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Unveiling the positive impacts of the genus *Rhodococcus* on plant and environmental health

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ABSTRACT

Organic farming has emerged as a sustainable solution to the adverse effects (diminished nutritional value, compromised food quality, environmental contamination, and public health hazards) that are usually associated with harmful chemical pesticides. To overcome such loss, one must explore the plant-associated microbes that are the naturally occurring root commensal and could positively improve crop health. In this review, we highlight the importance of the bacterial genus Rhodococcus, a subset of Actinobacteria that carries immense potential in enhancing crop yield and is associated with bioremediation of toxic pesticides and other chemicals to improve soil health. However, it has been noticed that few species of *Rhodococcus* are pathogenic for the plant (*R. fascians*) as well as humans/animals (*R. equi*). But still, the majority of *Rhodococcus* isolates are found to be non-pathogenic and carry substantial beneficial traits. Here, we have attempted to comprise those beneficial traits of the different members of the genus *Rhodococcus*. The main emphasis of this review article is to explore the major areas such as enzyme production, phytohormone synthesis, growth regulation, siderophore production, bioremediation, organic compound degradation, and environmental pollution control. Opinions towards the applications of advanced methodologies for utilizing the cumulative prospective potential of the genus *Rhodococcus* have also been discussed in the different sections of the review. Conclusively, this article gathers the scattered information from the past and recent literature about this bacteria and provides the future direction about how it can improve plant/soil health and eliminate toxic chemicals and environmental pollutants.

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1 Introduction

Modern agriculture practices have reached a state where the food demands are not easy to fulfil due to the increasing global population and agricultural land crisis. Therefore, no other option was left to overuse chemical fertilizers and harmful pesticides to increase crop yield. However, these hazardous chemicals can adversely affect human and environmental health (Islam and Karim 2020). Therefore, a pressing need is required to draw attention to organic farming and put a hold on the over-usage of these kinds of chemicals. Recent reports have indicated the role of symbiotic microbes in tackling abiotic and biotic stress in plants (Sharma et al. 2024) and approaching a healthy environment (Hartman et al. 2023). The present review has discussed the diverse roles played by the different members of the genus *Rhodococcus* (an aerobic, nonsporulating, nonmotile Gram-positive bacteria closely related to *Mycobacterium* and *Corynebacterium*) for various applications in the improvement of plant/soil health as well as biodegradation of toxic chemical fertilizers, pesticides, and environmental pollutants. Marginal pathogenicity of certain *Rhodococcus* species (*R. equi* and *R. fascians*) has also been reported, but predominantly existing Rhodococcus species are found non-pathogenic (Vázquez-Boland and Meijer 2019). The major highlights of this review is on (i) aniline (hazardous component of chemical pesticides) bioremediation by the *Rhodococcus* species (*A-deg 1* and *A-deg 2*) (Pande et al. 2022), (ii) p-nitrophenol and 2,4-dinitrophenol (2-DNP) degradation by *Rhodococcus RKJ300T* strain (Ghosh et al. 2010) as well as 2,4-DNP by the *Rhodococcus XM24D* strain (Hu et al. 2021), (iii) *Rhodococcus*-mediated breakdown of neonicotinoids, glyphosate, pesticides, and herbicides (Pang et al. 2020), (iv) role in siderophore-mediated metal detoxification, and role of quorum sensors and quenchers in microbiome (Saeed et al. 2021), and (v) enzymatic degradation of plastic (Zampolli et al. 2022). Conclusively, mechanistic investigation of the role of different *Rhodococcus* species in such important microbe-plant as well as microbe-environmental bio-processes can provide clues about the better understanding of genetic/molecular counterparts that will help advance the utility of *Rhodococcus* in sustainable agriculture and also in environmental bioremediation. In this direction, the present review has been written to gather recent and relevant information about the role of *Rhodococcus* in these versatile biological processes involved in maintaining plant health, bioremediation of toxic chemicals from soil/water, and environmental eco-balancing.

2 *Rhodococcus* in pesticide and insecticide degradation

Chemical-derived micronutrients, fertilizers, insecticides, and pesticides have been used widely to enhance crop productivity and fulfil the food demands of modern agriculture practices. This over-usage of such chemical products leads to their bioaccumulation in the plant product, soil, water, and environment, and ultimately could cause disastrous hazards for the animal kingdom in many ways. Among these chemicals, aniline is one of them, which is a breakdown product of several pesticides and herbicides (Chaturvedi 2022).

2.1 Aniline compounds degradation by *Rhodococcus*

One must target the utility of *Rhodococcus* bacteria in microbial bioremediation, where this bacterium can alternatively use the aniline as a source of nitrogen and carbon. Two strains of *Rhodococcus* (*R.A-deg11* and *R.A-deg-2*) can degrade aniline, as summarized in Figure 1 (Krivoruchko et al. 2023). However, the upper limit of aniline concentrations that Rhodococcus can detoxify is still unknown, which makes it difficult to use *Rhodococcus* strains for microbial-based aniline degradation. Therefore, we believe targeting the successful application of these bacteria in the agriculture sector as a set of safety and toxicity assessments is always necessary.

2.2 Nitro/para-nitro phenols degradation by *Rhodococcus*

Rhodococcus bacteria can also degrade p-nitrophenol and 4-NP (Takeo et al. 2018). However, in pesticide-affected areas, *R. imtechensis (RKJ300T)* efficiently reduces p-nitrophenol (PNP) and 2,4-dinitrophenol (2,4-DNP), demonstrating the ability of such microbes to decontaminate the soil from these toxic chemicals as shown in Figure 1 (Ghosh et al. 2010). Four enzymes in the *R. imtechensis RKJ300T* strain catalyze the conversion of 4-NP to maleylacetate (Santillan et al. 2020), and *R. rhodochrous* degrades malathion, but the involved genes and mechanisms are still unknown (Wrońska et al. 2016). Therefore, a better understanding of the mechanisms by which *R. imtechensis (RKJ300T)* degrades PNP and 2,4-DNP is required (Mawang et al. 2021). 4-nitrophenol (4-NP) is a chemical which is present in insecticides and fungicides, can cause headaches, tiredness, nausea, and cyanosis (a bluish colouring of the lips, ears, and fingernails), and it can irritate the eyes. The *Rhodococcus BUPNP1* strain produces an enzyme that can break down and utilize 4-NP as a carbon source for its growth and survival when no carbon and nitrogen source is available. Bacterial enzymes that can capably degrade the chemical substances (4-NP, 4-nitrocatechol (4-NC) and 1,2,4-benzenetriol) as carbon source belongs to the category of monooxygenases (MO). These MO enzymes in bacteria can capably convert 4-NP into 4-NC and trigger the release of nitrite ions to initiate the breakdown of 4-NP. Therefore, bacteria that contain MO can grow in the presence of 4-NP, 4-NC, and 1,2,4-benzenetriol. A progressive degradation primarily degrades 4-NP and subsequently carries out 4-NC degradation (Sengupta et al. 2019a). However, the cellular enzymes responsible for such processes stepwise have been identified earlier (Brookbank et al. 2021). But, in a recent study, MO enzymes have been mentioned as a responsible

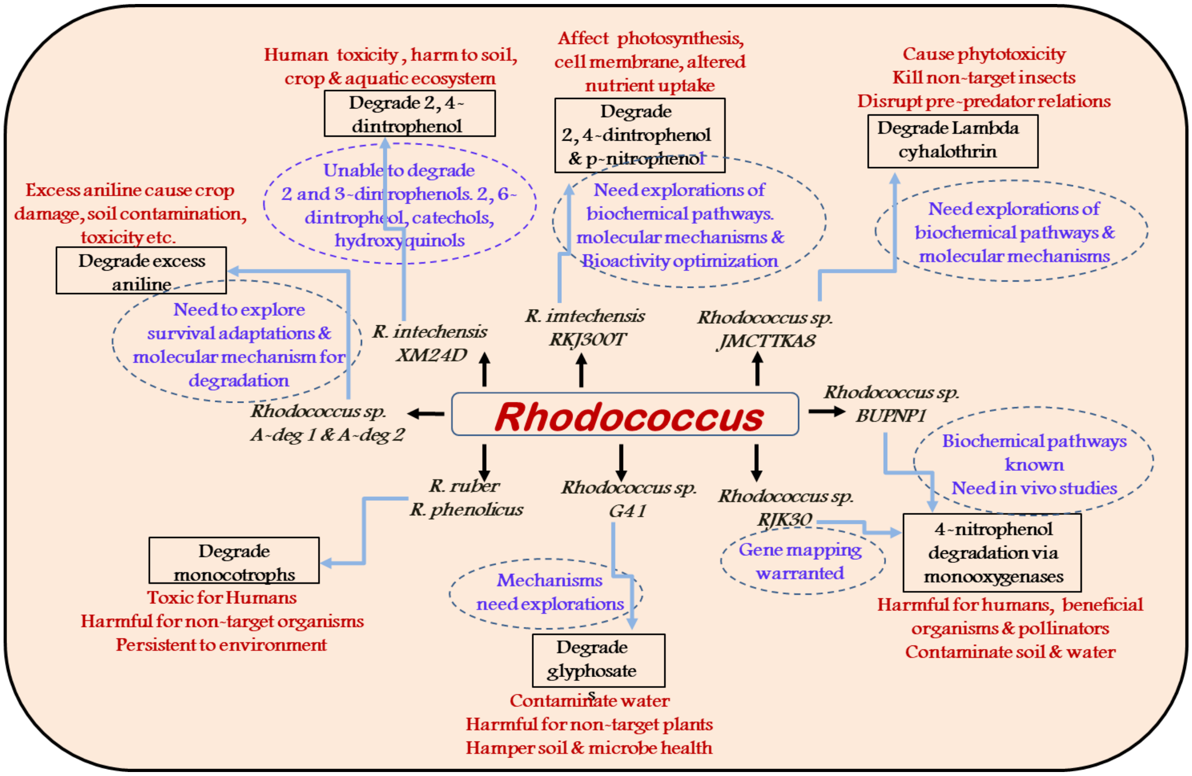

Figure 1 Schematic representation of the role of *Rhodococcus* species in pesticide and insecticide degradation as discussed briefly in the above section

molecule for the conversion of 4-NP into the less toxic, water-soluble compound (4-NC) and releases nitrite ions via synthesizing an unstable intermediate, which is essential for the process of 4-NP breakdown (Hecko et al. 2023). Interestingly, it was reported by Sengupta et al. (2019a) that the highest activity of MO was observed during the early exponential growth phase. In contrast, the abundance of alcohol dehydrogenase (ADH) was observed during the exponential growth phase of the *Rhodococcus BUPNP1* strain, and this enzyme can cause the breakdown of 4-NP. However, a deep understanding of these enzymes and associated pathways involved in bacteria-mediated degradation of 4-NP can be investigated by looking into the protein-protein interactions, pathway analysis, and conservancy (Kaushik et al. 2022). A better understanding of the concept of developing microbial consortia to enhance the potential of the 4-NP degradation can be achieved by assembling a variety of bacterial strains to break down contaminants collectively in a much better way (Zhang and Zhang 2022). The degradation of 4-NP by *Rhodococcus FXJ9.536* strain at different temperatures was evaluated, and it was observed that the degradation was optimal at 28°C but less effective at 10°C. During the degradation process, intermediates 4-nitrocatechol and 1,2,4-benzenetriol have been identified (Huang et al. 2022). The *R. tibetensis FXJ9.536* genes peg.5460, and peg.3921 were involved in 4-NP degradation (Figure 1). The lower degradation at 10°C may be due to decreased enzyme activity. The breakdown of 4-NP by *Rhodococcus* bacteria is dependent on temperatures between 28-30°C. The gene encoding 4-hydroxyphenyl acetate 3-monooxygenase was found in cold-adapted *Rhodococcus* strains, including *R. erythropolis* and *R. qingshengii*, possibly associated with the degradation of 4-NP (Bordin et al. 2021).

It has been reported that in the pesticides and industrial waste polluted areas, two chemical compounds (PNP and 2,4-DNP) are present predominantly (Hu et al. 2021). The strain *Rhodococcus RKJ300* was isolated from pesticide-laden Punjab State soils at 30°C via a serial dilution plating method. These bacteria grow well on minimal agar media supplemented with 0.5 mM PNP or 2,4-DNP as carbon and energy sources, representing that the *Rhodococcus RKJ300* strain can capably degrade PNP and 2,4-DNP (Ghosh et al. 2006). Compound 2,4-DNP contains two nitrogen groups on its benzene ring, the most often used pesticides, herbicides, and fungicides (Aslam et al. 2023). Meanwhile, the *Rhodococcus XM24D* strain utilizes 2,4-DNP as a source of carbon and nitrogen (Figure 1). Interestingly, the *Rhodococcus XM24D* strain can break down 4-PNP and 2C4NP efficiently but is incapable of degrading 2,6-NP, 2-NP, 3-NP, 4-nitrocatechol, hydroxyquinol, catechol and hydroquinone (Xiang et al. 2022). Research on the *Rhodococcus XM24D* strain that exposed to 2,4-DNP stress has revealed that 12 out of 17 genes in the relevant pathway were remain unregulated, including NADPH-dependent

F420 oxidoreductase (dnpB), hydrolase (dnpC), and coenzyme F420 biosynthesis pathway genes. The gene cluster comprises five PNP degradation genes of the *Rhodococcus XM24D* strain. The PNP and 2C4NP degradation pathways predominantly enhance the expression of these genes. Like the *R. imtechensis* and *R. RKJ300* strains, the *R. XM24D* strain degrades PNP and mineralizes 2C4NP (Alam and Saha 2022). Furthermore, the ecological consequences of *R. XM24D* must be addressed to ensure its mutually beneficial coexistence in the environment. In-depth molecular biology studies may reveal the breakdown processes of 2,4-DNP, PNP, and 2-C-4-NP to understand and exploit metabolic regulation (Kim et al. 2018; Swangjang 2022). However, using *R. JMCTTKA8* strain is promising in approaching the bioremediation of a persistent insecticide (lambda-cyhalothrin) (Sakr and Rashad 2023). Therefore, exploring the use of microbes in bioremediation processes under variable environmental conditions can be approached, which is certainly achieved by using *Rhodococcus* bacteria (Raffa and Chiampo 2021; Thi Mo et al. 2022). However, better utilization of such chemicals in minimal amounts for pest management can be achieved by the adoption of a new approach (Yousef et al. 2023), which can help to synthesize the advanced active formulation of such chemicals ingredients and thus reduce hazardous effects of chemicals on the environment (Camara et al. 2019). Conventional pest control methods are not enough to decompose such chemicals, and the risk of bioaccumulation in the environment of these chemicals remains on high alert (Okoye et al. 2022).

2.3 Monocrotophos degradation by *Rhodococcus*

Neonicotinoids are another popular class of pesticides used in more than 120 countries globally. They destroy pests by targeting their central nervous system (Costas-Ferreira and Faro 2021), and most of the neonicotinoid treatments also protect plant seedlings, increasing Bt toxin tolerance(D'Ambrosio et al. 2020). According to Parte and Kharat (2019) imidacloprid and clothianidin have their respective half-lives of 3000 and 6931 days. Meanwhile, thiamethoxam and acetamiprid have 353 and 450 days of soil half-live, respectively (Bhattacherjee et al. 2020). These chemicals enter the water sources and subsequently enter the food chain. The long environmental lifespan and negative impacts of these chemicals on unspecific insects raised concerns about their applications in the agricultural sector. It also affects the population of essential pollinators, including bees, butterflies, dragonflies, and wild bees, which have lost their behaviour, immunity, and survival. Increased neonicotinoid use has also been connected to bird population reduction. Only a portion of the active chemical protects the crops, while the remaining compound is dispersed in the environment, harming soil microbial populations and their living creatures, including earthworms, amphibians, and aquatic insects (Glen-Karolczyk et al. 2021). Recent studies have shown that certain bacteria can break down the neonicotinoids (imidacloprid and acetamiprid) (Thi Mo et al. 2022). Bacteria (*R. phenolicus and R. ruber*), isolated from pesticide-contaminated soils can break down monocrotophos and mineralize acetochlor in six days (Ahirwar 2023). Acetamiprid biodegradation is efficiently increased by adding carbon and nitrogen sources (Xu et al. 2020; Rasool et al. 2022). *Rhodococcus* bacteria can metabolize chemical substances such as neonicotinoids. However, the capacity of *Rhodococcus* bacteria to break down the pesticides and its adaptation to the soil environment, as well as its interactions with other microorganisms in the soil, can only determine its utility for neonicotinoid bioremediation (Dai et al. 2021).

2.4 Glyphosates degradation by *Rhodococcus*

Many organophosphate herbicides in agriculture and forestry use glyphosate to suppress broadleaf weeds and grasses. However, environmental concerns have been raised because of its impact on soil health. Response surface methodology (RSM) involves optimizing glyphosate degradation to decrease environmental and health issues (Firdous et al. 2020). There are two major pathways for degrading glyphosate. One of the pathways involves glyphosate oxidoreductase, which breaks the C-N bond and releases glyoxylate. The second pathway uses C-P bond lyase to convert glyphosate into sarcosine and inorganic phosphorus. Sarcosine oxidase converts it to glycine, an amino acid that can be further utilized for protein synthesis (Singh et al. 2020). Inorganic phosphate in the soil can prevent glyphosate's bacterial degradations and generate toxic aminomethylphosphonic acid (AMPA) (Sun et al. 2019). Therefore, efforts are required to find solutions for safe and efficient glyphosate degradation and removal of AMPA residues (Castrejón-Godínez et al. 2021). Interestingly, reports have demonstrated that the *R. soli G41* strain degraded 42.7% of glyphosate in seven days, and this bacterium can grow very well and attain maximum optical density at 30°C and pH 7.0. The *R. soli G41* strain reduced glyphosate in nonsterile soil and enhanced weeds' germination by 10% in contaminated soil, where weeds have shown soil healing potential (Nguyen et al. 2022). Another study also revealed that *R. soli G41* contains an enzyme (sarcosine oxidase) and utilizes sarcosine instead of AMPA, which is more environmentally friendly (Pérez Rodríguez et al. 2019). Sarcosine oxidase is essential for converting glyphosate to phosphate by C-P lyase. The soxA gene in *R. soli G41* was 98.9% similar to that in *R. opacus* and included sarcosine oxidase; potentially, this newly identified *R. soli G41* strain may help remediate glyphosate-contaminated soil (Pérez Rodríguez et al. 2019).

3 *Rhodococcus* in AHL degradation mediated quorum quenching

In microbes, N-acyl homoserine lactone (AHL) degradation has been reported as a novel method for quorum quenching (QQ) by using the enzyme (lactonases and acylases) (Kusada et al. 2017).

Exploring the QQ pathway in disease-specific pathogenic bacteria may be beneficial in reducing bacterial resistance. Importantly, the *Rhodococcus* bacteria can break down AHL through certain enzymatic degradative pathways (Figure 2). However, targeting the QQ employing *Rhodococcus* enzymes (lactonases and acylases) may help inhibit the biofilm formation in pathogenic bacteria (Murugayah and Gerth 2019; Sikdar and Elias 2020). This strategy has been meaningful for reducing the disease burden caused by pathogenic microbes and maintaining the balance between pathogenic and non-pathogenic bacterial populations. Because biofilms are essential for the colonization and survival of bacteria, these QQ mechanisms in *Rhodococcus* species have demonstrated a great potential for inhibiting biofilm formation (Paluch et al. 2020). *Rhodococcus* species enriched with AHL-degrading enzymes have demonstrated predominant expression of oxidoreductases (Ryu et al. 2020). AHLs are involved in the quorum sensing-mediated pathogenicity of certain pathogenic bacteria and biofilm formation, and the ability of the *R. erythropolis* W2 strain to destroy these bacteria depends on the simultaneous activity of different QQ enzymes (Figure 2) (Chakraborty et al. 2023). When the production of AHL in a pathogenic species, such as *E. caratovora,* is hampered, survival diminishes, decreasing its pathogenicity. Interestingly, *Rhodococcus* strains (*LS31* and *PI33*) have shown strong inhibitory effects on OHHL and pectate lyase activity when grown together with *E. carotovora* (Sarveswari and Solomon 2019*).* In the *Rhodococcus* strain *LS31*, one can more clearly understand the suppression mechanism of quorum sensors by lactonases and acylases-mediated AHL breakdown (Park et al. 2006). In other species of *Agrobacterium*, AHLases such as AttM can digest c-butyrolactone, but the mechanism is still elusive. Therefore, it was earlier directed that a deeper mechanistic understanding of the relationship between lactonase and acylase enzymes must be explored (Kumar et al. 2022). The ability of the *R. erythropolis W2* strain to degrade AHLs reflects the relevance of AHL turnover under varying environmental conditions where the length of the acyl chain affects the level of AHL degradation (Utari et al. 2017). Biochemical pathways analysis of the enzymes produced by different *Rhodococcus* strains can develop new approaches to control the AHL mediated pathogenicity in microbes (Rehman et al. 2022). However, LC-ESI/MS employed investigations on AHL degradation by *Rhodococcus* strains (*LS31* and *PI33*) demonstrated that the *Rhodococcus LS31* synthesize several byproducts from N-hexanoyl-L-homoserine lactone (HHL) more rapidly and enhance AHL degradation (Taşkan and Taşkan 2021). Such observations indicated the putative role of AHLases in releasing homoserine lactone rings that indirectly affect the density of the final product.

On the other side, bioremediation traits of *Rhodococcus* bacteria were demonstrated by agar-based immobilization assays carried out on synthetic polymers where biphenyl metabolization was mediated with the help of limonene (Tyumina et al. 2023). Cumin oil containing cumin aldehyde and cumene initiates the co-metabolization process of trichloroethylene by Rhodococcus strain

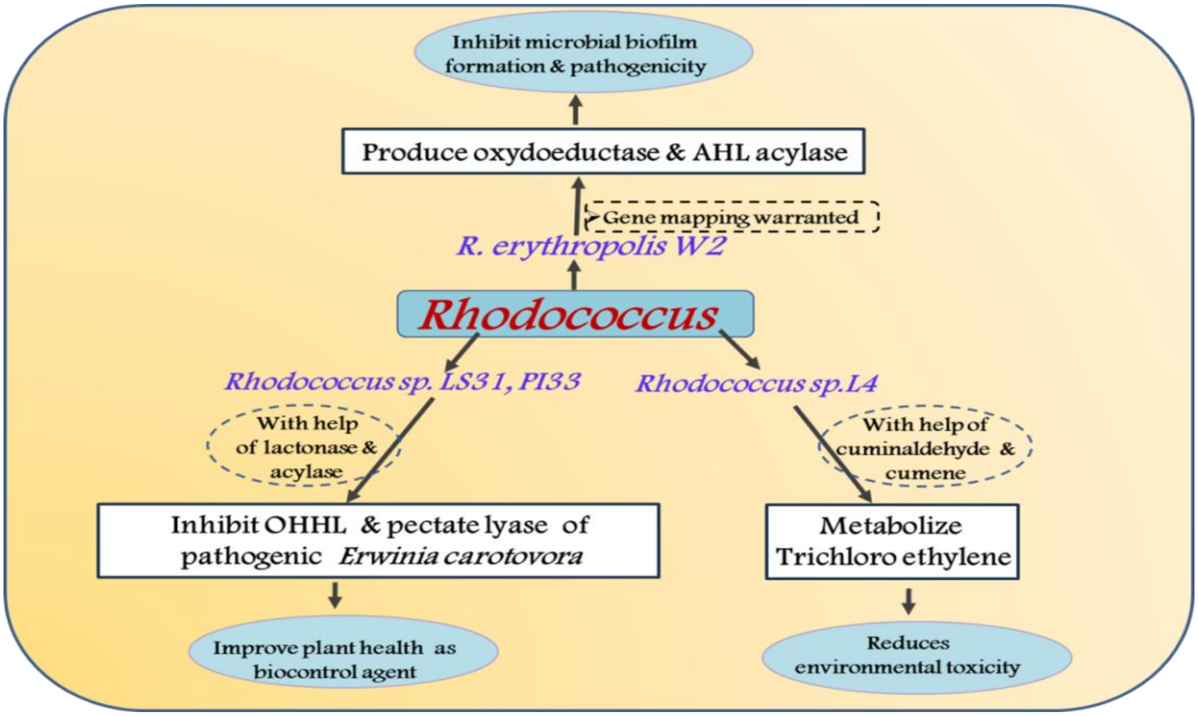

Figure 2 Illustration of the role of the symbiotic bacterium *Rhodococcus* in providing plant benefits and eco-protection via enhanced quorum quenching.

L4, indicating that one pathway could be targeted for environmental detoxification (Suttinun et al. 2010). If we overlook in total, enzymes (lactonases and acylases) have been the key players in QQ processes (Dubert et al. 2017). The complicated enzymatic pathways of *Rhodococcus* strains highlight their potential in modulating quorum sensing, microbial behaviour, and responses to environmental stressors (Barbey et al. 2018). The degradation of AHL has several potential uses, from preventing disease spread to cleaning polluted areas by *Rhodococcus* bacteria (Prazdnova et al. 2022).

4 *Rhodococcus* as a siderophore producer and metal scavenger

Siderophores are complex molecules with remarkable metal-binding abilities, and they play a crucial role in many biological processes, such as metal-ion metabolism and degradation (Gomes et al. 2024). Siderophore production by different *Rhodococcus* species (*R. qingshengii*, *R. erythropolis*, and *R. jostii*) has taken the lead in revealing the complex gene clusters and metabolic pathways that could control the metabolism of metal-containing compounds (Khilyas et al. 2021). The reported literature has demonstrated that the *Rhodococcus* metabolites (heterobactins and rhequichelin) are hydroxamate- and catecholate-type siderophores, respectively. Two nonribosomal peptide synthases (NRPSs) and siderophore-producing clusters have sequence homology (da Silveira et al. 2020). The heterobactin gene clusters of *R. qingshengii BKS* 20-40, the *Rhodococcus* strain *ADH*, and *R. erythropolis SK121* have 100% identity, while the erythrochelin gene cluster shares 57%. *R. qingshengii S10* produces siderophores in liquid M9 medium and on chrome azurol S (CAS) agar under iron-deficient conditions. The bacteria grow and produce catalase and urease in the presence of NaCl at pH values ranging from 5 to 9. The *R. qingshengii S10* genome contains twelve trehalose-producing genes that protect against desiccation, temperature variations, and high salinity (Khilyas et al. 2021). However, a deeper understanding of the functional differences between these clusters, especially genes with different sequences, could shed light on the factors that lead to siderophore diversity and their distinct roles. Rhodochelin, a principal secondary metabolite, was identified, and genome analysis revealed the responsible gene clusters. The rhodochelin-producing cluster (rhc) contains the entire bimodular NRPS synthetase, rhcB, and genes for export and import (rhcC, D, F). The crucial enzyme isochorismatase (rhcA) is in the rhc cluster. In an operon with rhcA, a dhbE-like gene is near two additional 2,3-DHB-producing genes, dhbC and dhbA. This operon covers the 2,3-DHB pathway from chorismate to adenylate (Puja et al. 2023). Siderophore synthesis was reduced in a gene knockout study targeting key genes in clusters (rhcB, dhbE, rmo, and rft) (Yin et al. 2023). *R. erythropolis B7g* has shown promise in siderophore synthesis and metal interactions (Retamal-Morales et al. 2018). Genome investigation of *R. erythropolis B7g* revealed two siderophore biosynthesis-related gene clusters. One cluster produces heterobactins and mixed catecholate-hydroxamate siderophores, while the other produces requichelin siderophores, whose nature is unknown. When. *R erythropolis B7g* was grown in a specialized medium to produce apo-heterobactin S2 and heterobactin B as siderophores. Optimizing the growth conditions with supplementation with glucose, n-hexadecane, and casamino acids increased the production of siderophores. For instance, adding 30 mM glucose and 1% casamino acids to 1 L culture medium increased the siderophore concentration and improved production efficiency (Srimathi and Suji 2019). Complete genomic and transcriptomic analyses of both symbiotic partners (plants and microbes) that take up nutrients via siderophores are necessary (Hofmann et al. 2021).

A study investigated siderophore production by the bacterium *R. jostii RHA1* under various growth conditions revealed. It was observed that *R. jostii RHA1* produced siderophores in response to iron deficiency, as demonstrated by a positive CAS assay (Srimathi and Suji 2019). In the subsequent step, CAS-positive supernatant was purified using ion exchange chromatography to identify siderophores. These iron-chelating chemical peaks were observed in the HPLC chromatogram. These peaks were misplaced under iron-rich growth conditions, confirming their association with iron scarcity. Liquid chromatography-mass spectrometry (LC–MS) revealed the behaviours of these peaks and their expression patterns. One peak resembled that of rhodochelin (a secretory bacterial siderophore), whereas a companion peak resembled that of rhodochelin, which lacked a modified ornithine residue (Pathak et al. 2024). Thus, *Rhodococcus* bacteria play a pivotal role in sustainable agriculture through siderophore production. The siderophore activity of *R. jostii* was enhanced by its interaction with 4HBA (Yasin et al. 2023). *R. rhodochorus GD02* can produce siderophores essential for iron uptake and metabolism. Interestingly, enzyme 4HBA plays a significant role in siderophore synthesis, particularly under iron-limited conditions. When iron is abundantly available, siderophore production is inhibited (Pathak et al. 2024). It was also evident that the *R. jostii* RHA1 gene, which produces rhodochelin, was similar to the gene cluster that produces 2,3-DHB in *R. rhodochorus GD02* but had different siderophore expression profiles. NRPS genes, which are important for siderophore production, were identified in *R. rhodochorus GD02* but are poorly characterized. Additionally, anti-SMASH analysis could identify secondary metabolite biosynthesis-related gene clusters, which seem to be involved in metallophore synthesis and could also be responsible for synthesizing other compounds, such as siderophores. This suggests that *R. rhodochorus GD02* has a complex genetic landscape related to siderophores that needs to be studied in more depth to understand siderophore production fully (Ward et al. 2018). One must target the recent approaches of OMICs that include transcriptomics, proteomics, metabolomics and integrative bioinformatics platforms for elucidation of pathways, protein-protein interaction and other metabolites cross-talk for a thorough investigation of siderophore production as well as respective metabolic processes.

5 *Rhodococcus* and plastic degradation

Rhodococcus bacteria also have a peculiar ability to degrade plastic material and offer hope to solve the non-degradable plastic burden-related environmental issues (Bacha et al. 2023). In a comparative bioinformatics study, analysis of 669 *Rhodococcus* genomes revealed genetic components involved in plastic and polymer breakdown, where 24% of bacteria target the CC backbone and 18% target heteroatomic polymer degradation, with 57% of these bacteria possessing enzymes for degrading poly-3 hydroxybutyrate (PHB) and polybutylene adipate-co-terephthalate (PBAT). Further in-depth analysis showed that *R. pyridinivorans, R. qingshengii,* and *R. hoagii* degraded the CC backbone of the plastic (Figure 3) (Zampolli et al. 2023). *Rhodococcus* species with enzymes (multicopper oxidases, alkane monooxygenases, and cytochrome P450 hydroxylases) may break down plastic (Mohanan et al. 2020). Initial studies suggested that extracellular secretion signals and enzyme types such as cutinase and PU esterase degrade heteroatomic backbone plastic. Polyester breakdown enzymes (carboxylesterase, PLA-depolymerase, and PHB-depolymerase) were consistently prevalent in *R. triamomae* (Ke et al. 2017). Understanding the molecular mechanisms underlying the degradation of various polymers is essential, as elucidating the biochemical pathways and enzymatic reactions can provide insights into the substrate selectivity, kinetics, and structural characteristics of these enzymes and elucidate the molecular basis of the plastic-degrading capabilities of the genus *Rhodococcus* (Cai et al. 2023). A study showed that the textile, pesticide, and fertilizer industries waste materials in waste materials that are enriched in anthraquinone (AC) compounds, which are ultimately deposited gradually in agricultural land. Unfortunately, these ACs contain an anthraquinone ring that harms microbes, plants, and animals (Safiarian et al. 2023). The *R. pyridinivorans GF3* strain degrades AC by breaking the anthraquinone ring into catechol and salicylic acid. However, the enzymes and genes that drive this process remain elusive and must be investigated in detail. So far, *R. pyridinivorans GF3* strain has been tested for the capacity to degrade 1-aminoanthraquinone-2-sulfonic acid (ASA-2) (Wang et al. 2022). ASA-2 breakdown produced catechol, 3-amino-4-sulfophthalic acid, salicylic acid, and 3-amino-4-sulfosalicylic acid. Gene analysis revealed that CYP450 and short-chain dehydrogenase/reductase are upregulated in *R. pyridinivorans GF3* during ASA-2 exposure, demonstrating their roles in AC oxidation and hydroxylation. The expression of catechol metabolism genes, which break down the AC compound and produce ATP through the TCA cycle, was upregulated (Figure 3) (Wang et al. 2022). The strains *R. pyridinivorans X1* and *X2* exhibited enhanced tolerance to phenolic contaminants, attributed to mutations identified through genome sequencing. These mutations were detected in genes associated with phosphotransferase, MFS transporter, AcrR regulator, and GlpD regulator, which collectively contribute to increased phenol tolerance and degradation capabilities in the transformed strains

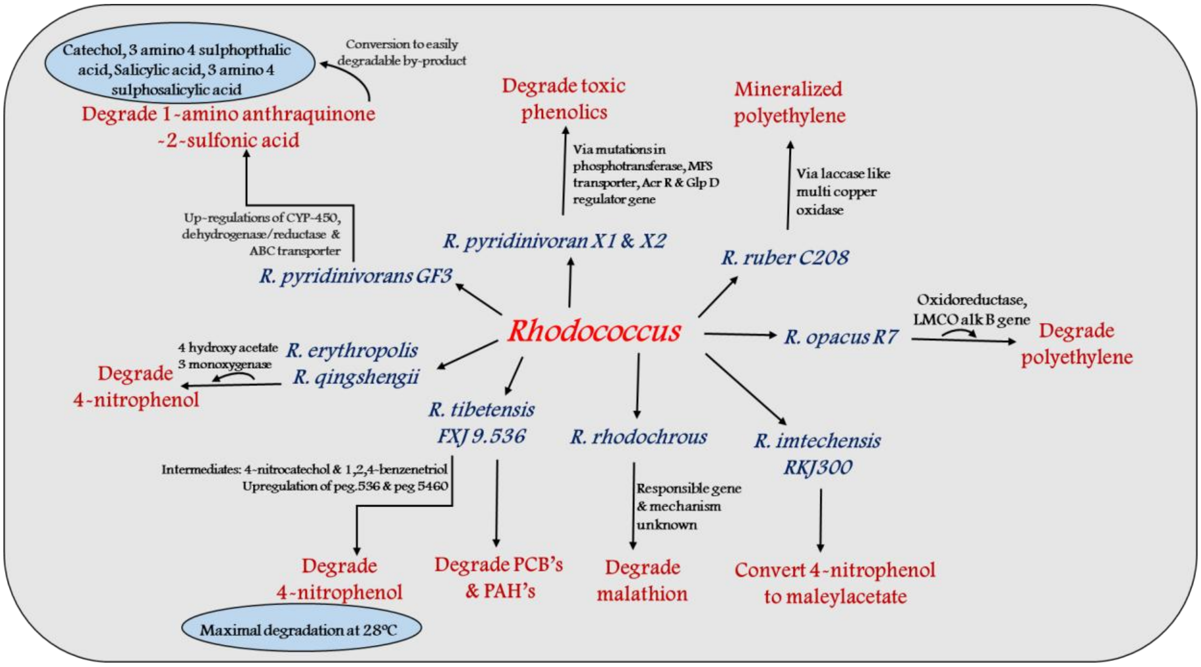

Figure 3 Highlights the roles of the bacterium *Rhodococcus* in plastics and toxin degradation.

(Wang et al. 2022). Notably, bacteria's polyethylene (PE) degradation can be influenced by acidity, photooxidation, and heat (Ghatge et al. 2020). The *R. ruber C208* strain mineralizes PE without external stimuli, and bacterial laccase-like multicopper oxidase (LMCO) decreases the molecular weight of PE (Zampolli et al. 2024). Similar to *R. ruber C208*, another strain, *R. opacus R7*, exhibit growth and survival capabilities by degrading PE and using it as a carbon source. *R. opacus R7* RNA sequencing revealed elevated expression of genes responsible for oxidoreductase activity, hydrocarbon catabolism type and other activities (Figure 3). The overexpression of three LMCO genes (LMCO1, 2, 3) suggested that these genes play an important role in early PE oxidation. The highly expressed alkB gene degrades medium-chain n-alkanes and shows that *R. opacus R7* can degrade PE (Zampolli et al. 2021). The *R. tibetensis FXJ9.536* strain was discovered on the Qinghai–Tibet Plateau (QTP). This strain degrades QTP organic pollutants such as polychlorinated biphenyl (PCBs) and polyaromatic hydrocarbons (PAHs) (Huang et al. 2022). Our attention must be directed towards approaches which help identify new plastic-degrading enzymes from *Rhodococcus* bacteria. One must explore global proteomics analysis to discover the uncharacterized unique enzymes from the *Rhodococcus* bacteria.

6 *Rhodococcus* and environmental stress adaptation

Rhodococcus bacteria can also encounter environmental stressors that result in adaptation and resilience against abiotic stress (Kuhl et al. 2021). A mechanistic study between the fungal pathogen, abscisic acid (ABA) levels in sugar beet plants, and counter-current mechanisms of *Rhodococcus* have been investigated in the past (Rangel et al. 2020). *C. beticola* is a pathogenic fungus that can elevate the ABA levels in the sugar beet plants during the infection cycle. This ABA level enhancement in sugar beet can make plants more susceptible to other pathogens. Because ABA hampers the immune system of plants, excess ABA leaches into the soil through dead shoot tissues and root turnover, thus changing the amount of ABA in the soil (Figure 4) (Brookbank et al. 2021). This delicate equilibrium between ABA synthesis and breakdown contributes to oxidative changes within the system, with CYP707A2 monooxygenase emerging as a crucial player in this cyclic process (Rai et al. 2021). Therefore, a deep understanding of the modulating interactions between plants and fungi and their respective resultant effects on the ABA availability in the soil has been important while considering plant health and resistance to pathogenic diseases (Begum et al. 2019).

The *Rhodococcus P1Y* strain uses ABA as a carbon and energy source (Yuzikhin et al. 2021). Phaseic and dehydrophaseic acids are predominantly derived from the modification of cyclohexene by ABA. Researchers have shown that the *Rhodococcus P1Y* strain can degrade ABA to dehydrovomifoliol in a synthetic nutrient medium using ABA as the sole carbon and energy source (Bordin et al. 2021). However, the process of converting ABA to dehydrovomifoliol is still unknown. By analyzing the genome of the

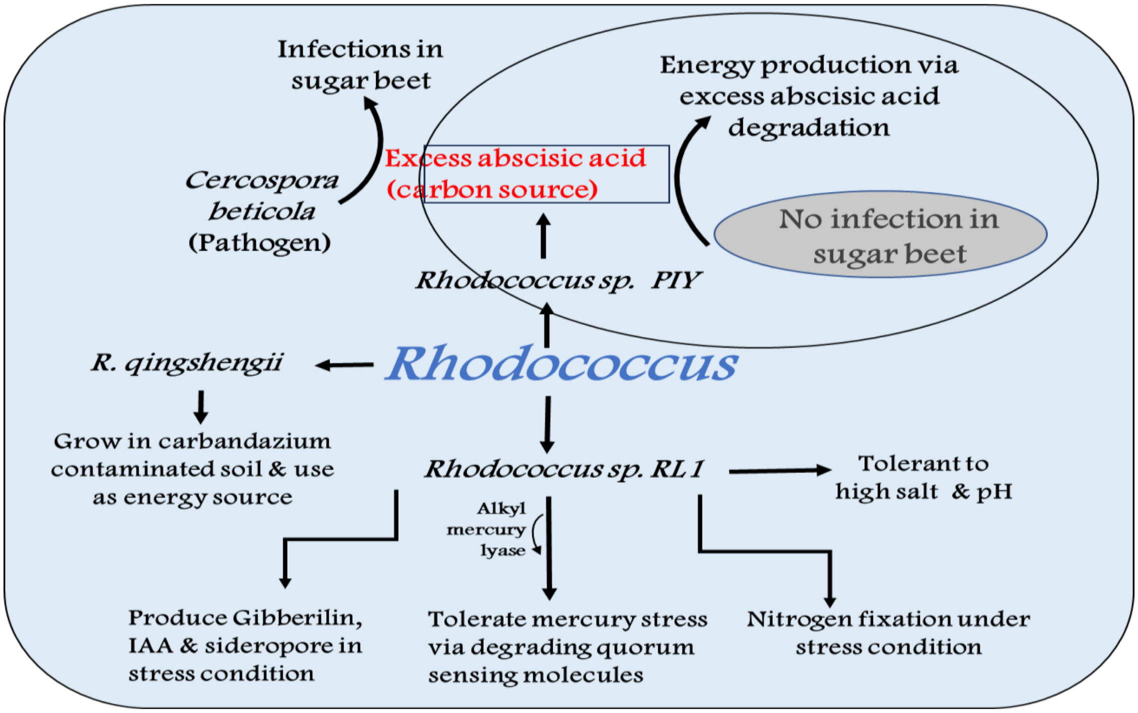

Figure 4 Explaining the *Rhodococcus* sp.-mediated stress adaptation and resilience mechanisms to establish healthy symbioses between plants and soil microbes

Table 1 Different roles of *Rhodococcus* species in the bioremediation and metabolism processes

S. N.	Strain	Application	Mechanism	Reference
1	*Rhodococcus* sp. *A-deg 1* and *A-deg 2*	Degrade aniline	Degradation of aniline and consumption as a single carbon source. Mechanism unknown	Krivoruchko et al. 2023
2	*R. imtechensis RKJ300T* strain	Degrade p-nitrophenol (PNP) and 2,4-dinitrophenol (2,4-DNP)	Degradation of PNP and 2,4-DNP by consuming as a single carbon source. Mechanism unknown	Ghosh et al. 2006
3	*Rhodococcus JMCTTKA8* strain	Degrade Lambda cyhalothrin (pesticide)	Breakdown and consumption of Lambda cyhalothrin byproducts as major source of energy. Mechanism unknown	Djouaka et al. 2018
4	*R. phenolicus* and *R. ruber*	Degrade monocrotophos and mineralized acetochlor	Monocrotophos (MCP-1 and MCP-2) degradation and acetochlor mineralization by a known mechanism	Srinivasulu et al. 2017
5	*Rhodococcus BUPNP1*strain	4-NP metabolization	Monooxygenase dependent degradation of 4-NP, 4-NC, and 1,2,4-benzenetriol to use as single carbon source and release nitite ions.	Sengupta et al. 2019b
6	*Rhodococcus RKJ300* strain	Degrade PNP or 2,4-DNP	Degradation via oxidative and reductive processes creates chlorohydroquinone and generates hydroquinone as an intermediate.	Ghosh et al. 2010
7	*R. soli G41* strain	Glyphosate degradation	Glyphosate degradation via sarcosine oxidase and C-P lysis turns glyphosate into phosphate.	Nguyen et al. 2022
8	*Rhodococcus XM24D* strain	Degrade 2,4-DNP and its analogue	Biosynthetic genes involved in 2,4-DNP degradation include dnpB and dnpC, F420 oxidoreductases, and F420 coenzyme	Hu et al. 2021
9	*R. erythropolisW2* strain	Quorum quencher	Quenching of quorum sensing by N-acylhomoserine lactone (AHL) degradation and inhibiting bacterial cross-talk.	Uroz et al. 2005
10	*Rhodococcus* strain (*LS31* and *PI33I*)	Inhibition of AHLs type OHHL and Pectate lysin	Lowering of AHLs, especially OHHL (N-(3-oxohexanoyl)-L-homoserine lactone) in *Erwinia carotovora* via pectate lyase activity.	Park et al. 2006
11	*Rhodococcus L4* strain	Metabolize trichloroethylene (TCE)	TCE degradation via enzyme cumene aldehyde and cumene.	Suttinun et al. 2010
12	*R. pyridinivorans, R. qingshengii*, and *R. hoagii*	Degrade plastic C-C backbone of plastics	Enzymatic degradation of C-C backbone by para-nitrobenzylesterase and carboxylesterase.	Mohanan et al. 2020
13	*R. triatomae*	Polyester breakdown	Polyester degradation mediated by enzymes: Carboxylesterase, PLA-depolymerase, and PHB-depolymerase	Zampolli et al. 2022
14	*R. pyridinivorans GF3* strain	Degrade anthraquinone compounds	Breakdown of anthraquinone compounds by enzymatic cleavage of anthraquinone ring.	Wang et al. 2022
15	*R. pyridinivorans X1* and *X2* strain	Phenol tolerance and degradation	Enzymatic metabolization of phenol by phosphotransferase, MFS transporter, AcrR regulator, and GlpD regulator.	Peng et al. 2022
16	*R. ruber C208* strain	Polyethylene (PE) mineralization	Mineralizes of PE without external stimuli where the bacterial laccase-like multicopper oxidase (LMCO) decreases the PE molecular weight.	Zampolli et al. 2021
17	*R. tibetensis* FXJ9.536 strain	Degrade polyaromatic hydrocarbon (PAH) polychlorinated biphenyl (PCB) sand	Breakdown of organic pollutants such as PCBs and PAHs by generating intermediates (4-nitrocatechol and 1,2,4-benzenetriol).	Huang et al. 2022
18	*RhodococcusP1Y* strain	Degrade excess Abscisic acid (ABA)	ABA is utilized as its only carbon source, and energy is converted into specific metabolites, such as dehydrophaseic acid.	Yuzikhin et al. 2021
19	*Rhodococcus RL1* strain	Stress tolerance	Removal of harmful compounds from the environment. Such as quorum-quenching, mercury resistance, high-salt, extreme pH, osmotic stress resilience, biofilm formation, and the production of compounds that help plants grow and the soil stay fertile. Mechanisms Unknown	Kuhl et al. 2021

Rhodococcus RL1 strain, scientists have identified a large number of genes related to stress tolerance, bioremediation of toxic compounds, and colonization of rhizospheric biota to ensure the establishment of beneficial interactions between plants and microbes (Figure 4) (Kuhl et al. 2021). This genetic profile suggests that the *Rhodococcus RL1* strain is a tool required for interactions with other organisms, including plants, and can survive in various abiotic stress situations. *In vitro* tests were performed to analyze the practical implications of the genomic potential of the *Rhodococcus RL1* strain. The *Rhodococcs RL1* strain broke down quorum-quenching signals (important for bacterial cross-talk) and tolerated mercury stress. The *Rhodococcus RL1* strain contains genes encoding an enzyme (alkyl-mercury lyase) and a DNA-binding protein (merR family), which allows it to grow quickly in the presence of mercury (Kuhl et al. 2019). *Rhodococcs RL1* was also reported to be resistant to high salt levels (up to 7.5% NaCl), extreme acidic pH ranges (pH 2-5), and osmotic stress conditions. The strain *Rhodococcs RL1* can also form biofilms, which are important for initiating many microbial interactions (Kuhl et al. 2021). The ability of *R. cholerae RL1* to produce IAA and siderophores that collect iron from the environment helps improve soil fertility and helps in healthy plant growth. A summary of the prospective contributions of the genus *Rhodococcus* to the phytoremediation and metabolism of complex environmental pollutants is provided in Table 1.

Conclusions And Future Prospectus

The multifaceted capabilities of the bacterium *Rhodococcus* have suggested that it is an important microbe for improving plant and soil health and balancing the ecological environment. By harnessing their diverse enzymatic pathways and genetic traits, one can look forward to their respective synchronized coexistence between the agriculture sector and environmental pollution control, which could help us achieve sustainable development goals. However, through bioremediation and eco-friendly pest control, the genus *Rhodococcus* also contributes to mitigating the adverse effects of chemical toxic materials and promoting a healthy ecosystem. Concurrently, because of their ability to degrade hazardous pollutants and plastics by modulating quorum sensing ability and assisting in plant-fungal interactions, *Rhodococcus* species have been highlighted as a combination of beneficial traits because of their remarkable adaptability and resilience for improving the health of soils, plants and ecosystems. However, to gain more knowledge about the molecular mechanism, biological pathways, and protein-protein interactions responsible for such unusual traits of genus *Rhodococcus*, a detailed study will be required by employing diverse OMICs platforms. One must plan the genomics, transcriptomics, proteomics, and metabolomics investigations about the above-discussed *Rhodococcus* strains to get deeper insight into exclusive properties of genus *Rhodococcus*, and should integrate the independent outcomes by in-depth bioinformatics analysis to get more holistic bio-molecular view of multidisciplinary functional traits of genus *Rhodococcus*.

Abbreviations

2,4-DNP--2,4-Dinitrophenol; 4-NC--4-Nitrocatechol; 4-NP--4-Nitrophenol; ABA--Abscisic acid; ACs-- Anthraquinone compounds; ADH--Alcohol dehydrogenase; AHL--N-acyl homoserine lactone; AMPA--Aminomethylphosphonic acid; ASA-2--1-aminoanthraquinone-2-sulfonic acid; CAS--Chrome azurol S; HHL--N-hexanoyl-L-homoserine lactone; MO--Monooxygenase; NRPS--Nonribosomal peptide synthase; PBAT--Poly(butylene adipate-coterephthalate); PNP--Para-nitrophenol; QQ--Quorum quenching; QTP--Qinghai–Tibet Plateau; TCE--Trichloroethylene;

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Conflicts of interest

The authors declare no competitive or financial conflicts of interest.

Consent to subjects and ethics statement

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Data availability statement

The data presented in this study are available upon request from the corresponding author.

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