4) Organic carbon – Nitrogen ratio (CN), measured using an

elemental analyser (Flash 2000, CHN-O Analyzer, Thermo Scientific, Waltham, Massachusetts, United States).

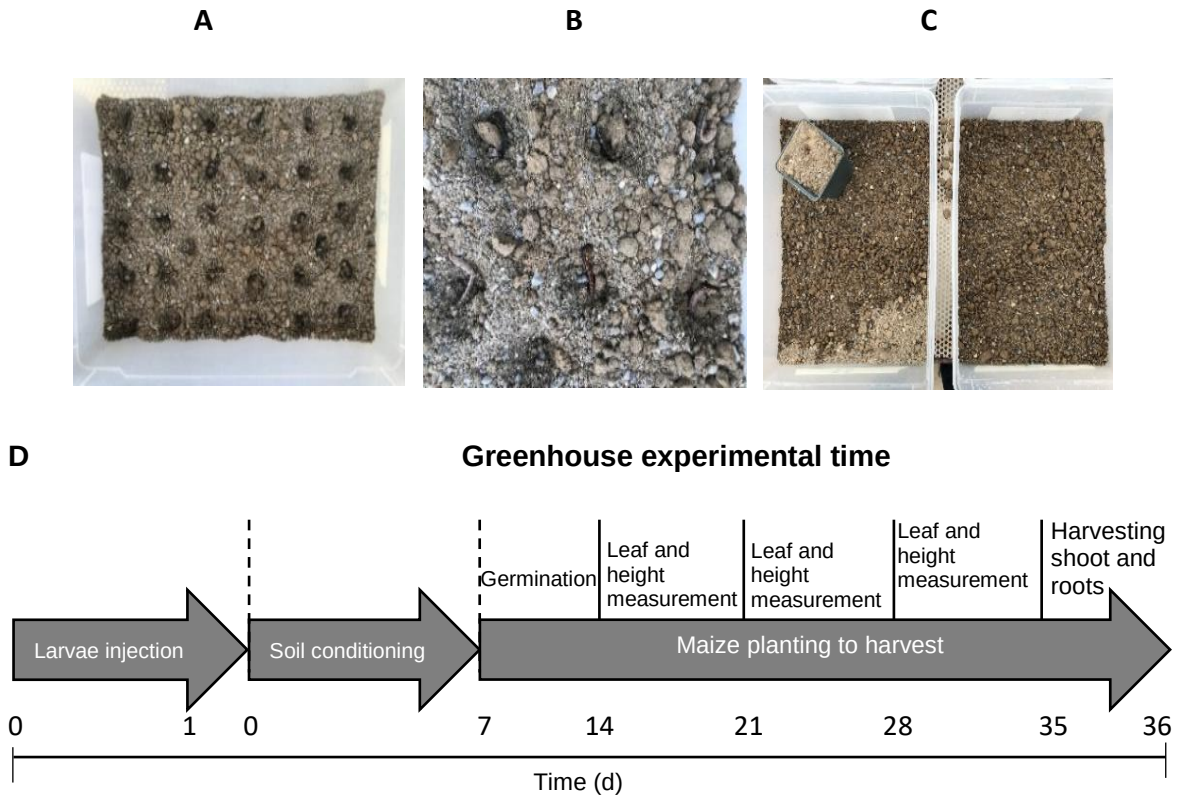

Figure 1. Experimental procedure from soil conditioning to plant harvest. **A** – Holes created on the soil surface to bury cadavers, **B** – Cadavers placed in holes, **C** – Cadavers buried with soil and moistened with sprinkles of water on the surface, and **D** – Greenhouse experimental time.

Soil conditioning with water extracts of *Photorhabdus*-infected *S. frugiperda* cadavers

To condition soil with water extracts of *Photorhabdus*-infected *S. frugiperda* cadavers, either 80 *Photorhabdus*-infected *S. frugiperda* cadavers or 80 MK larvae were macerated in 18ml of autoclaved water. Then, the water extracts were filtered using 20 µm syringe filters. The amount of solvent used for the extraction corresponds to a 1: 10 ratio, as each larvae weighted in average 22.5 mg. The resulting water extracts were added to 5,840 g of experimental soil and homogenised. The conditioned soil was left under greenhouse conditions and regularly moistened for seven days (Fig. 1). Control soil was treated in a similar manner with autoclaved water. After this time period, the conditioned soil was homogenized and transferred to 0.5l square plastic pots and used to plant maize (var. Delprim) plants. Plant growth and biomass accumulation were evaluated regularly as described below.

Soil conditioning with cell-free *Photorhabdus* culture supernatants

To prepare cell-free *Photorhabdus* culture supernatants, 25 ml of LB broth medium was inoculated with a single colony of *Photorhabdus* bacteria in Erlenmeyer flasks and incubated overnight at 28 °C and 180 rpm of constant agitation for 14-16 hours. The overnight cultures

were transferred into sterile 50 ml centrifuge tubes and centrifuged at 20,000 rpm for 5 minutes. Then, 18 ml of cell-free *Photorhabdus* culture supernatants was extracted for use in soil conditioning, and the remaining supernatants plus the bacterial pellets in the centrifuge tubes were discarded. The extracted supernatants were added to 5,840 g of experimental soil and homogenised. Control soil was treated in a similar manner with autoclaved water. The conditioned soil was left under greenhouse conditions and moistened regularly for seven days. After this time period, the conditioned soil was again homogenised and transferred to 0.5l square plastic pots and used to plant maize (var. Delprim) plants. Plant growth and biomass accumulation were evaluated regularly as described in the plant growth measurements below. These experiments were repeated thrice.

Sterilisation and soil re-inoculation experiments

To evaluate whether changes in soil-conditioning mediated changes in soil microbial communities impact plant growth and biomass accumulation, sterilisation and re-inoculation experiments were conducted. In the first phase, I conditioned experimental soil with *Photorhabdus*-infected insect cadavers as described above. In the second phase, I autoclaved a portion of the conditioned soil and then complemented it by mixing it with 10% of non-autoclaved soil previously conditioned with *Photorhabdus*-infected insect cadavers or with MK insect larvae. Re-inoculated soil treatments have been shown to re-establish their natural microbial communities (Thuerig et al., 2009; Li et al., 2019). The resulting soils were left under the greenhouse for 7 days before using them for planting. Plants were then grown on three soil types: non-autoclaved experimental soil, soil conditioned with *Photorhabdus*-infected insect cadavers or with MK insect larvae, and autoclaved conditioned soil mixed with 10% soil conditioned with *Photorhabdus*-infected insect cadavers or with MK insect larvae. Plant growth and biomass accumulation in these three soil types were regularly evaluated as described below. The experiments were repeated thrice.

Plant Growth Measurements

To evaluate plant growth and plant biomass accumulation, I measured the following parameters: plant height, and leaf length and width of the plant's first and second leaves at three time points: two, three, and four weeks after germination. The plant height was measured from the soil surface to the point where the first leaf starts to bend. The leaf length was measured from the leaf collar to the leaf tip, and the leaf width was measured from where the leaf was widest apart. Four weeks after germination, I carefully harvested the plants and washed their roots with running water to remove soil particles. I then detached the roots, leaves and stems using scissors, and finally determined the fresh shoots and root biomasses using a digital weighing scale.

Statistical analysis

Statistical analyses were performed by the analysis of variance (ANOVA) technique using the SigmaPlot 15.0 software. All Pairwise Multiple Comparisons between the mean values of treatments were performed using the Holm-Sidak method at $p \leq 0.05$. A one-sample T-test was conducted using Microsoft Excel to determine if the fold changes in the total plant biomass induced by each soil conditioning treatment significantly differ from the mean hypothesis ($\mu=0$) across experiments. The soil physicochemical properties were analysed using R software version (v 4.4.2; R Development Core Team, 2024).

Results

Soil properties

To test the differences in the soil chemical properties, I compared the bioavailable phosphorus (P), Organic Nitrogen (N), Carbon (C), and Soil Organic Matter (SOM) content in soil conditioned with *Photorhabdus*-infected insect cadavers or mechanically killed larvae, water extracts of toxins derived from macerated *Photorhabdus*-infected insect cadavers, and cell-free *Photorhabdus* culture supernatants with non-conditioned soil as the control. No significant differences were observed in P, N, C and SOM in all the different soil conditioning treatments compared to the controls (Fig. S1). I further examined the correlations between soil chemical properties and plant growth. Overall, no significant associations were detected across soil conditioning treatments. Only the bioavailable P was significantly correlated with plant growth in soils conditioned with water extracts of toxins from *Photorhabdus*-infected insect cadavers (Fig. S2, S3, S4 and S5). Altogether, these findings underscore the role of *Photorhabdus* toxins and bioactive metabolites in driving plant growth promotion, beyond the influence of the soil chemical properties.

Soil conditioning with *Photorhabdus*-infected insect cadavers often improves plant growth

To test whether the different soil conditioning treatments influence plant growth, I conducted greenhouse experiments and compared maize plants grown in non-conditioned soils and soil conditioned with *Photorhabdus*-infected insect cadavers or with mechanically killed insect larvae. In seven independent experiments, plant biomass production was impacted by the different soil conditioning treatments in a treatment-specific manner (Fig. 2). In each experiment, neutral or positive effects of the different soil conditioning treatments on plant biomass were more often observed than negative effects (Fig. 2). The biomass produced by plants grown on conditioned soils was up to 55% greater than the biomass produced by plants grown on non-conditioned control soils. In only two cases, we observed a significant reduction in plant biomass, i.e. in experiments four and seven, where the soil conditioning with cadavers infected with *Photorhabdus* bacteria reduced plant biomass in a strain-specific manner. When

all seven experiments were analysed together, plants grown on soils conditioned with mechanically killed larvae or with *Photorhabdus*-infected insect cadavers significantly produced more total biomass than plants grown on non-conditioned control soils (Fig. 2). However, no significant differences in the following plant growth traits were observed across treatments: height, leaf length width and number of crown roots (Fig. S6).

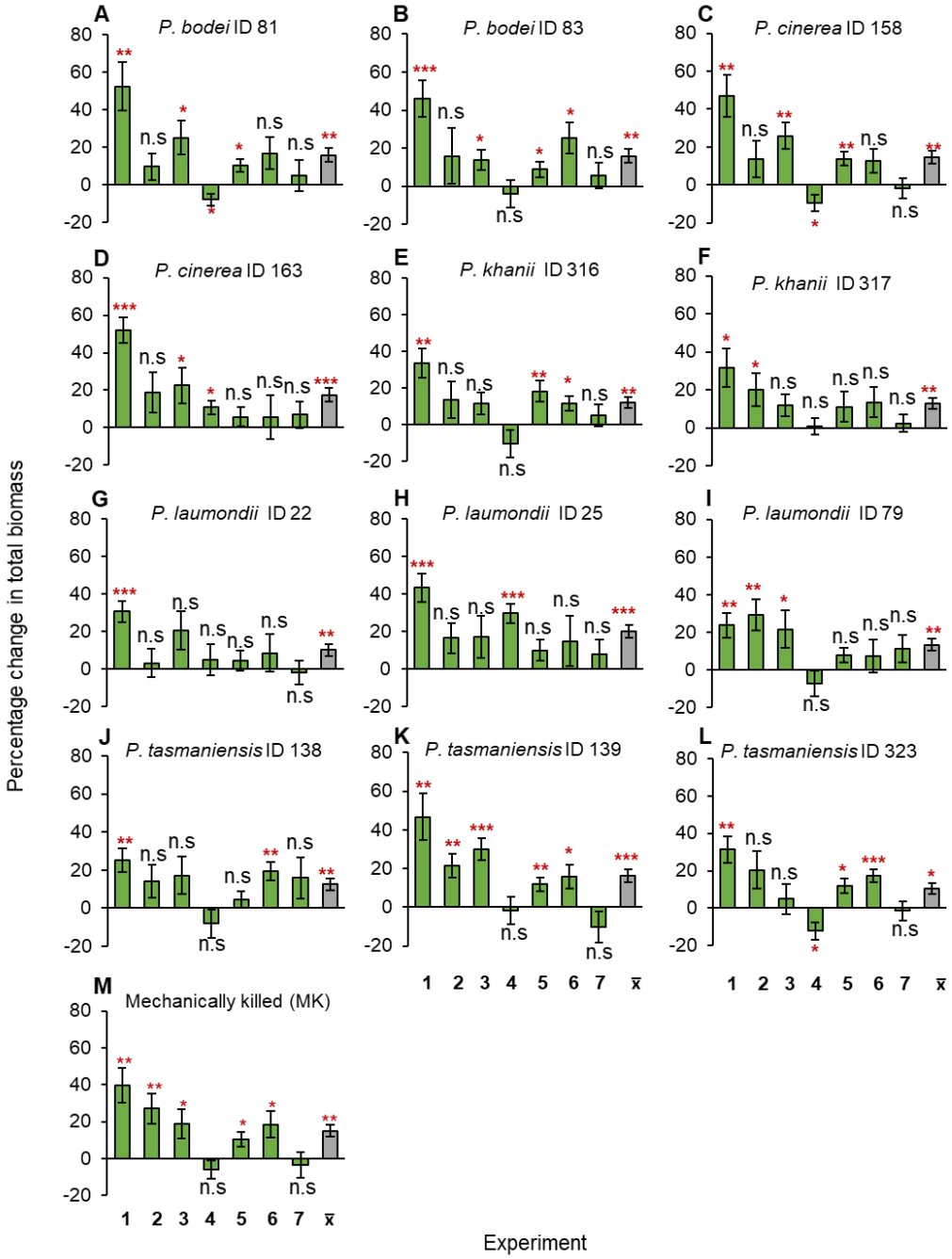

Figure 2. Fold change in total biomass of plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers or mechanically killed larvae. Graphs A–M display the total biomass induced by soil conditioning with insect larvae killed by each *Photorhabdus* strain. In the graphs, the green bars (mean ± SE) represent the fold changes in total biomass observed in three independent experiments compared to the controls. The grey bars represent the overall mean (**x̄**) total biomass of all experiments combined. Asterisks above the bars indicate statistical differences (LSD 0.05) between the treatments and the control at a significance level of $p < 0.05$, using a one-sample T-test.

Soil conditioning with water extracts of toxins from *Photorhabdus*-infected insect cadavers or *Photorhabdus* cell-free supernatant improves plant growth

To test whether soil conditioning with *Photorhabdus* toxins and metabolites influences plant growth, I compared maize plants grown in non-conditioned control soils with plants grown on soil conditioned with water extracts of toxins derived from *Photorhabdus*-infected insect cadavers or mechanically killed insect larvae, and *Photorhabdus* cell-free supernatant. In three independent experiments, neutral or positive effects of the different soil conditioning treatments on plant biomass were observed in independent experiments (Fig. 3). When all three experiments were analysed together, plants grown on soil conditioned with water extracts of toxins derived from macerated *Photorhabdus*-infected insect cadavers significantly increased plant total biomass by 10 – 26% more than the control plants. Contrary to the results of soil conditioning with mechanically killed insect larvae, the total biomass of plants grown on soil conditioned with water extracts of macerated, mechanically killed larvae was consistently insignificant across experiments (Fig. 3). In the soil conditioned with the different cell-free *Photorhabdus* culture supernatants, the plant total biomass was significantly improved by 11 – 20% more than the control (Fig. 4) in all soil conditioning treatments. However, no significant differences were observed in the plant traits: heights, leaf length, width and number of crown roots of plants grown on all the above-mentioned soil conditioning treatments (Fig. S7 and S8).

Sterilisation and soil re-inoculation experiments

To evaluate whether the changes in soil microbial communities mediated by soil-conditioning impact plant growth and biomass accumulation, I set up sterilisation and re-inoculation experiments and compared maize plants grown in non-conditioned soils and plants grown in soil complemented with soil preconditioned with *Photorhabdus*-infected insect cadavers or with MK insect larvae. In three independent experiments, no significant differences were observed in the plant heights, leaf length, width and number of crown roots (Fig. S9). However, plant biomass production was impacted by soil complementation treatments. In independent experiments, significant positive effects on plant biomass were observed more in experiments 1 and 2, and more neutral than positive effects were observed in experiment 3 (Fig. 5). In experiment 3, a significant difference in plant biomass was only observed in plants grown on soils complemented with soil preconditioned with insect cadavers killed by *Photorhabdus* strains ID22. When all three experiments were analysed, the plants grown on all the complemented soil treatments significantly produced more total biomass (16 – 30%) than plants grown on non-conditioned control soils (Fig. 5).

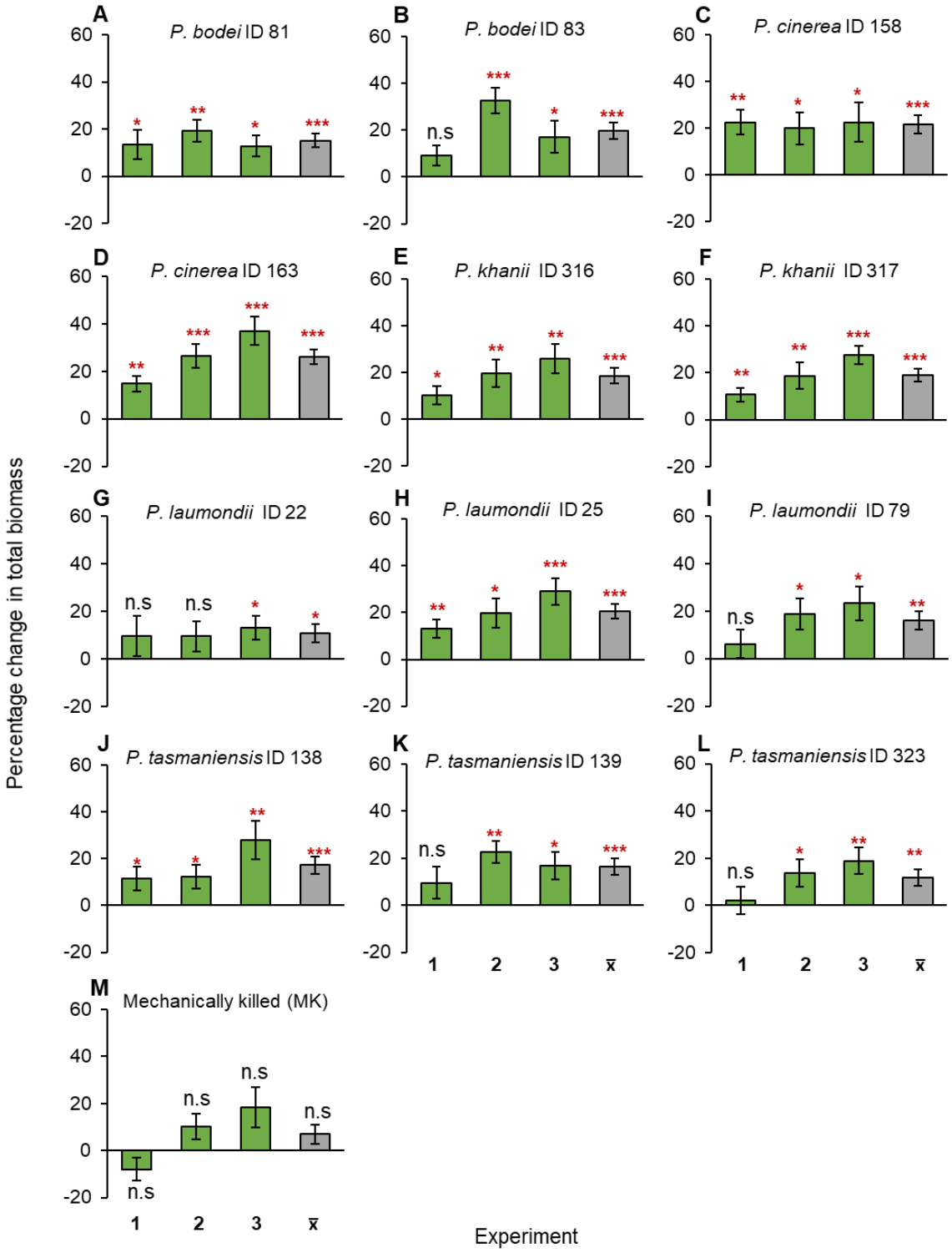

Figure 3. Fold change in total biomass of plants grown on soils conditioned with water extracts of toxins from *Photorhabdus*-infected insect cadavers or mechanically killed larvae. Graphs A–M display the total biomass induced by soil conditioning with toxin extract of each *Photorhabdus* strain. In the graphs, the green bars (mean ± SE) represent the fold changes in total biomass observed in three independent experiments compared to the controls. The grey bars represent the overall mean (**x̄**) total biomass of all experiments combined. Asterisks above the bars indicate statistical differences (LSD 0.05) between the treatments and the control at a significance level of $p < 0.05$, using a one-sample T-test.

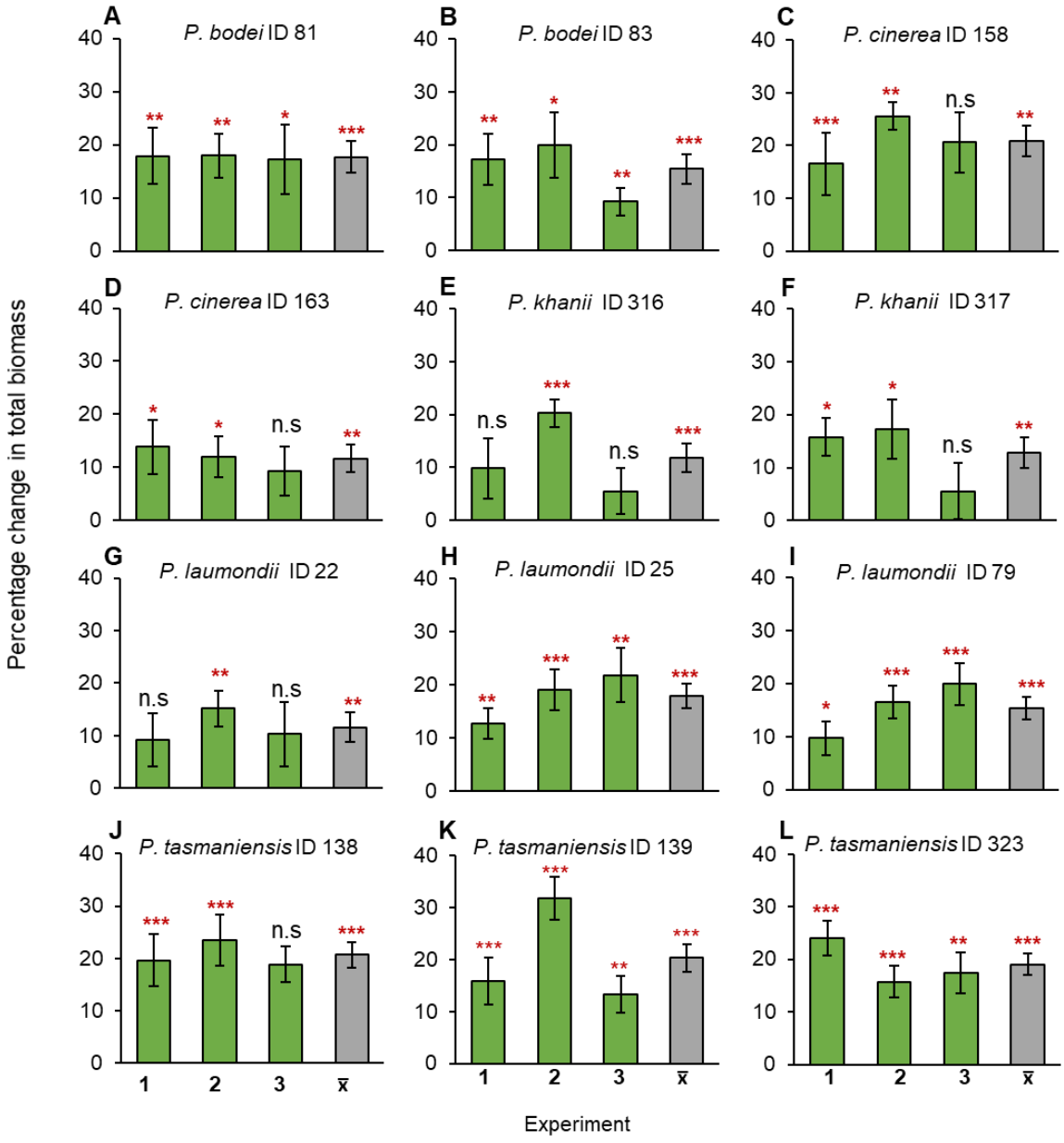

Figure 4. Fold change in total biomass of plants grown on soils conditioned with *Photorhabdus* cell-free supernatants. Graphs A–L display the total biomass induced by soil conditioning with cell-free supernatants of each *Photorhabdus* strain. In the graphs, the green bars (mean ± SE) represent the fold changes in total biomass observed in three independent experiments compared to the controls. The grey bars represent the overall mean (**x̄**) total biomass of all experiments combined. Asterisks above the bars indicate statistical differences (LSD 0.05) between the treatments and the control at a significance level of $p < 0.05$, using a one-sample T-test.

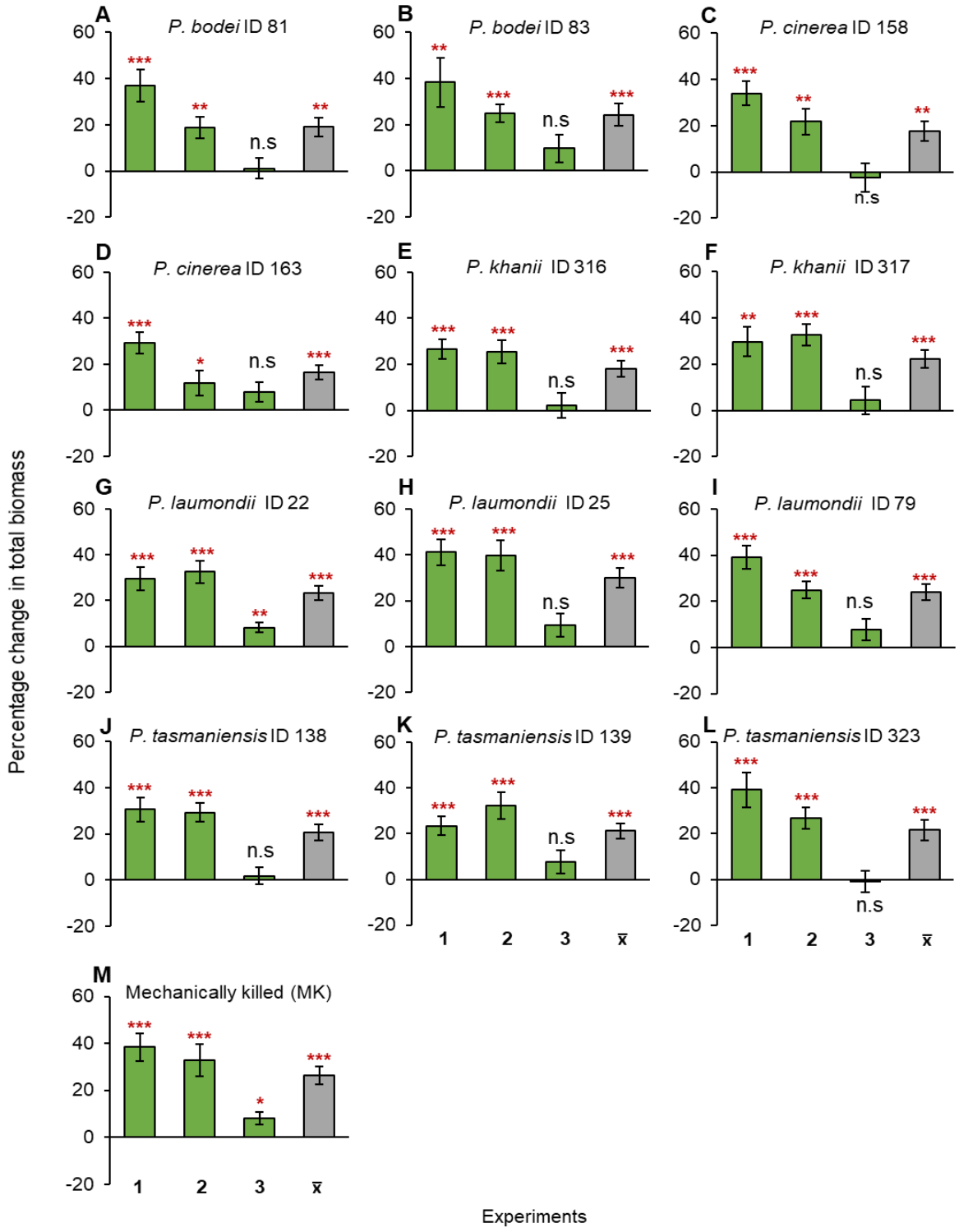

Figure 5. Fold change in total biomass of plants grown on soils complemented with soil previously conditioned with *Photorhabdus*-infected insect cadavers or mechanically killed larvae. Graphs A–M display the total biomass induced by autoclaved soil complemented with live soil previously conditioned with insect larvae killed by each *Photorhabdus* strain. In the graphs, the green bars (mean ± SE) represent the fold changes in total biomass observed in three independent experiments compared to the controls. The grey bars represent the overall mean ($\bar{x}$) total biomass of all experiments combined. Asterisks above the bars indicate statistical differences (LSD 0.05) between the treatments and the control at a significance level of $p < 0.05$, using a one-sample T-test.

Supplementary figures

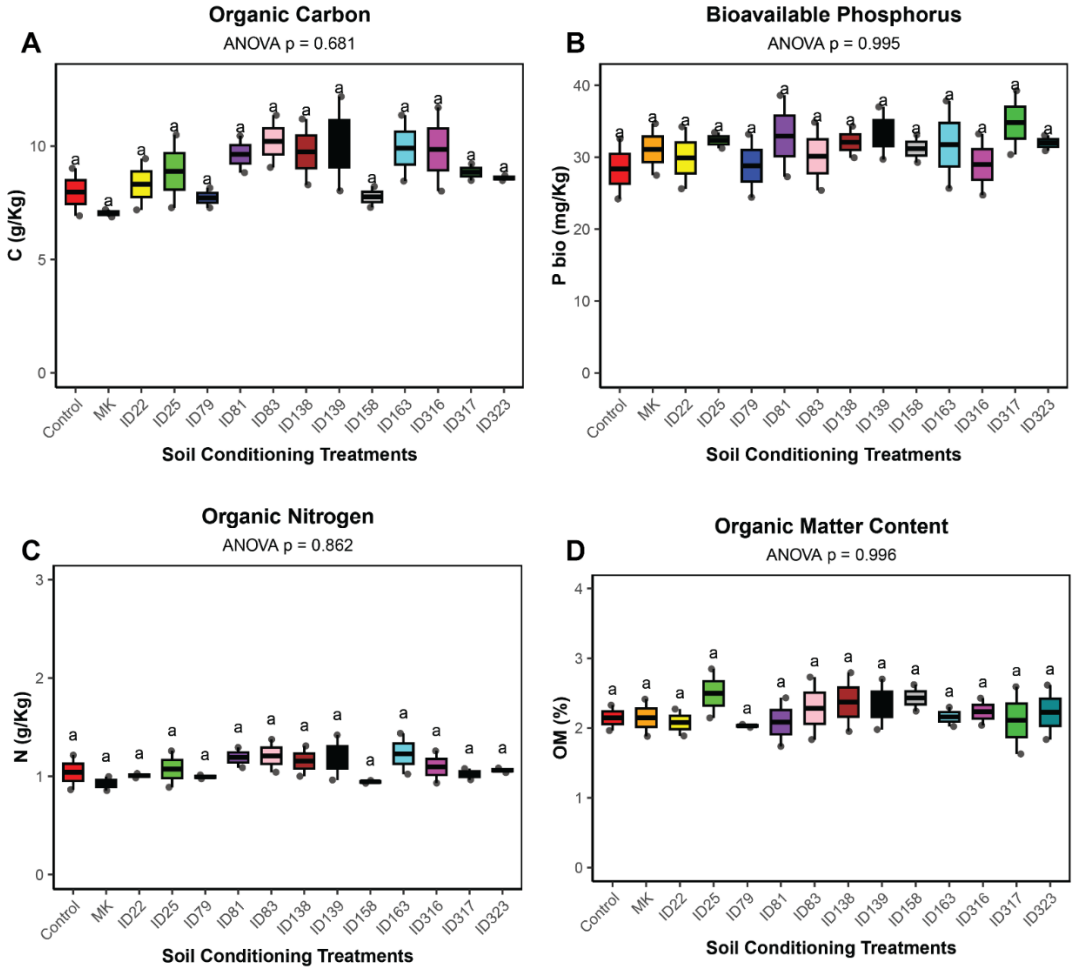

Figure S1. A–D represent soil properties for different soil conditioning treatments. The dots on the boxplots represent the raw data. The black lines in the boxes represent the median values of all variables. Control is non-conditioned soil; MK is soil conditioning with mechanically killed insect larvae, and ID22–323 are soils conditioned with insect larvae killed by the different *Photorhabdus* strains. Asterisks and ns in the plot area represent significant differences among soil conditioning treatments compared to the control, as determined by Tukey's honest significant difference test, $p < 0.05$.

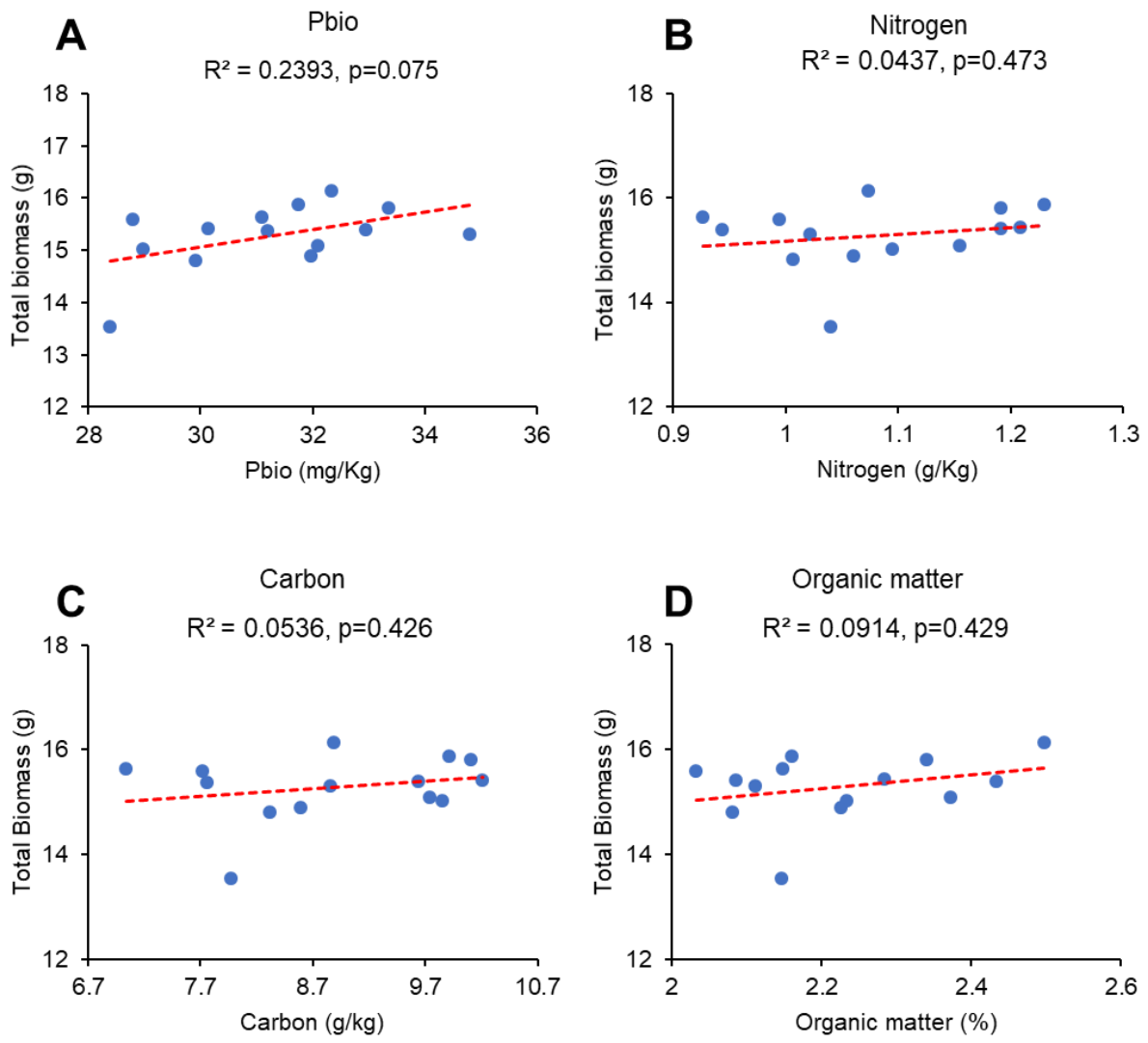

Figure S2. The scatter plots illustrate the relationship between plant total biomass produced and the levels of soil chemical properties in soils conditioned with *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

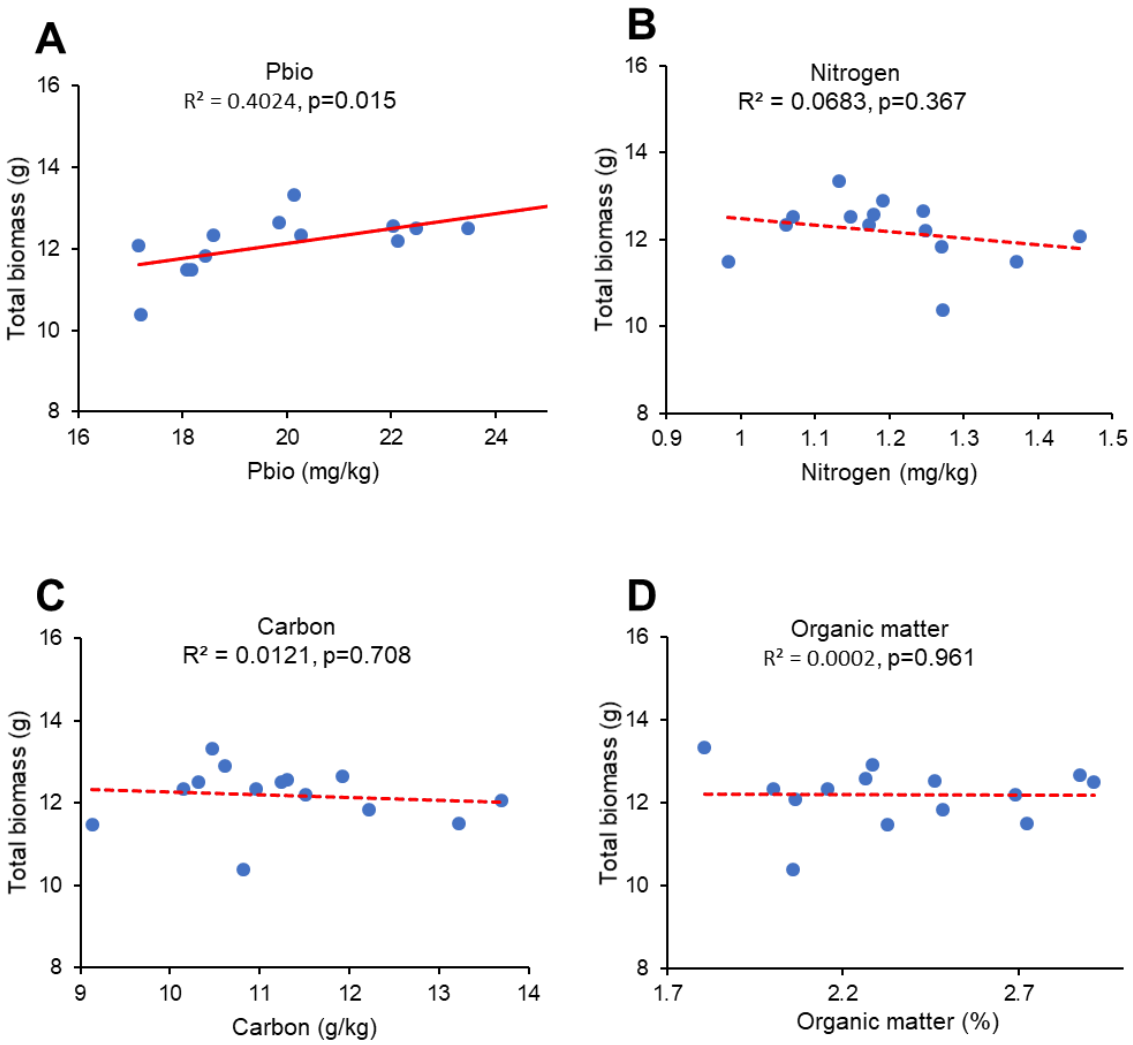

Figure S3: The scatter plots illustrate the relationship between plant total biomass produced and the levels of soil chemical properties in soils conditioned with water extracts of toxins from *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

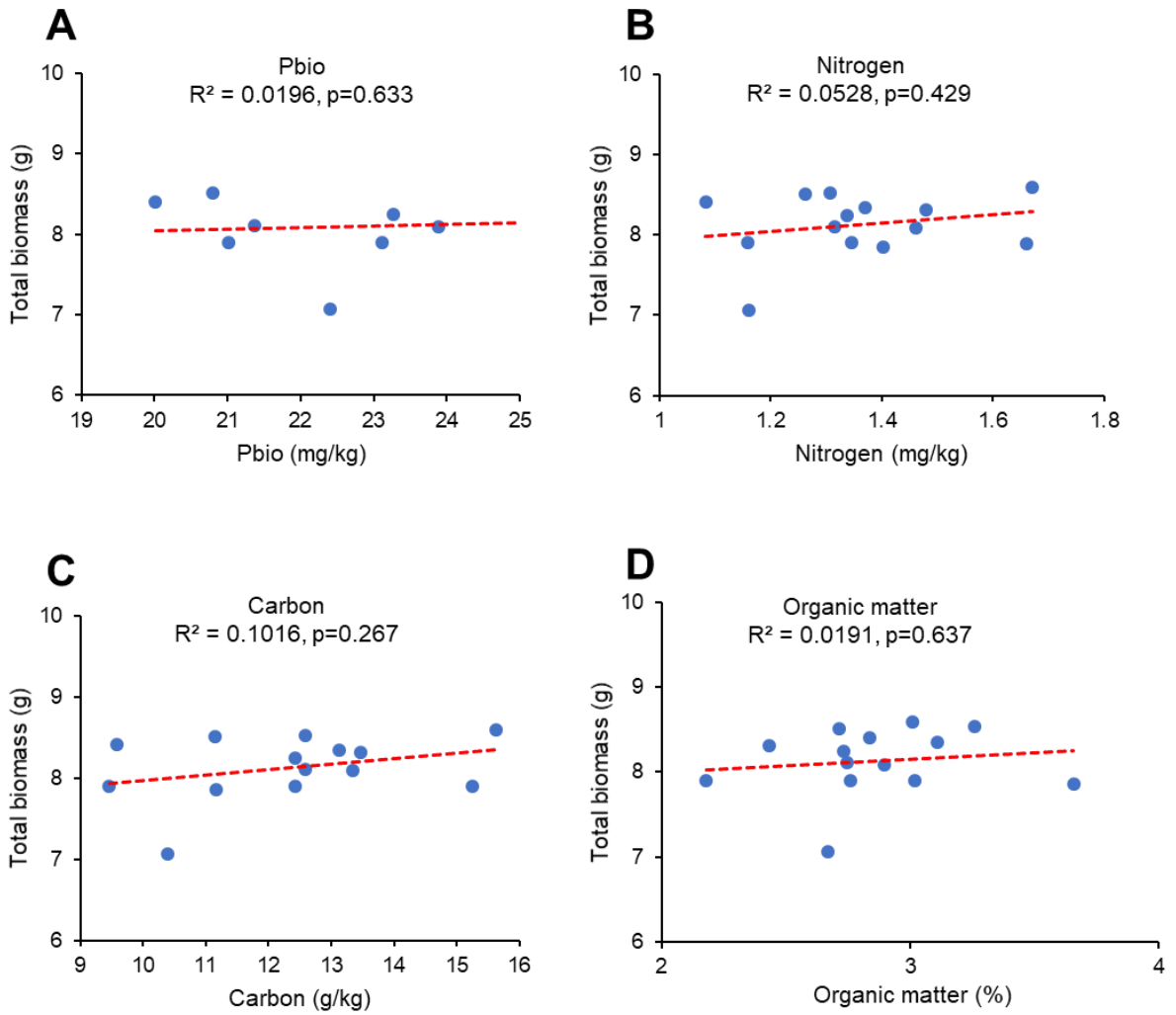

Figure S4: The scatter plots illustrate the relationship between plant total biomass produced and the levels of soil chemical properties in soils conditioned with cell-free supernatants of *Photorhabdus* bacteria. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

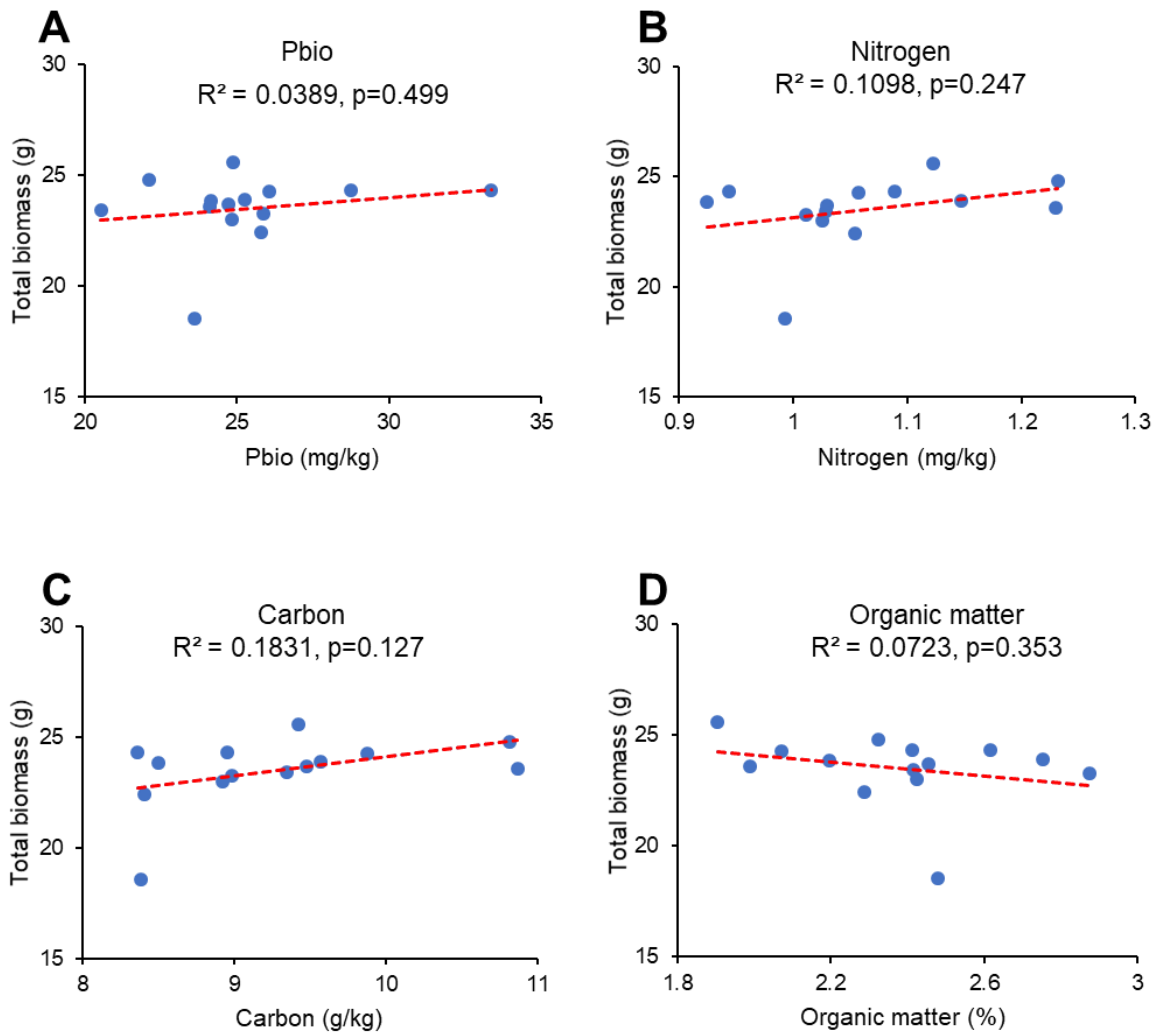

Figure S5: The scatter plots illustrate the relationship between plant total biomass produced and the levels of soil chemical properties in soils complemented with soil previously conditioned with *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

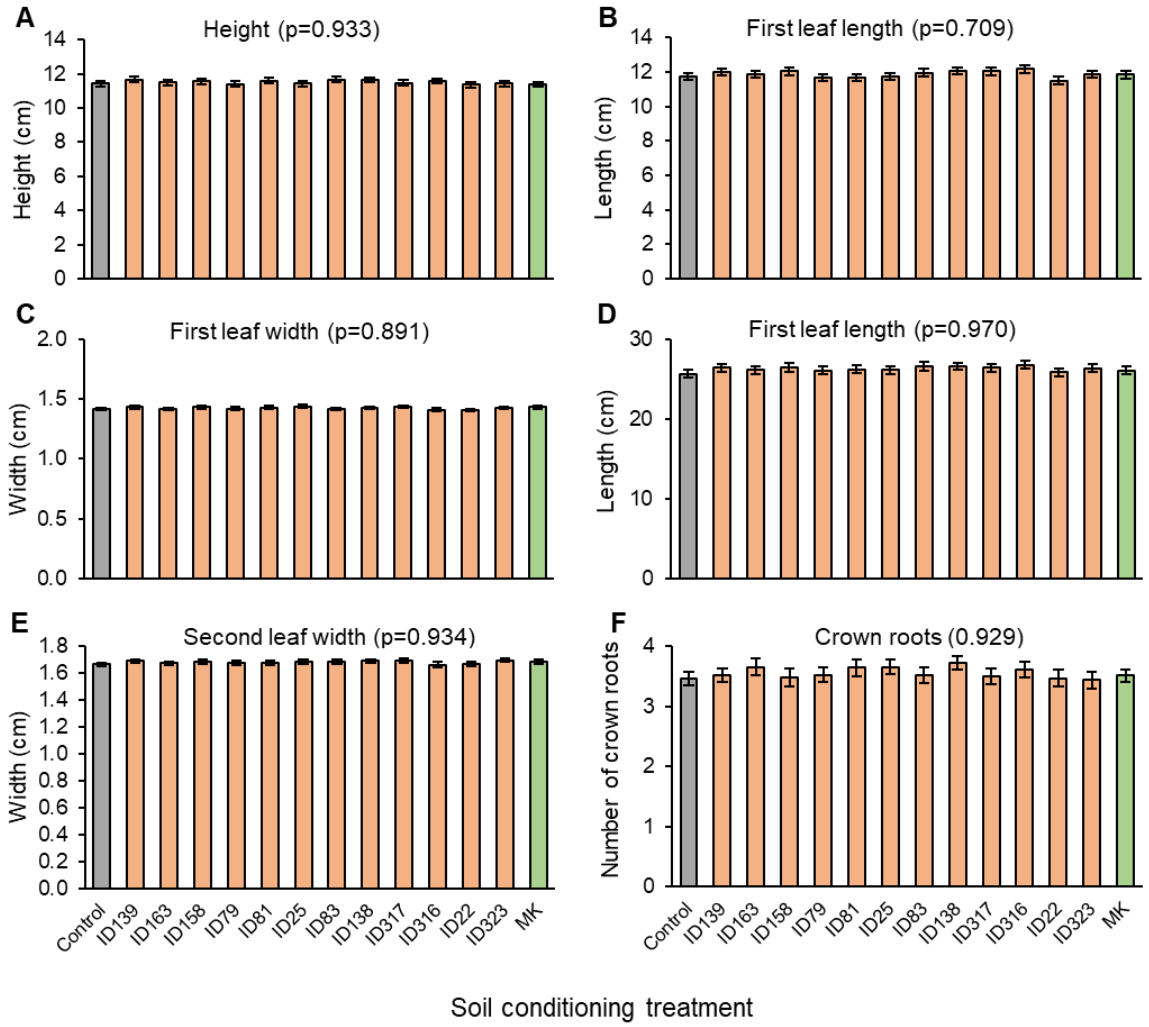

Figure S6. Graphs A–E display the mean measurements of plant height. First leaf length, width, second leaf length, width and F represent the number of crown roots of plants grown on unconditioned control soil (grey bars), soil conditioned with *Photorhabdus*-infected insect cadavers (orange bars) or mechanically killed larvae (green bars). The plant growth measurements and crown roots were statistically assessed by one-way ANOVA and Holm-Sidak test for multiple comparisons.

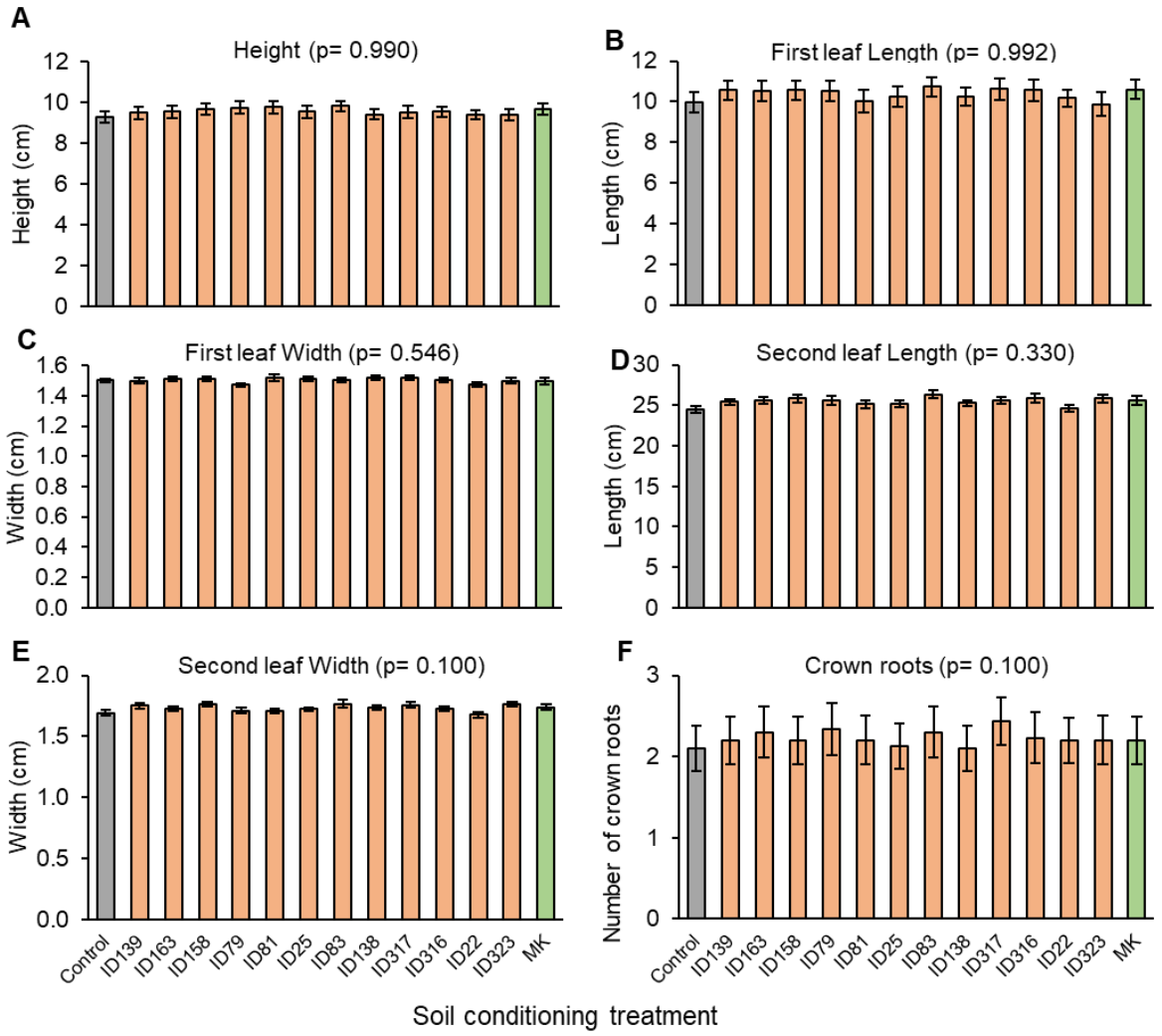

Figure S7. Graphs A–E display the mean measurements of plant height. First leaf length, width, second leaf length, width and F represent the number of crown roots of plants grown on unconditioned control soil (grey bars), soil conditioned with water extract of toxins from *Photorhabdus*-infected insect cadavers (orange bars) or mechanically killed larvae (green bars). The plant growth measurements and crown roots were statistically assessed by one-way ANOVA and Holm-Sidak test for multiple comparisons.

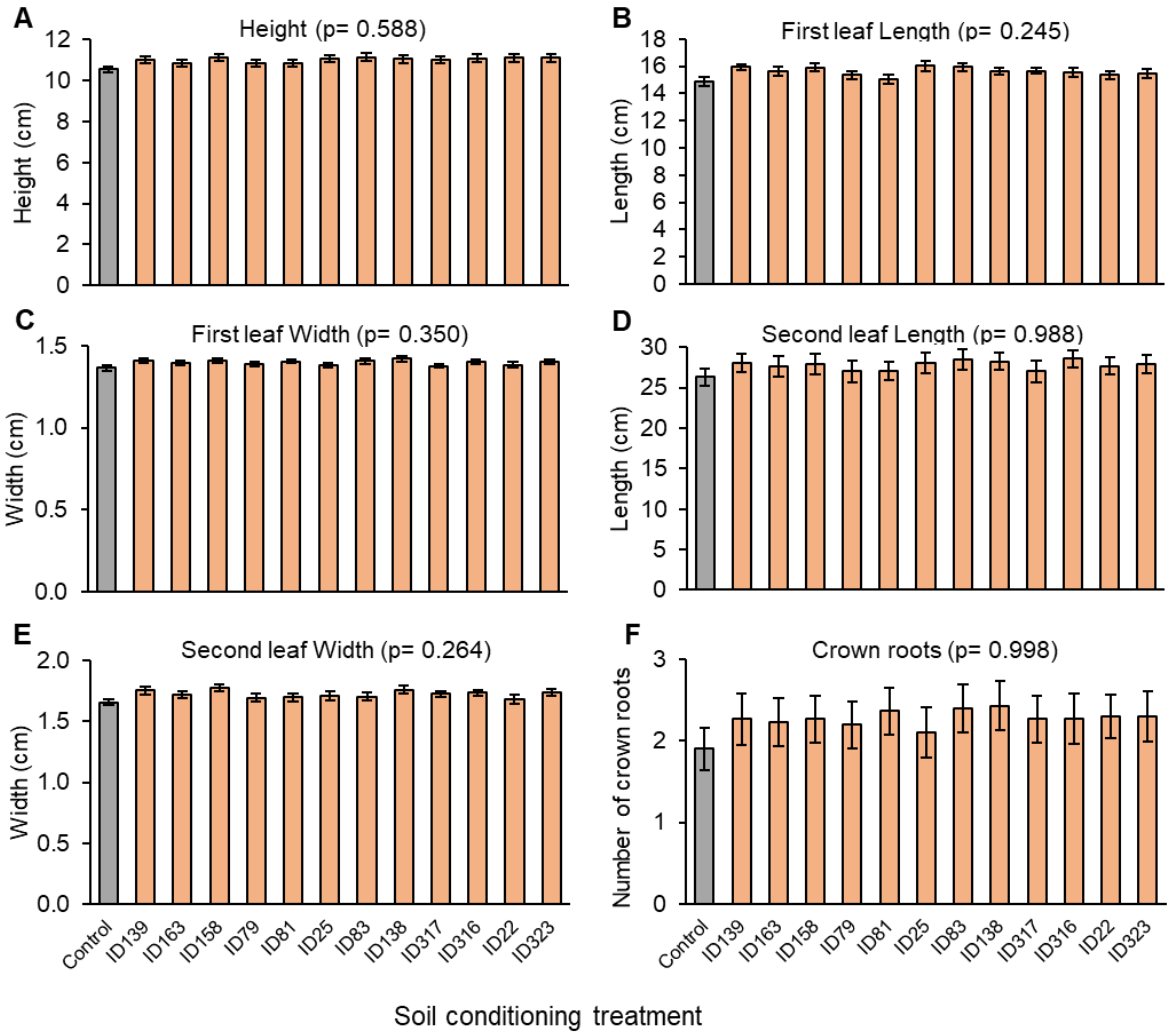

Figure S8. Graphs A–E display the mean measurements of plant height. First leaf length, width, second leaf length, width and F represent the number of crown roots of plants grown on unconditioned control soil (grey bars) and soil conditioned with *Photorhabdus* cell-free supernatants (orange bars). The plant growth measurements and crown roots were statistically assessed by one-way ANOVA and Holm-Sidak test for multiple comparisons.

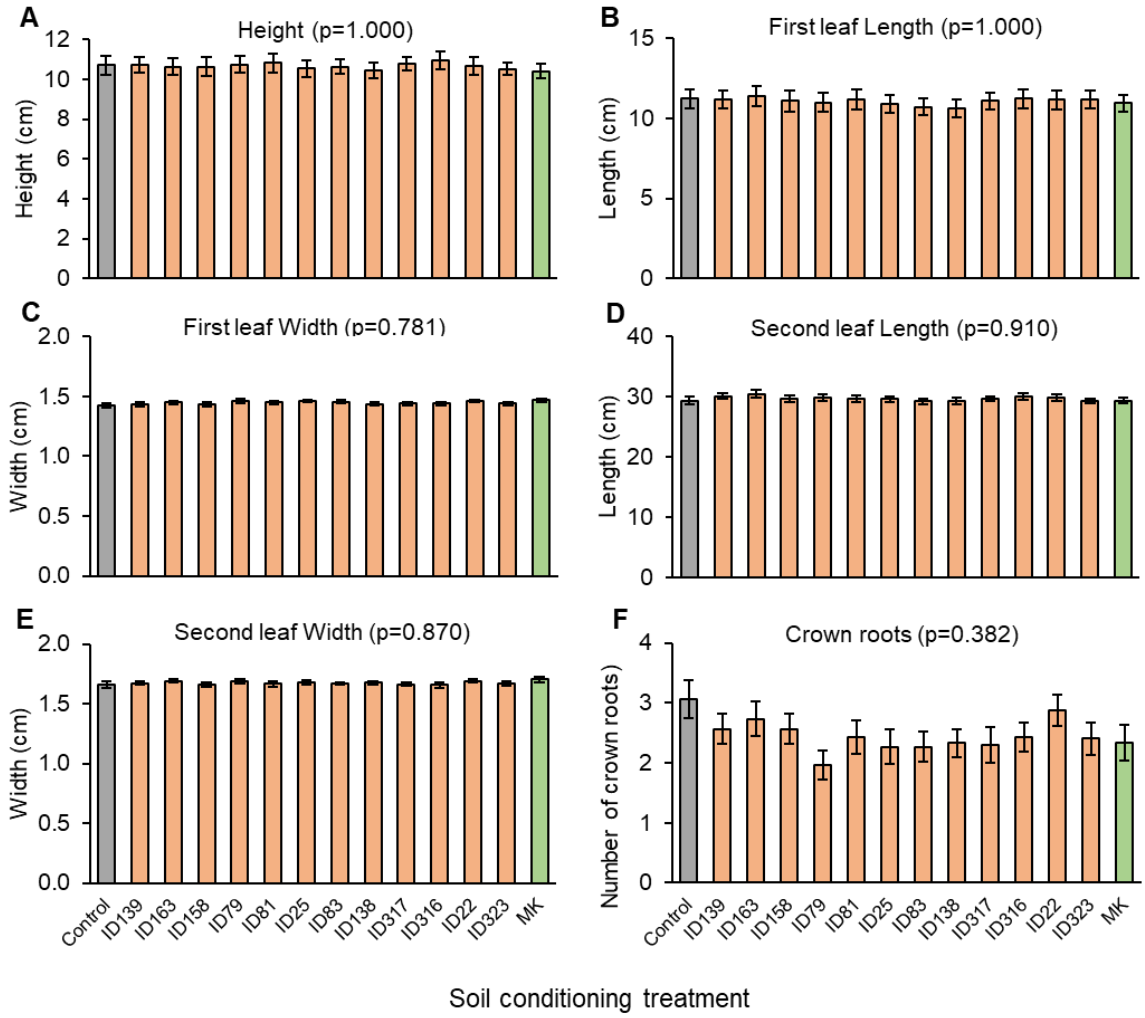

Figure S9. Graphs A–E display the mean measurements of plant height. First leaf length, width, second leaf length, width and F represent the number of crown roots of plants grown on unconditioned control soil (grey bars), autoclaved soil complemented with soil previously conditioned with *Photorhabdus*-infected insect cadavers (orange bars), or mechanically killed larvae (green bars). The plant growth measurements and crown roots were statistically assessed by one-way ANOVA and Holm-Sidak test for multiple comparisons.

Discussion

This study demonstrated that soil conditioning with *Photorhabdus*-infected insect cadavers or MK insect larvae, toxins from *Photorhabdus*-infected insect cadavers, and cell-free supernatants or complementing sterilised soil with soil conditioned with *Photorhabdus*-infected insect cadavers significantly improves plant growth in a greenhouse environment. This is encouraging for growers as *Photorhabdus* bacteria will offer dual benefits of pest control and plant growth promotion in fields where the bacteria are applied by foliar spraying or soil drenching (Abdel-Razek, 2003; Mohan et al., 2003; Vyas et al., 2008; Shahina et al., 2011; Aatif et al., 2014; Kakade et al., 2023; Abdisa et al., 2024). These results are consistent with laboratory experiments, where Ullah et al., (2013) showed that *Photorhabdus* strains *P. temperata* M1021 and *P. luminescens* TT01 improved plant growth when the bacteria were inoculated in rice plant seedlings.

In this study, a significant increase in plant biomass was observed in soils conditioned with MK insect larvae, similar to studies that used insect materials such as cadavers, frass and exuviae for soil amendment (Schmitt and de Vries, 2020; Anyega et al., 2021; van de Zande et al., 2024). This is because insect-based materials such as MK larvae, exuviae and frass contain a large reserve of plant-available nitrogen (Frost and Hunter, 2007; Fielding et al., 2013). Although this treatment improved plant growth, the soil conditioning treatment with MK insect larvae differs from other soil conditioning treatments with *Photorhabdus*-infected insect cadavers and more so, in their mechanisms of plant growth enhancement. Whilst MK insects directly introduce nutrients in the soil, *Photorhabdus*-infected insect cadavers are likely depleted in nutrients but full of bacterial biomass and their sub-products, such as toxins and secondary metabolites. When insect cadavers are in the soil, they decompose quickly and release organic nitrogen to plants in a more readily available form (Hunter, 2001; Fagan et al., 2002; Behie and Bidochka, 2013). Insects weigh approximately 10% organic nitrogen and contain carbohydrates, lipids, protein and chitin (Fagan et al., 2002; Barragán-Fonseca et al., 2022). This makes decomposing insect cadavers richer in ammonium and nitrate levels that can have more lasting effects in the soil (Hunter, 2001; Schimel and Bennett, 2004; Yang, 2004; Behie and Bidochka, 2013; Song et al., 2015). Additionally, insect-based organic materials can stimulate the growth of soil-beneficial rhizobacteria and accelerate their activities to break down organic nitrogen and other nutrients in a plant-available form (Fagan et al., 2002; Sharp, 2013; De Tender et al., 2019). The soil chemical property results showed that soil conditioning tended to increase or decrease soil properties in a treatment-dependent manner, but no significant differences were observed in soil bioavailable P, N, C and SOM compared to the control, nor their correlation with plant growth. This underscores the role of *Photorhabdus* toxins and bioactive metabolites in promoting plant growth. These variations in soil nutrients could be attributed to the growth of soil microorganisms after soil conditioning. The build-up of

microbial communities is associated with heavy consumption of organic matter and carbon, which consequently affects the availability of other soil organic nutrients, as observed in the experiments (Campbell et al., 2022; Duan et al., 2023). In Chapter 3, I observed that soil conditioning with MK larvae or insect cadavers killed by the different *Photorhabdus* strains favoured the growth of more beneficial bacteria and nematodes than the non-conditioned control soil. This indicates that the insignificant differences in soil nutrients might be transient, as the higher abundance of beneficial microbes might have driven the recovery of organic soil nutrients and later improved plant growth (Coban et al., 2022; Philippot et al., 2024). Therefore, the improved plant growth observed in the soil treatment with MK insect larvae can be attributed to the release of nutrients and the abundance of soil-beneficial rhizobacteria over plant pathogens, as reported in previous studies involving soil treatment with insect-based materials (Trivedi et al., 2020; Wantulla et al., 2023; van de Zande et al., 2024).

In my experiments, the exact mechanisms of plant growth stimulation in soils conditioned with *Photorhabdus*-infected insect cadavers or *Photorhabdus* toxins could be explained in two ways. One possible mechanism behind these effects could be the release of bioactive metabolites such as Resorcinol, siderophores, indole-3-acetic acid and Gibberellin groups by *Photorhabdus* bacteria (Ullah et al., 2013, 2014; Muangpat et al., 2022). Any or all of the abovementioned bioactive metabolites stimulate plant growth upon direct interaction with plants (Keswani et al., 2022; Timofeeva et al., 2022; Bibi et al., 2023; Etesami and Glick, 2024). These hormone-driven processes culminate in accelerated plant growth, enhanced biomass generation, and higher crop yields (Orozco-Mosqueda et al., 2023). In this study, soil conditioning with either water extract of toxins and metabolites from *Photorhabdus*-infected insect cadavers or cell-free supernatants significantly increased plant growth. However, the total biomass of plants grown on soil conditioned with water extracts of macerated MK larvae was consistently insignificant across experiments, thus highlighting the *Photorhabdus*-specific effects via their toxins and metabolites in enhancing plant growth in soil conditioned with *Photorhabdus*-infected insect cadavers or *Photorhabdus* toxins or *Photorhabdus* cell-free supernatants. The improvement of plant growth through the production of active metabolites has been reported in many studies of bacterial association with crops (Wilson et al., 2006; Seshadri et al., 2007; Mishra et al., 2009; Pindi et al., 2014; Armada et al., 2016; Bandopadhyay, 2020; Yi et al., 2022). To understand the metabolic and biochemical mechanisms through which *Photorhabdus* bacteria promote plant growth, there is a need to identify the *Photorhabdus* toxins and metabolites associated with the observed plant growth promotion. Another mechanism behind the increased plant growth could be the changes in microbial communities through soil legacy-mediated effects of *Photorhabdus* toxins and metabolites. As such, I conducted sterilisation and re-inoculation experiments to investigate the link between changes in soil microbial communities caused by *Photorhabdus* toxins and

their soil feedback on plant growth. I demonstrated that plants grown on autoclaved soils complemented with only 10% of living soil previously conditioned with *Photorhabdus*-infected insect cadavers or MK insect larvae significantly produced more total biomass than those grown on non-conditioned control soil. These results were consistent with those obtained in the experiment with plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers or MK insect larvae, indicating that the microbial communities, probably dominated by beneficial microbes in conditioned soil, were successfully established in autoclaved soil and positively impacted plant growth. The differences in the soil microbial community composition of the different soil conditioning treatments are discussed in Chapter 3. These results agree with studies that reported improved plant growth in soils inoculated with beneficial microbial agents (Hernández-Montiel et al., 2017; Prisa, 2020; Reis et al., 2022). Changes in microbial communities can drive plant-soil feedback and impact plants in many ways, including enhancing growth and resistance against herbivores and pathogens (Bever et al., 2012; Hu et al., 2018; Pineda et al., 2020; Benitez et al., 2021; Gfeller et al., 2023). Microbial control agents produce toxins and bioactive compounds whose activities can alter soil microbial communities and their belowground activities, and in turn affect plant growth positively, negatively or in a neutral manner (Pfender et al., 1996; Natsch et al., 1998; Wamberg et al., 2003; Kozdrój et al., 2004; Prévost et al., 2006; Lioussanne et al., 2010; Gao et al., 2012; Zhaolei et al., 2017; Bahram et al., 2018; Dong et al., 2019). As soil microbes are sensitive to changes in the soil environment (Kuang et al., 2018), it could be possible that *Photorhabdus* toxins and metabolites impacted the soil microbial community, favouring the growth of beneficial microbes that consequently increased plant growth in conditioned soil. Therefore, I conclude that both the *Photorhabdus* toxins and metabolites, as well as the microbial communities, influenced plant growth in soils conditioned with *Photorhabdus*-infected insect cadavers. The influence of *Photorhabdus* toxins and MK insect larvae on the microbial community assembly and their impact on plant growth are discussed in Chapter 3.

Altogether, irrespective of the exact mechanisms, I report that soil conditioning with *Photorhabdus*-infected insect cadavers or MK insect larvae, *Photorhabdus* cell-free supernatants, water extracts of *Photorhabdus*-killed larvae but not of MK-killed insects, or complementing sterilised soil with soil conditioned with *Photorhabdus*-infected insect cadavers significantly improves plant growth in a greenhouse environment, offering promise for field conditions.

Chapter 2

Soil legacy effects of *Photorhabdus* metabolites on plant physiology and resistance

Abstract

The application of beneficial microorganisms (such as bacteria and fungi) in agriculture impacts plant physiology and consequently their resistance to herbivore attack via Microbial Induced Resistance. Whether *Photorhabdus* bacteria cause similar effects remains unclear. To fill this knowledge gap, I conditioned soils with *Photorhabdus*-killed insect cadavers or with mechanically killed insect larvae. Then, I measured the performance of *Diabrotica balteata* and *Spodoptera frugiperda* larvae feeding on plants grown on the different soil conditioning treatments or on control, non-conditioned soils. To investigate how soil conditioning treatments might influence insect performance, I profiled plant responses at the metabolic level. I observed neutral to negative effects of plants grown on the different soil conditioning treatments on the growth of both *D. balteata* and *S. frugiperda.* More specifically, plants grown on soils conditioned with insect larvae killed by *Photorhabdus* strains ID79, ID139, ID158, ID163, and ID323 were more resistant to the attack of *D. balteata* larvae, and the larval weights were reduced by 15 – 20%, whereas the plants grown on soils conditioned with insect larvae infected with *Photorhabdus* strains ID22, ID138 and ID158 were more resistant to the attack of *S. frugiperda* larvae, and reduced their weights by 10 – 59%. Only the plants that grew on soils conditioned with insect cadavers killed by the *Photorhabdus* strain ID158 significantly suppressed the feeding of both *D. balteata* and *S. frugiperda* larvae. No significant differences were observed in the performance of both herbivore larvae on plants grown on soil conditioned with mechanically killed insect larvae and other soil conditioning treatments.

When the chemical profiles of leaves and roots of plants grown on the different soil conditioning treatments were analysed, the plants that resisted the attack of *D. balteata* and *S. frugiperda* larvae in the insect performance experiments accumulated distinct metabolites in their roots and leaves, enabling resistance against the herbivores. Notably, twelve metabolites from the groups of alkaloids, benzoxazinoids, fatty acids, terpenoids, shikimates and phenylpropanoids were upregulated in the roots of resistant plants. In the leaves, eight defensive metabolites from the groups of amino acids, fatty acids, and phenylpropanoids were significantly accumulated. Up to eight root and four-leaf metabolites were only accumulated in the resistant, but not the susceptible and control plants. These results suggest that soil conditioning with infected insect cadavers killed by selected *Photorhabdus* strains confers systemic responses in plants and negatively affects the feeding of herbivores in maize crops.

Introduction

Plant resistance to herbivores is a key part of integrated pest management and helps to reduce the application of synthetic pesticides in agriculture (Schoonhoven et al., 2005; Prasanna et al., 2018; 2021). While plants are immobile and unable to hide for protection, they possess a natural immune system that enables them to recognise attacks and respond with appropriate defensive mechanisms (Carreno-Quintero et al., 2012; Fernie and Tohge, 2017; Zaynab et al., 2018; Erb and Reymond, 2019). As a means of protection, plants produce and release metabolites as chemical defenses against attackers (Pickett et al., 1999; Hartmann, 2007; Turlings and Erb, 2018; Zaynab et al., 2018). However, in addition to the plant's natural defense system, it has been recognised that beneficial microbes can improve plant resistance and enhance the plant's ability to fend off a wide range of pests and pathogens (Pozo et al., 2020; Thomas et al., 2023). This can benefit cultivated crops as they have a relatively reduced degree of variation in plant defense mechanisms (Alonso-Blanco and Koornneef, 2000; Gols et al., 2008; Anderson and Mitchell-Olds, 2011).

In agriculture, soil beneficial microorganisms, such as bacteria and fungi, have been mainly used as inoculants to enhance plant growth (Trivedi et al., 2017; Compant et al., 2019; Singh et al., 2020). Besides improving plant growth, these microbes help plants to tolerate abiotic stress and also enhance their resistance to pathogens and insects (Pineda et al., 2017; Van Oosten et al., 2017; Heinen et al., 2018; De Kesel et al., 2021; Sanchez-Mahecha et al., 2022). Beneficial microbes influence plant resistance in two ways. First, they can mediate the production of plant metabolites or directly produce compounds that negatively affect insect herbivores – this is termed microbe-induced resistance (MIR) (Rashid and Chung, 2017; Pozo et al., 2020; De Kesel et al., 2021). These microbes induce systemic resistance in plants by producing toxic metabolites against herbivores (Ryu et al., 2004; Sharifi et al., 2018; Pozo et al., 2020). Such microbially-induced resistance in plants reduces the growth of herbivores and enhances mortality (Gruden et al., 2020). Indeed, well-studied bacteria such as *Bacillus* species have been reported to induce resistance in *Arabidopsis* and broccoli plants against aphids and facilitate the release of plant metabolites that attract parasitoids (Gadhave et al., 2016; Rashid et al., 2017). As the benefits are evident in agriculture, microbial-induced resistance in plants has been recognised as an emerging tool for sustainable crop protection (Minchev et al., 2024). Secondly, beneficial microbes, especially those inoculated by soil application or seed treatment, can alter soil microbial communities and indirectly affect plant growth and resistance against herbivores and pathogens through microbial community-mediated effects (Hu et al., 2018; Pineda et al., 2020; Pang et al., 2021; Yu et al., 2021). Studies on microbial communities have demonstrated that changes in the diversity and abundance of soil microbes can significantly impact plant metabolism and consequently plant resistance (Turner et al., 2013; Trivedi et al., 2020). For example, application of plant growth-

promoting microbes altered the rhizosphere microbial community of strawberry and oilseed crops, and the changes were associated with improved growth and resistance against herbivores (Deng et al., 2019; Jiménez et al., 2020). The soil conditioning effects of beneficial microbes enable plants to interact with diverse soil microbial communities that can determine the constituents and concentration of metabolites released by plants against herbivory (Bezemer et al., 2005; Eisenhauer et al., 2010; Kabouw et al., 2011; Trivedi et al., 2020).

Photorhabdus bacteria, a symbiont of the entomopathogenic nematodes from the *Heterorhabditis* genera, is one of the microbial agents applied in agriculture as foliar sprays or by soil drenching to control above and below-ground insect pests (Abdel-Razek, 2003; Mohan et al., 2003; Vyas et al., 2008; Shahina et al., 2011; Aatif et al., 2014; Kakade et al., 2023; Abdisa et al., 2024). In their growth environments, *Photorhabdus* bacteria produces many different toxins and metabolites with antibacterial, insecticidal, antimicrobial, antifungal, and antiparasitic properties (Waterfield et al., 2005; Eleftherianos et al., 2007; Ffrench-Constant et al., 2007; Bode, 2009; Tobias et al., 2016; Muangpat et al., 2017; Antonello et al., 2018; Eroglu et al., 2019). However, many studies are limited to the control efficacy of *Photorhabdus* bacteria against pests and soil pathogens, while the bacteria may have consequences on plant growth and resistance. In Chapter 1, I showed in greenhouse experiments that soils conditioned with toxins and metabolites released from decomposing *Photorhabdus*-infected insect cadavers or water extracts of toxins from *Photorhabdus*-infected larvae or cell-free supernatants enhanced the growth of maize plants. In Chapter 3, I showed that soil conditioning with *Photorhabdus*-infected insect cadavers significantly alters the microbial communities, resulting in a higher diversity of beneficial bacteria and nematodes. These changes in the soil microbes corresponded with the increased biomass of plants grown on conditioned soil, as reported in Chapter 1. While the soil legacy effect of *Photorhabdus* bacteria and its toxins on plant growth and microbial community is known, there is a poor understanding of the impact of soil conditioning with *Photorhabdus*-infected insect cadavers on plant resistance. It has been demonstrated that changes in the plant metabolomes via soil conditioning effects can enhance the plant's ability to produce many classes of defense metabolites against herbivores and plant pathogens (Deng et al., 2019; Jiménez et al., 2020; Trivedi et al., 2020). However, the evidence for this hypothesis in plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers is still lacking.

To bridge this knowledge gap, I assessed the performance of the root-feeding herbivore *D. balteata* and the leaf-feeding herbivore *S. frugiperda* larvae on maize plants grown in soils conditioned with *Photorhabdus*-infected insect cadavers. Additionally, I employed metabolomics to analyse the changes in the chemical profiles of the roots and leaves of plants grown in the different soil conditioning treatments. I hypothesised that conditioning the soil with *Photorhabdus*-infected insect cadavers would alter the chemical profiles of plants and that

these changes would, in turn, affect the performance of both root- and leaf-feeding herbivores. This study provides new insights into the multifunctional roles of *Photorhabdus* bacteria and their toxins beyond direct pest control and improving plant growth, highlighting their contributions to enhancing the plants' defensive mechanisms against herbivores.

Materials and Methods

Insects and Insect Rearing

Spodoptera frugiperda larvae were fed on an artificial diet (in g/Kg: soy milk 31.7, wheat germ 90, sugar 36.56, dried yeast 17.81, cholesterol 0.5, methylparaben 1, sorbic acid 2.3, ascorbic acid 2.46, vitamin B complex 0.184, chloramphenicol 0.269 and agar 27.5). The adults were kept in insect-rearing cages with a constant supply of water and a 10% sucrose solution. Eggs were collected twice a week. Insect rearing was maintained under a controlled temperature (25 ± 2°C). Larvae at 4-6th instar were used for all the soil conditioning experiments. *Diabrotica balteata* eggs were supplied by Syngenta (Stein, Switzerland) every week and incubated under a controlled temperature (25 ± 2°C) until hatching. The *D. balteata* larvae were fed on 4-day-old fresh maize roots, and second-instar larvae were used to conduct the experiments.

Bacterial strains

The *Photorhabdus* bacterial strains used in this experiment were selected from five species in the phylogenetic tree of *Photorhabdus* bacteria (Table 1), and cultured in lysogeny broth (LB) agar plates at 28°C. Bacterial strains were re-plated monthly, and the cultures were refreshed from glycerol stocks every six months.

Table 1: *Photorhabdus* bacteria strains used in the study

Species	Strain
P. bodei	ID81
	ID83
P. cinerea	ID158
	ID163
P. khanii subsp*. khanii*	ID316
	ID317
P. laumondii subsp*. laumondii*	ID22
	ID25
	ID79
P. tasmaniensis	ID138
	ID139
	ID323

Insect infection assays

Spodoptera frugiperda larvae were infected with the different *Photorhabdus* strains by directly injecting bacterial cultures into their bodies. To this end, ten microliters (10 µL) of bacterial suspensions were injected at the back, neck or behind the last pair of false legs using the

Hamilton syringe. To prepare the bacterial suspensions, 25 ml of LB broth medium was inoculated with a single colony of *Photorhabdus* bacteria and incubated overnight at 28 °C and 180 rpm of constant agitation for 14-16 hours. Before injecting the larvae, the overnight liquid culture optical density (OD_{600}) was measured and adjusted to OD_{600}=1. The injections were performed using a Hamilton syringe, and the injected larvae were kept at room temperature in plastic trays. Insect mortalities were recorded at regular intervals for 96h, and *Photorhabdus*-infected insect cadavers were used for soil conditioning experiments as described below.

Soil conditioning with *Photorhabdus*-infected *S. frugiperda* cadavers

To condition soil with *Photorhabdus*-infected *S. frugiperda* cadavers or mechanically killed (MK) larvae, field soil was mixed with sand (0-4mm) at a 1:1 ratio (hereafter referred to as experimental soil). Then, desired amounts of soil-sand mixture were transferred to plastic containers, and *Photorhabdus*-killed or MK larvae were buried equidistantly from each other. Five *Photorhabdus*-infected or MK insect larvae per 365g of soil (equivalent to soil filled in 0.5L square plastic pots) were used. The conditioned soil was left under greenhouse conditions and moistened regularly for seven days. Control soil was treated in a similar manner, but no insect cadavers were buried. After this period, the conditioned soil was homogenised and then transferred to 0.5 L square plastic pots to plant maize (var. Delprim).

Herbivore performance

To evaluate whether soil conditioning with *Photorhabdus*-infected insect cadavers affects plant resistance to herbivore attack, *S. frugiperda* and *D. balteata* larvae were fed on 10-day-old maize plants grown on conditioned soils. To evaluate *D. balteata* growth, 10 second-instar larvae were placed in solo cups and presented with fresh maize roots harvested from plants grown on conditioned soil. Then, maize roots and larvae were covered with a thin layer of organic soil. Five independent replicates were set up per soil conditioning treatment. Fresh roots were added inside the solo cups every two days for ten days, and larvae were counted and weighted on the 8^{th} and 10^{th} days.

To evaluate *S. frugiperda* growth, 2^{nd} instar larvae were placed in Petri dishes and presented with maize leaves harvested from plants grown on conditioned soil to feed on. Ten larvae per Petri dish and five independent replicates per soil conditioning treatment were set up. Fresh leaves were added to the plates every day for four days, and larvae were counted and weighed every day. All the experiments were repeated thrice.

Metabolomics

Maize tissue collection and sample preparation for metabolite analyses

To evaluate plant responses to soil conditioning with *Photorhabdus*-infected insect cadavers at the metabolic level, metabolomics experiments were conducted in 10-day-old maize plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers, with mechanically

killed insect larvae and non-conditioned soil as the control. Five biological replicates per treatment were analysed (n = 5). To collect the metabolomics samples, I removed 10-day-old maize plants from the planting pots, washed the roots with running water to remove the soil particles, and carefully detached the leaves and roots from the stem using scissors. I then wrapped the roots and leaves of each plant separately in aluminium foil and immediately froze them in liquid nitrogen. All the samples were thereafter stored at -80 °C for 72 hours.

Untargeted metabolomics

Flash frozen samples of roots and leaf tissues were ground separately to a fine powder under liquid nitrogen using a mortar and pestle. Fifty milligrams of the powder were weighed in a 2ml safe-lock Eppendorf tube, and 4-8 glass beads (diameter 2-3mm) and 1 mL of methanol:water:formic acid buffer (25:75:0.1 v/v/v) were added to the powder. The samples were subjected to extraction in a Qiagen tissue lyser for 3 min at 30 Hz, followed by centrifugation at 14,000 × g for 3 min. After centrifugation, 400 µL of the supernatant was recovered in a new Eppendorf tube and stored at -80°C. The sample extracts were then analysed by ultra-high-performance liquid chromatography-quadrupole time-of-flight mass spectrometry (UHPLC-QTOFMS).

The system was controlled using MassLynx version 4.1. An Acquity UPLC™ HSS T3 column (100 × 2.1 mm, 1.8 µm) was maintained at 25 °C, operating at a 0.4 mL/min flow rate. The mobile phases comprised water with 0.05% formic acid (solvent A) and acetonitrile with 0.05% formic acid (solvent B). A segmented gradient was applied, increasing from 0% to 50% B over 7.5 minutes, followed by a transition to 100% B over the next 2.5 minutes, and an injection volume of 2 µL. Mass spectrometry (MS) detection was performed using negative electrospray ionisation and data-dependent acquisition (DDA) mode. A resolution of 20,000 at m/z 554 was used, and data were collected in centroid mode. The capillary and cone voltages were set at -2.0 kV and -25 V, respectively. The source and desolvation temperatures were set at 120 °C and 400 °C, respectively, while the gas flows for desolvation, the cone and the collision gas (argon) were set at 900 L/h, 50 L/h, and 2.0 L/min flow rate, respectively. The settings for DDA included a mass range for MS1 from 50 to 1200 Da, with a scan time of 0.15 seconds. The top three MS/MS were selected, each with a 0.15-second scan time. The intensity threshold was set to 6,500 counts per second, and the MS/MS selection window was 4 Da. Peak deisotoping was activated, with dynamic exclusion set to 2.0 seconds after acquisition. An exclusion list containing the 10 most intense background ions was generated from a blank sample run prior to the sample analysis. A ramped collision energy was applied in MS/MS acquisition, ranging from 5–40 V at m/z 50 to 20–70 V at m/z 1200. Quality control samples were prepared by pooling aliquots from all samples, which were run four times before the sample batch and approximately every 30 samples during the batch.

The raw data were imported into Progenesis QI (Waters) for peak picking. The feature containing (.csv) and MS/MS data (.msp) was generated and exported to the global natural products (GNPs)(https://gnps.ucsd.edu) to establish molecular networks using a Feature-Based Molecular Networking (FBMN) visible analyses. The FBMN parameters were set as follows: mass tolerance for both precursor and MS/MS fragment ions at 0.02 Da, the minimum pairs cosine score at 0.7, minimum matched fragment ions at 6, Top K at 10, the maximum connected component size was 100, and the maximum shift between precursors was 500 Da. The resultant molecular networks were visualised with Cytoscape version 3.9.1.

Statistical analyses

Statistical analyses were performed using the analysis of variance (ANOVA) technique on SigmaPlot 16.0 software. All Pairwise Multiple Comparisons between the mean values of treatments were performed using the Holm-Sidak method at $p \leq 0.05$. A one-sample T-test was conducted using Microsoft Excel to determine if the fold changes in the larval weights induced by each bacterial strain significantly differed from the mean hypothesis ($\mu=0$) across experiments. To visualise an overview of the UHPLC-QTOFMS fingerprints, a Principal Component Analysis (PCA) was performed at the initial steps of data exploration. To compare the metabolic responses of plants grown under different soil conditioning treatments, a Partial Least-Squares Discriminant Analysis (PLS-DA) was conducted to identify the metabolic differences in the roots and leaves of resistant and susceptible plants. The cross-validation of the PLS-DA models was performed using quality assessment (Q^2) and R-squared (R^2) parameters. The features that were upregulated in the resistant plants and not present in the susceptible and control plants were selected for metabolite identification. The PCA and PLS-DA were produced using the software R 4.4.2 (R Core Team, 2024).

Results

Impact of soil conditioning with *Photorhabdus*-infected insect cadavers on plant resistance to root and leaf-feeding herbivores

Across three independent experiments, neutral, positive and negative effects on insect performance were observed in a strain-specific manner (Fig. 1). When the three experiments were evaluated together, I observed that plants growing in soils conditioned with insect cadavers killed by strains ID139, ID158, ID163, ID79 and ID 323 were more resistant to the attack of *D. balteata* larvae. The average weights of the *D. balteata* larvae that fed on plants grown on these soil conditioning treatments were significantly reduced by 15 – 20% (Fig. 1). Neutral effects on insect performance were observed in larvae that fed on the roots of plants grown on soils conditioned with mechanically killed larvae and insect cadavers killed by *Photorhabdus* strains ID22, ID25, ID81, ID83, ID138, ID317, and ID316. Consequently, the

average weight of *D. balteata* larvae that fed on plants grown on these soil conditioning treatments was not statistically significant in a one-sample t-test (Fig. 1).

On the other hand, when *S. frugiperda* larvae were fed on the leaves harvested from maize plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers, I often observed neutral effects on the insect performance when the three independent experiments were evaluated together. Only the plants grown on soils conditioned with insect cadavers killed by *Photorhabdus* strains ID158, ID22 and ID138 were more resistant to the attack of *S. frugiperda* larvae and the average larval weights were reduced by 10 – 59% less than the control (Fig. 2). I also observed that only the plants that grew on soils conditioned with insect cadavers killed by the *Photorhabdus* strain (ID158) significantly suppressed the feeding of both *D. balteata* and *S. frugiperda* larvae. The feeding of both *S. frugiperda* and *D. balteata* larvae on the plants grown on soil conditioned with mechanically killed insect larvae was not affected, and no significant differences were observed in larval performance. I recorded the mortality of larvae in three independent experiments. The mortality of *D. balteata* larvae was only significant in larvae that fed on plants grown on soils conditioned with insect larvae killed by *Photorhabdus* strains ID139 and ID317. The mortality of *S. frugiperda* larvae was statistically insignificant across all treatments.

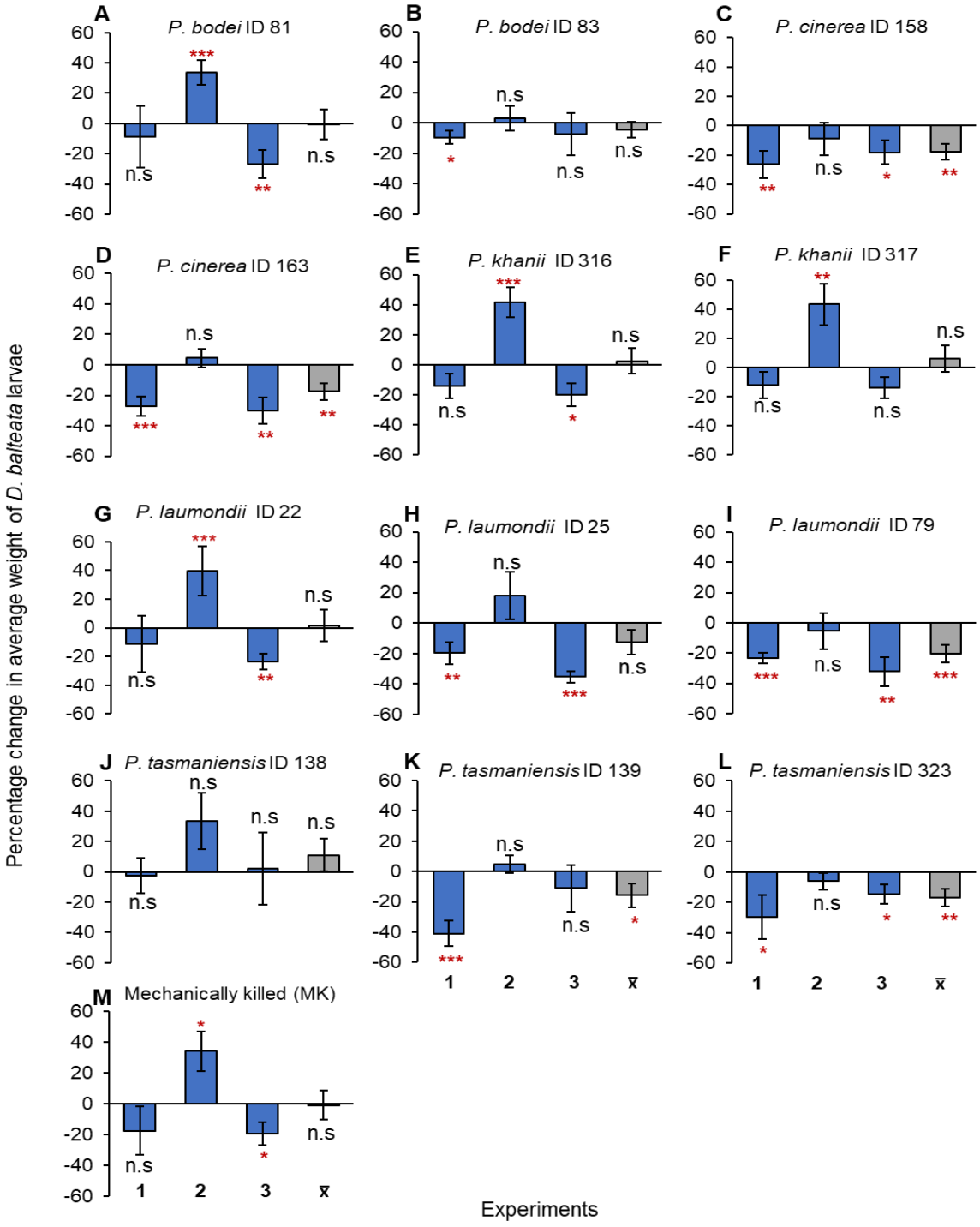

Figure 1. Graphs A–M represent the performance of *D. balteata* larvae feeding on maize plants grown on soils conditioned with insect larvae killed by each *Photorhabdus* strain in three experiments. The bars (mean ± SE) in blue represent fold changes in the weight of *D. balteata* larvae in each experiment compared to the control. The grey bars represent the larval mean (x̄) weight across experiments. Asterisks above the bars indicate statistical differences (LSD 0.05) between the treatments and the control at a significance level of $p < 0.05$, using a one-sample T-test.

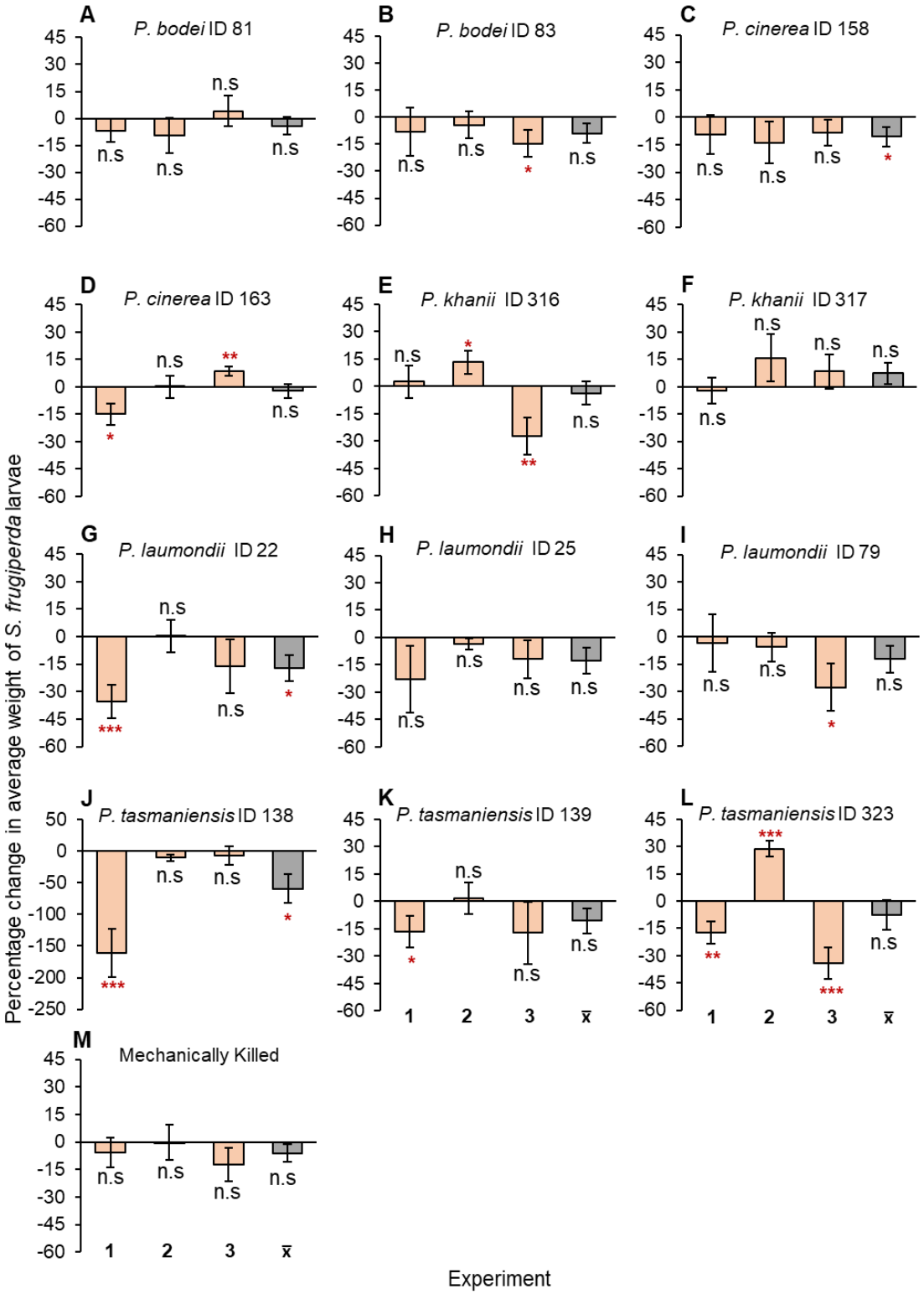

Figure 2. Graphs A–M represent the performance of *S. frugiperda* larvae feeding on maize plants grown on soils conditioned with insect larvae killed by each *Photorhabdus* strain in three experiments. The bars (mean ± SE) in orange represent fold changes in the weight of *S. frugiperda* larvae in each experiment compared to the control. The grey bars depict the mean (x̄) larval weight across all experiments. Asterisks above the bars denote statistical differences (LSD 0.05) between the treatments and the control at a significance level of $p < 0.05$, based on a one-sample T-test.

Soil conditioning with insect cadavers killed by selected *Photorhabdus* strains induces metabolic responses in plants

To evaluate plant responses to soil conditioning at the metabolic level, I analysed the small molecular weight metabolites in the roots and leaves of plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers, mechanically killed insect larvae or non-conditioned soil as the control. Plants grown on the different soil conditioning treatments were categorised as “Resistant” and “Susceptible” based on the insect performance experimental results. I performed the Partial Least-Squares Discriminant Analysis (PLS-DA) to highlight the soil conditioning treatments that induced resistance responses in plant roots and leaves. The PLS-DA revealed that changes in the plant metabolites resulting from the soil conditioning treatments occurred in a treatment-specific manner. Notably, plants grown on soils conditioned with insect cadavers killed by *Photorhabdus* strains ID139, ID158, ID163, ID79, or ID 323 were highlighted to possess distinctive root metabolites that might be involved in resistance response against the attack of *D. balteata* (Fig. 3). On the leaves, only the plants grown on the soil conditioned with insect cadavers killed by *Photorhabdus* strains ID158, ID22 or ID138 were marked to have distinctive metabolites from the others (Fig. 3). These findings correlate with the insect performance experiments, where plants grown on these soil conditioning treatments resisted the attack of *D. balteata* and *S. frugiperda*.

To identify the metabolic changes in the roots and leaves of resistant plants, I analysed the low-weight metabolites produced by the plants, focusing on the most abundant metabolites highlighted on the enhanced molecular network. I observed that resistant plants exhibited higher levels of certain distinct compounds than susceptible plants. In the roots of resistant plants, twelve metabolites from the groups of alkaloids, benzoxazinoids, fatty acids, shikimates, phenylpropanoids, and terpenoids were upregulated (Table S1). Only four metabolites, namely Aromadendrin, Compound ID 196, Imidazole alkaloids, and (6R,9R,10R)-6,9,10-trihydroxyoctadec-7-enoic acid, were present in both resistant and susceptible plants, but were significantly upregulated in resistant plants. The other eight metabolites including 4-[(6R)-6-hydroxy-5,5-dimethylcyclohexen-1-yl] benzoic acid, 2 cis-Abscisic Acid, Canthoside B, Apigenin 7-sulfate, Pimarane and Isopimarane diterpenoids, Ajugaciliatin A, GDIMBOA and Tinosineside B, were only detected in resistant plants and not in “susceptible” or control plants (Fig. 4). In the leaves, eight metabolites from the groups of amino acids, fatty acids, and phenylpropanoids were upregulated (Table 1). Four of these metabolites identified as (2R)-2-ammonio-3-phenylpropanoate, L-Tryptophan, 1-Acyl-sn-glycero-3-phosphoglycerol (N-C16:1), and 2 cis-Abscisic Acid, were found in both susceptible and resistant plants, but were significantly upregulated in resistant plants. The other four metabolites identified as Cephalosporins, Cherimola cyclopeptide, PC (16:0/18:2(9Z,12Z)) 1-hexadecanoyl-2-(9Z,12Z-octadecadienoyl)-sn-glycero-3-phosphocholine, and PA (22:4(7Z,10Z,13Z,16Z)

/22:2(13Z,16Z)) were accumulated only in resistant plants (Fig. 5). Notably, only 2 cis-Abscisic Acid were upregulated in the roots and leaves of resistant plants. No significant correlation was observed after examining the relationships between metabolite abundance and insect performance. with the performance of *D. balteata* and *S. frugiperda* larvae. Only three metabolites in the leaves (2-ammonio-3-phenylpropanoate, L-Tryptophan and Cherimola cyclopeptide) tended to negatively affect insect performance (Fig. S2). Altogether, these results indicate that soil conditioning with *Photorhabdus*-infected insect cadavers induces metabolic responses in the roots and leaves of plants, and that the metabolic patterns between resistant and susceptible plants differ.

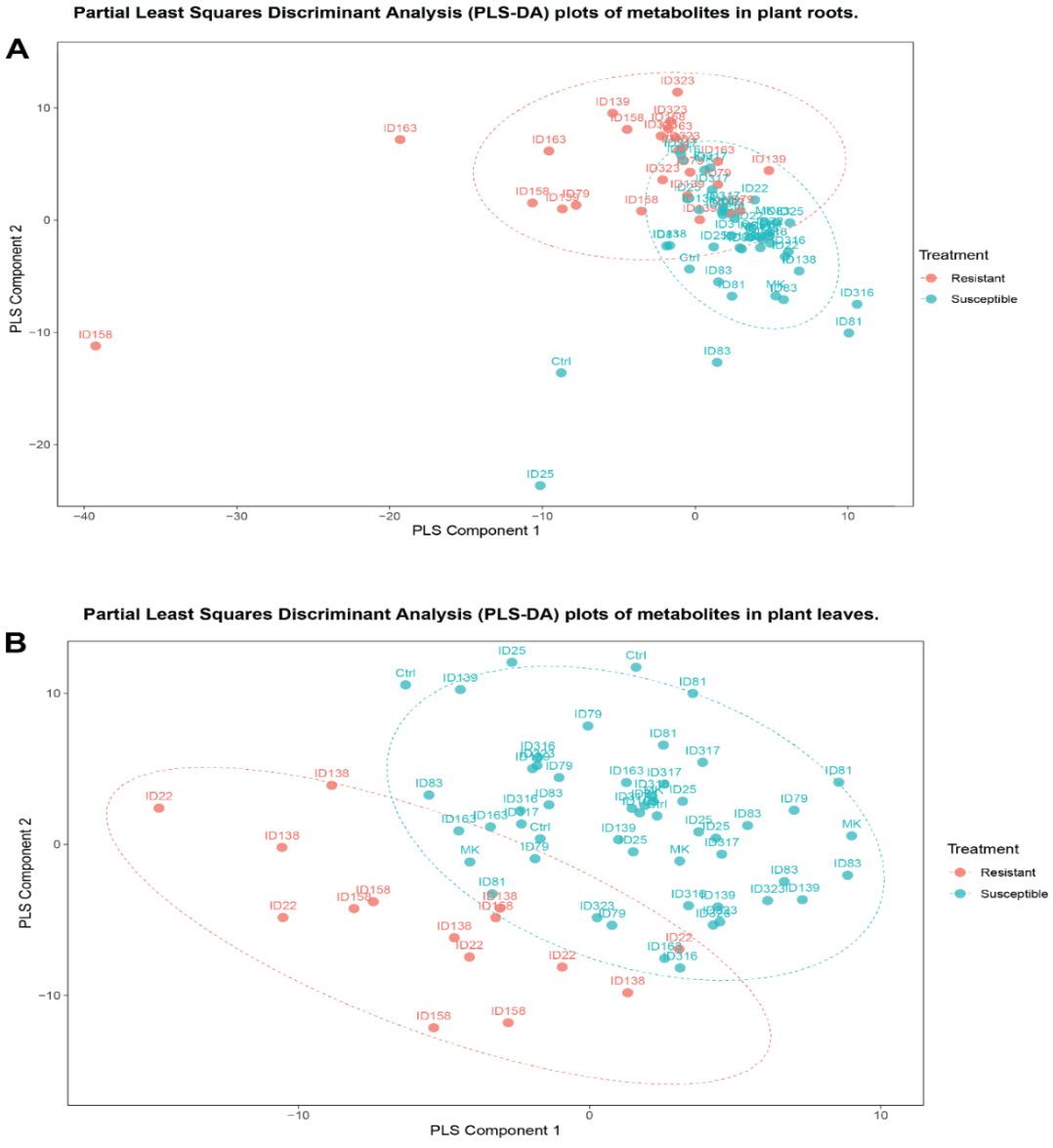

Figure 3. Partial Least-Squares Discriminant Analysis (PLS-DA) plots of metabolites in (A) roots and (B) leaves of plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers, mechanically killed insect larvae and non-conditioned soil.

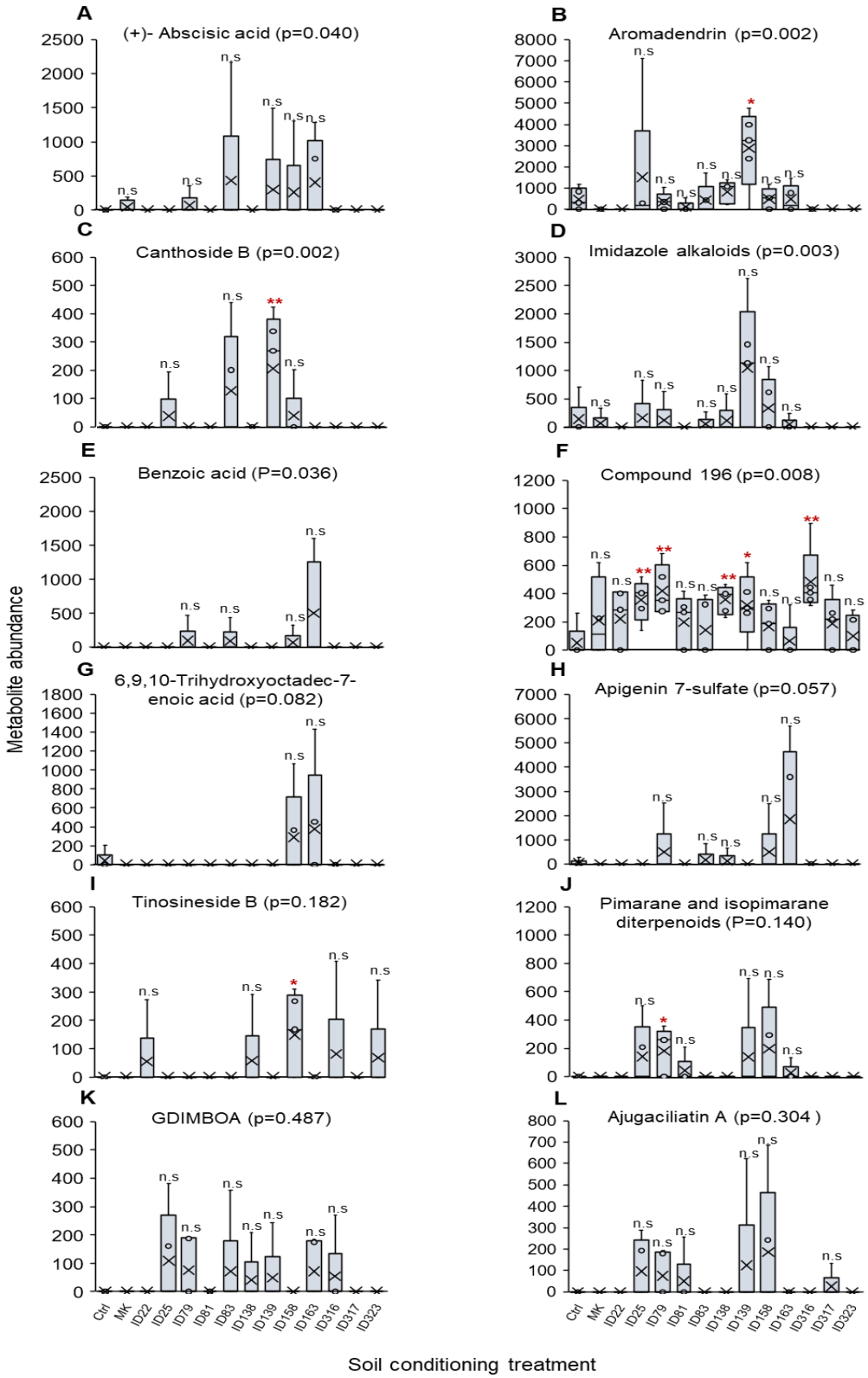

Figure 4. A–L Relative abundance of low molecular weight metabolites upregulated in the roots of plants grown under different soil conditioning treatments. The dots on the boxplots represent the raw data. The black cross (X) in the boxes represents the median values of all variables. Ctrl – non-conditioned control soil, MK – soil conditioning with mechanically killed larvae, and ID22–323 represent soil conditioning treatments with insect cadavers killed by the different *Photorhabdus* strains. Asterisks above the bars indicate statistical differences between the treatments and the control at a significance level of $p < 0.05$, by one-way ANOVA with Tukey HSD test for multiple comparisons.

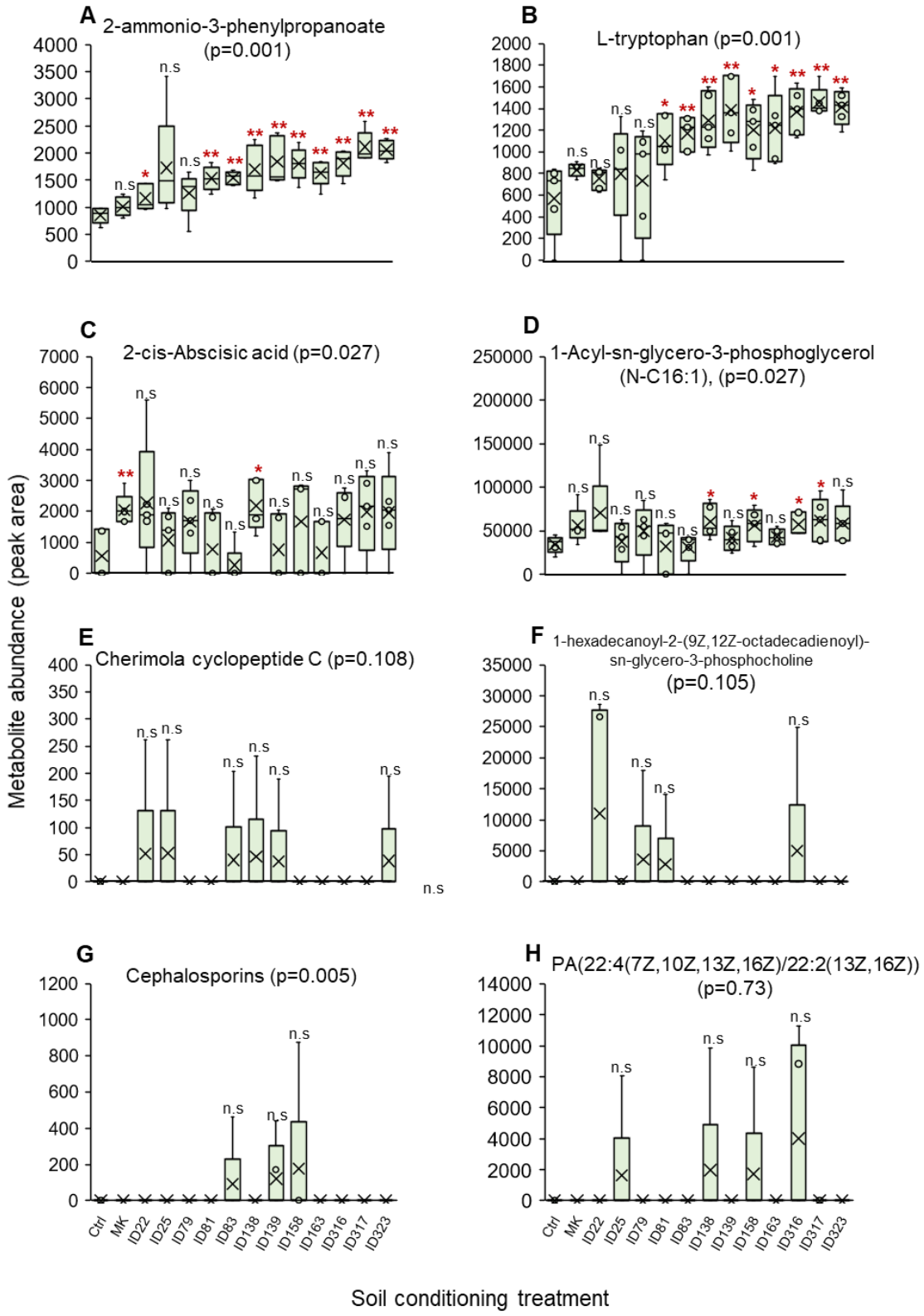

Figure 5. A–H Relative abundance of low molecular weight metabolites upregulated in the leaves of plants grown under different soil conditioning treatments. The dots on the boxplots represent the raw data. The black cross (X) in the boxes represents the median values of all variables. Ctrl – non-conditioned control soil, MK – soil conditioning with mechanically killed larvae, and ID22–323 represent soil conditioning treatments with insect cadavers killed by the different *Photorhabdus* strains. Asterisks above the bars indicate statistical differences between the treatments and the control at a significance level of $p < 0.05$, by one-way ANOVA with Tukey HSD test for multiple comparisons.

Table 1. List of annotated metabolites upregulated in resistant plants

ID	Metabolite	Family	m/z	p-value	The plant part accumulated in
106	Benzoic acid	Terpenoids	245.1180082	0.036	Roots
130	2 cis-Abscisic Acid	Terpenoids	265.1443499	0.04	Roots
152	Aromadendrin	Alkaloids	287.0558557	0.002	Roots
196	Compound id 196	Alkaloids	305.1502976	0.008	Roots
501	Imidazole alkaloids	Alkaloids	413.1447281	0.003	Roots
580	Canthoside B	Unknown	445.134756	0.002	Roots
285	6,9,10-trihydroxyoctadec-7-enoic acid	Fatty acids	329.2332015	0.082	Roots
342	Apigenin 7-sulfate	Shikimates and Phenylpropanoids	349.0018846	0.057	Roots
953	Pimarane and Isopimarane diterpenoids	Terpenoids	655.3330362	0.14	Roots
978	Ajugaciliatin A	Terpenoids	669.3121824	0.304	Roots
334	GDIMBOA	Benzoxazinoid	344.0980292	0.487	Roots
891	Tinosineside B	Alkaloids	597.2182435	0.182	Roots
28	2-ammonio-3-phenylpropanoate	Amino acids	164.071264	0.001	Leaves
60	L-Tryptophan	Amino acids	203.0823064	0.001	Leaves
663	1-Acyl-sn-glycero-3-phosphoglycerol (N-C16:1)	Fatty Acids	481.2571387	0.027	Leaves
785	2 cis-Abscisic Acid	Amino Acids	549.2441131	0.027	Leaves
654	Cephalosporins	Amino Acids	478.0412101	0.005	Leaves
1003	Cherimola cyclopeptide	Peptides	691.3543569	0.108	Leaves
1113	PC (16:0/18:2(9Z,12Z)) $ 1-hexadecanoyl-2-(9Z,12Z-octadecadienoyl)-sn-glycero-3-phosphocholine	Shikimates and Phenylpropanoids	802.5595557	0.105	Leaves
1115	PA(22:4(7Z,10Z,13Z,16Z)/22:2(13Z,16Z))	Unknown	803.56318	0.73	Leaves

Supplementary figures

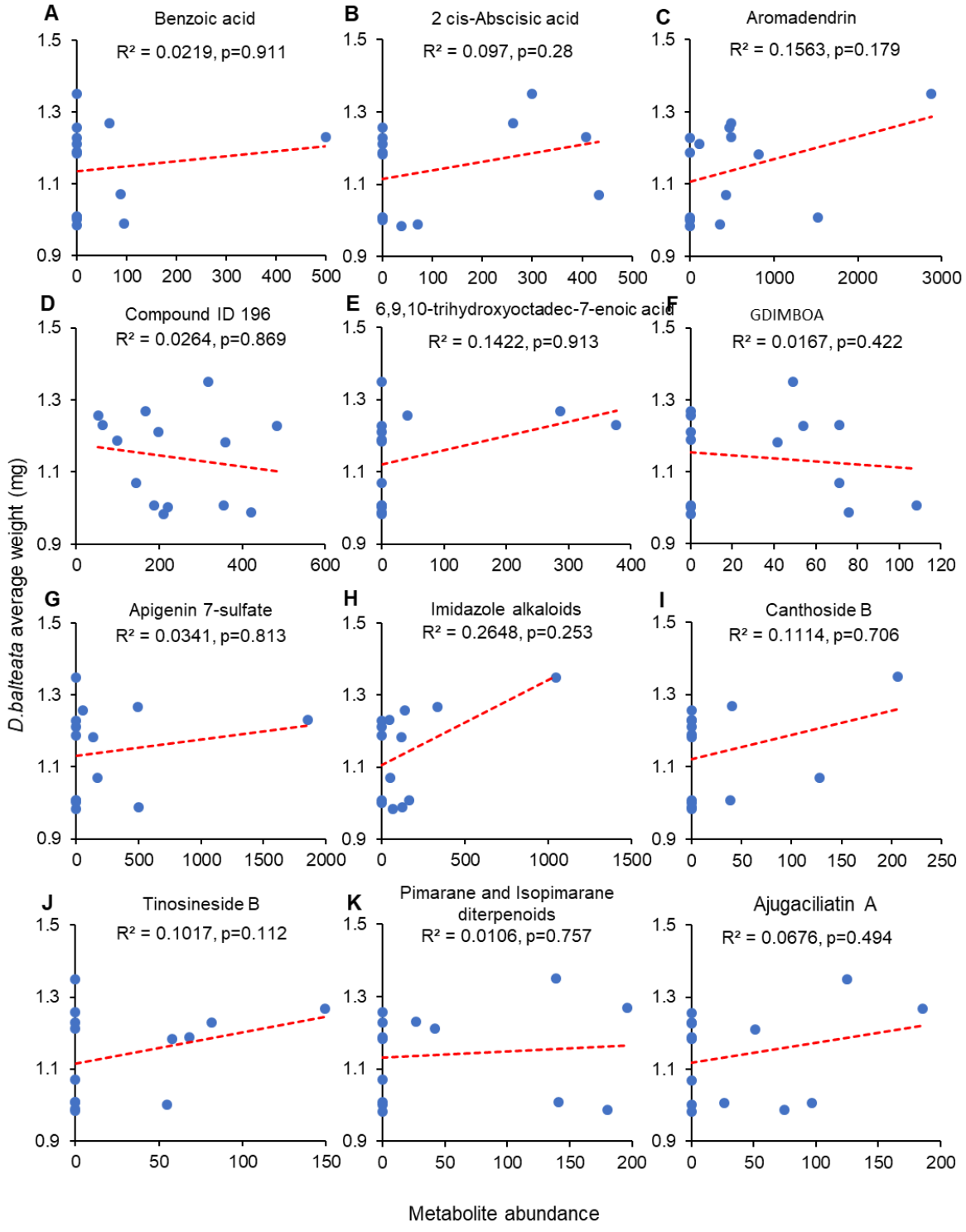

Figure S1. The scatter plots illustrate the relationship between plant total biomass produced and the levels of metabolites upregulated in the roots of plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

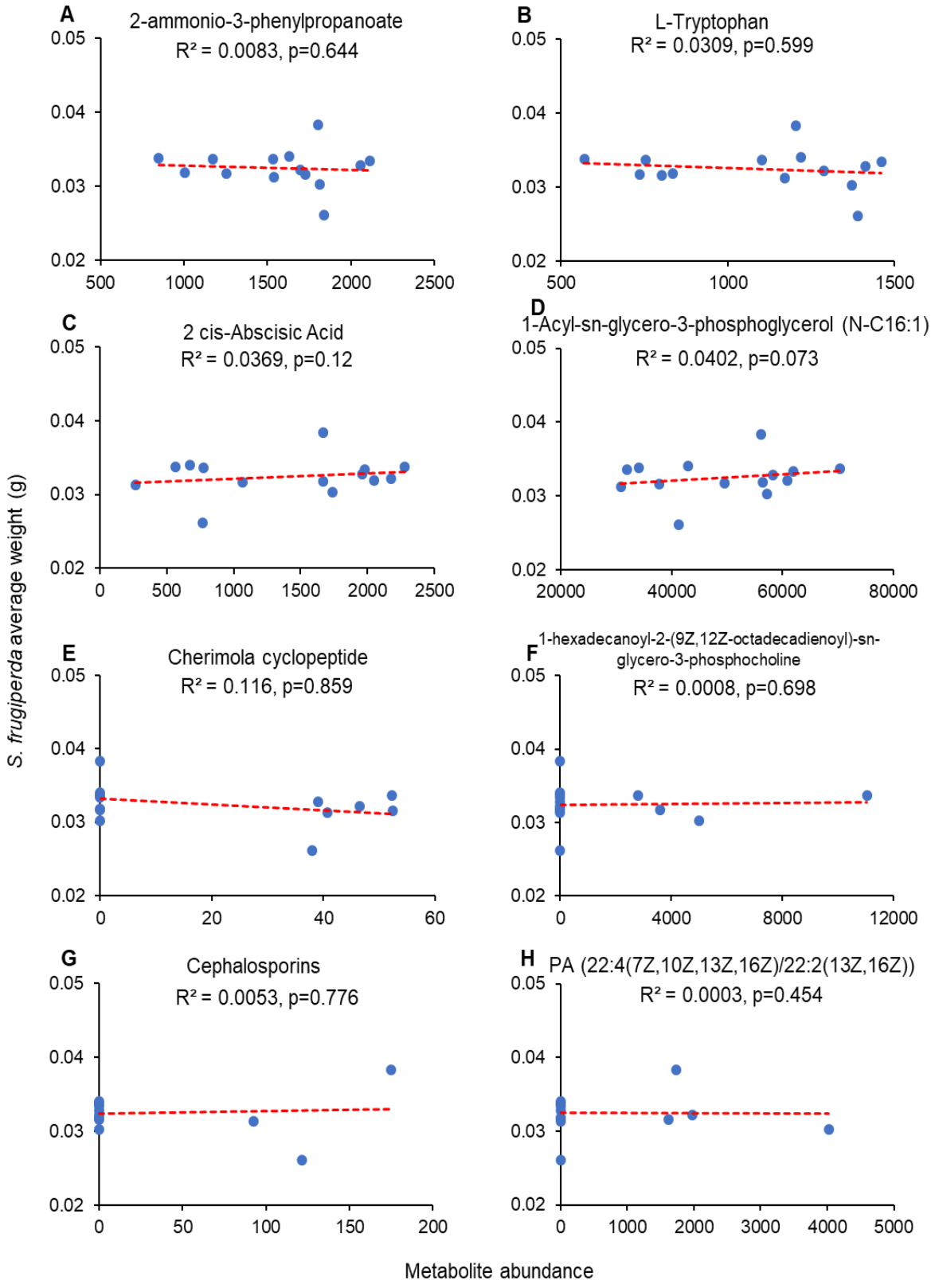

Figure S2. The scatter plots A–H illustrate the relationship between plant total biomass produced and the levels of metabolites upregulated in the leaves of plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

Discussion

Root and leaf feeding herbivore performance

In this study, I have shown that the performance of *D. balteata* and *S. frugiperda* larvae feeding on maize plants grown on soil conditioned with *Photorhabdus*-infected insect cadavers is affected negatively, or neutrally and that these effects are dependent on the *Photorhabdus* strain used to kill *S. frugiperda* larvae used for soil conditioning. Out of the *Photorhabdus* strains used to infect cadavers for soil conditioning, the plants grown on soils conditioned with insect cadavers killed by strains ID79, ID139, ID158, ID163, and ID323 were more resistant to the attack of *D. balteata* larvae, whereas plants grown on soils conditioned with insect cadavers killed by strains ID22, ID138, and ID158 resisted the attack of *S. frugiperda* larvae. These results are consistent with studies that reported suppressive effects of plants grown on soils conditioned with microbial agents against root-feeding insects (Gange, 2001; Oddsdottir et al., 2010; Yang et al., 2014; Santos et al., 2014) and leaf-feeding herbivores (Martinuz et al., 2012; Megali et al., 2015; Gadhave and Gange, 2016; Brock et al., 2018; Dorta et al., 2020). These negative effects against herbivory have been suggested to be mediated by the changes in plant secondary metabolites caused by the microorganisms incorporated in the soil (Gange, 2007; Santos et al., 2014; Van Geem et al., 2015). The differences in resistance of plants used in this study could be due to the variations in the defense metabolites accumulated in the plants, driven by the soil conditioning effects of the different *Photorhabdus* strains used to kill insect larvae. It has been shown that *Photorhabdus* bacteria produce many metabolites that can impact plant growth and health, such as Trans-cinnamic acid, siderophore, resorcinol, terpene, and nucleoside (Muangpat et al., 2022). These bioactive compounds have been characterised to contribute to plant growth, resistance and or can be part of the signalling network for the release of defense compounds against insect herbivores and pathogens (Roba, 2021; Timofeeva et al., 2022; Toffolatti et al., 2021; Yang et al., 2023; Witte and Herde, 2024). However, the production of certain metabolites varies among *Photorhabdus* strains (Tobias et al., 2017; Muangpat et al., 2022; Ardpairin et al., 2024), which may explain the differences in the plant response against herbivore attack. Furthermore, the differences in metabolite production of *Photorhabdus* bacteria may lead to strain-specific soil legacies that influence plant resistance, with effects that can be neutral, positive, or negative against insect pests (Hu et al., 2018; Pineda et al., 2020; Pang et al., 2021; Yu et al., 2021). Moreover, soil conditioning with certain microbial species has been shown to determine the diversity of soil microbial communities that plants interact with, which interaction can determine the constituents and concentration of metabolites released by plants and their effectiveness against herbivory (Bezemer et al., 2005; Eisenhauer et al., 2010; Kabouw et al., 2011; Trivedi et al., 2020). These factors could explain why soil conditioning with cadavers killed by certain *Photorhabdus* strains resulted in a strong plant resistance effect.

The present study also reports that plants grown on soils conditioned with insect cadavers infected with some *Photorhabdus* strains showed a neutral effect on the performance of both *D. balteata* and *S. frugiperda* larvae. These neutral effects observed in the present study are not surprising, as these have also been reported in several studies that evaluated the performance of roots and leaf-feeding insects on plants grown on soils conditioned with other microbial agents (Herman et al., 2008; Kempel et al., 2009; Koricheva et al., 2009; Currie et al., 2011; Pineda et al., 2012; Van Geem et al., 2015; Bernaola et al., 2018; Bernaola and Stout, 2019; Friman et al., 2020). This could suggest that soil conditioning did not induce systemic resistance in plants, and the little suppressive effect is probably due to the local defense barrier produced by plants. In other studies of microbial-plant-herbivore systems involving microbial soil inoculation, little and neutral effects on herbivore performance have been linked with herbivore speciality in feeding on the host crop (Van Oosten et al., 2008; Pineda et al., 2010). Reports have shown that microbial-induced plant resistance more often negatively affects generalist rather than specialist pests (Pineda et al., 2020; Lin et al., 2022; Wang et al., 2023). In our study, we used *S. frugiperda* larvae, a pest that is considered a specialist feeder on the crops in the Poaceae family, in which maize is included (Casmuz et al., 2010; Montezano et al., 2018). This means that *S. frugiperda* is better adapted to maize plants, and any resistance conferred through soil legacy-mediated effects would not affect their performance on maize plants. One of the known mechanisms of adapting to plant defense metabolites by *S. frugiperda* is glycosylation, a mechanism by which herbivores release UDP-glycosyltransferases (UGTs) enzymes to detoxify and control the stability, bioavailability, and activity of plant defensive metabolites (Meech et al., 2012). Studies revealed that *S. frugiperda* detoxifies DIMBOA, the main Benzoxazinoid (BXD) aglucone found in maize leaves, rendering the defense metabolite non-toxic (Maag et al., 2014; Wouters et al., 2014; Israni et al., 2020). Specifically, *S. frugiperda* larvae employ the UGT33 and UGT40 enzymes to glycosylate BXDs (Israni et al., 2020)**.** The detoxification strategy against BXDs has also been reported in *Diabrotica virgifera virgifera* and other Lepidoptera larvae including *S. littoralis*, *M. separata*, and *O. furnacalis* (Sasai et al., 2009; Kojima et al., 2010; Glauser et al., 2011; Maag et al., 2014; Phuong et al., 2016; Robert et al., 2017). In this study, only the plants grown on soils conditioned with insect cadavers killed by *Photorhabdus* strains ID158, ID22 and ID138 were more resistant to the attack of *S. frugiperda* larvae*.* We speculate that besides the BXDs, it is possible that other systemically induced defense metabolites in the maize plants contributed to the negative performance of *S. frugiperda* larvae.

This study investigated resistance in detached leaves and roots but did not account for the systemic changes that mediate interactions between herbivores in natural environments. For example, studies that have focused on metabolic reprogramming have shown that herbivore attack on the roots can have a strong effect on aboveground resistance to herbivores and vice-

versa (Van Dam et al., 2005; Soler et al., 2007; Kaplan et al., 2008; Erb et al., 2009, 2011; Yang et al., 2011; Marti et al., 2013). This reveals that the strong resistance effect observed in our experiment against *D. balteata* larvae feeding on the roots could also translate into enhanced resistance against above-ground herbivores feeding on the leaves via metabolic programming upon insect attack. Through whole plant experiments, further studies should explore the influence of root chemistry on the aboveground plant resistance in plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers to decipher whether the resistance compounds on the roots can be exported to attacked parts above ground to protect against leaf-feeding herbivores such as *S. frugiperda*.

Soil conditioning with insect cadavers killed by specific *Photorhabdus* strains induces metabolic responses in plants

We found that soil conditioning with *Photorhabdus*-infected insect cadavers induces plant resistance against herbivores. We hypothesised that plants that resisted the attack of *D. balteata* and *S. frugiperda* larvae in the insect performance experiments would exhibit changes in their roots and leaf metabolites, enabling resistance against the herbivores. The results have shown that soil conditioning with *Photorhabdus*-infected insect cadavers leads to significant upregulation of certain metabolites in plant leaves and roots, and that these metabolic responses are dependent on the *Photorhabdus* strain used to kill insect larvae for soil conditioning. We noted that only the plants that resisted the attack of *D. balteata* and *S. frugiperda* larvae in the insect performance experiment phase accumulated more distinct metabolites than the susceptible and the control plants. In the roots, Aromadendrin, Compound ID 196, Imidazole alkaloids, and 6,9,10-trihydroxyoctadec-7-enoic acid were significantly more abundant in plants grown on soils conditioned with insect cadavers killed by strains ID79, ID139, ID158, ID163, and ID323. These metabolites have many biological activities and could be involved in the defense mechanisms of plants (Hövelmann et al., 2019; Lee and Jeong, 2020; Mareya et al., 2020; Dozio et al., 2025). The distinct metabolites that were only accumulated in the roots of resistant plants included; 4-[(6R)-6-hydroxy-5,5-dimethylcyclohexen-1-yl] benzoic acid, 2 cis-Abscisic Acid, Canthoside B, Apigenin 7-sulfate, Pimarane and Isopimarane diterpenoids, Ajugaciliatin A, GDIMBOA and Tinosineside B. Many of these metabolites accumulated in the experimental plants have been reported in other studies as defensive compounds employed by plants against herbivores and pathogens (Erb et al., 2012; Johnson et al., 2016; Rasmann and Turlings, 2016; Reveglia et al., 2018; Zhang et al., 2024), making them possible candidates for the specific resistance observed against the root feeding herbivore. The metabolites Ajugaciliatin A, Canthoside B, Apigenin 7-sulfate and Tinosineside B naturally occur in plants, but have not yet been linked to plant defense. However, their biological activities, including antimicrobial, antioxidant, cytotoxic, and anti-estrogenic, among other properties, have been described (Gonzalez-Burgos and Gomez-

Serranillos, 2012; Dutta et al., 2021; Parveen et al., 2021; Allemailem et al., 2024; Ao et al., 2024), and thus, their accumulation in plants could directly contribute to resistance or be part of the signalling network for the release of defense compounds against insect pests.

In the leaves, the more abundant metabolites were; (2R)-2-ammonio-3-phenylpropanoate, L-Tryptophan, 1-Acyl-sn-glycero-3-phosphoglycerol (N-C16:1), 2 cis-Abscisic Acid, Cephalosporins, Cherimola cyclopeptide, PC (16:0/18:2(9Z,12Z)) 1-hexadecanoyl-2-(9Z,12Z-octadecadienoyl)-sn-glycero-3-phosphocholine and PA(22:4(7Z,10Z,13Z,16Z)/22:2(13Z,16Z)), all of which have been described to offer resistance against insect pests and pathogens (Irmisch et al., 2015; Mareya et al., 2020; Pan et al., 2019; Yadav et al., 2020; Pretorius et al., 2022; Rosa et al., 2023; Chekan et al., 2024; Li et al., 2025). The changes in the metabolic response observed in this study are consistent with studies by Muller et al. (2024), who showed that root exposure to *Photorhabdus* bioluminescence triggered the accumulation of defensive secondary metabolites in maize plants. Taken together, these results suggest that soil conditioning with *Photorhabdus*-infected insect cadavers killed by selected *Photorhabdus* strains confers systemic responses in maize plants that can suppress the feeding of below and aboveground herbivores.

Conclusion

Altogether, our study demonstrated that plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers have suppressive effects against the roots and leaf-feeding herbivores in a strain-specific manner. The plants that resisted the attack of *D. balteata* and *S. frugiperda* larvae in the insect performance experiments accumulated distinct metabolites in their roots and leaves, enabling resistance against the herbivores. As cultivated crops have a relatively reduced degree of variation in plant defense mechanisms in comparison to wild populations (Alonso-Blanco and Koornneef, 2000; Gols et al., 2008; Anderson and Mitchell-Olds, 2011), the results of this study demonstrate that soil conditioning with insect cadavers killed by selected *Photorhabdus* bacterial strains via plant-soil feedback can induce a systemic response that can protect plants against herbivore attack.

Chapter 3

Soil legacy effects of *Photorhabdus* metabolites on the soil microbial community

Abstract

Photorhabdus bacteria are often applied as foliar sprays or in soil drenching treatments to control above and below-ground insect pests, respectively. As a result, large amounts of *Photorhabdus* bacterial cells, toxins, and metabolites end up in the soil, and yet, their impact on non-target soil microbial organisms is unknown. This study investigated the response of soil microbial communities under three soil treatments: i) non-conditioned control soil, ii) soils conditioned with *Photorhabdus*-infected insect cadavers, and iii) soil conditioned with mechanically killed (MK) insect larvae. I used amplicon sequencing to determine the diversity and the relative abundance of bacterial, nematode, and fungal communities in the experimental soil treatments.

The results showed that soil conditioning treatments had a generally greater impact on the bacterial than on the fungal and nematode communities. Notably, the abundance of *Myroides odoratimimus, Serratia marcescens, Providencia rettgeri,* and *Alcaligenes faecalis* was higher in soils conditioned with *Photorhabdus*-infected insects than in soils conditioned with mechanically-killed (MK) insects or in non-conditioned control soils. I observed treatment-specific effects of soil conditioning on the nematode species abundance. Notably, *Aphelenchus sp., Acrobeloides sp., Cervidellus* sp*.,* and *Mesodorylaimus* sp*.* were exclusively abundant in soils conditioned with *Photorhabdus*-infected or with MK insects. *Aphelenchus* sp. and *Acrobeloides* sp. were found in all conditioned soils, whereas *Cervidellus* sp*., Mesodorylaimus sp., filenchus* sp*. and Diploscapter* sp. were observed in conditioned soils in a treatment-dependent manner.

Altogether, conditioned soil treatments were exclusively associated with beneficial bacteria and nematodes than the non-conditioned control soil, highlighting their potential contribution to the increased biomass of plants grown on conditioned soil, as reported in Chapter 1. I conclude that soil conditioning with MK or *Photorhabdus*-infected insect cadavers improves plant growth and promotes a high abundance of beneficial bacteria and nematodes in conditioned soil.

Introduction

The soil is a habitat for over 10^{30} microorganisms, including bacterial, archaeal, and eukaryotic groups with unique diversity and abundance (Whitman et al., 1998; Torsvik et al., 2002; Roesch et al., 2007; FAO et al., 2020). Soil microorganisms drive agricultural food production by performing important ecosystem functions, such as plant nutrient cycling, pest and disease suppression, and enhancing soil health (Bardgett et al., 2008; Rojas et al., 2016; Fierer, 2017; Schloter et al., 2018; Singh and Gupta, 2018). However, in agricultural settings, farming inputs and practices impact soil microbial communities and their belowground activities (Verbruggen et al., 2010; Bender et al., 2016; K. Li et al., 2022). Agricultural inputs used by farmers include microbial agents as biofertilizers, biopesticides or bioremediation to enhance crop yields (Glick, 2012; Berger et al., 2018; Pacios-Michelena et al., 2021; Kour et al., 2022). These microbial agents are delivered by foliar sprays, seed treatment or soil drenching, and in turn modify the soil microbial communities and their below-ground activities in crop fields via the release of toxic compounds in the microenvironment (Palma et al., 2014; Valldor et al., 2015; Zhaolei et al., 2017; Y. Li et al., 2022; Saha et al., 2022). The resultant changes in soil microbial communities can positively affect crop production through the recruitment of beneficial microorganisms that support plant growth or negatively via the accumulation of plant pathogens that reduce plant growth (Dudenhöffer et al., 2018; Santoyo et al., 2021; Zhang et al., 2022; Gul et al., 2023).

Photorhabdus bacteria, a symbiont of the entomopathogenic nematodes from the *Heterorhabditis* genera, is one of the microbial control agents applied as foliar sprays or by soil drenching to control above and below-ground insect pests (Abdel-Razek, 2003; Mohan et al., 2003; Vyas et al., 2008; Shahina et al., 2011; Aatif et al., 2014; Kakade et al., 2023; Abdisa et al., 2024). Its direct application without the EPN vector introduces a high density of *Photorhabdus* bacterial cells and their toxins and metabolites in the soil. Studies on *Photorhabdus* bacteria in the soil have found that the bacteria can survive and interact with plant roots (Eckstein and Heermann, 2019; Regaiolo et al., 2020). In Chapter 1, I evaluated *Photorhabdus* bacteria strains against *Spodoptera frugiperda* larvae and investigated the soil legacy effects of *Photorhabdus* bacteria via soil conditioning with *Photorhabdus*-infected insect cadavers on plant growth in a greenhouse condition. I demonstrated that plants grown on soil conditioned with *Photorhabdus*-infected insect cadavers produced significantly higher plant biomass than the non-conditioned control soil. Despite my understanding of the impact of soil conditioning with *Photorhabdus*-infected insect cadavers on plant performance and resistance to herbivores, their indirect effects on non-target resident soil microbial organisms are unknown.

Many studies on direct soil inoculation with different microbial control agents have reported varying effects including altering or having limited, transient or no effects on the soil microbial

communities (Kozdrój et al., 2004; Mayerhofer et al., 2019; Saha et al., 2022; Canfora et al., 2023; Fazal et al., 2024). Mechanistically, toxins released by the microbial agents in the soil environment have been implicated in altering the soil microbial community (Yan et al., 2007; Saha et al., 2022; Fazal et al., 2024). Moreover, toxins of some microbial control agents, such as *Bacillus thuringiensis* (Bt), can persist in the rhizosphere during crop life and continue to cause changes in the soil microbiome (Luo et al., 2017; Saha et al., 2022). *Photorhabdus* bacteria produce many toxins and metabolites with insecticidal, antimicrobial, acaricidal, cytotoxic, and antiparasitic properties that have been exploited against plant pathogens, pests, and diseases (Waterfield et al., 2005; Eleftherianos et al., 2007; Furgani et al., 2008; Bode, 2009; Grundmann et al., 2014; Tobias et al., 2016; Muangpat et al., 2017; Antonello et al., 2018; Vitta et al., 2018; Eroglu et al., 2019; Cevizci et al., 2020; Muangpat et al., 2022). Although the agricultural benefits of *Photorhabdus* toxins and metabolites are established, there remains a knowledge gap regarding the response of soil microorganisms to *Photorhabdus*-derived toxins and metabolites released into the soil ecosystem.

In this study, I examined the effect of soil conditioning with *Photorhabdus*-infected insect cadavers on soil microbial communities. I hypothesised that *Photorhabdus*-derived toxins and metabolites, released from decomposing insect cadavers, affect the soil microbial community. To test this hypothesis, soil conditioning experiments were set up in a greenhouse environment, and I collected samples of three soil treatments: i) non-conditioned control soil, ii) soil conditioned with *Photorhabdus*-infected insect cadavers, and iii) soil conditioned with mechanically killed (MK) insect larvae. Amplicon sequencing was used to examine the composition and diversity of bacterial, nematode, and fungal communities in the different experimental soil treatments. This study provides an understanding of the interactions among *Photorhabdus* bacterial cells and toxins and the resident soil microbial communities, providing new insights into the ecological impact of *Photorhabdus* bacteria on the soil ecosystems.

Materials and Methods

Insects and insect rearing

Spodoptera frugiperda larvae were fed on an artificial diet (in g/Kg: soy milk 31.7, wheat germ 90, sugar 36.56, dried yeast 17.81, cholesterol 0.5, methylparaben 1, sorbic acid 2.3, ascorbic acid 2.46, vitamin B complex 0.184, chloramphenicol 0.269 and agar 27.5). The adults were kept in insect-rearing cages with a constant supply of water and a 10% sucrose solution. Eggs were collected twice a week. Insect rearing was maintained under a controlled temperature (25 ± 2°C). Larvae at 4-6th instar were used for all the soil conditioning experiments.

Bacterial strains

The *Photorhabdus* bacterial strains used in this experiment were selected from five species in the phylogenetic tree of *Photorhabdus* bacteria (Table 1), and cultured in lysogeny broth (LB)

agar plates at 28°C. Bacterial strains were re-plated monthly, and the cultures were refreshed from glycerol stocks every six months.

Table 1: *Photorhabdus* bacteria strains used in the study

Species	Strain
P. bodei	ID81
	ID83
P. cinerea	ID158
	ID163
P. khanii subsp*. khanii*	ID316
	ID317
P. laumondii subsp*. laumondii*	ID22
	ID25
	ID79
P. tasmaniensis	ID138
	ID139
	ID323

Insect infection assays

Spodoptera frugiperda larvae were infected with the different *Photorhabdus* strains by directly injecting bacterial cultures into their bodies. To this end, ten microliters (10 µL) of bacterial suspensions were injected at the back, neck or behind the last pair of false legs using the Hamilton syringe. To prepare the bacterial suspensions, 25 ml of LB broth medium was inoculated with a single colony of *Photorhabdus* bacteria and incubated overnight at 28 °C and 180 rpm of constant agitation for 14-16 hours. Before injecting the larvae, the overnight liquid culture optical density (OD_{600}) was measured and adjusted to OD_{600}=1. The injections were performed using a Hamilton syringe, and the injected larvae were kept at room temperature in plastic trays. Insect mortalities were recorded at regular intervals for 96h, and *Photorhabdus*-infected insect cadavers were used for soil conditioning experiments as described below.

Soil conditioning with *Photorhabdus*-infected *S. frugiperda* cadavers

To condition the soil with *Photorhabdus*-infected insect cadavers, field soil was mixed with sand (0-4mm) at a 1 to 1 ratio (hereafter referred to as experimental soil). Then, desired amounts of soil-sand mixture were transferred to plastic containers, and *Photorhabdus*-infected *S. frugiperda* cadavers or MK larvae were buried equidistantly from each other (Fig. 1, Chapter 1). Five *Photorhabdus*-infected cadavers or five MK insect larvae per 365g of soil (equivalent to soil filled in 0.5l square plastic pots) were used. The conditioned soil was left under greenhouse conditions and moistened regularly for seven days. Control soil was treated in a similar manner, but no insect cadavers were buried. After this time, the different experimental soil treatments were homogenised and approximately 365g of soil samples from

soil conditioned with *Photorhabdus*-infected cadavers, MK insect larvae and non-conditioned control soil were collected. The experiment consisted of 14 soil conditioning treatments, from which three soil subsamples were prepared, resulting in 168 samples for microbial analysis across four independent experiments (14 treatments x 4 experiments x 3 sub-samples). These were stored at -20°C for soil chemical elements and microbial composition analyses.

DNA extraction

The total genomic DNA was extracted from a subsample of 200 mg of soil from each treatment using the TGuide S96 Magnetic Universal DNA Kit (DP812, Tiangen Biotech, Beijing, China), following the manufacturer's recommendations. The concentration of the extracted DNA was assessed using the Nanodrop 2000 (Thermo Fisher Scientific, Wilmington, USA).

After the DNA extraction, primers were designed according to the conserved region, and sequencing adapters were added to the ends of the primers. The bacterial universal primer set 338F: 5'-ACTCCTACGGGAGGCAGCA-3' and 806R: 5'-GGACTACHVGGGTWTCTAAT-3' was used to amplify the V3-V4 region of 16S rRNA gene from the genomic DNA extracted from each sample. The fungal primer ITS1 F: CTTGGTCATTTAGAGGAAGTAA; and ITS2 R: GCTGCGTTCTTCATCGATGC was used to amplify the ITS1 region, and the nematode primer set NF1: 5′-GGTGGTGCATGGCCGTTCTTAGTT-3' (Forward) and 18Sr2b-ad: 5′-TACAAAGGGCAGGGACGTAAT-3' (Reverse) was used to amplify the nematode nf1 region. Both the forward and reverse primers were ligated with sample-specific Illumina index sequences. After amplification, the PCR products were analysed by LabChip GX (Perkin Elmer, Waltham, USA) for fragment analysis and integrity assessment. The qualified library was sequenced on the Illumina Novaseq 6000 platform (Illumina, San Diego, USA) with paired-end 250 bp (PE250) mode. Library construction and sequencing were performed at Biomarker Technologies (BMKGENE) GmbH. To obtain Clean Reads without primer sequences, the Raw Reads were filtered using the Trimmomatic v0.33 software (Bolger et al., 2014) and the primer sequences were identified and removed using the cutadapt 1.9.1 software (Martin, 2011). The DADA2 (Callahan et al., 2016) method in QIIME2 2020.6 (Bolyen et al., 2019) was used for denoising, double-end sequence splicing, and removing chimeric sequences to obtain the final valid data (Non-chimeric Reads). Finally, using SILVA version 138 as the reference database for bacteria and nematodes, and the FASTQ release from UNITE version 9.0 for fungi, the naive Bayes classifier combined with the alignment method was used to perform taxonomic annotation on the feature sequences. The species classification information corresponding to each feature was obtained, and then the community composition of each sample was statistically analysed at each level (phylum, class, order, family, genus, species). The species abundance table at different classification levels was generated using QIIME software (Bolyen et al., 2019), and then the community structure diagram at each taxonomic level of the sample was drawn using the R package *vegan* (Oksanen et al., 2001).

Data Analysis

All microbial community analyses and high-quality graphs were produced using the R package *vegan* (Oksanen et al., 2001). To determine the differences in the soil microbial community composition between samples, the Principal Coordinate Analysis (PCoA) and PERMANOVA (Permutational multivariate analysis of variance) were conducted on Bray-Curtis distances in the R package *vegan* (Oksanen et al., 2001).

Results

Soil conditioning with *Photorhabdus*-infected insect cadavers changes the soil bacterial and nematode but not the fungal communities

i) Microbial Community Composition

To investigate the impact of the different soil conditioning treatments on the soil microbial community composition, soil samples were analysed by profiling the bacterial V3-V4 region, the nf1 regions for nematodes and the fungal ITS1 region of the ribosomal operon. I compared the microbial communities of non-conditioned control soil and soil conditioned with *Photorhabdus*-infected insect cadavers or mechanically killed (MK) insect larvae to the lowest taxonomic rank possible. The results showed that soil conditioning with *Photorhabdus*-infected insect cadavers or MK insect larvae significantly altered the bacterial community than the fungal and nematode communities. The dominant bacterial species identified were: *Myroides odoratimimus, Serratia marcescens, Providencia rettgeri,* and *Alcaligenes faecalis.* In addition, among the most abundant bacterial taxa, we found the orders *Gaiellales* sp.*, Gemmatimonas* sp.*,* and *Vicinamibacterales* sp*.* (Fig. 1). It was observed that soils conditioned with *Photorhabdus*-infected insect cadavers or MK insect larvae were significantly enriched with bacteria species *M. odoratimimus, S. marcescens, P.rettgeri, and A. faecalis*, which were not detected in non-conditioned control soils (Fig. 2). Importantly, the abundance of *M. odoratimimus, S. marcescens, P. rettgeri,* and *A. faecalis* was higher (5 – 29%) in soils conditioned with *Photorhabdus*-infected insect cadavers than in soils conditioned with MK insect larvae (Only 1 – 3%), pointing to *Photorhabdus*-dependent and independent effects on soil microbial communities (Fig. 2).

The fungal community composition did not differ between soil conditioning treatments. The dominant fungal species were: *Mortierella wolfii, Cercophora samala, Gibellulopsis serrae, Solicoccozyma aeria, Fusarium circinatum, Fusarium equiseti,* and *Fusarium solani* (Fig. 1). All these were detected in both conditioned and non-conditioned control soil (Fig. 3). Regarding the nematode communities, the most dominant genera were *Cephalobus sp., Aphelenchus sp., Pratylenchus* sp., *Filenchus* sp., *Acrobeloides* sp., *Cervidellus* sp., *Diploscapter* sp., and *Mesodorylaimus* sp*.* (Fig. 1). There were significant differences in the abundance of some nematode species in conditioned soils when compared with non-conditioned control soil, and

soil conditioning treatment-specific effects on the nematode species abundance were observed (Fig. 4). Notably, *Cephalobus* sp*.* and *Acrobeloides* sp. were significantly impacted by the soil conditioning treatments. *Aphelenchus* sp., *Acrobeloides* sp., *Cervidellus* sp., and *Mesodorylaimus* sp*.* were exclusively detected in soils conditioned with *Photorhabdus*-infected insect cadavers or with MK insect larvae, but not in control soils. While the abundance of *Cervidellus* sp., *Mesodorylaimus* sp., *filenchus* sp., *Diploscapter* sp. and *Pratylenchus* sp. were detected in conditioned soil in a treatment-specific manner (Fig. 4).

ii) Microbial Diversity

To investigate the effect of different soil conditioning treatments on microbial diversity, I compared microbial communities across treatments using Principal Coordinates Analysis (PCoA) and Permutational Analysis of Variance (PERMANOVA) based on Bray-Curtis distances. In this study, soil conditioning with *Photorhabdus*-infected insect cadavers significantly influenced bacterial communities. The PCoA analysis, using Bray-Curtis distance matrices, showed a higher dissimilarity index in the bacterial community across most of the soil conditioning treatments compared to the control group. Additionally, the PERMANOVA test confirmed a significant effect of soil conditioning on the bacterial community composition (Fig. 5). In contrast, the PCoA analyses showed no dissimilarity in the fungal community and the PERMANOVA revealed no significant effect of soil conditioning on the fungal community composition across treatments (Fig. 5). Similarly, from a global view, no significant differences in the nematode community were observed (Fig. 5). However, individual species were significantly impacted by soil conditioning when compared with the control (Fig. 4). Overall, these findings demonstrate that the legacy effects of soil conditioning with *Photorhabdus*-infected insect cadavers and MK insect larvae altered the bacterial and nematode communities, while the fungal communities remained stable.

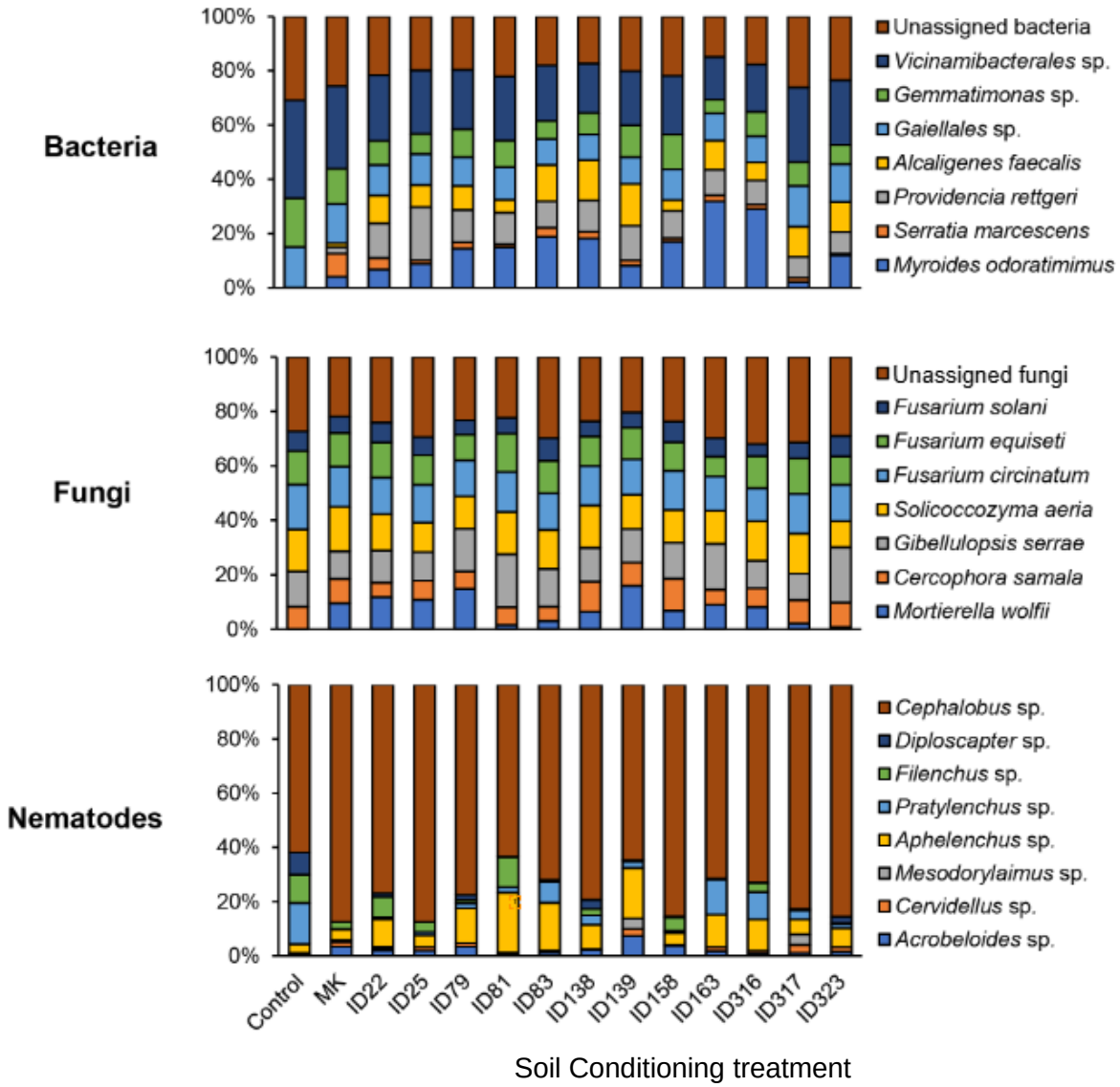

Figure 1. Relative abundance of identified soil bacteria, fungi and nematode species to the lowest taxonomic rank in the different soil conditioning treatments. The colours represent distinct species (bacteria and Fungi), and genera (nematodes). The stacked columns are the top eight taxa in relative abundance at the genus level.

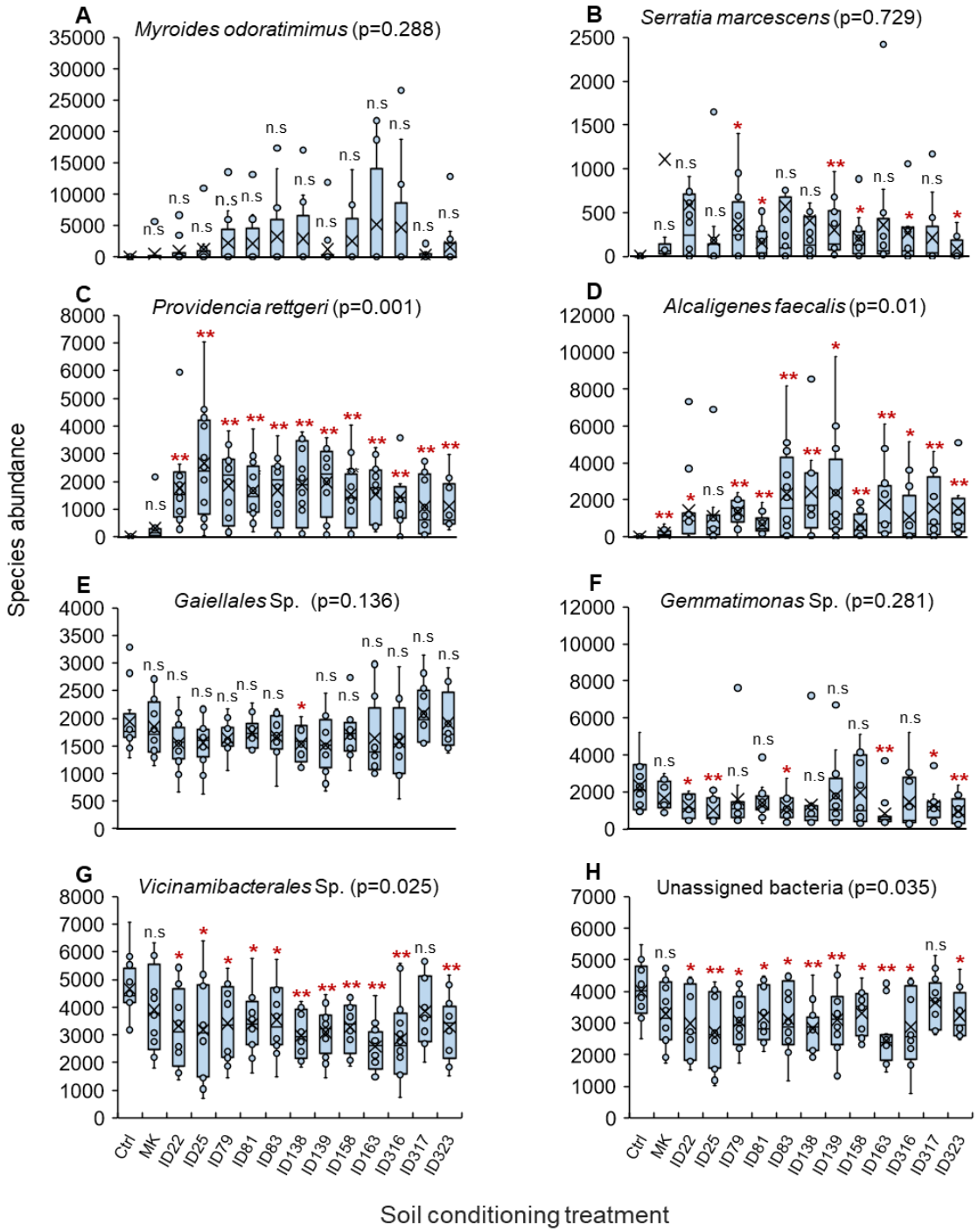

Figure 2. A–H represent the analysis of the alterations in the abundance of each bacterial species under different soil conditioning treatments. The dots on the boxplots represent the raw data. The black cross (X) in the boxes represents the median values of all variables. Ctrl, non-conditioned soil; MK, soil conditioning with mechanically killed insect larvae; ID22–323, soils conditioned with insect larvae killed by the different *Photorhabdus* strains. Asterisks above the bars indicate statistical differences between the treatments and the control at a significance level of $p < 0.05$, by one-way ANOVA with Tukey HSD test for multiple comparisons.

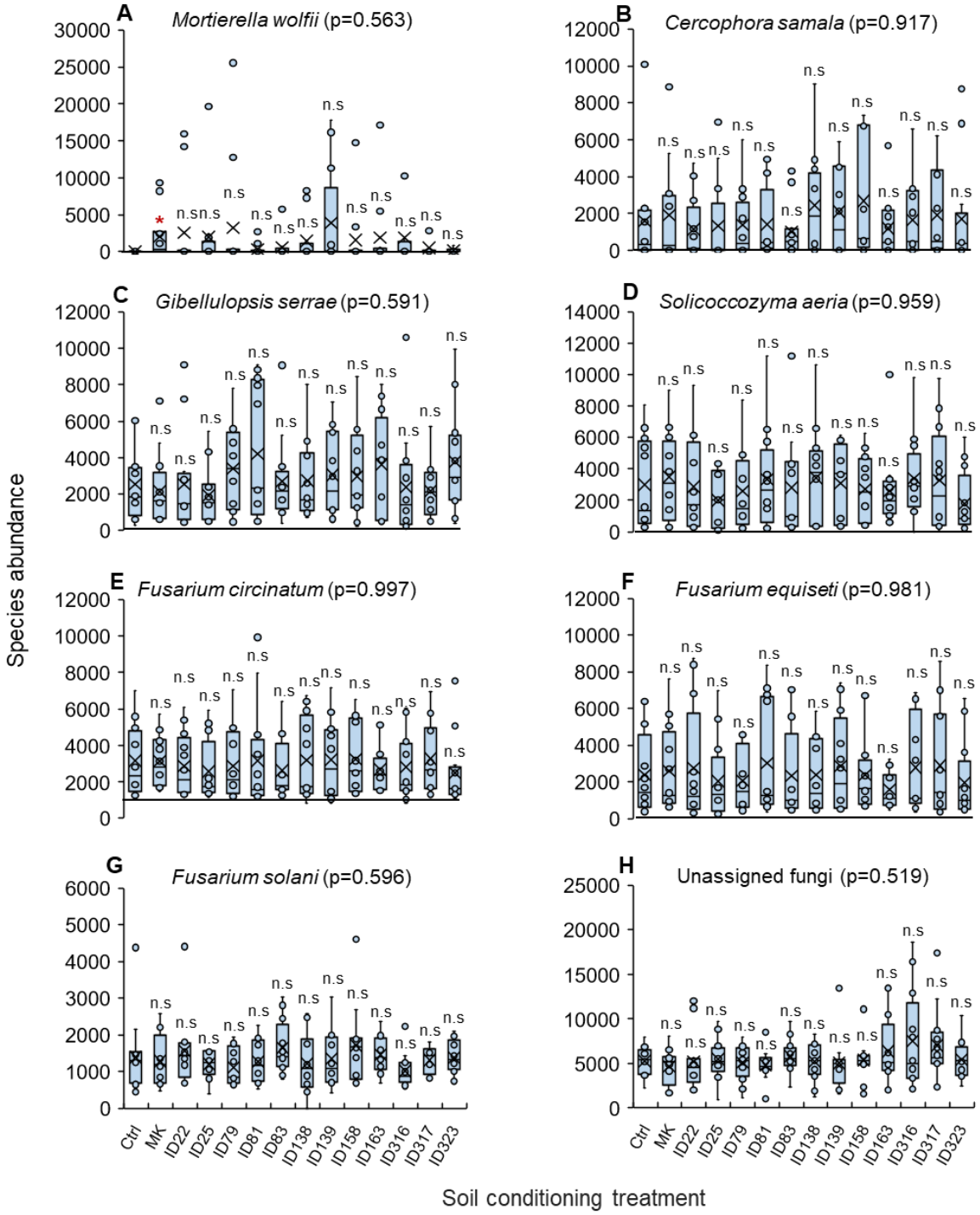

Figure 3. A–H represent the analysis of the alterations in the abundance of each fungal species under different soil conditioning treatments. The dots on the boxplots represent the raw data. The black cross (X) in the boxes represents the median values of all variables. Ctrl, non-conditioned soil; MK, soil conditioning with mechanically killed insect larvae; ID22–323, soils conditioned with insect larvae killed by the different *Photorhabdus* strains. Asterisks above the bars indicate statistical differences between the treatments and the control at a significance level of $p < 0.05$, by one-way ANOVA with Tukey HSD test for multiple comparisons.

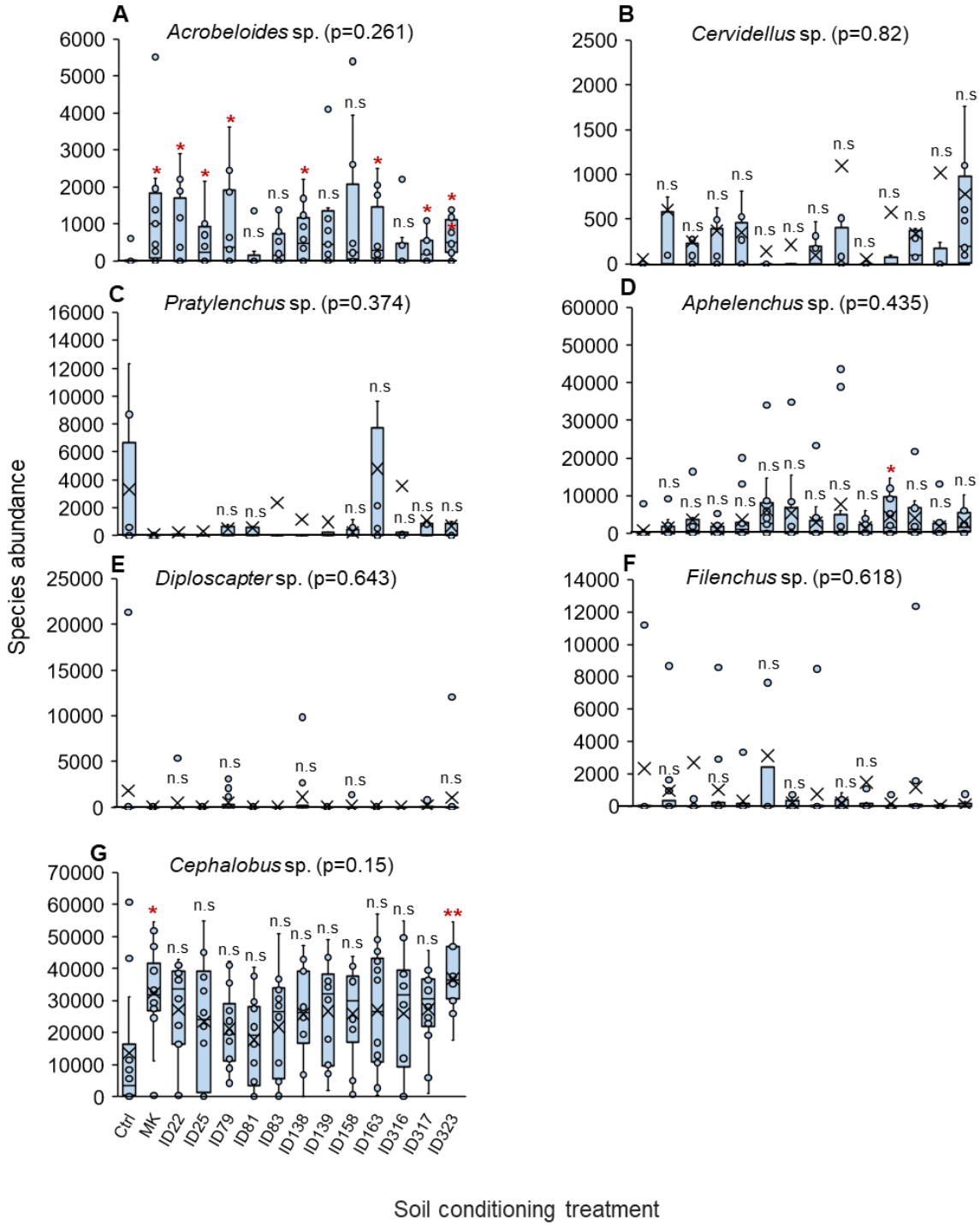

Figure 4. A–G represent the analysis of the alterations in the abundance of each nematode species under different soil conditioning treatments. The dots on the boxplots represent the raw data. The black cross (X) in the boxes represents the median values of all variables. Ctrl, non-conditioned soil; MK, soil conditioning with mechanically killed insect larvae; ID22–323, soils conditioned with insect larvae killed by the different *Photorhabdus* strains. Asterisks above the bars indicate statistical differences between the treatments and the control at a significance level of $p < 0.05$, by one-way ANOVA with Tukey HSD test for multiple comparisons.

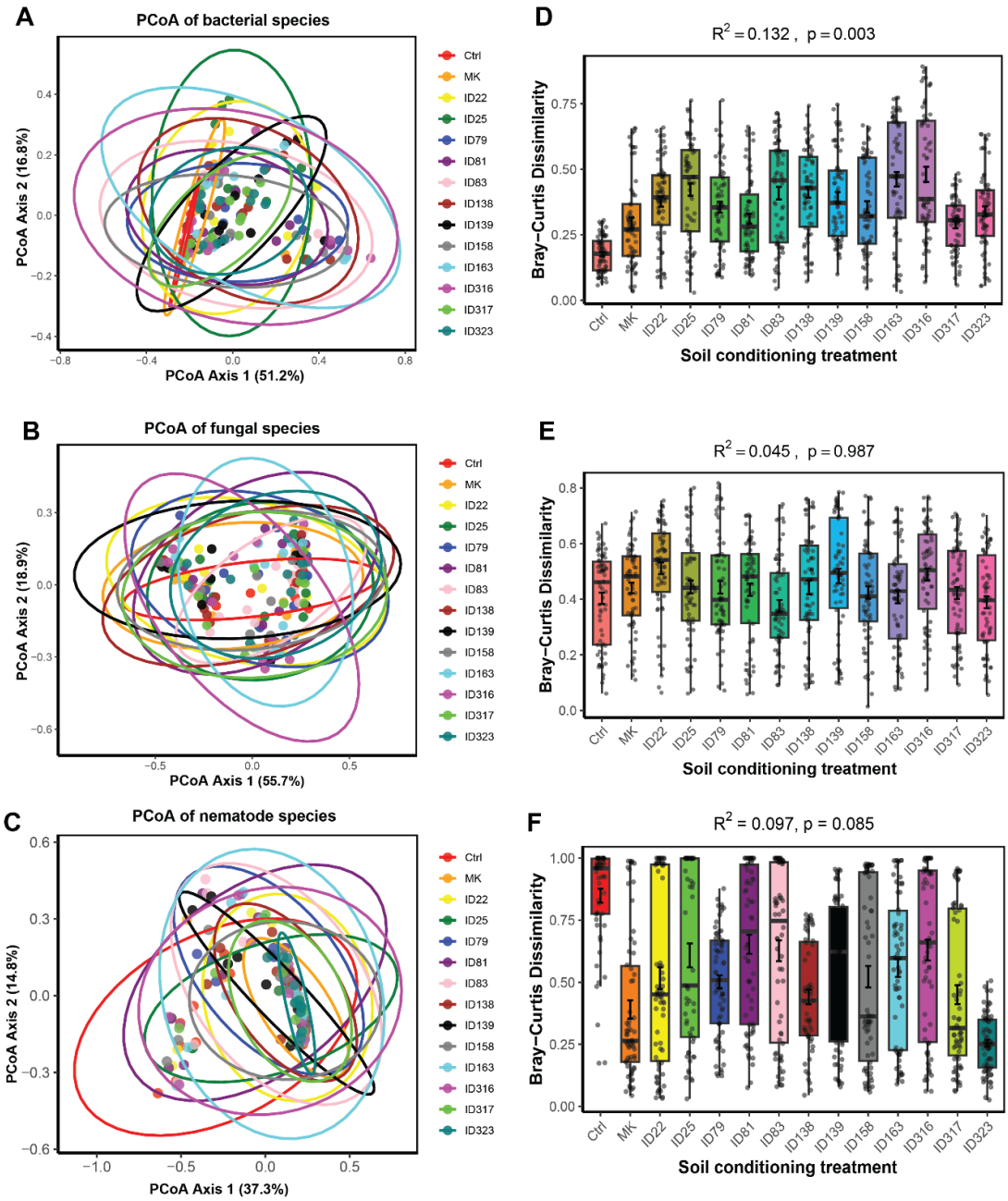

Figure 5. A–C are Principal coordinates analyses (PCoAs), using Bray-Curtis distances representing the bacterial, fungal, and nematode communities of the non-conditioned soil (control), soil conditioned with insect cadavers killed by different *Photorhabdus* strains or mechanically killed larvae (MK). The colours represent samples of the different soil conditioning treatments. The ellipses indicate the 95% confidence intervals per treatment. D-F are outputs of PERMANOVA on Bray-Curtis dissimilarities, showing R^2 and p-values for soil conditioning effect on the soil bacterial, fungal, and nematode communities, respectively.

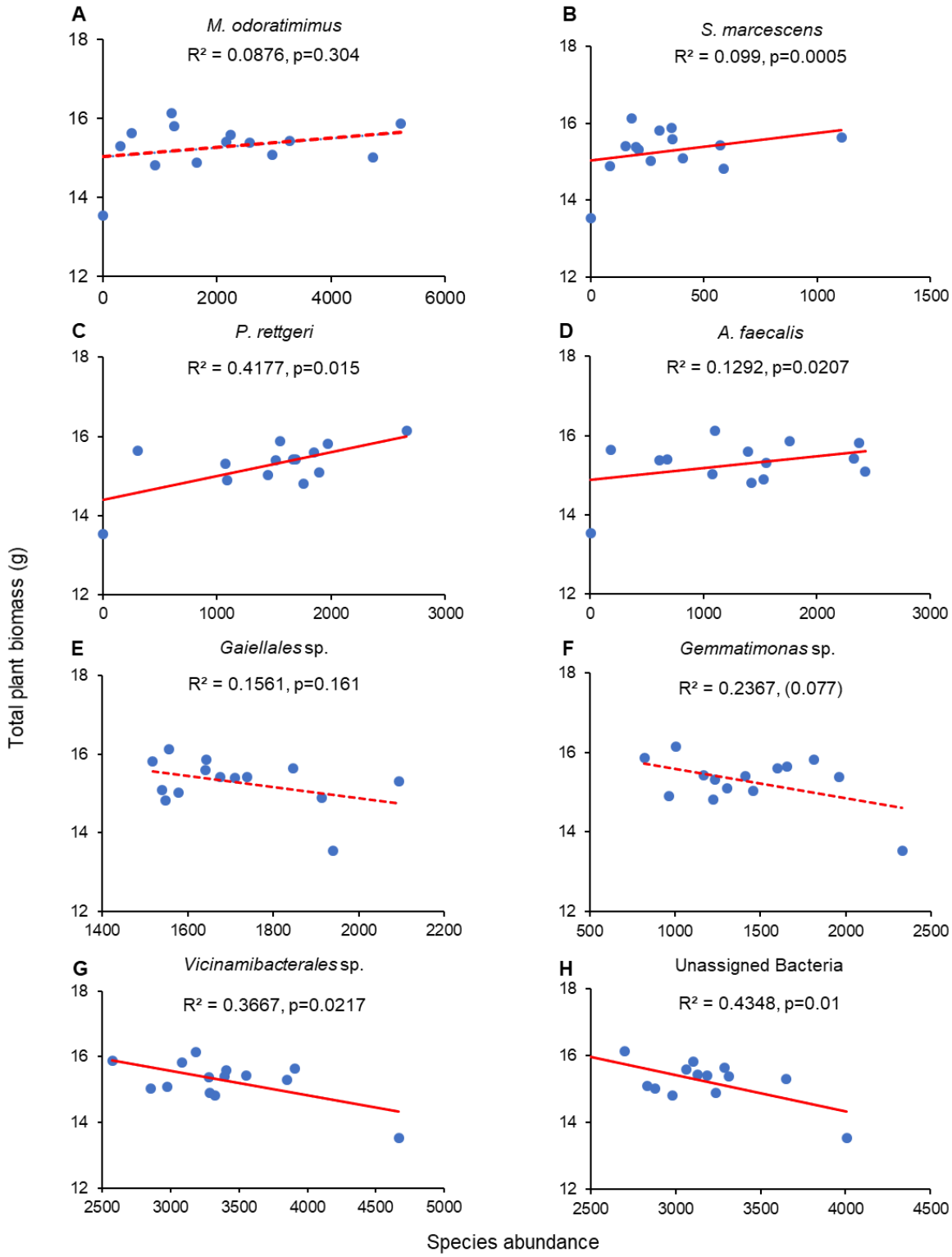

Figure S1. The scatter plots A–H illustrate the relationship between plant total biomass produced and bacterial species abundance in soils conditioned with *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

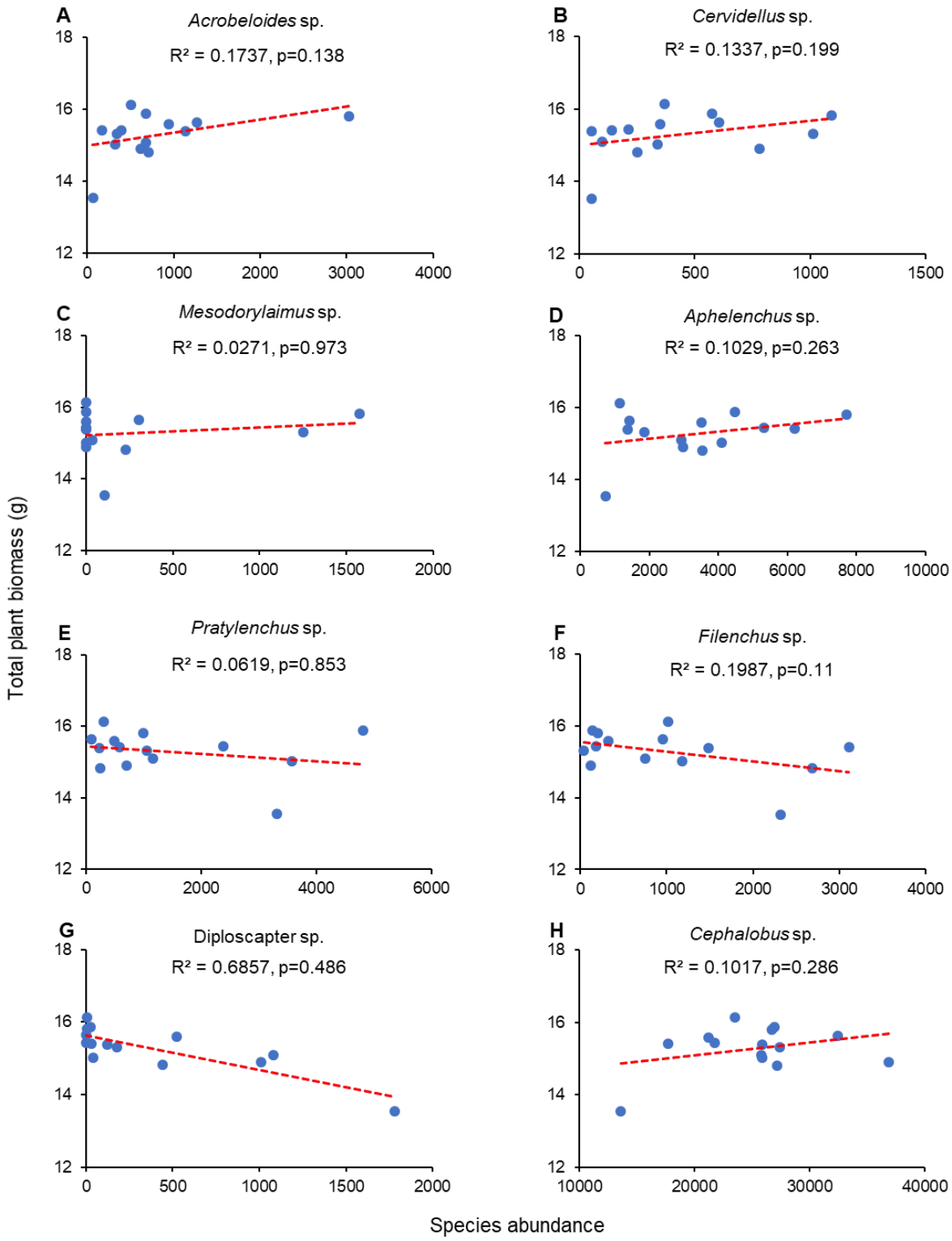

Figure S2. The scatter plots A–H illustrate the relationship between plant total biomass produced and nematode species abundance in soils conditioned with *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

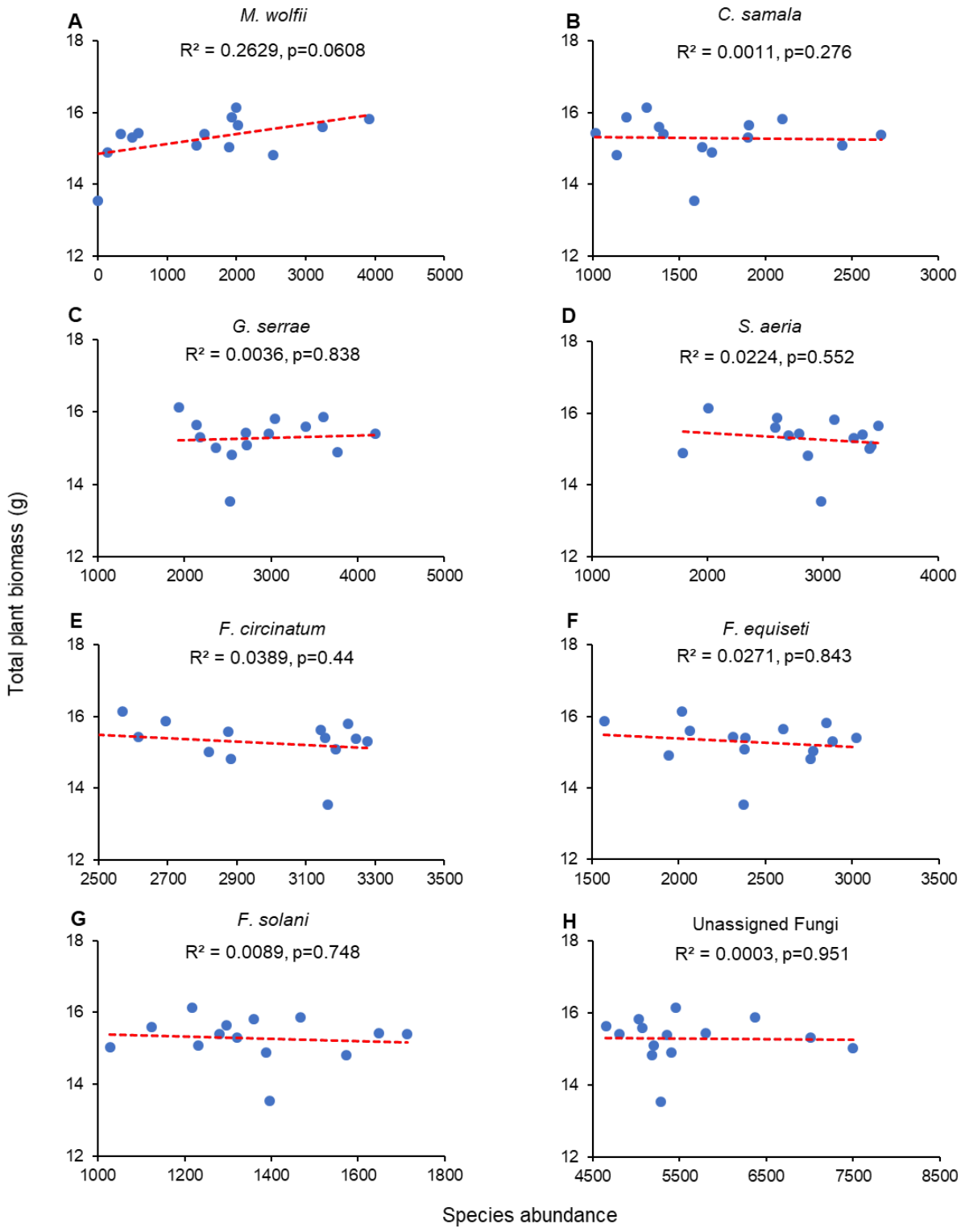

Figure S3. The scatter plots A–H illustrate the relationship between plant total biomass produced and fungal species abundance in soils conditioned with *Photorhabdus*-infected insect cadavers. Each data point corresponds to a soil conditioning treatment. Correlation relationships were assessed by Pearson's test.

Discussion

This study demonstrates that soil conditioning treatments has a generally greater impact on the bacterial than on the fungal and nematode communities. However, similar to the bacterial species, the abundance of some nematode species was significantly abundant in conditioned soils, and not in non-conditioned control soil, although the overall nematode community diversity was not statistically significant. The changes observed in the bacterial and nematode species are consistent with studies that reported changes in the bacterial and nematode species in soils inoculated with bacterial control agents (Kozdrój et al., 2004; Čerevková et al., 2018; Saha et al., 2022). For instance, inoculating soil with *Pseudomonas* species, *P. chlororaphis* and *P. putida* altered the bacterial community and their composition from a Gram-positive to Gram-negative dominant community in maize rhizosphere (Kozdrój et al., 2004). Similarly, Bt toxins applied directly in soil or released by Bt-transgenic crops as exudates altered the soil bacterial and nematode community composition (Griffiths et al., 2007; Yan et al., 2007; Neher et al., 2014; Čerevková et al., 2018; Fazal et al., 2024).

The resultant changes in soil microbial communities can positively or negatively affect plant growth (Santoyo et al., 2021; Zhang et al., 2022). This study showed that among the dominant bacterial species, *Myroides odoratimimus, Serratia marcescens, Providencia rettgeri,* and *Alcaligenes faecalis* were more abundant in soils conditioned with *Photorhabdus*-infected insect cadavers and MK insect larvae, not the non-conditioned control soil. All these are beneficial bacteria that have plant growth promotion properties in the form of nutrient cycling (You et al., 2015; Jiang et al., 2021; Jia et al., 2022; Salaskar et al., 2022; Asaturova et al., 2023; Liu et al., 2024; Patel et al., 2024). Additionally, their functions extend to plant protection against pests and pathogens and improve the stress tolerance of plants (You et al., 2015; Shan et al., 2019; Ferioun et al., 2023). In the nematode community, the most dominant genera were *Cephalobus* sp., *Aphelenchus* sp., *Pratylenchus* sp., *Filenchus* sp., *Acrobeloides* sp., *Cervidellus* sp., *Diploscapter* sp.*,* and *Mesodorylaimus* sp*.* These are beneficial nematodes categorised as bacterial feeders, fungal feeders, and omnivores, with only nematodes from the genus *Pratylenchus* sp*.* being plant pathogenic (Čerevková et al., 2018; Melakeberhan et al., 2021). More nematode species were observed in conditioned soils than in non-conditioned soil, as evidenced by the absence of *Aphelenchus* sp*., Acrobeloides* sp*., Cervidellus* sp*.,* and *Mesodorylaimus* sp*.* in non-conditioned control soil. These nematode species had a positive correlation with plant growth. The abundance of nematode species was observed in conditioned soils in a treatment-dependent manner. Previous studies have shown that the production of certain toxins and metabolites varies among *Photorhabdus* strains (Tobias et al., 2017; Muangpat et al., 2022; Ardpairin et al., 2024). Consequently, the absence of some nematode species in certain soil conditioning treatments may be attributed to the differences in the diversity of toxins and metabolites produced by the different *Photorhabdus* strains, which

can have a varied impact on the nematode community. Additionally, the fungivorous and bacterivorous nematodes identified in conditioned soil reproduce either through uniparental methods, such as hermaphroditism or parthenogenesis, or through amphimixis (Vats et al., 2004; Lahl et al., 2006; Kim et al., 2021). Their population densities are directly linked to food availability (dos Santos et al., 2008). Studies that have investigated the life-history traits and population growth of fungivorous and bacterivorous nematodes reported that the population of these nematodes increase rapidly when their prey hosts are highly abundant (Okada et al., 2005; dos Santos et al., 2008; Gansfort et al., 2018; Kanwar et al., 2021; Zhao et al., 2022). Therefore, the high abundance of beneficial nematodes observed in certain soil conditioning treatments may be linked to the abundance of suitable prey hosts, which promote rapid reproduction in nematode populations (Arancon et al., 2003; Zhao et al., 2022).

This study also demonstrated that soil conditioning with *Photorhabdus*-infected insect cadavers did not affect the fungal community. This could be because the amount of *Photorhabdus* toxins released in the soil was insufficient to affect the fungal community. Rasool et al. (2023) reported that changes in soil fungal communities depend on the density of the inoculant in the soil. In their experiments, the fungal communities only changed when *M. brunneum* was applied by soil drenching, but not seed treatment, because of increased *M. brunneum* abundance and persistence in drenched soil. Nonetheless, the results of the present study are consistent with soil inoculation studies with entomopathogenic fungal and bacterial species that only produced limited, transient or no effects on the soil fungal community (Kirchmair et al., 2008; Schwarzenbach et al., 2009; Gao et al., 2012; Hirsch et al., 2013; McKinnon et al., 2018; Mayerhofer et al., 2019; Canfora et al., 2023). Moreover, transient effects disappeared and the fungal community stabilised in a short time (Gao et al., 2012).

The fungal community consisted of a few beneficial species, namely *Mortierella wolfii* and *Solicoccozyma aeria* (Li et al., 2020; Ozimek and Hanaka, 2020; Carvajal et al., 2024). The majority were plant pathogenic fungal species, including *Gibellulopsis serrae, Fusarium circinatum, Fusarium equiseti, Fusarium solani* (Giraldo and Crous, 2019; Gibert et al., 2022; Ghosal and Datta, 2024; Woodward et al., 2025). Overall, the most dominant plant pathogens in non-conditioned control soil were *Pratylenchus* sp. *and Fusarium* spp. These are problematic plant pathogens in crop production (Reen et al., 2019; Chukwudi et al., 2021). Specifically, *Fusarium* colonises plant roots, hindering protein synthesis and the normal transport of water to aboveground parts of the plant (Chukwudi et al., 2021; Bryła et al., 2022). *Pratylenchus* plant-parasitic nematodes damage plant roots and limit nutrient concentrations and uptake in plants (Reen et al., 2019; Thompson and Clewett, 2021; Owen et al., 2023; Briar et al., 2023). Moreover, yield losses due to *Pratylenchus* sp. have been reported up to 50% in wheat (Thompson et al., 2000; Reen et al., 2014; 2019). The infestation of these plant

pathogens in the absence of their specialist natural enemies could be responsible for the underperformance of plants in non-conditioned control soil.

Altogether, the composition of the bacterial, fungal and nematode communities with more beneficial microbes in soil conditioned with *Photorhabdus*-infected insect cadavers and MK larvae is strongly associated with the improved plant growth observed in Chapter 1. One explanation for this result is that *Photorhabdus* toxins and metabolites from decomposing insect cadavers might have suppressed soil-borne plant pathogens and reduced competitors for nutrient resources, thus encouraging the growth of the beneficial bacteria, nematodes and fungi (Webster et al., 2002; Singh and Forst, 2016; Stock, 2019; Dominelli et al., 2022). For the soils conditioned with MK insect larvae, which do not contain any toxins, the growth of the microbes may be attributed to the organic materials such as organic nitrogen, carbohydrates, lipids, protein and chitin in soil by the decomposing insect cadavers (Fagan et al., 2002; Barragán-Fonseca et al., 2022). These insect-based organic materials accelerate the growth and activities of microbial decomposers and soil-beneficial rhizobacteria (Fagan et al., 2002; Sharp, 2013; De Tender et al., 2019). Secondly, soil conditioning may have accelerated the growth of beneficial bacteria, nematodes and fungi that are heavy feeders of plant pathogens, possibly playing a role in suppressing soil-borne pathogens observed in the non-conditioned control soil. For instance, the nematode *Mesodorylaimus* species are predators of many plant pathogenic nematodes, including *R. reniformis* and *R. similis* (Cabos et al., 2013; Kanwar et al., 2021), whereas *Aphelenchus* sp*.* feeds on plant parasitic fungal pathogens (Okada and Kadota, 2003; Haraguchi and Yoshiga, 2020). These bacterivorous and fungivorous nematodes also accelerate nutrient release for plant uptake and enhance plant resistance to pathogens (Trap et al., 2016; Li et al., 2024). In addition, bacterial species, *M. odoratimimus, S. marcescens, P. rettgeri,* and *A. faecalis* protect plants against pests and pathogens (You et al., 2015; Shan et al., 2019; Ferioun et al., 2023). Therefore, the beneficial bacteria and nematode species enriched in conditioned soil might have suppressed and ameliorated the negative effects of plant parasitic nematodes and fungal pathogens. This provides a superior advantage for improved growth in plants grown in conditioned soil, as discussed in Chapter 1.

Conclusion

This study reports the response of microbial communities to soil conditioning with *Photorhabdus*-infected insect cadavers. Soil conditioning produced a generally greater impact on the bacterial and nematode communities, but not on the fungal. Conditioned soil treatments were exclusively associated with a high abundance of beneficial bacteria and nematodes, which positively correlated with the high biomass of plants grown on conditioned soil, as discussed in Chapter 1. These findings suggest that utilising *Photorhabdus* bacteria in pest control could improve plant growth via decomposing *Photorhabdus*-infected insect cadavers and maximise yields without adding external inputs.

General discussion

Entomopathogenic nematodes (EPNs) from the *Heterorhabditis* genera and their symbionts, *Photorhabdus* bacteria, are biological agents used to control agricultural pests. These biocontrol agents are commonly used to control belowground herbivores, but recent developments have enabled their usage as foliar treatments against leaf herbivores (Acharya et al., 2020; Fallet, 2022a; 2022b). The nematodes carry the symbionts in their intestines and release them immediately after penetrating a suitable insect host (Ffrench-Constant et al., 2003; Bode, 2009). However, the bacteria have often been isolated and applied by soil drenching or foliar spraying without the vectoring nematodes to target belowground and aboveground pests, respectively (Abdel-Razek, 2003; Mohan et al., 2003; Vyas et al., 2008; Shahina et al., 2011; Aatif et al., 2014; Kakade et al., 2023; Abdisa et al., 2024). The control efficacy of *Photorhabdus* bacteria has been demonstrated against a wide range of pests, pathogens and parasites (Ahantarig et al., 2009; Orozco et al., 2016; Shawer et al., 2018; Vitta et al., 2018; Vicente-Díez et al., 2021; 2023). The soil application of *Photorhabdus* bacteria introduces massive amounts of bacterial cells and their toxins and metabolites into the soil. Moreover, *Photorhabdus* bacteria produce bioactive compounds that may impact plant physiology, performance and resistance to insect attack (Regaiolo et al., 2020; Muangpat et al., 2022). Understanding the complex interactions among *Photorhabdus* bacteria, and or their toxins and metabolites, soil microbial organisms, plants, and herbivores is crucial in revealing the environmental impact of *Photorhabdus* bacteria. It clarifies whether the application of *Photorhabdus* bacteria supports sustainable agriculture and can be safely integrated with other methods, or if they pose greater risks than currently restricted pest control agents.

In my PhD thesis, I demonstrate that soil conditioning with *Photorhabdus*-infected insect cadavers, mechanically killed (MK) insect larvae, *Photorhabdus* cell-free supernatants, or water extracts of toxins derived from *Photorhabdus*-killed larvae (but not from MK-killed insects) significantly improves plant growth in a greenhouse environment. In the first instance, I found that plants growing in soils conditioned with *Photorhabdus*-infected insect cadavers or MK insect larvae accumulated more biomass than those in non-conditioned control soil. Interestingly, the results obtained with the MK larvae soil conditioning treatment indicated two main mechanisms for enhancing plant growth: *Photorhabdus*-specific effects in the form of toxins and metabolites, and *Photorhabdus*-independent effects resulting from the introduction of insect biomass in the soil. Consequently, I used various approaches to determine the exact mechanisms of plant growth stimulation in conditioned soil.

To establish *Photorhabdus*-specific effects on plant biomass accumulation, I grew plants in soils conditioned with water extracts of toxins derived from macerated *Photorhabdus*-killed larvae, or MK larvae, under greenhouse conditions. Additionally, I complemented this experiment by growing plants in soil conditioned with cell-free *Photorhabdus* culture

supernatants. The results confirmed that soil conditioning with *Photorhabdus* cell-free supernatants or water extracts from *Photorhabdus*-killed larvae significantly improved plant growth, whereas conditioning with extracts from MK insect larvae did not. Further, I measured and compared soil chemical properties, including bioavailable phosphorus, organic nitrogen, carbon, and soil organic matter content of the different conditioning treatments and examined the correlations between these soil chemical properties and plant growth. My findings showed no significant differences in the soil chemical properties among the different conditioning treatments, nor their correlation with plant growth. Altogether, these findings underscore the role of *Photorhabdus* toxins and bioactive metabolites in promoting plant growth. Indeed, studies by Muangpat et al. (2022) reported many *Photorhabdus* bioactive metabolites, including siderophores, resorcinol, indole-3-acetic acid, and gibberellin groups. The roles of these metabolites in plant growth promotion have been documented in many plant-microbe interaction studies (Wilson et al., 2006; Seshadri et al., 2007; Mishra et al., 2009; Pindi et al., 2014; Armada et al., 2016; Bandopadhyay, 2020; Yi et al., 2022). Although insect biomass can promote plant growth by releasing plant-available nitrogen (Fagan et al., 2002; Barragán-Fonseca et al., 2022), these findings demonstrate that *Photorhabdus* toxins and bioactive metabolites are the main drivers of plant growth in conditioned soil.

In a separate experiment, I performed soil sterilisation and re-inoculation experiments to establish the link between changes in soil microbial communities, driven by *Photorhabdus* toxins, and their subsequent impact on plant growth. I found that plants grown in autoclaved soils supplemented with just 10% of living soil previously conditioned with *Photorhabdus*-infected insect cadavers or MK insect larvae produced significantly more total biomass than those grown in non-conditioned control soil. This research provides evidence that both *Photorhabdus* metabolites and alterations in microbial communities induced by *Photorhabdus* toxins and metabolites contribute to enhanced plant growth. The contribution of the microbial community is supported by the response of soil microbial communities observed in conditioned soil. The microbial community analyses showed that soil conditioned with *Photorhabdus*-infected insect cadavers or MK insect larvae had a generally greater abundance of beneficial bacteria and nematodes than the non-conditioned control soil. Notably, the abundance of bacterial species *M. odoratimimus, S. marcescens, P. rettgeri,* and *A. faecalis,* as well as nematodes, *Aphelenchus* sp., *Acrobeloides* sp., *Cervidellus* sp., and *Mesodorylaimus* sp., was higher in soils conditioned with *Photorhabdus*-infected or with MK insects. I noted that the abundance of these beneficial bacterial and nematode species was higher (5 – 29%) in soils conditioned with *Photorhabdus*-infected insect cadavers than in soils conditioned with MK insect larvae (Only 1 – 3%), pointing to *Photorhabdus*-dependent and independent effects on soil microbial communities. Studies have reported that the nematode *Mesodorylaimus* sp. is a predator of many plant pathogenic nematodes, including *R. reniformis* and *R. similis* (Cabos

et al., 2013; Kanwar et al., 2021), whereas *Aphelenchus* sp. feeds on plant parasitic fungal pathogens (Okada and Kadota, 2003; Haraguchi and Yoshiga, 2020). These bacterivorous and fungivorous nematodes also accelerate nutrient release for plant uptake and enhance plant resistance to pathogens (Trap et al., 2016; Li et al., 2024). In addition, bacterial species, *M. odoratimimus, S. marcescens, P. rettgeri, and A. faecalis* protect plants against pests and pathogens (You et al., 2015; Shan et al., 2019; Ferioun et al., 2023). In this study, these beneficial bacterial and nematode species positively correlated with plant growth enhancement, suggesting why plants grown on soil conditioned with *Photorhabdus*-infected insect cadavers or MK insect larvae outperformed those grown on non-conditioned control soil. Therefore, soil conditioning with MK or *Photorhabdus*-infected insect cadavers modulates the microbial community towards a structure that promotes the abundance of beneficial bacteria and nematodes, and in turn enhances plant growth and resistance.

My thesis also explored the impact of soil conditioning on plant resistance to two important pests of maize plants, *D. balteata* and *S. frugiperda* larvae. In my experiments, I fed *D. balteata* and *S. frugiperda ad libitum* with fresh roots and leaves of maize plants grown on soil conditioned with *Photorhabdus*-infected insect cadavers, MK insect larvae or non-conditioned control soil. I demonstrated that plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers have suppressive effects against the root and leaf-feeding herbivores in a strain-specific manner, while conditioning soil with MK larvae does not increase resistance against the two herbivores. More specifically, plants grown on soils conditioned with insect larvae killed by *Photorhabdus* strains ID79, ID139, ID158, ID163, and ID323 were more resistant to the attack of *D. balteata* larvae, and the larval weights were reduced by 15 – 20%. The metabolites, Aromadendrin, Compound ID 196, Imidazole alkaloids, and 6,9,10-trihydroxyoctadec-7-enoic acid were significantly abundant in the roots of resistant plants than in control and susceptible plants. These metabolites are reported to have many biological activities and could be involved in the defense mechanisms of plants (Hövelmann et al., 2019; Lee and Jeong, 2020; Mareya et al., 2020; Dozio et al., 2025). The distinct metabolites that were only accumulated in the roots of resistant plants included; 4-[(6R)-6-hydroxy-5,5-dimethylcyclohexen-1-yl] benzoic acid, 2 cis-Abscisic Acid, Canthoside B, Apigenin 7-sulfate, Pimarane and Isopimarane diterpenoids, Ajugaciliatin A, GDIMBOA and Tinosineside B. Many of these have been described as defensive compounds employed by plants against herbivores and pathogens (Erb et al., 2012; Johnson et al., 2016; Rasmann and Turlings, 2016; Reveglia et al., 2018; Zhang et al., 2024), making them possible candidates for the resistance observed against *D. balteata*. Other metabolites detected in the roots, which have not yet been linked to plant defense, included Ajugaciliatin A, Canthoside B, Apigenin 7-sulfate and Tinosineside B. However, their biological activities, including antimicrobial, antioxidant, cytotoxic, and anti-estrogenic properties, have been described (Gonzalez-Burgos

and Gomez-Serranillos, 2012; Dutta et al., 2021; Parveen et al., 2021; Allemailem et al., 2024; Ao et al., 2024), and thus, their upregulation in plants could directly contribute to resistance or be part of the signalling network for the release of defense compounds against insect pests.

The plants grown on soils conditioned with insect larvae killed by *Photorhabdus* strains ID22, ID138, and ID158 resisted the attack of *S. frugiperda* larvae, and reduced their weights by 10 – 59%. Only the plants that grew on soils conditioned with insect larvae killed by the *Photorhabdus* strain ID158 significantly suppressed the feeding of both *D. balteata* and *S. frugiperda* larvae. At the metabolic level, plants that resisted the attack of *D. balteata* and *S. frugiperda* larvae in the insect performance experiments accumulated distinct metabolites in their roots and leaves, enabling resistance against the herbivores. Notably, twelve metabolites from the groups of alkaloids, benzoxazinoids, fatty acids, terpenoids, shikimates and phenylpropanoids were upregulated in the roots of resistant plants. In the leaves, eight metabolites from the groups of amino acids, fatty acids, and phenylpropanoids were significantly upregulated. Specifically, (2R)-2-ammonio-3-phenylpropanoate, L-Tryptophan, 1-Acyl-sn-glycero-3-phosphoglycerol (N-C16:1), 2 cis-Abscisic Acid, Cephalosporins, Cherimola cyclopeptide, PC (16:0/18:2(9Z,12Z)) 1-hexadecanoyl-2-(9Z,12Z-octadecadienoyl)-sn-glycero-3-phosphocholine and PA(22:4(7Z,10Z,13Z,16Z)/22:2(13Z,16Z)) were the most abundant metabolites detected in the leaves of resistant plants. All these metabolites have been described to offer resistance against insect pests and pathogens (Irmisch et al., 2015; Mareya et al., 2020; Pan et al., 2019; Yadav et al., 2020; Pretorius et al., 2022; Rosa et al., 2023; Chekan et al., 2024; Li et al., 2025). The changes in the metabolic response observed are consistent with studies by Muller et al. (2024), who showed that root exposure to *Photorhabdus* bioluminescence triggered the accumulation of defensive secondary metabolites in maize plants. Taken together, these results suggest that soil conditioning with *Photorhabdus*-infected insect cadavers confers systemic defensive responses in plants, with negative impacts on herbivores feeding on maize crops.

The main objective of my PhD thesis was to investigate the soil legacy effects of *Photorhabdus* bacteria on plant physiology, performance, and resistance to insect attacks. The project aimed to provide evidence on the interactions among *Photorhabdus* bacteria (including their toxins and metabolites), plants, herbivores, and soil microbial organisms. The findings of this PhD thesis will encourage farmers who are using *Photorhabdus* bacteria in their crop fields, allowing them to increase yields while reducing reliance on chemical pest control. The concept of microbial-induced resistance as a sustainable pest control strategy has garnered attention from researchers in Europe. The outcomes of this research will inform the scientific community about the environmental implications of *Photorhabdus* bacteria and their role in supporting sustainable agriculture, ultimately stimulating research in exploring *Photorhabdus* strains to develop innovative approaches to crop protection.

Research outlook

In Chapter 1, this thesis reported that soil conditioning with *Photorhabdus*-infected insect cadavers, or *Photorhabdus* toxins and metabolites, significantly improves plant growth in a greenhouse environment. Indeed, *Photorhabdus* bacteria produce bioactive metabolites whose roles in plant growth promotion have been documented in many plant-microbe interaction studies (Wilson et al., 2006; Seshadri et al., 2007; Mishra et al., 2009; Pindi et al., 2014; Armada et al., 2016; Bandopadhyay, 2020; Yi et al., 2022). However, there is a need to understand the metabolic and biochemical mechanisms through which *Photorhabdus* bacteria promote plant growth. Research should focus on isolating and characterising the metabolites of the different *Photorhabdus* strains used in this study, and establishing the linkages between the metabolites and their functions in promoting plant growth and resistance. Further work should also analyse the *Photorhabdus* secondary metabolite-biosynthetic gene clusters (BGCs) and establish their distribution in the different *Photorhabdus* strains. *Photorhabdus* bacteria have different BGCs, depending on their strain relationships (Muangpat et al., 2022). This knowledge will enable transposition mutagenesis techniques to select specific genes and examine their role in promoting plant growth and resistance to herbivores. Finally, the BGC expression of bacteria can be shaped by many factors, including bacterial growth environments (Hughes and Andersson, 2017; Lorková et al., 2025; Salamzade and Kalan, 2025). In this study, soil conditioning was conducted using supernatants from *Photorhabdus* bacteria grown in lysogeny broth (LB), as well as toxins and metabolites from *Photorhabdus*-killed insect larvae. These represent two different growth environments with distinct food resources, which may affect the expression of metabolites and various gene clusters. Therefore, it might be necessary to establish the differences in metabolic profiles of *Photorhabdus* cell-free culture supernatants and water extracts of toxins and metabolites derived from macerated *Photorhabdus*-killed larvae.

In a separate experiment, I demonstrated that soil conditioning significantly altered the bacterial and nematode community, with a higher abundance of beneficial bacteria and nematodes than in non-conditioned control soil. There is a need to isolate the beneficial bacteria and nematodes and establish the extent to which specific species, individually or in combination, contribute to plant growth and resistance to herbivore attacks. *Photorhabdus* bacterial strains are now being applied in agriculture. Thus, a thorough understanding of how microbial species accumulated in soils conditioned with *Photorhabdus*-infected insect cadavers impact plant growth and stress resilience in agricultural systems is needed.

In this thesis, I demonstrated that maize plants grown on soils conditioned with *Photorhabdus*-killed insect cadavers negatively affect the performance of two important pests: *D. balteata* and *S. frugiperda* larvae. I also showed that maize plants that resisted the attacks of these

herbivores accumulated distinct metabolites in their leaves and roots, which might be responsible for defense against insects. The roots accumulated more metabolites than leaves, and consequently, the root-feeding *D. balteata* larvae were more affected than *S. frugiperda* feeding on the leaves. In this work, I investigated resistance in detached leaves and roots, but did not account for the systemic changes that mediate interactions between herbivores in natural environments. For example, studies that have focused on metabolic reprogramming have shown that herbivore attack on the roots can have a strong effect on aboveground resistance to herbivores and vice versa (Van Dam et al., 2005; Soler et al., 2007; Kaplan et al., 2008; Erb et al., 2009, 2011; Yang et al., 2011; Marti et al., 2013). This reveals that the strong resistance effect observed against *D. balteata* larvae feeding on the roots could also translate into enhanced resistance against above-ground herbivores feeding on the leaves via metabolic programming upon insect attack. Further studies should explore the influence of root chemistry on the aboveground plant resistance in plants grown on soils conditioned with *Photorhabdus*-infected insect cadavers to decipher whether the resistance compounds on the roots can be exported to attacked parts above ground to protect against leaf-feeding herbivores such as *S. frugiperda*. Secondly, there is a need to investigate the resistance expression of other plant species, like legumes or vegetable crops, when grown on soils conditioned with *Photorhabdus*-killed insect cadavers. Efforts should also be focused on evaluating the resistance compounds accumulated in those plants, and their control efficacy against problematic root and leaf herbivores of those crops. Third, microbial-induced secondary metabolites can be accumulated in flowers and seeds, which could impact beneficial insects (Zamioudis et al., 2015; Godschalx et al., 2016). The extent to which resistance compounds occur in flowers and nectar of plants grown on soils conditioned with *Photorhabdus*-killed insect cadavers, and their effects on pollinators, remains unclear. Additionally, it has been shown that changes in nectar chemistry and scent determine pollinator attraction and survival (Becklin et al., 2011; Davis et al., 2019, 2023), and research into the impacts of nectar toxicity with plant secondary metabolites on pollinator health has been recommended (Rothman et al., 2020; Schmitt et al., 2021; Barberis et al., 2023). The potential effects of metabolites accumulated in plants grown on soils conditioned with *Photorhabdus*-killed insect cadavers on pollinators can be of particular interest because recently, the silent dramatic decline in the global insect populations has been given attention (van der Sluijs, 2020); thus, in the pursuit of sustainable agriculture, the impacts of microbial soil conditioning and pest control technologies on non-target organisms need to be assessed.

References

Aatif, H. M., Javed, N., Khan, S. A., Lali, S. P. and Ullah, M. I. (2014) Evaluation of persistence and effectiveness of bacterial cell suspensions and culture filtrates against M. incognita on brinjal, *Archives Of Phytopathology And Plant Protection*, 47(20), pp. 2447–2457, [online] Available at: http://www.tandfonline.com/doi/abs/10.1080/03235408.2014.880571.

Abdel-Razek, A. S. (2003) Pathogenic effects of Xenorhabdus nematophilus and Photorhabdus luminescens (Enterobacteriaceae) against pupae of the Diamondback Moth, Plutella xylostella (L.), *Anzeiger fur Schadlingskunde*, 76(4), pp. 108–111.

Abdisa, E., Park, H., Kwon, J., Jin, G., Esmaeily, M. and Kim, Y. (2024) Enhancement of an entomopathogenic fungal virulence against the seedcorn maggot, Delia platura , by suppressing immune responses with a bacterial culture broth of Photorhabdus temperata subsp. temperata, *Archives of Insect Biochemistry and Physiology*, 115(3), [online] Available at: https://onlinelibrary.wiley.com/doi/10.1002/arch.22103.

Abrahams, P., Bateman, M., Beale, T., Clottey, V., Cock, M., Colmenarez, Y., Corniani, N., Day, R., Early, R., Godwin, J. and Gomez, J. (2017) Fall armyworm: impacts and implications for Africa. Evidence note (2), *Center for Agriculture and Bioscience International-CABI*.

Acharya, R., Hwang, H.-S., Mostafiz, M. M., Yu, Y.-S. and Lee, K.-Y. (2020) Susceptibility of various developmental stages of the fall armyworm, Spodoptera frugiperda, to entomopathogenic nematodes, *Insects*, 11(12), p. 868, [online] Available at: https://www.mdpi.com/2075-4450/11/12/868.

Adams, B. J. and Nguyen, K. B. (2002) Taxonomy and systematics., In Gaugler, R. (ed.), *Entomopathogenic nematology*, Wallingford, CABI, pp. 1–33, [online] Available at: http://www.cabi.org/cabebooks/ebook/20023023440.

Adekanmbi, A. A., Shu, X., Zou, Y. and Sizmur, T. (2022) Legacy effect of constant and diurnally oscillating temperatures on soil respiration and microbial community structure, *European Journal of Soil Science*, 73(6), [online] Available at: https://bsssjournals.onlinelibrary.wiley.com/doi/10.1111/ejss.13319.

Ahantarig, A., Chantawat, N., Waterfield, N. R., Ffrench-Constant, R. and Kittayapong, P. (2009) PirAB toxin from Photorhabdus asymbiotica as a larvicide against dengue vectors, *Applied and Environmental Microbiology*, 75(13), pp. 4627–4629.

Akhurst, R. and Smith, K. (2002) Regulation and safety., In *Entomopathogenic nematology*, Wallingford, CABI, pp. 311–332, [online] Available at: http://www.cabi.org/cabebooks/ebook/20023023456.

Al-Sarar, A., Hall, F. R. and Downer, R. A. (2006) Impact of spray application methodology on the development of resistance to cypermethrin and spinosad by fall armyworm Spodoptera frugiperda (JE Smith), *Pest Management Science*, 62(11), pp. 1023–1031.

Albazazz, A. M. and Aljuboori, F. K. (2024) Morphological and morphometrical characterization of the nematode genus Filenchus spp. associated with olive trees in Iraq, *IOP Conference Series: Earth and Environmental Science*, 1371(3), p. 032048, [online] Available at: https://iopscience.iop.org/article/10.1088/1755-1315/1371/3/032048.

Allemailem, K. S., Almatroudi, A., Alharbi, H. O. A., AlSuhaymi, N., Alsugoor, M. H., Aldakheel, F. M., Khan, A. A. and Rahmani, A. H. (2024) Apigenin: A bioflavonoid with a promising role in disease prevention and treatment, *Biomedicines*, 12(6), p. 1353, [online] Available at: https://www.mdpi.com/2227-9059/12/6/1353.

Alonso-Blanco, C. and Koornneef, M. (2000) Naturally occurring variation in Arabidopsis: An underexploited resource for plant genetics, *Trends in Plant Science*, pp. 22–29.

Alouw, J. C. and Miller, N. J. (2015) Effects of benzoxazinoids on specialist and generalist

Diabrotica species, *Journal of Applied Entomology*, 139(6), pp. 424–431, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/jen.12194.

Anderson, J. T. and Mitchell-Olds, T. (2011) Ecological genetics and genomics of plant defences: Evidence and approaches, *Functional Ecology*, 25(2), pp. 312–324.

Antonello, A. M., Sartori, T., Folmer Correa, A. P., Brandelli, A., Heermann, R., Rodrigues Júnior, L. C., Peres, A., Romão, P. R. T. and Da Silva, O. S. (2018) Entomopathogenic bacteria Photorhabdus luminescens as drug source against Leishmania amazonensis, *Parasitology*, 145(8), pp. 1065–1074, [online] Available at: https://doi.org/10.1017/S0031182017002001.

Anyega, A. O., Korir, N. K., Beesigamukama, D., Changeh, G. J., Nkoba, K., Subramanian, S., van Loon, J. J. A., Dicke, M. and Tanga, C. M. (2021) Black soldier fly-composted organic fertilizer enhances growth, yield, and nutrient quality of three key vegetable crops in Sub-Saharan Africa, *Frontiers in Plant Science*, 12, [online] Available at: https://www.frontiersin.org/articles/10.3389/fpls.2021.680312/full.

Ao, R., Li, M.-Y., Yang, F.-F., Bao, J., Zhang, J.-S. and Zhang, H. (2024) Targeted discovery of clerodane diterpenoids from Tinospora sinensis as immunomodulatory agents, *Fitoterapia*, 178, p. 106174, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0367326X24003575.

Arancon, N. Q., Galvis, P., Edwards, C. and Yardim, E. (2003) The trophic diversity of nematode communities in soils treated with vermicompost, *Pedobiologia*, 47(5–6), pp. 736–740, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0031405604702619.

Ardpairin, J., Subkrasae, C., Dumidae, A., Pansri, S., Homkaew, C., Meesil, W., Kumchantuek, T., Phoungpetchara, I., Dillman, A. R., Pavesi, C., Bode, H. B., Tandhavanant, S., Thanwisai, A. and Vitta, A. (2024) Symbiotic bacteria associated with entomopathogenic nematodes showed molluscicidal activity against Biomphalaria glabrata, an intermediate host of Schistosoma mansoni, *Parasites & Vectors*, 17(1), p. 529, [online] Available at: https://parasitesandvectors.biomedcentral.com/articles/10.1186/s13071-024-06605-x.

Armada, E., Probanza, A., Roldán, A. and Azcón, R. (2016) Native plant growth promoting bacteria Bacillus thuringiensis and mixed or individual mycorrhizal species improved drought tolerance and oxidative metabolism in Lavandula dentata plants, *Journal of Plant Physiology*, Elsevier GmbH., 192, pp. 1–12, [online] Available at: http://dx.doi.org/10.1016/j.jplph.2015.11.007.

Asaturova, A. M., Tomashevich, N. S., Dubyaga, V. M., Zhevnova, N. A., Pavlova, M. D. and Homyak, A. I. (2023) Bacterial strains from the bioresource collection of the Federal State Budgetary Scientific Institution of the Federal Scientific Center for Biological Plant Protection, which have growth-stimulating activity against winter wheat plants, *Russian Agricultural Sciences*, 49(S2), pp. S248–S256, [online] Available at: https://link.springer.com/10.3103/S1068367423080049.

Bahram, M., Hildebrand, F., Forslund, S. K., Anderson, J. L., Soudzilovskaia, N. A., Bodegom, P. M., Bengtsson-Palme, J., Anslan, S., Coelho, L. P., Harend, H., Huerta-Cepas, J., Medema, M. H., Maltz, M. R., Mundra, S., Olsson, P. A., Pent, M., Põlme, S., Sunagawa, S., Ryberg, M., Tedersoo, L. and Bork, P. (2018) Structure and function of the global topsoil microbiome, *Nature*, Springer US, 560(7717), pp. 233–237, [online] Available at: http://dx.doi.org/10.1038/s41586-018-0386-6.

Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S. and Vivanco, J. M. (2006) The role of root exudates in rhizosphere interactions with plants and other organisms, *Annual Review of Plant Biology*, 57(1), pp. 233–266, [online] Available at: https://www.annualreviews.org/doi/10.1146/annurev.arplant.57.032905.105159.

Banda, S.L.C., Corredor, P.D. and Corredor, S.G. (2004) Efecto de la asociación patilla (Citrullus lanatus) con maíz (Zea mays) sobre la población y el daño causado por tres insectos

plaga y el rendimiento de estos cultivos en la Ciénaga Grande de Lorica, Córdoba, *Revista Colombiana de Entomología*, 30(2), pp. 161–169, [online] Available at: https://revistacolombianaentomologia.univalle.edu.co/index.php/SOCOLEN/article/view/9547
.

Bandopadhyay, S. (2020) Application of plant growth promoting bacillus thuringiensis as biofertilizer on abelmoschus esculentus plants under field condition, *Journal of Pure and Applied Microbiology*, 14(2), pp. 1287–1294.

Barberis, M., Calabrese, D., Galloni, M. and Nepi, M. (2023) Secondary metabolites in nectar-mediated plant-pollinator relationships, *Plants*, 12(3), p. 550, [online] Available at: https://www.mdpi.com/2223-7747/12/3/550.

Bardgett, R. D., Freeman, C. and Ostle, N. J. (2008) Microbial contributions to climate change through carbon cycle feedbacks, *The ISME Journal*, 2(8), pp. 805–814, [online] Available at: http://www.nature.com/articles/ismej200858.

Barragán-Fonseca, K. Y., Nurfikari, A., van de Zande, E. M., Wantulla, M., van Loon, J. J. A., de Boer, W. and Dicke, M. (2022) Insect frass and exuviae to promote plant growth and health, *Trends in Plant Science*, 27(7), pp. 646–654, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1360138522000073.

Bateman, M. L., Day, R. K., Luke, B., Edgington, S., Kuhlmann, U. and Cock, M. J. W. (2018) Assessment of potential biopesticide options for managing fall armyworm (Spodoptera frugiperda) in Africa, *Journal of Applied Entomology*, 142(9), pp. 805–819.

Baur, M. E., Kaya, H. K. and Strong, D. R. (1998) Foraging ants as scavengers on entomopathogenic nematode-killed insects, *Biological Control*, Academic Press, 12(3), pp. 231–236.

Becklin, K. M., Gamez, G., Uelk, B., Raguso, R. A. and Galen, C. (2011) Soil fungal effects on floral signals, rewards, and aboveground interactions in an alpine pollination web, *American Journal of Botany*, 98(8), pp. 1299–1308, [online] Available at: https://bsapubs.onlinelibrary.wiley.com/doi/10.3732/ajb.1000450.

Behie, S. and Bidochka, M. (2013) Insects as a nitrogen source for plants, *Insects*, 4(3), pp. 413–424, [online] Available at: https://www.mdpi.com/2075-4450/4/3/413.

Bender, S. F., Wagg, C. and van der Heijden, M. G. A. (2016) An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability, *Trends in Ecology & Evolution*, 31(6), pp. 440–452, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0169534716000616.

Benitez, M.-S., Ewing, P. M., Osborne, S. L. and Lehman, R. M. (2021) Rhizosphere microbial communities explain positive effects of diverse crop rotations on maize and soybean performance, *Soil Biology and Biochemistry*, 159, p. 108309, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071721001826.

Bennett, J. A. and Klironomos, J. (2019) Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers, *New Phytologist*, 222(1), pp. 91–96.

Berger, B., Patz, S., Ruppel, S., Dietel, K., Faetke, S., Junge, H. and Becker, M. (2018) Successful formulation and application of plant growth-promoting Kosakonia radicincitans in maize cultivation, *BioMed Research International*, 2018, pp. 1–8, [online] Available at: https://www.hindawi.com/journals/bmri/2018/6439481/.

Bernaola, L., Cosme, M., Schneider, R. W. and Stout, M. (2018) Belowground inoculation with Arbuscular mycorrhizal Fungi increases local and systemic susceptibility of rice plants to different pest organisms, *Frontiers in Plant Science*, 9, [online] Available at: https://www.frontiersin.org/article/10.3389/fpls.2018.00747/full.

Bernaola, L. and Stout, M. J. (2019) Effects of arbuscular mycorrhizal fungi on rice-herbivore interactions are soil-dependent, *Scientific Reports*, 9(1), p. 14037, [online] Available at: https://www.nature.com/articles/s41598-019-50354-2.

Bever, J. D., Platt, T. G. and Morton, E. R. (2012) Microbial population and community dynamics on plant roots and their feedbacks on plant communities, *Annual Review of Microbiology*, 66(1), pp. 265–283, [online] Available at: https://www.annualreviews.org/doi/10.1146/annurev-micro-092611-150107.

Bezemer, T. M., De Deyn, G. B., Bossinga, T. M., Van Dam, N. M., Harvey, J. A. and Van Der Putten, W. H. (2005) Soil community composition drives aboveground plant-herbivore-parasitoid interactions, *Ecology Letters*, 8(6), pp. 652–661.

Bibi, S., Ullah, R., Burni, T., Ullah, Z. and Kazi, M. (2023) Impact of resorcinol and biochar application on the growth attributes, metabolite contents, and antioxidant systems of tomato (Lycopersicon esculentum Mill.), *ACS Omega*, 8(48), pp. 45750–45762, [online] Available at: https://pubs.acs.org/doi/10.1021/acsomega.3c06233.

Birch, A. N. E., Begg, G. . and Squire, G. . (2011) How agro-ecological research helps to address food security issues under new IPM and pesticide reduction policies for global crop production systems, *Journal of Experimental Botany*, 62(10), pp. 3251–3261, [online] Available at: https://academic.oup.com/jxb/article-lookup/doi/10.1093/jxb/err064.

Blackburn, M. B., Domek, J. M., Gelman, D. B. and Hu, J. S. (2005) The broadly insecticidal Photorhabdus luminescens toxin complex a (Tca): Activity against the Colorado potato beetle, Leptinotarsa decemlineata, and sweet potato whitefly, Bemisia tabaci, *Journal of Insect Science*, 5, [online] Available at: www.hp.com.

Boaventura, D., Buer, B., Hamaekers, N., Maiwald, F. and Nauen, R. (2021) Toxicological and molecular profiling of insecticide resistance in a Brazilian strain of fall armyworm resistant to Bt Cry1 proteins, *Pest Management Science*, 77(8), pp. 3713–3726, [online] Available at: www.soci.org.

Bode, H. B. (2009) Entomopathogenic bacteria as a source of secondary metabolites, *Current Opinion in Chemical Biology*, 13(2), pp. 224–230.

Bolger, A. M., Lohse, M. and Usadel, B. (2014) Trimmomatic: a flexible trimmer for Illumina sequence data, *Bioinformatics*, 30(15), pp. 2114–2120, [online] Available at: https://academic.oup.com/bioinformatics/article/30/15/2114/2390096.

Bolyen, E., Rideout, J. R., Dillon, M. R. and et al. (2019) Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2, *Nature Biotechnology*, 37(8), pp. 852–857, [online] Available at: https://www.nature.com/articles/s41587-019-0209-9.

Bolzan, A., Padovez, F. E. O., Nascimento, A. R. B., Kaiser, I. S., Lira, E. C., Amaral, F. S. A., Kanno, R. H., Malaquias, J. B. and Omoto, C. (2019) Selection and characterization of the inheritance of resistance of Spodoptera frugiperda (Lepidoptera: Noctuidae) to chlorantraniliprole and cross-resistance to other diamide insecticides, *Pest Management Science*, 75(10), pp. 2682–2689, [online] Available at: www.soci.org.

Bradshaw, C. J. A., Leroy, B., Bellard, C., Roiz, D., Albert, C., Fournier, A., Barbet-Massin, M., Salles, J.-M., Simard, F. and Courchamp, F. (2016) Massive yet grossly underestimated global costs of invasive insects, *Nature Communications*, 7(1), p. 12986, [online] Available at: https://www.nature.com/articles/ncomms12986.

Briar, S. S., Khan, M. R. and Zwart, R. (2023) Nematode problems in pulse crops and their sustainable management, In *Nematode Diseases of Crops and their Sustainable Management*, Elsevier, pp. 183–204, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/B9780323912266000109.

Brillard, J., Duchaud, E., Boemare, N., Kunst, F. and Givaudan, A. (2002) The PhlA hemolysin from the entomopathogenic bacterium Photorhabdus luminescens belongs to the two-partner secretion family of hemolysins, *Journal of Bacteriology*, 184(14), pp. 3871–3878.

Brivio, M. F., Mastore, M. and Moro, M. (2004) The role of Steinernema feltiae body-surface lipids in host-parasite immunological interactions, *Molecular and Biochemical Parasitology*, 135(1), pp. 111–121.

Brock, A. K., Berger, B., Schreiner, M., Ruppel, S. and Mewis, I. (2018) Plant growth-promoting bacteria Kosakonia radicincitans mediate anti-herbivore defense in Arabidopsis thaliana, *Planta*, 248(6), pp. 1383–1392, [online] Available at: http://link.springer.com/10.1007/s00425-018-2964-0.

Bruno, P., Arce, C. C. M., Machado, R. A. R., Besomi, G., Spescha, A., Glauser, G., Jaccard, C., Benrey, B. and Turlings, T. C. J. (2022) Sequestration of cucurbitacins from cucumber plants by Diabrotica balteata larvae provides little protection against biological control agents, *Journal of Pest Science*, Springer Berlin Heidelberg, 96(3), pp. 1061–1075, [online] Available at: https://doi.org/10.1007/s10340-022-01568-3.

Bryła, M., Pierzgalski, A., Zapaśnik, A., Uwineza, P. A., Ksieniewicz-Woźniak, E., Modrzewska, M. and Waśkiewicz, A. (2022) Recent research on Fusarium mycotoxins in maize—A review, *Foods*, 11(21), p. 3465, [online] Available at: https://www.mdpi.com/2304-8158/11/21/3465.

Bussaman, P., Sermswan, R.W. and Grewal, P. S. (2006) Toxicity of the entomopathogenic bacteria Photorhabdus and Xenorhabdus to the mushroom mite (Luciaphorus sp.; Acari: Pygmephoridae), *Biocontrol Science and Technology*, 16(3), pp. 245–256, [online] Available at: https://www.tandfonline.com/doi/full/10.1080/09583150500335822.

Bussaman, P., Sobanboa, S., Grewal, P. S. and Chandrapatya, A. (2009) Pathogenicity of additional strains of Photorhabdus and Xenorhabdus (Enterobacteriaceae) to the mushroom mite Luciaphorus perniciosus (Acari: Pygmephoridae), *Applied Entomology and Zoology*, 44(2), pp. 293–299.

Cabos, R. Y. M., Wang, K. H., Sipes, B. S., Heller, W. P. and Matsumoto, T. K. (2013) Detection of plant-parasitic nematode dna in the gut of predatory and omnivorous nematodes, *Nematropica*, 43(1), pp. 44–48.

Cabral, C. M., Cherqui, A., Pereira, A. and Simões, N. (2004) Purification and characterization of two distinct metalloproteases secreted by the entomopathogenic bacterium Photorhabdus sp. strain Az29, *Applied and Environmental Microbiology*, 70(7), pp. 3831–3838.

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A. and Holmes, S. P. (2016) DADA2: High-resolution sample inference from Illumina amplicon data, *Nature Methods*, 13(7), pp. 581–583, [online] Available at: https://www.nature.com/articles/nmeth.3869.

Campbell, T. P., Ulrich, D. E. M., Toyoda, J., Thompson, J., Munsky, B., Albright, M. B. N., Bailey, V. L., Tfaily, M. M. and Dunbar, J. (2022) Microbial communities influence soil dissolved organic carbon concentration by altering metabolite composition, *Frontiers in Microbiology*, 12, [online] Available at: https://www.frontiersin.org/articles/10.3389/fmicb.2021.799014/full.

Campos-Herrera, R., Barbercheck, M., Hoy, C. W. and Stock, S. P. (2012) Entomopathogenic nematodes as a model system for advancing the frontiers of ecology, *Journal of Nematology*, 44(2), pp. 162–176.

Canarini, A., Schmidt, H., Fuchslueger, L., Martin, V., Herbold, C. W., Zezula, D., Gündler, P., Hasibeder, R., Jecmenica, M., Bahn, M. and Richter, A. (2021) Ecological memory of recurrent drought modifies soil processes via changes in soil microbial community, *Nature Communications*, 12(1), p. 5308, [online] Available at: https://www.nature.com/articles/s41467-021-25675-4.

Canfora, L., Tartanus, M., Manfredini, A., Tkaczuk, C., Majchrowska-Safaryan, A. and Malusà, E. (2023) The impact of Beauveria species bioinocula on the soil microbial community structure in organic strawberry plantations, *Frontiers in Microbiology*, 13, [online] Available at: https://www.frontiersin.org/articles/10.3389/fmicb.2022.1073386/full.

Carreno-Quintero, N., Acharjee, A., Maliepaard, C., Bachem, C. W. B., Mumm, R., Bouwmeester, H., Visser, R. G. F. and Keurentjes, J. J. B. (2012) Untargeted metabolic quantitative trait loci analyses reveal a relationship between primary metabolism and potato tuber quality, *Plant Physiology*, 158(3), pp. 1306–1318.

Carvajal, M., Godoy, L., Gebauer, M., Catrileo, D. and Albornoz, F. (2024) Screening for indole-3-acetic acid synthesis and 1-aminocyclopropane-carboxylate deaminase activity in soil yeasts from Chile uncovers Solicoccozyma terrea as an effective plant growth promoter, *Plant and Soil*, 496(1–2), pp. 83–93, [online] Available at: https://link.springer.com/10.1007/s11104-023-05906-x.

Carvalheiro, L. G., Bartomeus, I., Rollin, O., Timóteo, S. and Tinoco, C. F. (2021) The role of soils on pollination and seed dispersal, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1834), p. 20200171, [online] Available at: https://royalsocietypublishing.org/doi/10.1098/rstb.2020.0171.

Carvalho, R. A., Omoto, C., Field, L. M., Williamson, M. S. and Bass, C. (2013) Investigating the molecular mechanisms of organophosphate and pyrethroid resistance in the fall armyworm Spodoptera frugiperda, Vontas, J. (ed.), *PLoS ONE*, 8(4), p. e62268, [online] Available at: https://dx.plos.org/10.1371/journal.pone.0062268.

Casmuz, A., Juárez, M., Socías, M. G., Murúa, M. G., Prieto, S., Medina, S., Willink, E. and Gastaminza, G. (2010) Revisión de los hospederos del gusano cogollero del maíz, Spodoptera frugiperda (Lepidoptera: Noctuidae), *Revista de la Sociedad Entomologica Argentina …*, 69(3–4), pp. 209–231, [online] Available at: http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Revisión+de+los+hospederos+del+gusano+cogollero+del+maíz+,+Spodoptera+frugiperda+(+Lepidoptera+:+Noctuidae+)#0.

Castillo, J. C., Reynolds, S. E. and Eleftherianos, I. (2011) Insect immune responses to nematode parasites, *Trends in Parasitology*, Elsevier Ltd, 27(12), pp. 537–547, [online] Available at: http://dx.doi.org/10.1016/j.pt.2011.09.001.

Castillo, J. C., Shokal, U. and Eleftherianos, I. (2013) Immune gene transcription in Drosophila adult flies infected by entomopathogenic nematodes and their mutualistic bacteria, *Journal of Insect Physiology*, 59(2), pp. 179–185, [online] Available at: http://dx.doi.org/10.1016/j.jinsphys.2012.08.003.

Čerevková, A., Miklisová, D., Szoboszlay, M., Tebbe, C. C. and Cagáň, Ľ. (2018) The responses of soil nematode communities to Bt maize cultivation at four field sites across Europe, *Soil Biology and Biochemistry*, 119, pp. 194–202, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071718300233.

Cevizci, D., Ulug, D., Cimen, H., Touray, M., Hazir, S. and Cakmak, I. (2020) Mode of entry of secondary metabolites of the bacteria Xenorhabdus szentirmaii and X. nematophila into Tetranychus urticae, and their toxicity to the predatory mites Phytoseiulus persimilis and Neoseiulus californicus, *Journal of Invertebrate Pathology*, Elsevier, 174(May), p. 107418, [online] Available at: https://doi.org/10.1016/j.jip.2020.107418.

Chandrasena, D. I., Signorini, A. M., Abratti, G., Storer, N. P., Olaciregui, M. L., Alves, A. P. and Pilcher, C. D. (2018) Characterization of field-evolved resistance to Bacillus thuringiensis-derived Cry1F δ-endotoxin in Spodoptera frugiperda populations from Argentina, *Pest Management Science*, 74(3), pp. 746–754, [online] Available at: www.soci.org.

Chekan, J. R., Mydy, L. S., Pasquale, M. A. and Kersten, R. D. (2024) Plant peptides –

redefining an area of ribosomally synthesized and post-translationally modified peptides, *Natural Product Reports*, 41(7), pp. 1020–1059, [online] Available at: https://xlink.rsc.org/?DOI=D3NP00042G.

Chukwudi, U. P., Kutu, F. R. and Mavengahama, S. (2021) Mycotoxins in maize and implications on food security: A review, *Agricultural Reviews*, (Of), [online] Available at: https://arccjournals.com/journal/agricultural-reviews/R-140.

Clark, S. M., LeDoux, D. G., Seeno, T. S., Riley, E. G., Gilbert, A. J. and Sullivan, J. M. (2004) *Host plants of leaf beetle species occurring in the United States and Canada (Coleoptera: Megalopodidae, Orsodacnidae, Chrysomelidae, excluding Bruchinae)*, *Annals of the Entomological Society of America*, [online] Available at: https://www.zin.ru/animalia/coleoptera/pdf/clark_ledoux_et_al_2004.pdf.

Coban, O., De Deyn, G. B. and van der Ploeg, M. (2022) Soil microbiota as game-changers in restoration of degraded lands, *Science*, 375(6584), [online] Available at: https://www.science.org/doi/10.1126/science.abe0725.

Compant, S., Samad, A., Faist, H. and Sessitsch, A. (2019) A review on the plant microbiome: Ecology, functions, and emerging trends in microbial application, *Journal of Advanced Research*, 19, pp. 29–37.

Currie, A. F., Murray, P. J. and Gange, A. C. (2011) Is a specialist root-feeding insect affected by arbuscular mycorrhizal fungi?, *Applied Soil Ecology*, 47(2), pp. 77–83, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0929139310002593.

Cuthbertson, A. G. S., Walters, K. F. A., Northing, P. and Luo, W. (2007) Efficacy of the entomopathogenic nematode, Steinernema feltiae , against sweetpotato whitefly Bemisia tabaci (Homoptera: Aleyrodidae) under laboratory and glasshouse conditions, *Bulletin of Entomological Research*, 97(1), pp. 9–14, [online] Available at: https://www.cambridge.org/core/product/identifier/S0007485307004701/type/journal_article.

Van Dam, N. M., Raaijmakers, C. E. and Van Der Putten, W. H. (2005) Root herbivory reduces growth and survival of the shoot feeding specialist Pieris rapae on Brassica nigra, *Entomologia Experimentalis et Applicata*, 115(1), pp. 161–170, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1570-7458.2005.00241.x.

Damalas, C. and Koutroubas, S. (2018) Current status and recent developments in biopesticide use, *Agriculture*, 8(1), p. 13, [online] Available at: https://www.mdpi.com/2077-0472/8/1/13.

Davis, J. K., Aguirre, L. A., Barber, N. A., Stevenson, P. C. and Adler, L. S. (2019) From plant fungi to bee parasites: mycorrhizae and soil nutrients shape floral chemistry and bee pathogens, *Ecology*, 100(10), [online] Available at: https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.2801.

Davis, J. K., Cohen, A. D., Getman-Pickering, Z. L., Grab, H. L., Hodgden, B., Maher, R. M., Pelzer, C. J., Rangarajan, A., Ryan, M. R., Ugine, T. A. and Thaler, J. S. (2023) Agricultural soil legacy influences multitrophic interactions between crops, their pathogens and pollinators, *Proceedings of the Royal Society B: Biological Sciences*, 290(2011), [online] Available at: https://royalsocietypublishing.org/doi/10.1098/rspb.2023.1453.

Day, R., Abrahams, P., Bateman, M., Beale, T., Clottey, V., Cock, M., Colmenarez, Y., Corniani, N., Early, R., Godwin, J., Gomez, J., Moreno, P. G., Murphy, S. T., Oppong-Mensah, B., Phiri, N., Pratt, C., Silvestri, S. and Witt, A. (2017) Fall armyworm: Impacts and implications for Africa, *Outlooks on Pest Management*, 28(5), pp. 196–201.

Deng, S., Wipf, H. M.-L., Pierroz, G., Raab, T. K., Khanna, R. and Coleman-Derr, D. (2019) A plant growth-promoting microbial soil amendment dynamically alters the strawberry root bacterial microbiome, *Scientific Reports*, 9(1), p. 17677, [online] Available at:

https://www.nature.com/articles/s41598-019-53623-2.

Denno, R. F., Gruner, D. S. and Kaplan, I. (2008) Potential for entomopathogenic nematodes in biological control: a meta-analytical synthesis and insights from trophic cascade theory., *Journal of nematology*, 40(2), pp. 61–72, [online] Available at: http://www.ncbi.nlm.nih.gov/pubmed/19259522.

Derunkov, A. and Konstantinov, A. (2013) Taxonomic changes in the genus Diabrotica Chevrolat (Coleoptera: Chrysomelidae: Galerucinae): results of a synopsis of North and Central America Diabrotica species, *Zootaxa*, 3686(3), p. 301, [online] Available at: http://biotaxa.org/Zootaxa/article/view/zootaxa.3686.3.1.

Dhanasekaran, D. and Thangaraj, R. (2014) Microbial secondary metabolites are an alternative approaches against insect vector to prevent zoonotic diseases, *Asian Pacific Journal of Tropical Disease*, No longer published by Elsevier, 4(4), pp. 253–261.

Dominelli, N., Platz, F. and Heermann, R. (2022) The insect pathogen photorhabdus luminescens protects plants from phytopathogenic Fusarium graminearum via chitin degradation, Johnson, K. N. (ed.), *Applied and Environmental Microbiology*, 88(11), [online] Available at: https://journals.asm.org/doi/10.1128/aem.00645-22.

Dong, L., Li, Y., Xu, J., Yang, J., Wei, G., Shen, L., Ding, W. and Chen, S. (2019) Biofertilizers regulate the soil microbial community and enhance Panax ginseng yields, *Chinese Medicine (United Kingdom)*, BioMed Central, 14(1), pp. 1–14, [online] Available at: https://doi.org/10.1186/s13020-019-0241-1.

Dorta, S. de O., Balbinotte, J., Monnerat, R., Lopes, J. R. S., da Cunha, T., Zanardi, O. Z., de Miranda, M. P., Machado, M. A. and de Freitas-Astúa, J. (2020) Selection of Bacillus thuringiensis strains in citrus and their pathogenicity to Diaphorina citri (Hemiptera: Liviidae) nymphs, *Insect Science*, 27(3), pp. 519–530, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/1744-7917.12654.

Dozio, D., Sacchi, F., Pinto, A., Dallavalle, S., Annunziata, F. and Princiotto, S. (2025) Natural antifungal alkaloids for crop protection: An overview of the latest synthetic approaches, *Pharmaceuticals*, 18(4), p. 589, [online] Available at: https://www.mdpi.com/1424-8247/18/4/589.

Duan, M., Li, Y., Zhu, G., Wu, X., Huang, H., Qin, J., Long, S., Li, X., Feng, B., Qin, S., Liu, Q.-H., Li, C., Wang, L., Li, Q., He, T. and Wang, Z. (2023) Soil chemistry, metabarcoding, and metabolome analyses reveal that a sugarcane—Dictyophora indusiata intercropping system can enhance soil health by reducing soil nitrogen loss, *Frontiers in Microbiology*, 14, [online] Available at: https://www.frontiersin.org/articles/10.3389/fmicb.2023.1193990/full.

Dudenhöffer, J., Ebeling, A., Klein, A. and Wagg, C. (2018) Beyond biomass: Soil feedbacks are transient over plant life stages and alter fitness, Farrer, E. (ed.), *Journal of Ecology*, 106(1), pp. 230–241, [online] Available at: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12870.

Dutta, D., Bordoloi, M. J. and Bhattacharyya, N. K. (2021) Genus pothos: A review of chemical constituents and biological activities, *Rasayan Journal of Chemistry*, 14(04), [online] Available at: http://rasayanjournal.co.in/admin/php/upload/3313_pdf.pdf.

Early, R., González-Moreno, P., Murphy, S. T. and Day, R. (2018) Forecasting the global extent of invasion of the cereal pest Spodoptera frugiperda, the fall armyworm, *NeoBiota*, 40, pp. 25–50, [online] Available at: https://neobiota.pensoft.net/articles.php?id=28165.

Eben, A. and Barbercheck, M. E. (1996) Field observations on host plant associations enemies of diabroticite beetles (chrysomelidae: luperini) in veracruz, mexico, *ACTA ZOOLÓGICA MEXICANA (N.S.)*, (67), pp. 47–65, [online] Available at: https://azm.ojs.inecol.mx/index.php/azm/article/view/1756.

Eckstein, S. and Heermann, R. (2019) Regulation of phenotypic switching and heterogeneity in Photorhabdus luminescens cell populations, *Journal of Molecular Biology*, 431(23), pp. 4559–4568, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0022283619302116.

Ehlers, R.-U., Hiltpold, I., Kuhlmann, U. and Toepfer, S. (2008) Field results on the use of Heterorhabditis bacteriophora against the invasive maize pest Diabrotica virgifera virgifera, *Insect Pathog. Insect Parasit. Nematodes IOBC/wprs Bull*, 31, pp. 332–335.

Ehlers, R. U. (2005) Forum on safety and regulation., In Grewal, P. S., Ehlers, R. U., and Shapiro-Ilan, D. I. (eds.), *Nematodes as biocontrol agents*, UK, CABI Publishing, pp. 107–114, [online] Available at: http://www.cabi.org/cabebooks/ebook/20053223406.

Eisenhauer, N., Hörsch, V., Moeser, J. and Scheu, S. (2010) Synergistic effects of microbial and animal decomposers on plant and herbivore performance, *Basic and Applied Ecology*, 11(1), pp. 23–34.

Eleftherianos, I., Boundy, S., Joyce, S. A., Aslam, S., Marshall, J. W., Cox, R. J., Simpson, T. J., Clarke, D. J., Ffrench-Constant, R. H. and Reynolds, S. E. (2007) An antibiotic produced by an insect-pathogenic bacterium suppresses host defenses through phenoloxidase inhibition, *Proceedings of the National Academy of Sciences of the United States of America*, 104(7), pp. 2419–2424, [online] Available at: https://pnas.org/doi/full/10.1073/pnas.0610525104.

Eleftherianos, I., ffrench-Constant, R. H., Clarke, D. J., Dowling, A. J. and Reynolds, S. E. (2010) Dissecting the immune response to the entomopathogen Photorhabdus, *Trends in Microbiology*, 18(12), pp. 552–560.

Erb, M., Flors, V., Karlen, D., De Lange, E., Planchamp, C., D'Alessandro, M., Turlings, T. C. J. and Ton, J. (2009) Signal signature of aboveground-induced resistance upon belowground herbivory in maize, *The Plant Journal*, 59(2), pp. 292–302, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1365-313X.2009.03868.x.

Erb, M., Meldau, S. and Howe, G. A. (2012) Role of phytohormones in insect-specific plant reactions, *Trends in Plant Science*, 17(5), pp. 250–259, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1360138512000040.

Erb, M. and Reymond, P. (2019) Molecular interactions between plants and insect herbivores, *Annual Review of Plant Biology*, 70(1), pp. 527–557, [online] Available at: https://www.annualreviews.org/doi/10.1146/annurev-arplant-050718-095910.

Erb, M., Robert, C. A. M., Hibbard, B. E. and Turlings, T. C. J. (2011) Sequence of arrival determines plant-mediated interactions between herbivores, *Journal of Ecology*, 99(1), pp. 7–15, [online] Available at: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2745.2010.01757.x.

Eroglu, C., Cimen, H., Ulug, D., Karagoz, M., Hazir, S. and Cakmak, I. (2019) Acaricidal effect of cell-free supernatants from Xenorhabdus and Photorhabdus bacteria against Tetranychus urticae (Acari: Tetranychidae), *Journal of Invertebrate Pathology*, Elsevier, 160(December 2018), pp. 61–66, [online] Available at: https://doi.org/10.1016/j.jip.2018.12.004.

Etesami, H. and Glick, B. R. (2024) Bacterial indole-3-acetic acid: A key regulator for plant growth, plant-microbe interactions, and agricultural adaptive resilience, *Microbiological Research*, 281, p. 127602, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S094450132400003X.

Fagan, W. F., Siemann, E., Mitter, C., Denno, R. F., Huberty, A. F., Woods, H. A. and Elser, J. J. (2002) Nitrogen in insects: Implications for trophic complexity and species diversification, *The American Naturalist*, 160(6), pp. 784–802, [online] Available at: https://www.journals.uchicago.edu/doi/10.1086/343879.

Fallet, P., Bazagwira, D., Guenat, J. M., Bustos-Segura, C., Karangwa, P., Mukundwa, I. P., Kajuga, J., Degen, T., Toepfer, S. and Turlings, T. C. J. (2022) Laboratory and field trials reveal the potential of a gel formulation of entomopathogenic nematodes for the biological control of fall armyworm caterpillars (Spodoptera frugiperda), *Biological Control*, 176, p. 105086, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1049964422002511.

Fallet, P., De Gianni, L., Machado, R. A. R., Bruno, P., Bernal, J. S., Karangwa, P., Kajuga, J., Waweru, B., Bazagwira, D., Degen, T., Toepfer, S. and Turlings, T. C. J. (2022) Comparative screening of Mexican, Rwandan and commercial entomopathogenic nematodes to be used against invasive fall armyworm, Spodoptera frugiperda, *Insects*, 13(2), p. 205, [online] Available at: https://www.mdpi.com/2075-4450/13/2/205.

FAO (2018a) *Integrated management of the fall armyworm on maize: a guide for farmer field schools in Africa*, Rome, Italy, FAO, [online] Available at: https://www.fao.org/3/i8741en/I8741EN.pdf.

FAO (2020) New standards to curb the global spread of plant pests and diseases., [online] Available at: https://www.fao.org/newsroom/detail/New-standards-to-curb-the-global-spread-of-plant-pests-and-diseases/en.

FAO (2018b) Sustainable management of the Fall Armyworm in Africa A framework for partnership, (March), [online] Available at: https://www.fao.org/publications/card/en/c/4c559a77-82b3-4bb5-9b8d-2f16488c92ff/.

FAO and CABI (2019) *Community-based fall armyworm (Spodoptera frugiperda) monitoring, early warning and management*, *Community-based fall armyworm (Spodoptera frugiperda) monitoring, early warning and management. Training of Trainers Manual*, First Edit, [online] Available at: http://www.fao.org/3/CA2924EN/ca2924en.pdf.

FAO, ITPS, GSBI, CBD and EC (2020) *FAO, ITPS, GSBI, SCBD and EC. 2020. State of knowledge of soil biodiversity – Status, challenges and potentialities, summary for policy makers. Rome, FAO.*, *Soil in the Environment*.

Fazal, A., Yang, M., Han, H., Lu, G., Hao, C., Lai, X., Song, Y., Ma, H., Yin, T., Qi, J., Sun, S., Niu, K., Wen, Z. and Yang, Y. (2024) Impact of dual Bt-transgenic maize (2A7) on soil microbial communities and enzyme activities: A comparative study with control variety Z58, *Environmental Research*, 263, p. 120006, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0013935124019133.

Ferguson, J. E. and Metcalf, R. L. (1985) Cucurbitacins, *Journal of Chemical Ecology*, 11(3), pp. 311–318, [online] Available at: http://link.springer.com/10.1007/BF01411417.

Ferioun, M., Bouhraoua, S., Srhiouar, N., Tirry, N., Belahcen, D., Siang, T. C., Louahlia, S. and El Ghachtouli, N. (2023) Optimized drought tolerance in barley (Hordeum vulgare L.) using plant growth-promoting rhizobacteria (PGPR), *Biocatalysis and Agricultural Biotechnology*, 50, p. 102691, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1878818123000920.

Fernie, A. R. and Tohge, T. (2017) The genetics of plant metabolism, *Annual Review of Genetics*, 51, pp. 287–310.

Ffrench-Constant, R. H., Dowling, A. and Waterfield, N. R. (2007) Insecticidal toxins from Photorhabdus bacteria and their potential use in agriculture, *Toxicon*, Elsevier Ltd, 49(4), pp. 436–451, [online] Available at: http://dx.doi.org/10.1016/j.toxicon.2006.11.019.

Ffrench-Constant, R., Waterfield, N., Daborn, P., Joyce, S., Bennett, H., Au, C., Dowling, A., Boundy, S., Reynolds, S. and Clarke, D. (2003) Photorhabdus : towards a functional genomic analysis of a symbiont and pathogen, *FEMS Microbiology Reviews*, 26(5), pp. 433–456, [online] Available at: https://academic.oup.com/femsre/article-lookup/doi/10.1111/j.1574-6976.2003.tb00625.x.

Fielding, D. J., Trainor, E. and Zhang, M. (2013) Diet influences rates of carbon and nitrogen mineralization from decomposing grasshopper frass and cadavers, *Biology and Fertility of Soils*, 49(5), pp. 537–544, [online] Available at: http://link.springer.com/10.1007/s00374-012-0702-5.

Fierer, N. (2017) Embracing the unknown: disentangling the complexities of the soil microbiome, *Nature Reviews Microbiology*, 15(10), pp. 579–590, [online] Available at: https://www.nature.com/articles/nrmicro.2017.87.

Friman, J., Pineda, A., Gershenzon, J., Dicke, M. and van Loon, J. J. A. (2020) Differential effects of the rhizobacterium Pseudomonas simiae on above- and belowground chewing insect herbivores, *Journal of Applied Entomology*, 145(3), pp. 250–260, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/jen.12842.

Frost, C. J. and Hunter, M. D. (2007) Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses, *Oecologia*, 151(1), pp. 42–53, [online] Available at: http://link.springer.com/10.1007/s00442-006-0579-9.

Fukruksa, C., Yimthin, T., Suwannaroj, M., Muangpat, P., Tandhavanant, S., Thanwisai, A. and Vitta, A. (2017) Isolation and identification of Xenorhabdus and Photorhabdus bacteria associated with entomopathogenic nematodes and their larvicidal activity against Aedes aegypti, *Parasites and Vectors*, Parasites & Vectors, 10(1), pp. 1–10.

Furgani, G., Böszörményi, E., Fodor, A., Máthé-Fodor, A., Forst, S., Hogan, J. S., Katona, Z., Klein, M. G., Stackebrandt, E., Szentirmai, A., Sztaricskai, F. and Wolf, S. L. (2008) Xenorhabdus antibiotics: a comparative analysis and potential utility for controlling mastitis caused by bacteria, *Journal of Applied Microbiology*, 104(3), pp. 745–758, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2672.2007.03613.x.

Gadhave, K. R., Finch, P., Gibson, T. M. and Gange, A. C. (2016) Plant growth-promoting Bacillus suppress Brevicoryne brassicae field infestation and trigger density-dependent and density-independent natural enemy responses, *Journal of Pest Science*, 89(4), pp. 985–992, [online] Available at: http://link.springer.com/10.1007/s10340-015-0721-8.

Gadhave, K. R. and Gange, A. C. (2016) Plant-associated Bacillus spp. alter life-history traits of the specialist insect Brevicoryne brassicae L., *Agricultural and Forest Entomology*, 18(1), pp. 35–42, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/afe.12131.

Gámez-Virués, S. and Eben, A. (2005) Comparison of beetle diversity and incidence of parasitism in Diabroticina (Coleoptera: Chrysomelidae) species collected on cucurbits, *Florida Entomologist*, 88(March), pp. 72–76.

Gange, A. C. (2007) Insect–mycorrhizal interactions: patterns, processes, and consequences, In *Ecological Communities*, Cambridge University Press, pp. 124–144, [online] Available at: https://www.cambridge.org/core/product/identifier/CBO9780511542701A016/type/book_part.

Gange, A. C. (2001) Species-specific responses of a root- and shoot-feeding insect to arbuscular mycorrhizal colonization of its host plant, *New Phytologist*, 150(3), pp. 611–618, [online] Available at: https://nph.onlinelibrary.wiley.com/doi/10.1046/j.1469-8137.2001.00137.x.

Gansfort, B., Uthoff, J. and Traunspurger, W. (2018) Interactions among competing nematode species affect population growth rates, *Oecologia*, 187(1), pp. 75–84, [online] Available at: http://link.springer.com/10.1007/s00442-018-4109-3.

Gao, G., Yin, D., Chen, S., Xia, F., Yang, J., Li, Q. and Wang, W. (2012) Effect of biocontrol agent pseudomonas fluorescens 2P24 on soil fungal community in cucumber rhizosphere using T-RFLP and DGGE, *PLoS ONE*, 7(2).

Garlet, C. G., Gubiani, P. da S., Palharini, R. B., Moreira, R. P., Godoy, D. N., Farias, J. R. and

Bernardi, O. (2021) Field-evolved resistance to chlorpyrifos by Spodoptera frugiperda (Lepidoptera: Noctuidae): Inheritance mode, cross-resistance patterns, and synergism, *Pest Management Science*, 77(12), pp. 5367–5374.

Ge, S., Zhang, H., Liu, D., Lv, C., Cang, X., Sun, X., Song, Y., He, W., Chu, B., Zhao, S., Wu, Q., Yang, X. and Wu, K. (2022) Seasonal migratory activity of Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) across China and Myanmar, *Pest Management Science*, 78(11), pp. 4975–4982, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1002/ps.7120.

Van Geem, M., Harvey, J. A., Cortesero, A. M., Raaijmakers, C. E. and Gols, R. (2015) Interactions between a belowground herbivore and primary and secondary root metabolites in wild cabbage, *Journal of Chemical Ecology*, 41(8), pp. 696–707, [online] Available at: http://link.springer.com/10.1007/s10886-015-0605-7.

Georgis, R., Koppenhöfer, A. M., Lacey, L. A., Bélair, G., Duncan, L. W., Grewal, P. S., Samish, M., Tan, L., Torr, P. and van Tol, R. W. H. M. (2006) Successes and failures in the use of parasitic nematodes for pest control, *Biological Control*, Academic Press, 38(1), pp. 103–123.

Gerdes, E., Upadhyay, D., Mandjiny, S., Bullard-Dillard, R., Storms, M., Menefee, M. and Holmes, L. D. (2015) Photorhabdus Luminescens: Virulent properties and agricultural applications, *American Journal of Agriculture and Forestry*, 3(5), p. 171, [online] Available at: http://www.sciencepublishinggroup.com/journal/paperinfo?journalid=218&doi=10.11648/j.ajaf.20150305.12.

Gfeller, V., Waelchli, J., Pfister, S., Deslandes-Hérold, G., Mascher, F., Glauser, G., Aeby, Y., Mestrot, A., Robert, C. A. M., Schlaeppi, K. and Erb, M. (2023) Plant secondary metabolite-dependent plant-soil feedbacks can improve crop yield in the field, *eLife*, 12, pp. 1–20.

Ghosal, D. and Datta, B. (2024) Characterization, phylogenetic analysis and toxigenic potential of Fusarium incarnatum-equiseti species complex isolates associated with root rot disease in vegetables, *Journal of Phytopathology*, 172(4), [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/jph.13362.

Gibert, S., Edel-Hermann, V., Gautheron, E., Gautheron, N., Sol, J.-M., Capelle, G., Galland, R., Bardon-Debats, A., Lambert, C. and Steinberg, C. (2022) First report of Fusarium avenaceum , Fusarium oxysporum , Fusarium redolens , and Fusarium solani causing root rot in pea in France, *Plant Disease*, 106(4), p. 1297, [online] Available at: https://apsjournals.apsnet.org/doi/10.1094/PDIS-04-21-0833-PDN.

Giraldo, A. and Crous, P. W. (2019) Inside Plectosphaerellaceae, *Studies in Mycology*, 92(1), pp. 227–286, [online] Available at: https://www.ingentaconnect.com/content/10.1016/j.simyco.2018.10.005.

Glauser, G., Marti, G., Villard, N., Doyen, G. A., Wolfender, J., Turlings, T. C. J. and Erb, M. (2011) Induction and detoxification of maize 1,4-benzoxazin-3-ones by insect herbivores, *The Plant Journal*, 68(5), pp. 901–911, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1365-313X.2011.04740.x.

Glick, B. R. (2012) Plant growth-promoting Bacteria: mechanisms and applications, *Scientifica*, 2012, pp. 1–15, [online] Available at: http://www.hindawi.com/journals/scientifica/2012/963401/.

Godschalx, A. L., Stady, L., Watzig, B. and Ballhorn, D. J. (2016) Is protection against florivory consistent with the optimal defense hypothesis?, *BMC Plant Biology*, 16(1), p. 32, [online] Available at: https://bmcplantbiol.biomedcentral.com/articles/10.1186/s12870-016-0719-2.

Goergen, G., Kumar, P. L., Sankung, S. B., Togola, A. and Tamò, M. (2016) First Report of Outbreaks of the Fall Armyworm Spodoptera frugiperda (J E Smith) (Lepidoptera, Noctuidae), a New Alien Invasive Pest in West and Central Africa., Luthe, D. S. (ed.), *PloS one*, 11(10), p.

e0165632, [online] Available at: https://dx.plos.org/10.1371/journal.pone.0165632.

Gols, R., Bukovinszky, T., Van Dam, N. M., Dicke, M., Bullock, J. M. and Harvey, J. A. (2008) Performance of generalist and specialist herbivores and their endoparasitoids differs on cultivated and wild Brassica populations, *Journal of Chemical Ecology*, 34(2), pp. 132–143.

Gomiero, T., Pimentel, D. and Paoletti, M. G. (2011) Is there a need for a more sustainable agriculture?, *Critical Reviews in Plant Sciences*, 30(1–2), pp. 6–23, [online] Available at: http://www.tandfonline.com/doi/abs/10.1080/07352689.2011.553515.

Gonzalez-Burgos, E. and Gomez-Serranillos, M. P. (2012) Terpene compounds in nature: A review of their potential antioxidant activity, *Current Medicinal Chemistry*, 19(31), pp. 5319–5341, [online] Available at: http://www.eurekaselect.com/openurl/content.php?genre=article&issn=0929-8673&volume=19&issue=31&spage=5319.

Grewal, P. S., Ehlers, R. U. and Shapiro-Ilan, D. I. (2005) *Nematodes as biocontrol agents*, Grewal, P. S., Ehlers, R. U., and Shapiro-Ilan, D. I. (eds.), Wallingford, CABI, [online] Available at: http://www.cabi.org/cabebooks/ebook/20053223405.

Grewal, P. S., De Nardo, E. A. B. and Aguillera, M. M. (2001) Entomopathogenic nematodes: Potential for exploration and use in south America, *Neotropical Entomology*, 30(2), pp. 191–205.

Griffiths, B. S., Heckmann, L., Caul, S., Thompson, J., Scrimgeour, C. and Krogh, P. H. (2007) Varietal effects of eight paired lines of transgenic Bt maize and near-isogenic non- Bt maize on soil microbial and nematode community structure, *Plant Biotechnology Journal*, 5(1), pp. 60–68, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1467-7652.2006.00215.x.

Gruden, K., Lidoy, J., Petek, M., Podpečan, V., Flors, V., Papadopoulou, K. K., Pappas, M. L., Martinez-Medina, A., Bejarano, E., Biere, A. and Pozo, M. J. (2020) Ménage à trois: Unraveling the mechanisms regulating plant–microbe–arthropod interactions, *Trends in Plant Science*, 25(12), pp. 1215–1226, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1360138520302193.

Grundmann, F., Kaiser, M., Schiell, M., Batzer, A., Kurz, M., Thanwisai, A., Chantratita, N. and Bode, H. B. (2014) Antiparasitic Chaiyaphumines from Entomopathogenic Xenorhabdus sp. PB61.4, *Journal of Natural Products*, 77(4), pp. 779–783.

Gul, N., Wani, I. A., Mir, R. A., Nowshehri, J. A., Aslam, Shabana, Gupta, R., Verma, S. and Aslam, Saima (2023) Plant growth promoting microorganisms mediated abiotic stress tolerance in crop plants: a critical appraisal, *Plant Growth Regulation*, 100(1), pp. 7–24, [online] Available at: https://link.springer.com/10.1007/s10725-022-00951-5.

Gulcu, B., Hazir, S. and Kaya, H. K. (2012) Scavenger deterrent factor (SDF) from symbiotic bacteria of entomopathogenic nematodes, *Journal of Invertebrate Pathology*, Academic Press, 110(3), pp. 326–333.

Gulcu, B., Hazir, S., Lewis, E. E. and Kaya, H. K. (2018) Evaluation of responses of different ant species (Formicidae) to the scavenger deterrent factor associated with the entomopathogenic nematode-bacterium complex, *European Journal of Entomology*, 115, pp. 312–317, [online] Available at: http://www.eje.cz/doi/10.14411/eje.2018.030.html.

Gutiérrez-Moreno, R., Mota-Sanchez, D., Blanco, C. A., Whalon, M. E., Terán-Santofimio, H., Rodriguez-Maciel, J. C. and DiFonzo, C. (2019) Field-evolved resistance of the fall armyworm (Lepidoptera: Noctuidae) to synthetic insecticides in Puerto Rico and Mexico, *Journal of Economic Entomology*, 112(2), pp. 792–802.

Hannula, S. E., Heinen, R., Huberty, M., Steinauer, K., De Long, J. R., Jongen, R. and

Bezemer, T. M. (2021) Persistence of plant-mediated microbial soil legacy effects in soil and inside roots, *Nature Communications*, Springer US, 12(1), pp. 1–13, [online] Available at: http://dx.doi.org/10.1038/s41467-021-25971-z.

Haraguchi, S. and Yoshiga, T. (2020) Potential of the fungal feeding nematode Aphelenchus avenae to control fungi and the plant parasitic nematode Ditylenchus destructor associated with garlic, *Biological Control*, 143, p. 104203, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1049964419300209.

Hartmann, T. (2007) From waste products to ecochemicals: Fifty years research of plant secondary metabolism, *Phytochemistry*, 68(22–24), pp. 2831–2846, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0031942207005730.

Heinen, R., Biere, A., Harvey, J. A. and Bezemer, T. M. (2018) Effects of soil organisms on aboveground plant-insect interactions in the field: Patterns, mechanisms and the role of methodology, *Frontiers in Ecology and Evolution*, 6, [online] Available at: https://www.frontiersin.org/article/10.3389/fevo.2018.00106/full.

Herman, M. A. B., Nault, B. A. and Smart, C. D. (2008) Effects of plant growth-promoting rhizobacteria on bell pepper production and green peach aphid infestations in New York, *Crop Protection*, 27(6), pp. 996–1002, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0261219407003250.

Hernández-Montiel, L. G., Chiquito Contreras, C. J., Murillo Amador, B., Vidal Hernández, L., Quiñones Aguilar, E. E. and Chiquito Contreras, R. G. (2017) Efficiency of two inoculation methods of Pseudomonas putida on growth and yield of tomato plants, *Journal of soil science and plant nutrition*, 17(4), pp. 1003–1012, [online] Available at: http://www.scielo.cl/scielo.php?script=sci_arttext&pid=S0718-95162017000400012&lng=en&nrm=iso&tlng=en.

Hirsch, J., Galidevara, S., Strohmeier, S., Devi, K. U. and Reineke, A. (2013) Effects on diversity of soil fungal community and fate of an artificially applied Beauveria bassiana strain assessed through 454 pyrosequencing, *Microbial Ecology*, 66(3), pp. 608–620, [online] Available at: http://link.springer.com/10.1007/s00248-013-0249-5.

Hirsh, I. S. and Barbercheck, M. E. (1996) Effects of host plant and cucurbitacin on growth of larval Diabrotica undecimpunctata howardi, *Entomologia Experimentalis et Applicata*, 81(1), pp. 47–51, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1570-7458.1996.tb02013.x.

Hosseinvand, M., Eskandari, A. and Ghaderi, R. (2021) The genus Basiria Siddiqi, 1959 (Nematoda: Tylenchidae) from Dezful region, Iran, *Journal of Threatened Taxa*, 13(3), pp. 18004–18010, [online] Available at: https://threatenedtaxa.org/index.php/JoTT/article/view/6353.

Hövelmann, Y., Hahn, M., Hübner, F. and Humpf, H.-U. (2019) Detection of novel cytotoxic imidazole alkaloids in tomato products by LC-MS/MS, *Journal of Agricultural and Food Chemistry*, 67(13), pp. 3670–3678, [online] Available at: https://pubs.acs.org/doi/10.1021/acs.jafc.9b00461.

Hu, L., Robert, C. A. M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., Van Der Heijden, M. G. A., Schlaeppi, K. and Erb, M. (2018) Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota, *Nature Communications*, 9(1), pp. 1–13.

Hughes, D. and Andersson, D. I. (2017) Environmental and genetic modulation of the phenotypic expression of antibiotic resistance, *FEMS Microbiology Reviews*, 41(3), pp. 374–391, [online] Available at: https://academic.oup.com/femsre/article/41/3/374/3063351.

Hunter, M. D. (2001) Insect population dynamics meets ecosystem ecology: effects of

herbivory on soil nutrient dynamics, *Agricultural and Forest Entomology*, 3(2), pp. 77–84, [online] Available at: https://resjournals.onlinelibrary.wiley.com/doi/10.1046/j.1461-9563.2001.00100.x.

IPPC (2021) *Scientific review of the impact of climate change on plant pests – A global challenge to prevent and mitigate plant pest risks in agriculture, forestry and ecosystems*, *FAO on behalf of the IPPC Secretariat*, Rome, Italy, [online] Available at: https://doi.org/10.4060/cb4769en.

Irmisch, S., Zeltner, P., Handrick, V., Gershenzon, J. and Köllner, T. G. (2015) The maize cytochrome P450 CYP79A61 produces phenylacetaldoxime and indole-3-acetaldoxime in heterologous systems and might contribute to plant defense and auxin formation, *BMC Plant Biology*, 15(1), p. 128, [online] Available at: https://bmcplantbiol.biomedcentral.com/articles/10.1186/s12870-015-0526-1.

Israni, B., Wouters, F. C., Luck, K., Seibel, E., Ahn, S.-J., Paetz, C., Reinert, M., Vogel, H., Erb, M., Heckel, D. G., Gershenzon, J. and Vassão, D. G. (2020) The fall armyworm Spodoptera frugiperda utilizes specific UDP-glycosyltransferases to inactivate maize defensive benzoxazinoids, *Frontiers in Physiology*, 11, [online] Available at: https://www.frontiersin.org/articles/10.3389/fphys.2020.604754/full.

Jaccard, C., Cuny, M. A. C., Bustos-Segura, C., Arce, C. C. M., Giollo, L., Glauser, G. and Benrey, B. (2021) Squash Varieties Domesticated for Different Purposes Differ in Chemical and Physical Defense Against Leaf and Root Herbivores, *Frontiers in Agronomy*, 3, [online] Available at: https://www.frontiersin.org/articles/10.3389/fagro.2021.683936/full.

Jaffuel, G., Sbaiti, I. and Turlings, T. C. J. (2020) Encapsulated entomopathogenic nematodes can protect maize plants from diabrotica balteata larvae, *Insects*, 11(1).

Jia, R., Chen, J., Hu, L., Liu, X., Xiao, K. and Wang, Y. (2022) Alcaligenes faecalis Juj3 alleviates Plasmodiophora brassicae stress to cabbage via promoting growth and inducing resistance, *Frontiers in Sustainable Food Systems*, 6, [online] Available at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.942409/full.

Jiang, H., Li, S., Wang, T., Chi, X., Qi, P. and Chen, G. (2021) Interaction between halotolerant phosphate-solubilizing bacteria (Providencia rettgeri Strain TPM23) and rock phosphate improves soil biochemical properties and peanut growth in saline soil, *Frontiers in Microbiology*, 12, [online] Available at: https://www.frontiersin.org/articles/10.3389/fmicb.2021.777351/full.

Jiménez, J. A., Novinscak, A. and Filion, M. (2020) Inoculation with the plant-growth-promoting rhizobacterium Pseudomonas fluorescens LBUM677 impacts the rhizosphere microbiome of three oilseed crops, *Frontiers in Microbiology*, 11, [online] Available at: https://www.frontiersin.org/article/10.3389/fmicb.2020.569366/full.

Johnson, S. N., Benefer, C. M., Frew, A., Griffiths, B. S., Hartley, S. E., Karley, A. J., Rasmann, S., Schumann, M., Sonnemann, I. and Robert, C. A. M. (2016) New frontiers in belowground ecology for plant protection from root-feeding insects, *Applied Soil Ecology*, 108, pp. 96–107, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0929139316302116.

Johnson, S. N., Erb, M. and Hartley, S. E. (2016) Roots under attack: contrasting plant responses to below- and aboveground insect herbivory, *New Phytologist*, 210(2), pp. 413–418, [online] Available at: https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13807.

Kabouw, P., Kos, M., Kleine, S., Vockenhuber, E. A., van Loon, J. J. A., van der Putten, W. H., Van Dam, N. M. and Biere, A. (2011) Effects of soil organisms on aboveground multitrophic interactions are consistent between plant genotypes mediating the interaction, *Entomologia Experimentalis et Applicata*, 139(3), pp. 197–206.

Kakade, K., Patwardhan, R. and Pathade, G. (2023) Efficacy of Photorhabdus as a promising

entomopathogenic bacteria in the eco-friendly biocontrol of white grub larvae, *International Journal of Experimental Research and Review*, 35, pp. 149–159.

Kanwar, R. S., Patil, J. A. and Yadav, S. (2021) Prospects of using predatory nematodes in biological control for plant parasitic nematodes – A review, *Biological Control*, 160, p. 104668, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1049964421001389.

Kaplan, I., Halitschke, R., Kessler, A., Rehill, B. J., Sardanelli, S. and Denno, R. F. (2008) Physiological integration of roots and shoots in plant defense strategies links above- and belowground herbivory, *Ecology Letters*, 11(8), pp. 841–851, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2008.01200.x.

Kaya, H. K., Aguillera, M. M., Alumai, A., Choo, H. Y., de la Torre, M., Fodor, A., Ganguly, S., Hazir, S., Lakatos, T., Pye, A., Wilson, M., Yamanaka, S., Yang, H. and Ehlers, R. U. (2006) Status of entomopathogenic nematodes and their symbiotic bacteria from selected countries or regions of the world, *Biological Control*, Academic Press, 38(1), pp. 134–155.

Kempel, A., Brandl, R. and Schädler, M. (2009) Symbiotic soil microorganisms as players in aboveground plant–herbivore interactions – the role of rhizobia, *Oikos*, 118(4), pp. 634–640, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1600-0706.2009.17418.x.

De Kesel, J., Conrath, U., Flors, V., Luna, E., Mageroy, M. H., Mauch-Mani, B., Pastor, V., Pozo, M. J., Pieterse, C. M. J., Ton, J. and Kyndt, T. (2021) The induced resistance lexicon: Do's and don'ts, *Trends in Plant Science*, 26(7), pp. 685–691, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1360138521000029.

Keswani, C., Singh, S. P., García-Estrada, C., Mezaache-Aichour, S., Glare, T. R., Borriss, R., Rajput, V. D., Minkina, T. M., Ortiz, A. and Sansinenea, E. (2022) Biosynthesis and beneficial effects of microbial gibberellins on crops for sustainable agriculture, *Journal of Applied Microbiology*, 132(3), pp. 1597–1615, [online] Available at: https://academic.oup.com/jambio/article/132/3/1597/6988784.

Kiers, E. T., Leakey, R. R. B., Izac, A.-M., Heinemann, J. A., Rosenthal, E., Nathan, D. and Jiggins, J. (2008) Agriculture at a Crossroads, *Science*, 320(5874), pp. 320–321, [online] Available at: https://www.science.org/doi/10.1126/science.1158390.

Kim, J., Jaffuel, G. and Turlings, T. C. J. (2015) Enhanced alginate capsule properties as a formulation of entomopathogenic nematodes, *BioControl*, 60(4), pp. 527–535, [online] Available at: http://link.springer.com/10.1007/s10526-014-9638-z.

Kim, T., Yucheol, L. and Park, J.-K. (2021) First report and morphological description of two Acrobeloides species (Nematoda: Rhabditida: Cephalobidae) in South Korea, *Journal of Species Research*, 10(4), pp. 405–414.

Kirchmair, M., Neuhauser, S., Huber, L. and Strasser, H. (2008) The impact of soil treatment on soil mycobiota., *IOBC/Wprs Bulletin*, 31, pp. 239–244.

Klein, M. G. (2018) Efficacy against soil-inhabiting insect pests, In *Entomopathogenic Nematodes in Biological Control*, CRC Press, pp. 193–214, [online] Available at: https://www.taylorfrancis.com/books/9781351080194/chapters/10.1201/9781351071741-14.

Kojima, W., Fujii, T., Suwa, M., Miyazawa, M. and Ishikawa, Y. (2010) Physiological adaptation of the Asian corn borer Ostrinia furnacalis to chemical defenses of its host plant, maize, *Journal of Insect Physiology*, 56(9), pp. 1349–1355, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S002219101000137X.

Koricheva, J., Gange, A. C. and Jones, T. (2009) Effects of mycorrhizal fungi on insect herbivores: a meta-analysis, *Ecology*, 90(8), pp. 2088–2097, [online] Available at: https://esajournals.onlinelibrary.wiley.com/doi/10.1890/08-1555.1.

Kour, D., Khan, S. S., Kour, H., Kaur, T., Devi, R., Judy, C., Rai, P. K., McQuestion, C., Spells,

S., Bianchi, A., Mohan, R., Rai, A. K. and Yadav, A. N. (2022) Microbe-mediated bioremediation: Current research and future challenges, *Journal of Applied Biology & Biotechnology*, pp. 6–24, [online] Available at: https://jabonline.in/abstract.php?article_id=814&sts=2.

Kozdrój, J., Trevors, J. T. and Van Elsas, J. D. (2004) Influence of introduced potential biocontrol agents on maize seedling growth and bacterial community structure in the rhizosphere, *Soil Biology and Biochemistry*, 36(11), pp. 1775–1784.

Kuang, S., Su, Y., Wang, H., Yu, W., Lang, Q. and Matangi, R. (2018) Soil microbial community structure and diversity around the aging oil sludge in yellow river delta as determined by high-throughput sequencing, *Archaea*, 2018.

Kumela, T., Simiyu, J., Sisay, B., Likhayo, P., Mendesil, E., Gohole, L. and Tefera, T. (2018) Farmers' knowledge, perceptions, and management practices of the new invasive pest, fall armyworm (Spodoptera frugiperda) in Ethiopia and Kenya, *International Journal of Pest Management*, 65(1), pp. 1–9.

Lacey, L. A., Frutos, R., Kaya, H. K. and Vail, P. (2001) Insect pathogens as biological control agents: Do They Have a Future?, *Biological Control*, Academic Press, 21(3), pp. 230–248.

Lacey, L. A., Grzywacz, D., Shapiro-Ilan, D. I., Frutos, R., Brownbridge, M. and Goettel, M. S. (2015) Insect pathogens as biological control agents: Back to the future, *Journal of Invertebrate Pathology*, Academic Press, 132, pp. 1–41.

Lacey, L. A. and Shapiro-Ilan, D. I. (2008) Microbial control of insect pests in temperate orchard systems: Potential for incorporation into IPM, *Annual Review of Entomology*, pp. 121–144.

Lahl, V., Sadler, B. and Schierenberg, E. (2006) Egg development in parthenogenetic nematodes: variations in meiosis and axis formation, *The International Journal of Developmental Biology*, 50(4), pp. 393–397, [online] Available at: https://ijdb.ehu.eus/article/052030vl.

Lee, H.-S. and Jeong, G.-S. (2020) Aromadendrin inhibits T cell activation via regulation of Calcium influx and NFAT activity, *Molecules*, 25(19), p. 4590, [online] Available at: https://www.mdpi.com/1420-3049/25/19/4590.

Lewis, E. E. and Clarke, D. J. (2012) Nematode parasites and entomopathogens, *Insect Pathology*, Academic Press, pp. 395–424.

Li, F., Zhang, S., Wang, Y., Li, Y., Li, P., Chen, L., Jie, X., Hu, D., Feng, B., Yue, K. and Han, Y. (2020) Rare fungus, Mortierella capitata, promotes crop growth by stimulating primary metabolisms related genes and reshaping rhizosphere bacterial community, *Soil Biology and Biochemistry*, 151, p. 108017, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071720303138.

Li, G., Liu, T., Whalen, J. K. and Wei, Z. (2024) Nematodes: an overlooked tiny engineer of plant health, *Trends in Plant Science*, 29(1), pp. 52–63, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1360138523002261.

Li, K., DiLegge, M. J., Minas, I. S., Hamm, A., Manter, D. and Vivanco, J. M. (2019) Soil sterilization leads to re-colonization of a healthier rhizosphere microbiome, *Rhizosphere*, 12, p. 100176, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S2452219819301259.

Li, K., Wang, C., Zhang, H., Zhang, J., Jiang, R., Feng, G., Liu, X., Zuo, Y., Yuan, H., Zhang, C., Gai, J., Tian, J., Li, H., Sun, Y. and Yu, B. (2022) Evaluating the effects of agricultural inputs on the soil quality of smallholdings using improved indices, *CATENA*, 209, p. 105838, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0341816221006962.

Li, Q., Liu, Z., Jiang, Z., Jia, M., Hou, Z., Dou, D. and Yu, J. (2025) Phenylalanine metabolism-

dependent lignification confers rhizobacterium-induced plant resistance, *Plant Physiology*, 197(2), [online] Available at: https://academic.oup.com/plphys/article/doi/10.1093/plphys/kiaf016/8015619.

Li, Y., Wang, C., Ge, L., Hu, C., Wu, G., Sun, Y., Song, L., Wu, X., Pan, A., Xu, Q., Shi, J., Liang, J. and Li, P. (2022) Environmental behaviors of Bacillus thuringiensis (Bt) insecticidal proteins and their effects on microbial ecology, *Plants*, 11(9), p. 1212, [online] Available at: https://www.mdpi.com/2223-7747/11/9/1212.

Lin, D., Fang, Y., Li, L., Zhang, L., Gao, S., Wang, R. and Wang, J. (2022) The insecticidal effect of the botanical insecticide chlorogenic acid on Mythimna separata (Walker) is related to changes in MsCYP450 gene expression, *Frontiers in Plant Science*, 13, [online] Available at: https://www.frontiersin.org/articles/10.3389/fpls.2022.1015095/full.

Lioussanne, L., Perreault, F., Jolicoeur, M. and St-Arnaud, M. (2010) The bacterial community of tomato rhizosphere is modified by inoculation with arbuscular mycorrhizal fungi but unaffected by soil enrichment with mycorrhizal root exudates or inoculation with Phytophthora nicotianae, *Soil Biology and Biochemistry*, 42(3), pp. 473–483.

Lira, E. C., Bolzan, A., Nascimento, A. R. B., Amaral, F. S. A., Kanno, R. H., Kaiser, I. S. and Omoto, C. (2020) Resistance of Spodoptera frugiperda (Lepidoptera: Noctuidae) to spinetoram: inheritance and cross-resistance to spinosad, *Pest Management Science*, John Wiley and Sons Ltd, 76(8), pp. 2674–2680.

Liu, J., Liu, C., Zheng, J., Zhang, X., Zheng, K. and Zhuang, J. (2024) Response of plant endophyte communities to heavy metal stress and plant growth promotion by the endophyte Serratia marcescens (Strain JG1), *Plants*, 13(19), p. 2755, [online] Available at: https://www.mdpi.com/2223-7747/13/19/2755.

Lorková, Z., Cimermanová, M., Piknová, M., Adhvaryu, S., Pristaš, P. and Kisková, J. (2025) Environmental impact on the genome shaping of putative new Streptomyces species, *BMC Microbiology*, 25(1), p. 72, [online] Available at: https://bmcmicrobiol.biomedcentral.com/articles/10.1186/s12866-025-03779-x.

Luo, J. yu, ZHANG, S., ZHU, X. zhen, LU, L. min, WANG, C. yi, LI, C. hua, CUI, J. jie and ZHOU, Z. guo (2017) Effects of soil salinity on rhizosphere soil microbes in transgenic Bt cotton fields, *Journal of Integrative Agriculture*, CAAS. Publishing services by Elsevier B.V, 16(7), pp. 1624–1633, [online] Available at: http://dx.doi.org/10.1016/S2095-3119(16)61456-9.

Maag, D., Dalvit, C., Thevenet, D., Köhler, A., Wouters, F. C., Vassão, D. G., Gershenzon, J., Wolfender, J.-L., Turlings, T. C. J., Erb, M. and Glauser, G. (2014) 3-β-d-Glucopyranosyl-6-methoxy-2-benzoxazolinone (MBOA-N-Glc) is an insect detoxification product of maize 1,4-benzoxazin-3-ones, *Phytochemistry*, 102, pp. 97–105, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S003194221400137X.

Marchioro, C. A. and Krechemer, F. S. (2018) Potential global distribution of Diabrotica species and the risks for agricultural production, *Pest Management Science*, 74(9), pp. 2100–2109, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1002/ps.4906.

Mareya, C. R., Tugizimana, F., Di Lorenzo, F., Silipo, A., Piater, L. A., Molinaro, A. and Dubery, I. A. (2020) Adaptive defence-related changes in the metabolome of Sorghum bicolor cells in response to lipopolysaccharides of the pathogen Burkholderia andropogonis, *Scientific Reports*, 10(1), p. 7626, [online] Available at: https://www.nature.com/articles/s41598-020-64186-y.

Marti, G., Erb, M., Boccard, J., Glauser, G., Doyen, G. R., Villard, N., Robert, C. A. M., Turlings, T. C. J., Rudaz, S. and Wolfender, J. (2013) Metabolomics reveals herbivore-induced metabolites of resistance and susceptibility in maize leaves and roots, *Plant, Cell & Environment*, 36(3), pp. 621–639, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/pce.12002.

Martin, M. (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads, *EMBnet.journal*, 17(1), p. 10, [online] Available at: http://journal.embnet.org/index.php/embnetjournal/article/view/200.

Martínez-Medina, A., Biere, A. and Pozo, M. J. (2024) The imprint of microbe-induced plant resistance in plant-associated insects, *Trends in Plant Science*, 29(10), pp. 1062–1065, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1360138524001432.

Martinuz, A., Schouten, A., Menjivar, R. D. and Sikora, R. A. (2012) Effectiveness of systemic resistance toward Aphis gossypii (Hom., Aphididae) as induced by combined applications of the endophytes Fusarium oxysporum Fo162 and Rhizobium etli G12, *Biological Control*, 62(3), pp. 206–212, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1049964412001107.

Mayerhofer, J., Rauch, H., Hartmann, M., Widmer, F., Gschwend, F., Strasser, H., Leuchtmann, A. and Enkerli, J. (2019) Response of soil microbial communities to the application of a formulated Metarhizium brunneum biocontrol strain, *Biocontrol Science and Technology*, 29(6), pp. 547–564, [online] Available at: https://www.tandfonline.com/doi/full/10.1080/09583157.2019.1566953.

McKinnon, A. C., Glare, T. R., Ridgway, H. J., Mendoza-Mendoza, A., Holyoake, A., Godsoe, W. K. and Bufford, J. L. (2018) Detection of the entomopathogenic fungus Beauveria bassiana in the rhizosphere of wound-stressed Zea mays plants, *Frontiers in Microbiology*, 9, [online] Available at: https://www.frontiersin.org/article/10.3389/fmicb.2018.01161/full.

Megali, L., Schlau, B. and Rasmann, S. (2015) Soil microbial inoculation increases corn yield and insect attack, *Agronomy for Sustainable Development*, 35(4), pp. 1511–1519, [online] Available at: http://link.springer.com/10.1007/s13593-015-0323-0.

Melakeberhan, H., Maung, Z., Lartey, I., Yildiz, S., Gronseth, J., Qi, J., Karuku, G. N., Kimenju, J. W., Kwoseh, C. and Adjei-Gyapong, T. (2021) Nematode community-based soil food web analysis of ferralsol, lithosol and nitosol soil groups in ghana, kenya and malawi reveals distinct soil health degradations, *Diversity*, 13(3), p. 101, [online] Available at: https://www.mdpi.com/1424-2818/13/3/101.

Midega, C. A. O., Pittchar, J. O., Pickett, J. A., Hailu, G. W. and Khan, Z. R. (2018) A climate-adapted push-pull system effectively controls fall armyworm, Spodoptera frugiperda (J E Smith), in maize in East Africa, *Crop Protection*, 105, pp. 10–15, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0261219417303216.

Minchev, Z., Ramírez-Serrano, B., Dejana, L., Díaz, A. S. L., Zitlalpopoca-Hernandez, G., Orine, D., Saha, H., Papantoniou, D., García, J. M., González-Céspedes, A., Garbeva, P., Dam, N. M. van, Soler, R., Giron, D., Martínez-Medina, A., Biere, A., Hauser, T., Meyling, N. V., Rasmann, S. and Pozo, M. J. (2024) On testing the effectiveness of soil microbial inoculants in integrated pest management for commercial tomato production, [online] Available at: https://www.researchsquare.com/article/rs-3953202/v1.

Mishra, P. K., Mishra, S., Selvakumar, G., Bisht, J. K., Kundu, S. and Gupta, H. S. (2009) Coinoculation of Bacillus thuringeinsis-KR1 with Rhizobium leguminosarum enhances plant growth and nodulation of pea (Pisum sativum L.) and lentil (Lens culinaris L.), *World Journal of Microbiology and Biotechnology*, 25(5), pp. 753–761, [online] Available at: http://link.springer.com/10.1007/s11274-009-9963-z.

Moeser, J. and Vidal, S. (2004) Do alternative host plants enhance the invasion of the maize pest Diabrotica virgifera virgifera (Coleoptera: Chrysomelidae, Galerucinae) in Europe?, *Environmental Entomology*, 33(5), pp. 1169–1177, [online] Available at: https://academic.oup.com/ee/article-lookup/doi/10.1603/0046-225X-33.5.1169.

Mohan, S., Raman, R. and Gaur, H. S. (2003) Foliar application of Photorhabdus luminescens, symbiotic bacteria from entomopathogenic nematode Heterorhabditis indica, to kill cabbage

butterfly Pieris brassicae, *Current Science*, 84(11), p. 1397.

Montezano, D. G., Specht, A., Sosa-Gómez, D. R., Roque-Specht, V. F., Sousa-Silva, J. C., Paula-Moraes, S. V., Peterson, J. A. and Hunt, T. E. (2018) Host plants of Spodoptera frugiperda (Lepidoptera: Noctuidae) in the Americas, *African Entomology*, 26(2), pp. 286–300, [online] Available at: http://www.bioone.org/doi/10.4001/003.026.0286.

Muangpat, P., Meesil, W., Ngoenkam, J., Teethaisong, Y., Thummeepak, R., Sitthisak, S., Tandhavanant, S., Chantratita, N., Bode, H. B., Vitta, A. and Thanwisai, A. (2022) Genome analysis of secondary metabolite-biosynthetic gene clusters of Photorhabdus akhurstii subsp. akhurstii and its antibacterial activity against antibiotic-resistant bacteria, Dutta, T. K. (ed.), *PLOS ONE*, 17(9), p. e0274956, [online] Available at: https://dx.plos.org/10.1371/journal.pone.0274956.

Muangpat, P., Yooyangket, T., Fukruksa, C., Suwannaroj, M., Yimthin, T., Sitthisak, S., Chantratita, N., Vitta, A., Tobias, N. J., Bode, H. B. and Thanwisai, A. (2017) Screening of the antimicrobial activity against drug resistant bacteria of Photorhabdus and Xenorhabdus associated with entomopathogenic nematodes from Mae Wong National Park, Thailand, *Frontiers in Microbiology*, 8(JUN).

Muller, A., Morales-Montero, P., Boss, A., Hiltmann, A., Castaneda-Alvarez, C., Bhat, A. H., Arce, C. C. M., Glauser, G., Joyce, S. A., Clarke, D. J. and Machado, R. A. R. (2024) Bacterial bioluminescence is an important regulator of multitrophic interactions in the soil, *Cell Reports*, 43(10), p. 114817, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S2211124724011689.

Muraro, D. S., Oliveira Abbade Neto, D., Kanno, R. H., Kaiser, I. S., Bernardi, O. and Omoto, C. (2021) Inheritance patterns, cross-resistance and synergism in Spodoptera frugiperda (Lepidoptera: Noctuidae) resistant to emamectin benzoate, *Pest Management Science*, 77(11), pp. 5049–5057, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1002/ps.6545.

Nannipieri, P., Hannula, S. E., Pietramellara, G., Schloter, M., Sizmur, T. and Pathan, S. I. (2023) Legacy effects of rhizodeposits on soil microbiomes: A perspective, *Soil Biology and Biochemistry*, 184, p. 109107, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071723001694.

Natsch, A., Keel, C., Hebecker, N., Laasik, E. and Défago, G. (1998) Impact of Pseudomonas fluorescens strain CHA0 and a derivative with improved biocontrol activity on the culturable resident bacterial community on cucumber roots, *FEMS Microbiology Ecology*, 27(4), pp. 365–380.

Nealson, K. H., Schmidt, T. M. and Bleakley, B. (1990) Physiology and biochemistry of Xenorhabdus, In Gaugler, R. and Kaya, H. K. (eds.), *Entomopathogenic Nematodes in Biological Control*, Boca Raton, FL 33431, CRC Press Inc., p. 14, [online] Available at: https://www.cabdirect.org/cabdirect/abstract/19922317303.

Neher, D. A., Muthumbi, A. W. N. and Dively, G. P. (2014) Impact of coleopteran-active Bt corn on non-target nematode communities in soil and decomposing corn roots, *Soil Biology and Biochemistry*, 76, pp. 127–135, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071714001801.

Oddsdottir, E. S., Eilenberg, J., Sen, R., Harding, S. and Halldorsson, G. (2010) Early reduction of Otiorhynchus spp. larval root herbivory on Betula pubescens by beneficial soil fungi, *Applied Soil Ecology*, 45(3), pp. 168–174, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S092913931000051X.

Okada, H., Harada, H. and Kadota, I. (2005) Fungal-feeding habits of six nematode isolates in the genus Filenchus, *Soil Biology and Biochemistry*, 37(6), pp. 1113–1120, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071704004249.

Okada, H. and Kadota, I. (2003) Host status of 10 fungal isolates for two nematode species, Filenchus misellus and Aphelenchus avenae, *Soil Biology and Biochemistry*, 35(12), pp. 1601–1607, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071703002670.

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H. B. A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M. O., Lahti, L., Martino, C., McGlinn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C. J. F. and Weedon, J. (2001) Vegan: Community ecology package, *CRAN: Contributed Packages*, [online] Available at: https://cran.r-project.org/package=vegan.

Van Oosten, M. J., Pepe, O., De Pascale, S., Silletti, S. and Maggio, A. (2017) The role of biostimulants and bioeffectors as alleviators of abiotic stress in crop plants, *Chemical and Biological Technologies in Agriculture*, 4(1), p. 5, [online] Available at: http://chembioagro.springeropen.com/articles/10.1186/s40538-017-0089-5.

Van Oosten, V. R., Bodenhausen, N., Reymond, P., Van Pelt, J. A., Van Loon, L. C., Dicke, M. and Pieterse, C. M. J. (2008) Differential effectiveness of microbially induced resistance against herbivorous insects in Arabidopsis, *Molecular Plant-Microbe Interactions*®, 21(7), pp. 919–930, [online] Available at: https://apsjournals.apsnet.org/doi/10.1094/MPMI-21-7-0919.

Orozco-Mosqueda, M. del C., Santoyo, G. and Glick, B. R. (2023) Recent advances in the bacterial phytohormone modulation of plant growth, *Plants*, 12(3), p. 606, [online] Available at: https://www.mdpi.com/2223-7747/12/3/606.

Orozco, R. A., Molnár, I., Bode, H. and Stock, S. P. (2016) Bioprospecting for secondary metabolites in the entomopathogenic bacterium Photorhabdus luminescens subsp. sonorensis, *Journal of Invertebrate Pathology*, 141, pp. 45–52, [online] Available at: http://dx.doi.org/10.1016/j.jip.2016.09.008.

Owen, K., Walia, R. K., Yan, G. and Rahman Khan, M. (2023) Nematode problems in wheat and barley and their sustainable management, In *Nematode Diseases of Crops and their Sustainable Management*, Elsevier, pp. 97–131, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/B9780323912266000262.

Ozimek, E. and Hanaka, A. (2020) Mortierella species as the plant growth-promoting fungi present in the agricultural soils, *Agriculture*, 11(1), p. 7, [online] Available at: https://www.mdpi.com/2077-0472/11/1/7.

Pacios-Michelena, S., Aguilar González, C. N., Alvarez-Perez, O. B., Rodriguez-Herrera, R., Chávez-González, M., Arredondo Valdés, R., Ascacio Valdés, J. A., Govea Salas, M. and Ilyina, A. (2021) Application of streptomyces antimicrobial compounds for the control of phytopathogens, *Frontiers in Sustainable Food Systems*, 5, [online] Available at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.696518/full.

Palma, L., Muñoz, D., Berry, C., Murillo, J. and Caballero, P. (2014) Bacillus thuringiensis toxins: An overview of their biocidal activity, *Toxins*, 6(12), pp. 3296–3325.

Pan, S., Agyei, D., Jeevanandam, J. and Danquah, M. K. (2019) Bio-active peptides: Role in plant growth and defense, In *Natural Bio-active Compounds*, Singapore, Springer Singapore, pp. 1–29, [online] Available at: http://link.springer.com/10.1007/978-981-13-7438-8_1.

Pang, Z., Chen, J., Wang, T., Gao, C., Li, Z., Guo, L., Xu, J. and Cheng, Y. (2021) Linking plant secondary metabolites and plant microbiomes: A review., *Frontiers in plant science*, 12, p. 621276, [online] Available at: http://www.ncbi.nlm.nih.gov/pubmed/33737943.

Park, D., Ciezki, K., Van Der Hoeven, R., Singh, S., Reimer, D., Bode, H. B. and Forst, S. (2009) Genetic analysis of xenocoumacm antibiotic production in the mutnalistir bacterium Xenorhabdus nematophila, *Molecular Microbiology*, 73(5), pp. 938–949, [online] Available at:

http://www.genoscope.cns.fr/agc/mage/.

Park, Y. and Kim, Y. (2000) Eicosanoids rescue Spodoptera exigua infected with Xenorhabdus nematophilus, the symbiotic bacteria to the entomopathogenic nematode Steinernema carpocapsae, *Journal of Insect Physiology*, 46(11), pp. 1469–1476, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0022191000000718.

Parveen, A., Ali, Z., Fantoukh, O., Alhusban, M., Wang, W., Chittiboyina, A. G. and Khan, I. A. (2021) Undescribed phenylpropanoid and a dimeric sesquiterpenoid possessing a rare cyclobutane ring from Tinospora sinensis, *Natural Product Research*, 35(21), pp. 3955–3962, [online] Available at: https://www.tandfonline.com/doi/full/10.1080/14786419.2020.1752207.

Patel, S. K., Singh, S., Benjamin, J. C., Singh, V. R., Bisht, D. and Lal, R. K. (2024) Plant growth-promoting activities of Serratia marcescens and Pseudomonas fluorescens on Capsicum annuum L. plants, *Ecological Frontiers*, 44(4), pp. 654–663, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S2950509724000054.

Paudel Timilsena, B., Niassy, S., Kimathi, E., Abdel-Rahman, E. M., Seidl-Adams, I., Wamalwa, M., Tonnang, H. E. Z., Ekesi, S., Hughes, D. P., Rajotte, E. G. and Subramanian, S. (2022) Potential distribution of fall armyworm in Africa and beyond, considering climate change and irrigation patterns, *Scientific Reports*, 12(1), p. 539, [online] Available at: https://www.nature.com/articles/s41598-021-04369-3.

Pfender, W. F., Fieland, V. P., Ganio, L. M. and Seidler, R. J. (1996) Microbial community structure and activity in wheat straw after inoculation with biological control organisms, *Applied Soil Ecology*, 3(1), pp. 69–78.

Philippot, L., Chenu, C., Kappler, A., Rillig, M. C. and Fierer, N. (2024) The interplay between microbial communities and soil properties, *Nature Reviews Microbiology*, 22(4), pp. 226–239, [online] Available at: https://www.nature.com/articles/s41579-023-00980-5.

Philippot, L., Raaijmakers, J. M., Lemanceau, P. and van der Putten, W. H. (2013) Going back to the roots: the microbial ecology of the rhizosphere, *Nature Reviews Microbiology*, 11(11), pp. 789–799, [online] Available at: https://www.nature.com/articles/nrmicro3109.

Phuong, T. T. T., Yamamoto, M., Fujii, T., Kojima, W., Matsuo, T. and Ishikawa, Y. (2016) Comparison of the ability to catabolize DIMBOA, a maize antibiotic, between Ostrinia furnacalis and Ostrinia scapulalis (Lepidoptera: Crambidae), with reference to their hybrids, *Applied Entomology and Zoology*, 51(1), pp. 143–149, [online] Available at: http://link.springer.com/10.1007/s13355-015-0383-2.

Pickett, J. A., Smiley, D. W. M. and Woodcock, C. M. (1999) Secondary metabolites in plant-insect interactions: dynamic systems of induced and adaptive responses, In pp. 91–115, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S006522960860227X.

Pindi, P. K., Sultana, T. and Vootla, P. K. (2014) Plant growth regulation of Bt-cotton through Bacillus species, *3 Biotech*, 4(3), pp. 305–315.

Pineda, A., Kaplan, I. and Bezemer, T. M. (2017) Steering soil microbiomes to suppress aboveground insect pests, *Trends in Plant Science*, 22(9), pp. 770–778, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1360138517301395.

Pineda, A., Kaplan, I., Hannula, S. E., Ghanem, W. and Bezemer, T. M. (2020) Conditioning the soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest, *New Phytologist*, 226(2), pp. 595–608, [online] Available at: https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.16385.

Pineda, A., Zheng, S.-J., van Loon, J. J. A., Pieterse, C. M. J. and Dicke, M. (2010) Helping plants to deal with insects: the role of beneficial soil-borne microbes, *Trends in Plant Science*, 15(9), pp. 507–514, [online] Available at:

https://linkinghub.elsevier.com/retrieve/pii/S1360138510001007.

Pineda, A., Zheng, S. -J., van Loon, J. J. A. and Dicke, M. (2012) Rhizobacteria modify plant–aphid interactions: a case of induced systemic susceptibility, *Plant Biology*, 14(s1), pp. 83–90, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1438-8677.2011.00549.x.

Poinar, G. O. J. (1979) *Nematodes for biological control of insects*, CRC Press Inc. Boca Raton, Florida USA, [online] Available at: https://www.cabi.org/isc/abstract/19800870498.

Pouokam, G. B., Album, W. L., Ndikontar, A. S. and Sidatt, M. E. H. (2017) A pilot study in cameroon to understand safe uses of pesticides in agriculture, risk factors for farmers' exposure and management of accidental cases, *Toxics*, 5(4), [online] Available at: www.mdpi.com/journal/toxics.

Pozo, M. J., Benedicte R. Albrectsen, Eduardo R. Bejarano, E. de la P., Herrero, S., Ainhoa Martinez-Medina, V. P., Ravnskov, S., Williams, M. and Biere., A. (2020) Three-way interactions between plants, microbes, and arthropods (PMA): Impacts, mechanisms, and prospects for sustainable plant protection, *The Plant Cell*, 32(7), [online] Available at: https://academic.oup.com/plcell/article/doi/10.1105/tpc.120.tt0720/6115734.

Prasanna, B., Bruce, A., Beyene, Y., Makumbi, D., Gowda, M., Asim, M., Martinelli, S., Parimi, S., author bmprasanna, C. and Pakistan, B. (n.d.) *Host plant resistance in maize to fall armyworm fall armyworm in Asia: A guide for integrated pest management*, [online] Available at: www.genebanks.org/genebanks/cimmyt/.

Prasanna, B., Huesing, J. E., Eddy, R. and Peschke, V. M. (2018) *Fall Armyworm in Africa: A GUIDE FOR INTEGRATED PEST MANAGEMENT*, [online] Available at: www.maize.org.

Pretorius, C. J., Steenkamp, P. A., Tugizimana, F., Piater, L. A. and Dubery, I. A. (2022) Metabolomic characterisation of discriminatory metabolites involved in halo blight disease in oat cultivars caused by Pseudomonas syringae pv. coronafaciens, *Metabolites*, 12(3), p. 248, [online] Available at: https://www.mdpi.com/2218-1989/12/3/248.

Prévost, K., Couture, G., Shipley, B., Brzezinski, R. and Beaulieu, C. (2006) Effect of chitosan and a biocontrol streptomycete on field and potato tuber bacterial communities, *BioControl*, 51(4), pp. 533–546.

Prisa Domenico (2020) Optimised fertilisation with zeolitites containing plant growth promoting Rhizobacteria (PGPR) in Ranunculus asiaticus, *GSC Biological and Pharmaceutical Sciences*, 10(1), pp. 096–102, [online] Available at: https://gsconlinepress.com/journals/gscbps/node/1117.

Qi, G.-J., Ma, J., Wan, J., Ren, Y.-L., McKirdy, S., Hu, G. and Zhang, Z.-F. (2021) Source regions of the first immigration of fall armyworm, Spodoptera frugiperda (Lepidoptera: Noctuidae) invading Australia, *Insects*, 12(12), p. 1104, [online] Available at: https://www.mdpi.com/2075-4450/12/12/1104.

R Core Team (2024) A language and environment for statistical computing,.

Rashid, M. H.-O.-, Khan, A., Hossain, M. T. and Chung, Y. R. (2017) Induction of systemic resistance against aphids by endophytic Bacillus velezensis YC7010 via expressing phytoalexin deficient4 in Arabidopsis, *Frontiers in Plant Science*, 8, [online] Available at: http://journal.frontiersin.org/article/10.3389/fpls.2017.00211/full.

Rashid, M. H.-O. and Chung, Y. R. (2017) Induction of systemic resistance against insect herbivores in plants by beneficial soil microbes, *Frontiers in Plant Science*, 8, [online] Available at: http://journal.frontiersin.org/article/10.3389/fpls.2017.01816/full.

Rasmann, S. and Turlings, T. C. (2016) Root signals that mediate mutualistic interactions in the rhizosphere, *Current Opinion in Plant Biology*, 32, pp. 62–68, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1369526616301005.

Rasool, S., Groos, M., Hannula, S. E. and Biere, A. (2025) Bioinoculant-induced plant resistance is modulated by interactions with resident soil microbes, *Environmental Microbiome*, 20(1), p. 7, [online] Available at: https://environmentalmicrobiome.biomedcentral.com/articles/10.1186/s40793-025-00667-9.

Rasool, S., Markou, A., Hannula, S. E. and Biere, A. (2023) Effects of tomato inoculation with the entomopathogenic fungus Metarhizium brunneum on spider mite resistance and the rhizosphere microbial community, *Frontiers in Microbiology*, 14, [online] Available at: https://www.frontiersin.org/articles/10.3389/fmicb.2023.1197770/full.

Ray, D. K., Mueller, N. D., West, P. C. and Foley, J. A. (2013) Yield trends are insufficient to double global crop production by 2050, Hart, J. P. (ed.), *PLoS ONE*, 8(6), p. e66428, [online] Available at: https://dx.plos.org/10.1371/journal.pone.0066428.

Reen, R. A., Mumford, M. H. and Thompson, J. P. (2019) Novel sources of resistance to root-lesion nematode (Pratylenchus thornei) in a new collection of wild cicer species (C. reticulatum and C. echinospermum) to improve resistance in cultivated chickpea (C. arietinum), *Phytopathology®*, 109(7), pp. 1270–1279, [online] Available at: https://apsjournals.apsnet.org/doi/10.1094/PHYTO-02-19-0047-R.

Reen, R. A., Thompson, J. P., Clewett, T. G., Sheedy, J. G. and Bell, K. L. (2014) Yield response in chickpea cultivars and wheat following crop rotations affecting population densities of Pratylenchus thornei and arbuscular mycorrhizal fungi, *Crop and Pasture Science*, 65(5), p. 428, [online] Available at: http://www.publish.csiro.au/?paper=CP13441.

Regaiolo, A., Dominelli, N., Andresen, K. and Heermann, R. (2020) The biocontrol agent and insect pathogen photorhabdus luminescens interacts with plant roots, *Applied and Environmental Microbiology*, 86(17).

Reis, M. N. O., Vitorino, L. C., Lourenço, L. L. and Bessa, L. A. (2022) Microbial inoculation improves growth, nutritional and physiological aspects of glycine max (L.) Merr., *Microorganisms*, 10(7), p. 1386, [online] Available at: https://www.mdpi.com/2076-2607/10/7/1386.

Reveglia, P., Cimmino, A., Masi, M., Nocera, P., Berova, N., Ellestad, G. and Evidente, A. (2018) Pimarane diterpenes: Natural source, stereochemical configuration, and biological activity, *Chirality*, 30(10), pp. 1115–1134, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1002/chir.23009.

Ribeiro, L. P., Blume, E., Bogorni, P. C., Dequech, S. T. B., Brand, S. C. and Junges, E. (2012) Compatibility of Beauveria bassiana commercial isolate with botanical insecticides utilized in organic crops in southern Brazil, *Biological Agriculture & Horticulture*, 28(4), pp. 223–240, [online] Available at: http://www.tandfonline.com/doi/abs/10.1080/01448765.2012.735088.

Roba, K. (2021) The role of terpene (secondary metabolite), *Natural Products Chemistry & Research*, 9(8), pp. 1–11.

Robert, C. A., Zhang, X., Machado, R. A., Schirmer, S., Lori, M., Mateo, P., Erb, M. and Gershenzon, J. (2017) Sequestration and activation of plant toxins protect the western corn rootworm from enemies at multiple trophic levels, *eLife*, 6, [online] Available at: https://elifesciences.org/articles/29307.

Roesch, L. F. W., Fulthorpe, R. R., Riva, A., Casella, G., Hadwin, A. K. M., Kent, A. D., Daroub, S. H., Camargo, F. A. O., Farmerie, W. G. and Triplett, E. W. (2007) Pyrosequencing enumerates and contrasts soil microbial diversity, *The ISME Journal*, 1(4), pp. 283–290, [online] Available at: http://www.nature.com/articles/ismej200753.

Rojas, R. V., Achouri, M., Maroulis, J. and Caon, L. (2016) Healthy soils: A prerequisite for sustainable food security, *Environmental Earth Sciences*, 75(3), p. 180, [online] Available at: http://link.springer.com/10.1007/s12665-015-5099-7.

Rosa, R., Hajko, L., Franczuk, J., Zaniewicz-Bajkowska, A., Andrejiová, A. and Mezeyová, I. (2023) Effect of L-tryptophan and L-glutamic acid on carrot yield and its quality, *Agronomy*, 13(2), p. 562, [online] Available at: https://www.mdpi.com/2073-4395/13/2/562.

Rothman, J. A., Russell, K. A., Leger, L., McFrederick, Q. S. and Graystock, P. (2020) The direct and indirect effects of environmental toxicants on the health of bumblebees and their microbiomes, *Proceedings of the Royal Society B: Biological Sciences*, 287(1937), p. 20200980, [online] Available at: https://royalsocietypublishing.org/doi/10.1098/rspb.2020.0980.

Ryu, C.-M., Farag, M. A., Hu, C.-H., Reddy, M. S., Kloepper, J. W. and Paré, P. W. (2004) Bacterial volatiles induce systemic resistance in Arabidopsis, *Plant Physiology*, 134(3), pp. 1017–1026, [online] Available at: https://academic.oup.com/plphys/article/134/3/1017/6112257.

Saba, F. (1970) Host plant spectrum and temperature limitations of diabrotica balteata, *The Canadian Entomologist*, 102(6), pp. 684–691, [online] Available at: https://doi.org/10.4039/Ent102684-6.

Sadekuzzaman, M., Park, Y., Lee, S., Kim, K., Jung, J. K. and Kim, Y. (2017) An entomopathogenic bacterium, Xenorhabdus hominickii ANU101, produces oxindole and suppresses host insect immune response by inhibiting eicosanoid biosynthesis, *Journal of Invertebrate Pathology*, Academic Press, 145, pp. 13–22.

Saha, N. D., Chaudhary, A., Singh, A. K. and Bhowmick, A. (2022) Evaluation of Bt cotton effects on belowground microbial community structure and function in tropical western India, *International Journal of Environmental Science and Technology*, 19(8), pp. 7411–7424, [online] Available at: https://link.springer.com/10.1007/s13762-021-03543-4.

Salamzade, R. and Kalan, L. R. (2025) Context matters: assessing the impacts of genomic background and ecology on microbial biosynthetic gene cluster evolution, Klassen, J. L. (ed.), *mSystems*, 10(3), [online] Available at: https://journals.asm.org/doi/10.1128/msystems.01538-24.

Salaskar, D. A., Padwal, M. K., Gupta, A., Basu, B. and Kale, S. P. (2022) Proteomic perspective of cadmium tolerance in Providencia rettgeri Strain KDM3 and its in-situ bioremediation potential in rice ecosystem, *Frontiers in Microbiology*, 13, [online] Available at: https://www.frontiersin.org/articles/10.3389/fmicb.2022.852697/full.

Salazar-Gutiérrez, J. D., Castelblanco, A., Rodríguez-Bocanegra, M. X., Teran, W. and Sáenz-Aponte, A. (2017) Photorhabdus luminescens subsp. akhurstii SL0708 pathogenicity in Spodoptera frugiperda (Lepidoptera: Noctuidae) and Galleria mellonella (Lepidoptera: Pyralidae), *Journal of Asia-Pacific Entomology*, Elsevier, 20(4), pp. 1112–1121, [online] Available at: http://dx.doi.org/10.1016/j.aspen.2017.08.001.

Salles, L. A. (2000) Eficiência do inseticida thiamethoxam (actara) no controle das pragas de solo da batata, Diabrotica speciosa (col., Chrysomelidae) e heteroderes spp. (col., Elateridae), *Current Agricultural Science and Technology*, 6, pp. 149–151, [online] Available at: https://periodicos.ufpel.edu.br/ojs2/index.php/CAST/article/view/323.

Sanchez-Mahecha, O., Klink, S., Heinen, R., Rothballer, M. and Zytynska, S. (2022) Impaired microbial N -acyl homoserine lactone signalling increases plant resistance to aphids across variable abiotic and biotic environments, *Plant, Cell & Environment*, 45(10), pp. 3052–3069, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/pce.14399.

Santos, F., Peñaflor, M. F. G. V., Paré, P. W., Sanches, P. A., Kamiya, A. C., Tonelli, M., Nardi, C. and Bento, J. M. S. (2014) A novel interaction between plant-beneficial rhizobacteria and roots: Colonization induces corn resistance against the root herbivore Diabrotica speciosa, Zeng, R.-S. (ed.), *PLoS ONE*, 9(11), p. e113280, [online] Available at: https://dx.plos.org/10.1371/journal.pone.0113280.

dos Santos, G. A. P., Derycke, S., Fonsêca-Genevois, V. G., Coelho, L. C. B. B., Correia, M. T. S. and Moens, T. (2008) Differential effects of food availability on population growth and fitness of three species of estuarine, bacterial-feeding nematodes, *Journal of Experimental Marine Biology and Ecology*, 355(1), pp. 27–40, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0022098107005448.

Santoyo, G., Guzmán-Guzmán, P., Parra-Cota, F. I., Santos-Villalobos, S. de los, Orozco-Mosqueda, M. del C. and Glick, B. R. (2021) Plant growth stimulation by microbial consortia, *Agronomy*, 11(2), p. 219, [online] Available at: https://www.mdpi.com/2073-4395/11/2/219.

Sasai, H., Ishida, M., Murakami, K., Tadokoro, N., Ishihara, A., Nishida, R. and Mori, N. (2009) Species-specific glucosylation of DIMBOA in larvae of the rice armyworm, *Bioscience, Biotechnology, and Biochemistry*, 73(6), pp. 1333–1338, [online] Available at: https://academic.oup.com/bbb/article/73/6/1333-1338/5947628.

Savary, S., Willocquet, L., Pethybridge, S. J., Esker, P., McRoberts, N. and Nelson, A. (2019) The global burden of pathogens and pests on major food crops, *Nature Ecology & Evolution*, 3(3), pp. 430–439, [online] Available at: https://doi.org/10.1038/s41559-018-0793-y.

Schimel, J. P. and Bennett, J. (2004) Nitrogen mineralization: Challenges of a changing paradigm, *Ecology*, 85(3), pp. 591–602, [online] Available at: http://doi.wiley.com/10.1890/03-8002.

Schloter, M., Nannipieri, P., Sørensen, S. J. and van Elsas, J. D. (2018) Microbial indicators for soil quality, *Biology and Fertility of Soils*, 54(1), pp. 1–10, [online] Available at: http://link.springer.com/10.1007/s00374-017-1248-3.

Schmitt, A., Roy, R. and Carter, C. J. (2021) Nectar antimicrobial compounds and their potential effects on pollinators, *Current Opinion in Insect Science*, 44, pp. 55–63, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S2214574521000304.

Schmitt, E. and de Vries, W. (2020) Potential benefits of using Hermetia illucens frass as a soil amendment on food production and for environmental impact reduction, *Current Opinion in Green and Sustainable Chemistry*, 25, p. 100335, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S2452223620300225.

Schoonhoven, L. M., Loon, J. J. A. van. and Dicke, M. (2005) *Insect-plant biology*, Oxford University Press.

Schroer, S. and Ehlers, R.-U. (2005) Foliar application of the entomopathogenic nematode Steinernema carpocapsae for biological control of diamondback moth larvae (Plutella xylostella), *Biological Control*, 33(1), pp. 81–86, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1049964404002476.

Schroer, S., Sulistyanto, D. and Ehlers, R. -U. (2005) Control of Plutella xylostella using polymer-formulated Steinernema carpocapsae and Bacillus thuringiensis in cabbage fields, *Journal of Applied Entomology*, 129(4), pp. 198–204, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1439-0418.2005.00952.x.

Schwarzenbach, K., Enkerli, J. and Widmer, F. (2009) Effects of biological and chemical insect control agents on fungal community structures in soil microcosms, *Applied Soil Ecology*, 42(1), pp. 54–62, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0929139309000298.

Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., Pyšek, P., van Kleunen, M., Weber, E., Winter, M. and Blasius, B. (2015) Global trade will accelerate plant invasions in emerging economies under climate change, *Global Change Biology*, 21(11), pp. 4128–4140, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/gcb.13021.

Seshadri, S., Ignacimuthu, S., Vadivelu, M. and Lakshminarasimhan, C. (2007) Inorganic

phosphate solubilization by two insect pathogenic Bacillus sp, In *First International Meeting on Microbial Phosphate Solubilization*, Dordrecht, Springer Netherlands, pp. 351–355, [online] Available at: http://link.springer.com/10.1007/978-1-4020-5765-6_56.

Shahina, F., Tabassum, K. A., Salma, J. and Mahreen, G. (2011) Biopesticidal affect of Photorhabdus luminescens agaisnt Galleria mellonella larvae and subterranena termite (Termitidae: Macrotermis), *Pakistan Journal of Nematology*, 29(1), pp. 35–43.

Shan, S., Wang, W., Song, C., Wang, M., Sun, B., Li, Y., Fu, Y., Gu, X., Ruan, W. and Rasmann, S. (2019) The symbiotic bacteria Alcaligenes faecalis of the entomopathogenic nematodes Oscheius spp. exhibit potential biocontrol of plant- and entomopathogenic fungi, *Microbial Biotechnology*, 12(3), pp. 459–471, [online] Available at: https://sfamjournals.onlinelibrary.wiley.com/doi/10.1111/1751-7915.13365.

Shapiro-Ilan, D. I., Cottrell, T. E., Mizell, R. F., Horton, D. L., Behle, R. W. and Dunlap, C. A. (2010) Efficacy of Steinernema carpocapsae for control of the lesser peachtree borer, Synanthedon pictipes: Improved aboveground suppression with a novel gel application, *Biological Control*, 54(1), pp. 23–28, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1049964409002990.

Shapiro-Ilan, D. I. and Grewal, P. S. (2008) Entomopathogenic nematodes and insect management, In Capinera, J. L. (ed.), *Encyclopedia of Entomology*, Dordrecht, Springer Netherlands, pp. 1336–1340, [online] Available at: http://link.springer.com/10.1007/978-1-4020-6359-6_3599.

Shapiro-Ilan, D. I., Han, R. and Qiu, X. (2014) Production of entomopathogenic nematodes: Mass production of beneficial organisms, *Invertebrates and Entomopathogens*, Academic Press, pp. 321–355.

Shapiro-Ilan, D. I. and Lewis, E. E. (eds.) (2024) *Entomopathogenic nematodes as biological control agents*, GB, CABI, [online] Available at: http://www.cabidigitallibrary.org/doi/book/10.1079/9781800620322.0000.

Sharanabasappa, D., Kalleshwaraswamy, C. M., Asokan, R., Mahadeva Swamy, H. M., Maruthi, M. S., Pavithra, H. B., Hegde, K., Navi, S. T., S., P. and Goergen, G. (2018) First report of the fall armyworm, Spodoptera frugiperda (J E Smith) (Lepidoptera: Noctuidae), an alien invasive pest on maize in India, *Pest Management in Horticultural Ecosystems*, 24(1), pp. 23–29.

Sharifi, R., Lee, S. and Ryu, C. (2018) Microbe-induced plant volatiles, *New Phytologist*, 220(3), pp. 684–691, [online] Available at: https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.14955.

Sharp, R. (2013) A review of the applications of chitin and its derivatives in agriculture to modify plant-microbial interactions and improve crop yields, *Agronomy*, 3(4), pp. 757–793, [online] Available at: https://www.mdpi.com/2073-4395/3/4/757.

Shawer, R., Donati, I., Cellini, A., Spinelli, F. and Mori, N. (2018) Insecticidal Activity of Photorhabdus luminescens against Drosophila suzukii, *Insects*, 9(4), p. 148, [online] Available at: http://www.mdpi.com/2075-4450/9/4/148.

Shrestha, Y. K. and Lee, K. Y. (2012) Oral toxicity of Photorhabdus culture media on gene expression of the adult sweetpotato whitefly, Bemisia tabaci, *Journal of Invertebrate Pathology*, Academic Press, 109(1), pp. 91–96.

Sicard, M., Hinsinger, J., Le Brun, N., Pages, S., Boemare, N. and Moulia, C. (2006) Interspecific competition between entomopathogenic nematodes (Steinernema) is modified by their bacterial symbionts (Xenorhabdus), *BMC Evolutionary Biology*, 6, pp. 1–9.

da Silva, O. S., Prado, G. R., da Silva, J. L. R., Silva, C. E., da Costa, M. and Heermann, R.

(2013) Oral toxicity of Photorhabdus luminescens and Xenorhabdus nematophila (Enterobacteriaceae) against Aedes aegypti (Diptera: Culicidae), *Parasitology Research*, 112(8), pp. 2891–2896, [online] Available at: http://link.springer.com/10.1007/s00436-013-3460-x.

Da Silva, W. J., Pilz-Júnior, H. L., Heermann, R. and Da Silva, O. S. (2020) The great potential of entomopathogenic bacteria Xenorhabdus and Photorhabdus for mosquito control: a review, *Parasites and Vectors*, BioMed Central, 13(1), pp. 1–14, [online] Available at: https://doi.org/10.1186/s13071-020-04236-6.

Singh, B. K., Trivedi, P., Egidi, E., Macdonald, C. A. and Delgado-Baquerizo, M. (2020) Crop microbiome and sustainable agriculture, *Nature Reviews Microbiology*, 18(11), pp. 601–602, [online] Available at: https://www.nature.com/articles/s41579-020-00446-y.

Singh, J. S. and Gupta, V. K. (2018) Soil microbial biomass: A key soil driver in management of ecosystem functioning, *Science of The Total Environment*, 634(1), pp. 497–500, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0048969718311331.

Singh, S. and Forst, S. (2016) Antimicrobials and the natural biology of a bacterial-nematode symbiosis, In Hurst, C. (ed.), *Advances in environmental mcrobiology, 2*, Springer, Cham, pp. 101–119, [online] Available at: http://link.springer.com/10.1007/978-3-319-28068-4_5.

Singh, S., Reese, J. M., Casanova-Torres, Á. M., Goodrich-Blair, H. and Forst, S. (2014) Microbial population dynamics in the hemolymph of Manduca sexta infected with Xenorhabdus nematophila and the entomopathogenic nematode Steinernema carpocapsae, *Applied and Environmental Microbiology*, 80(14), pp. 4277–4285.

Sisay, B., Tefera, T., Wakgari, M., Ayalew, G. and Mendesil, E. (2019) The efficacy of selected synthetic insecticides and botanicals against fall armyworm, spodoptera frugiperda, in maize, *Insects*, 10(2).

van der Sluijs, J. P. (2020) Insect decline, an emerging global environmental risk, *Current Opinion in Environmental Sustainability*, 46, pp. 39–42, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1877343520300671.

Soler, R., Bezemer, T. M., Cortesero, A. M., Van der Putten, W. H., Vet, L. E. M. and Harvey, J. A. (2007) Impact of foliar herbivory on the development of a root-feeding insect and its parasitoid, *Oecologia*, 152(2), pp. 257–264, [online] Available at: https://link.springer.com/10.1007/s00442-006-0649-z.

Song, J., Wu, D., Shao, P., Hui, D. and Wan, S. (2015) Ecosystem carbon exchange in response to locust outbreaks in a temperate steppe, *Oecologia*, 178(2), pp. 579–590, [online] Available at: http://link.springer.com/10.1007/s00442-015-3248-z.

Sparks, T. C. and Nauen, R. (2015) IRAC: Mode of action classification and insecticide resistance management, *Pesticide Biochemistry and Physiology*, Academic Press, 121, pp. 122–128.

Stock, S. P. (2019) Partners in crime: symbiont-assisted resource acquisition in Steinernema entomopathogenic nematodes, *Current Opinion in Insect Science*, Elsevier Inc, 32, pp. 22–27, [online] Available at: https://doi.org/10.1016/j.cois.2018.10.006.

Storer, N. P., Babcock, J. M., Schlenz, M., Meade, T., Thompson, G. D., Bing, J. W. and Huckaba, R. M. (2010) Discovery and characterization of field resistance to Bt maize: Spodoptera frugiperda (Lepidoptera: Noctuidae) in Puerto Rico, *J. Econ. Entomol*, 103(4), pp. 1031–1038, [online] Available at: https://academic.oup.com/jee/article/103/4/1031/2199574.

Sun, X., Hu, C., Jia, H., Wu, Q., Shen, X., Zhao, S., Jiang, Y. and Wu, K. (2021) Case study on the first immigration of fall armyworm, Spodoptera frugiperda invading into China, *Journal of Integrative Agriculture*, 20(3), pp. 664–672, [online] Available at:

https://linkinghub.elsevier.com/retrieve/pii/S209531191962839X.

Tallamy, D. W., Whittington, D. P., Defurio, F., Fontaine, D. A., Gorski, P. M. and Gothro, P. W. (1998) Sequestered cucurbitacins and pathogenicity of Metarhizium anisopliae (Moniliales: Moniliaceae) on spotted cucumber beetle eggs and larvae, *Environmental Entomology*, 27(2), pp. 366–372, [online] Available at: https://academic.oup.com/ee/article-lookup/doi/10.1093/ee/27.2.366.

De Tender, C., Mesuere, B., Van der Jeugt, F., Haegeman, A., Ruttink, T., Vandecasteele, B., Dawyndt, P., Debode, J. and Kuramae, E. E. (2019) Peat substrate amended with chitin modulates the N-cycle, siderophore and chitinase responses in the lettuce rhizobiome, *Scientific Reports*, 9(1), p. 9890, [online] Available at: https://www.nature.com/articles/s41598-019-46106-x.

Thomas, G., Rusman, Q., Morrison, W. R., Magalhães, D. M., Dowell, J. A., Ngumbi, E., Osei-Owusu, J., Kansman, J., Gaffke, A., Pagadala Damodaram, K. J., Kim, S. J. and Tabanca, N. (2023) Deciphering plant-insect-microorganism signals for sustainable crop production, *Biomolecules*, 13(6), p. 997, [online] Available at: https://www.mdpi.com/2218-273X/13/6/997.

Thompson, J. P. and Clewett, T. G. (2021) Impacts of root-lesion nematode (Pratylenchus thornei) on plant nutrition, biomass, grain yield and yield components of susceptible/intolerant wheat cultivars determined by nematicide applications, *Agronomy*, 11(2), p. 296, [online] Available at: https://www.mdpi.com/2073-4395/11/2/296.

Thompson, J. P., Greco, N., Eastwood, R., Sharma, S. B. and Scurrah, M. (2000) Integrated control of nematodes of cool season food legumes, In pp. 491–506, [online] Available at: http://link.springer.com/10.1007/978-94-011-4385-1_45.

Thuerig, B., Fließbach, A., Berger, N., Fuchs, J. G., Kraus, N., Mahlberg, N., Nietlispach, B. and Tamm, L. (2009) Re-establishment of suppressiveness to soil- and air-borne diseases by re-inoculation of soil microbial communities, *Soil Biology and Biochemistry*, 41(10), pp. 2153–2161, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0038071709002715.

Timofeeva, A. M., Galyamova, M. R. and Sedykh, S. E. (2022) Bacterial siderophores: Classification, biosynthesis, perspectives of use in agriculture, *Plants*, 11(22), p. 3065, [online] Available at: https://www.mdpi.com/2223-7747/11/22/3065.

Tobias, N. J., Mishra, B., Gupta, D. K., Sharma, R., Thines, M., Stinear, T. P. and Bode, H. B. (2016) Genome comparisons provide insights into the role of secondary metabolites in the pathogenic phase of the Photorhabdus life cycle, *BMC Genomics*, BMC Genomics, 17(1), pp. 1–11, [online] Available at: http://dx.doi.org/10.1186/s12864-016-2862-4.

Tobias, N. J., Wolff, H., Djahanschiri, B., Grundmann, F., Kronenwerth, M., Shi, Y.-M., Simonyi, S., Grün, P., Shapiro-Ilan, D., Pidot, S. J., Stinear, T. P., Ebersberger, I. and Bode, H. B. (2017) Natural product diversity associated with the nematode symbionts Photorhabdus and Xenorhabdus, *Nature Microbiology*, 2(12), pp. 1676–1685, [online] Available at: http://www.nature.com/articles/s41564-017-0039-9.

Toepfer, S., Kurtz, B. and Kuhlmann, U. (2010) Influence of soil on the efficacy of entomopathogenic nematodes in reducing Diabrotica virgifera virgifera in maize, *Journal of Pest Science*, 83(3), pp. 257–264.

Toffolatti, S. L., Maddalena, G., Passera, A., Casati, P., Bianco, P. A. and Quaglino, F. (2021) Role of terpenes in plant defense to biotic stress, In *Biocontrol Agents and Secondary Metabolites*, Elsevier, pp. 401–417, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/B9780128229194000168.

Torsvik, V., Øvreås, L. and Thingstad, T. F. (2002) Prokaryotic diversity-magnitude, dynamics, and controlling factors, *Science*, 296(5570), pp. 1064–1066, [online] Available at: https://www.science.org/doi/10.1126/science.1071698.

Toubarro, D., Avila, M. M., Montiel, R. and Simões, N. (2013) A Pathogenic Nematode Targets Recognition Proteins to Avoid Insect Defenses, *PLoS ONE*, 8(9), p. 75691, [online] Available at: http://www.megasoftware.net/mega4/index.html.

Trap, J., Bonkowski, M., Plassard, C., Villenave, C. and Blanchart, E. (2016) Ecological importance of soil bacterivores for ecosystem functions, *Plant and Soil*, 398(1–2), pp. 1–24, [online] Available at: http://link.springer.com/10.1007/s11104-015-2671-6.

Trivedi, P., Leach, J. E., Tringe, S. G., Sa, T. and Singh, B. K. (2020) Plant–microbiome interactions: from community assembly to plant health, *Nature Reviews Microbiology*, 18(11), pp. 607–621, [online] Available at: https://www.nature.com/articles/s41579-020-0412-1.

Trivedi, P., Schenk, P. M., Wallenstein, M. D. and Singh, B. K. (2017) Tiny microbes, big yields: enhancing food crop production with biological solutions, *Microbial Biotechnology*, 10(5), pp. 999–1003, [online] Available at: https://sfamjournals.onlinelibrary.wiley.com/doi/10.1111/1751-7915.12804.

Turlings, T. C. J. and Erb, M. (2018) Tritrophic interactions mediated by herbivore-induced plant volatiles: Mechanisms, ecological relevance, and application potential, *Annual Review of Entomology*, 63(1), pp. 433–452, [online] Available at: https://www.annualreviews.org/doi/10.1146/annurev-ento-020117-043507.

Turner, T. R., James, E. K. and Poole, P. S. (2013) The plant microbiome, *Genome Biology*, 14(6), p. 209, [online] Available at: http://genomebiology.biomedcentral.com/articles/10.1186/gb-2013-14-6-209.

Ullah, I., Khan, A. R., Jung, B. K., Khan, A. L., Lee, I. J. and Shin, J. H. (2014) Gibberellins synthesized by the entomopathogenic bacterium, photorhabdus temperata M1021 as one of the factors of rice plant growth promotion, *Journal of Plant Interactions*, Taylor & Francis, 9(1), pp. 775–782, [online] Available at: http://dx.doi.org/10.1080/17429145.2014.942956.

Ullah, I., Khan, A. R., Park, G. S., Lim, J. H., Waqas, M., Lee, I. J. and Shin, J. H. (2013) Analysis of phytohormones and phosphate solubilization in Photorhabdus spp., *Food Science and Biotechnology*, 22(SUPPL. 1), pp. 25–31.

Valldor, P., Miethling-Graff, R., Martens, R. and Tebbe, C. C. (2015) Fate of the insecticidal Cry1Ab protein of GM crops in two agricultural soils as revealed by 14C-tracer studies, *Applied Microbiology and Biotechnology*, 99(17), pp. 7333–7341.

Vats, R., Kanwar, R. S. and Bajaj, H. K. (2004) Biology of Seinura paratenugiudata Geraert,.

Verbruggen, E., Röling, W. F. M., Gamper, H. A., Kowalchuk, G. A., Verhoef, H. A. and van der Heijden, M. G. A. (2010) Positive effects of organic farming on below-ground mutualists: large-scale comparison of mycorrhizal fungal communities in agricultural soils, *New Phytologist*, 186(4), pp. 968–979, [online] Available at: https://nph.onlinelibrary.wiley.com/doi/10.1111/j.1469-8137.2010.03230.x.

Viana, P. A. and Marochi, A. I. (2002) Controle químico da larva de Diabrotica spp. na cultura do milho em sistema de plantio direto, *Revista Brasileira de Milho e Sorgo*, 1(2), pp. 1–11, [online] Available at: http://www.bibliotekevirtual.org/index.php/2013-02-07-03-02-35/2013-02-07-03-03-11/1127-rbms/v01n02/11616-controle-quimico-da-larva-de-diabrotica-spp-na-cultura-do-milho-em-sistema-de-plantio-direto.html.

Vicente-Díez, I., Blanco-Pérez, R., Chelkha, M., Puelles, M., Pou, A. and Campos-Herrera, R. (2021) Exploring the use of entomopathogenic nematodes and the natural products derived from their symbiotic bacteria to control the grapevine moth, Lobesia botrana (Lepidoptera: Tortricidae), *Insects*, 12(11), p. 1033, [online] Available at: https://www.mdpi.com/2075-4450/12/11/1033.

Vicente-Díez, I., Pou, A. and Campos-Herrera, R. (2023) The deterrent ability of Xenorhabdus

nematophila and Photorhabdus laumondii compounds as a potential novel tool for Lobesia botrana (Lepidoptera: Tortricidae) management, *Journal of Invertebrate Pathology*, 198, p. 107911, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0022201123000289.

Vitta, A., Thimpoo, P., Meesil, W., Yimthin, T., Fukruksa, C., Polseela, R., Mangkit, B., Tandhavanant, S. and Thanwisai, A. (2018) Larvicidal activity of Xenorhabdus and Photorhabdus bacteria against Aedes aegypti and Aedes albopictus, *Asian Pacific Journal of Tropical Biomedicine*, 7(1), pp. 31–36.

van de Voorde, T. F. J., van der Putten, W. H. and Martijn Bezemer, T. (2011) Intra- and interspecific plant-soil interactions, soil legacies and priority effects during old-field succession, *Journal of Ecology*, 99(4), pp. 945–953, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2745.2011.01815.x.

Vyas, R. V., Patel, B., Maghodia, A. and Patel, D. J. (2008) Significance of metabolites of native Xenorhabdus, a bacterial symbiont of Steinernema, for suppression of collar rot and root knot diseases of groundnut, *Indian Journal of Biotechnology*, 7(3), pp. 371–377.

Walsh, G. C., Ávila, C. J., Cabrera, N., Nava, D. E., Pinto, A. de S. and Weber, D. C. (2020) Biology and management of pest diabrotica species in South America, *Insects*, pp. 1–18, [online] Available at: www.mdpi.com/journal/insects.

Wamberg, C., Christensen, S., Jakobsen, I., Müller, A. K. and Sørensen, S. J. (2003) The mycorrhizal fungus (Glomus intraradices) affects microbial activity in the rhizosphere of pea plants (Pisum sativum), *Soil Biology and Biochemistry*, 35(10), pp. 1349–1357.

Wang, R., Zhang, Q., Qu, C., Wang, Q., Wang, J. and Luo, C. (2023) Toxicity, baseline of susceptibility, detoxifying mechanism and sublethal effects of chlorogenic acid, a potential botanical insecticide, on Bemisia tabaci, *Frontiers in Plant Science*, 14, [online] Available at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1150853/full.

Wantulla, M., van Loon, J. J. A. and Dicke, M. (2023) Soil amendment with insect exuviae causes species-specific changes in the rhizosphere bacterial community of cabbage plants, *Applied Soil Ecology*, 188, p. 104854, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S0929139323000525.

Waterfield, N., Kamita, S. G., Hammock, B. D. and Ffrench-Constant, R. (2005) The Photorhabdus Pir toxins are similar to a developmentally regulated insect protein but show no juvenile hormone esterase activity, *FEMS Microbiology Letters*, 245(1), pp. 47–52.

Webster, J. M., GenHui, C., KaiJi, H. and JianXiong, L. (2002) Bacterial metabolites., In Gaugler, R. (ed.), *Entomopathogenic nematology*, Wallingford, CABI, pp. 99–114, [online] Available at: http://www.cabi.org/cabebooks/ebook/20023023445.

Whitman, W. B., Coleman, D. C. and Wiebe, W. J. (1998) Prokaryotes: The unseen majority, *Proceedings of the National Academy of Sciences of the United States of America*, 95(12), pp. 6578–6583.

Willer, H., Schlatter, B. and Trávníček, J. (2023) The world of organic agriculture statistics and emerging trends 2023, p. 360, [online] Available at: https://www.fibl.org/en/shop-en/1254-organic-world-2023.

Wilson, M. K., Abergel, R. J., Raymond, K. N., Arceneaux, J. E. L. and Byers, B. R. (2006) Siderophores of Bacillus anthracis, Bacillus cereus, and Bacillus thuringiensis, *Biochemical and Biophysical Research Communications*, 348(1), pp. 320–325.

Witte, C.-P. and Herde, M. (2024) Nucleotides and nucleotide derivatives as signal molecules in plants, Ort, D. (ed.), *Journal of Experimental Botany*, 75(22), pp. 6918–6938, [online] Available at: https://academic.oup.com/jxb/article/75/22/6918/7754297.

Woodward, S., Amin, H., Martín-García, J., Solla, A., Diaz-Vazquez, R., Romeralo, C., Alves, A., Pinto, G., Herron, D., Fraser, S., Zas, R., Doğmuş-Lehtijärvi, H. T., Bonello, P., Wingfield, M. J., Witzell, J. and Diez, J. J. (2025) Host-pathogen interactions in the pine- Fusarium circinatum pathosystem and the potential for resistance deployment in the field, *Forest Pathology*, 55(2), [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/efp.70020.

Wouters, F. C., Reichelt, M., Glauser, G., Bauer, E., Erb, M., Gershenzon, J. and Vassão, D. G. (2014) Reglucosylation of the benzoxazinoid DIMBOA with inversion of stereochemical configuration is a detoxification strategy in Lepidopteran herbivores, *Angewandte Chemie International Edition*, 53(42), pp. 11320–11324, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1002/anie.201406643.

Wu, D., Ma, Y., Yang, T., Gao, G., Wang, D., Guo, X. and Chu, H. (2022) Phosphorus and zinc are strongly associated with belowground fungal communities in wheat field under long-term fertilization, Gralnick, J. A. (ed.), *Microbiology Spectrum*, 10(2), [online] Available at: https://journals.asm.org/doi/10.1128/spectrum.00110-22.

Wurst, S. and Ohgushi, T. (2015) Do plant- and soil-mediated legacy effects impact future biotic interactions?, Allen, E. (ed.), *Functional Ecology*, 29(11), pp. 1373–1382, [online] Available at: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.12456.

Yadav, V., Wang, Z., Wei, C., Amo, A., Ahmed, B., Yang, X. and Zhang, X. (2020) Phenylpropanoid pathway engineering: An emerging approach towards plant defense, *Pathogens*, 9(4), p. 312, [online] Available at: https://www.mdpi.com/2076-0817/9/4/312.

Yan, W.-D., Shi, W.-M., Li, B.-H. and Zhang, M. (2007) Overexpression of a foreign Bt gene in cotton affects the low-molecular-weight components in root exudates, *Pedosphere*, 17(3), pp. 324–330, [online] Available at: https://linkinghub.elsevier.com/retrieve/pii/S1002016007600393.

Yang, B., Li, Z., Liu, S., Yang, J., Wang, P., Liu, H., Zhou, X., Liu, L., Wu, Z. and Yang, S. (2023) Novel cinnamic acid derivatives as a versatile tool for developing agrochemicals for controlling plant virus and bacterial diseases by enhancing plant defense responses, *Pest Management Science*, 79(7), pp. 2556–2570, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1002/ps.7433.

Yang, F., Morsello, S., Head, G. P., Sansone, C., Huang, F., Gilreath, R. T. and Kerns, D. L. (2018) F2 screen, inheritance and cross-resistance of field-derived Vip3A resistance in Spodoptera frugiperda (Lepidoptera: Noctuidae) collected from Louisiana, USA, *Pest Management Science*, 74(8), pp. 1769–1778, [online] Available at: www.soci.org.

Yang, H., Dai, Y., Wang, X., Zhang, Q., Zhu, L. and Bian, X. (2014) Meta-analysis of interactions between Arbuscular mycorrhizal fungi and biotic stressors of plants, *The Scientific World Journal*, 2014, pp. 1–7, [online] Available at: http://www.hindawi.com/journals/tswj/2014/746506/.

Yang, J. W., Yi, H., Kim, H., Lee, B., Lee, S., Ghim, S. and Ryu, C. (2011) Whitefly infestation of pepper plants elicits defence responses against bacterial pathogens in leaves and roots and changes the below-ground microflora, *Journal of Ecology*, 99(1), pp. 46–56, [online] Available at: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2745.2010.01756.x.

Yang, L. H. (2004) Periodical cicadas as resource pulses in North American forests, *Science*, 306(5701), pp. 1565–1567, [online] Available at: https://www.science.org/doi/10.1126/science.1103114.

Yeates, G. W., Bongers, T., De Goede, R. G., Freckman, D. W. and Georgieva, S. S. (1993) Feeding habits in soil nematode families and genera-an outline for soil ecologists., *Journal of nematology*, 25(3), pp. 315–31, [online] Available at: http://www.ncbi.nlm.nih.gov/pubmed/19279775.

Yi, Y., Luan, P., Wang, K., Li, G., Yin, Y., Yang, Y., Zhang, Q. and Liu, Y. (2022) Antifungal activity and plant growth-promoting properties of Bacillus mojovensis B1302 against Rhizoctonia cerealis, *Microorganisms*, 10(8).

You, C., Zhang, C., Feng, C., Wang, J. and Kong, F. (2015) Myroides odoratimimus, a biocontrol agent from the rhizosphere of tobacco with potential to control Alternaria alternata, *BioControl*, 60(4), pp. 555–564, [online] Available at: http://link.springer.com/10.1007/s10526-015-9654-7.

Yu, P., He, X., Baer, M., Beirinckx, S., Tian, T., Moya, Y. A. T., Zhang, X., Deichmann, M., Frey, F. P., Bresgen, V., Li, C., Razavi, B. S., Schaaf, G., von Wirén, N., Su, Z., Bucher, M., Tsuda, K., Goormachtig, S., Chen, X. and Hochholdinger, F. (2021) Plant flavones enrich rhizosphere Oxalobacteraceae to improve maize performance under nitrogen deprivation, *Nature Plants*, Springer US, 7(4), pp. 481–499, [online] Available at: http://dx.doi.org/10.1038/s41477-021-00897-y.

Zamioudis, C., Korteland, J., Van Pelt, J. A., van Hamersveld, M., Dombrowski, N., Bai, Y., Hanson, J., Van Verk, M. C., Ling, H., Schulze-Lefert, P. and Pieterse, C. M. J. (2015) Rhizobacterial volatiles and photosynthesis-related signals coordinate MYB 72 expression in Arabidopsis roots during onset of induced systemic resistance and iron-deficiency responses, *The Plant Journal*, 84(2), pp. 309–322, [online] Available at: https://onlinelibrary.wiley.com/doi/10.1111/tpj.12995.

van de Zande, E. M., Wantulla, M., van Loon, J. J. A. and Dicke, M. (2024) Soil amendment with insect frass and exuviae affects rhizosphere bacterial community, shoot growth and carbon/nitrogen ratio of a brassicaceous plant, *Plant and Soil*, 495(1–2), pp. 631–648, [online] Available at: https://link.springer.com/10.1007/s11104-023-06351-6.

Zaynab, M., Fatima, M., Abbas, S., Sharif, Y., Umair, M., Zafar, M. H. and Bahadar, K. (2018) Role of secondary metabolites in plant defense against pathogens, *Microbial Pathogenesis*, Elsevier Ltd, 124(August), pp. 198–202, [online] Available at: https://doi.org/10.1016/j.micpath.2018.08.034.

Zhang, H., Li, M., Lvha, A. and Zhang, S. (2024) Pimarane diterpenoids: sources, structures and biological activities, *Natural Product Research*, pp. 1–17, [online] Available at: https://www.tandfonline.com/doi/full/10.1080/14786419.2024.2426071.

Zhang, J., Klinkhamer, P. G. L., Vrieling, K. and Bezemer, T. M. (2022) The negative effects of soil microorganisms on plant growth only extend to the first weeks, Wagg, C. (ed.), *Journal of Plant Ecology*, 15(4), pp. 854–863, [online] Available at: https://academic.oup.com/jpe/article/15/4/854/6569138.

Zhang, X., van Doan, C., Arce, C. C. M., Hu, L., Gruenig, S., Parisod, C., Hibbard, B. E., Hervé, M. R., Nielson, C., Robert, C. A. M., Machado, R. A. R. and Erb, M. (2019) Plant defense resistance in natural enemies of a specialist insect herbivore, *Proceedings of the National Academy of Sciences*, 116(46), pp. 23174–23181, [online] Available at: https://pnas.org/doi/full/10.1073/pnas.1912599116.

Zhang X., Machado, R. A., Doan, C. V., Arce, C. C., Hu, L. and Robert, C. A. (2019) Entomopathogenic nematodes increase predation success by inducing cadaver volatiles that attract healthy herbivores, *eLife*, 8, [online] Available at: https://doi.org/10.7554/eLife.46668.001.

Zhao, J., Zhang, J., Zhu, X., Lu, J., Jin, B. and Chen, H. (2022) The life cycle of the bacterial-feeding nematode Diplolaimella stagnosa and its population growth in response to temperature and food availability, *Frontiers in Ecology and Evolution*, 10, [online] Available at: https://www.frontiersin.org/articles/10.3389/fevo.2022.953608/full.

Zhaolei, L., Naishun, B., Jun, C., Xueping, C., Manqiu, X., Feng, W., Zhiping, S. and Changming, F. (2017) Effects of long-term cultivation of transgenic Bt rice (Kefeng-6) on soil

microbial functioning and C cycling, *Scientific Reports*, 7(1), pp. 1–13.

Zhou, X., Kaya, H. K., Heungens, K. and Goodrich-Blair, H. (2002) Response of ants to a deterrent factor(s) produced by the symbiotic bacteria of entomopathogenic nematodes, *Applied and Environmental Microbiology*, 68(12), pp. 6202–6209.

Zhu, Y. C., Blanco, C. A., Portilla, M., Adamczyk, J., Luttrell, R. and Huang, F. (2015) Evidence of multiple/cross resistance to Bt and organophosphate insecticides in Puerto Rico population of the fall armyworm, Spodoptera frugiperda, *Pesticide Biochemistry and Physiology*, Academic Press, 122, pp. 15–21.