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Morpho-Molecular Characterization of Bacterial Endophytes from Different Banana (*Musa sp*.) Cultivars across Tamil Nadu, India

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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ABSTRACT

Banana (*Musa* spp.) is a major fruit crop in Tamil Nadu, but its productivity is severely affected by Fusarium wilt, caused by *Fusarium oxysporum* f. sp. *cubense* (*Foc*). Chemical management provides only limited, unsustainable control, emphasizing the need for eco-friendly approaches. Beneficial bacterial endophytes, which colonize plant tissues without causing harm, offer promise for plant growth promotion and biocontrol of pathogens. The present study aimed to isolate and identify bacterial endophytes from diverse banana cultivars across major growing regions of Tamil Nadu, with the long-term goal of developing sustainable disease management strategies. A survey-based experimental study was conducted at the Department of Plant Pathology, Faculty of

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Agriculture, Annamalai University, in collaboration with banana fields between July 2023 and May 2024. Field surveys were carried out in five districts representing AAA and AB genome groups cultivated on different soil types. Healthy pseudo stem and root tissues were collected, surface sterilized, and cultured on nutrient agar. Pure isolates were characterized through colony morphology, Gram staining, and biochemical assays (starch hydrolysis, citrate utilization, indole production, catalase, oxidase, methyl red). Genomic DNA was extracted by the CTAB method, and 16S rRNA gene fragments were amplified using universal primers. Ten morphologically distinct bacterial endophytes were identified. Gram-positive isolates included *Bacillus thuringiensis* and *B. velezensis*, while Gram-negative isolates comprised *Pseudomonas aeruginosa*, *Alcaligenes faecalis*, *Alcaligenes* sp., *Myroides odoratimimus*, *Stenotrophomonas maltophilia*, and *Providencia stuartii*. The isolates exhibited diverse colony and biochemical traits. Notably, *Bacillus* and *Pseudomonas* spp. are known for biocontrol and growth promotion, underscoring their potential for integration into eco-friendly management strategies against Fusarium wilt in banana cultivation.

Keywords: Banana (Musa spp.); bacterial endophytes; biochemical assay; 16S rRNA sequencing.

1. INTRODUCTION

Banana (*Musa* spp.) is one of the most important fruit crops worldwide, cultivated across more than 130 countries with an estimated annual production exceeding 125 million tonnes (FAO, 2023). India is the largest producer, contributing nearly 26% of global banana output, with Tamil Nadu being one of the leading banana growing states due to its diverse agro-ecological conditions, fertile soils, and efficient irrigation infrastructure (NHB, 2022). In 2023, Tamil Nadu recorded an estimated 109.37 thousand hectares under banana cultivation, producing 4,522.62 thousand tonnes (4.52 million tonnes), which corresponds to an average productivity of 41.3 tonnes per hectare. These figures highlight both the high yield potential of the crop and its critical role in sustaining the state's horticultural economy (CEIC Data, 2023a; CEIC Data, 2023b). The state supports cultivation of multiple genome groups, including AAA (e.g., Grand Naine), AAB (e.g., Red Banana), ABB (e.g., Monthan, Karpooravalli), and AB (e.g., Ney Poovan), each well adapted to specific soil types and climatic niches (Mustaffa & Kumar, 2012).

Despite its economic and nutritional importance, banana cultivation is challenged by serious biotic stresses, particularly Fusarium wilt caused by *Fusarium oxysporum* f. sp. *cubense* (*Foc*), which can cause yield losses up to 70-100% in susceptible cultivars (Ploetz, 2015; Azizan et al. 2025). The persistence of *Foc* in soil for decades and the lack of durable host resistance make management difficult. Conventional approaches such as chemical control, crop rotation and healthy planting material often provide limited success (Dita et al., 2018). This has created an urgent need for sustainable disease management strategies.

Endophytic bacteria that colonize internal plant tissues without causing apparent harm are increasingly recognized as key players in plant health and productivity (Compant et al., 2010). They can promote plant growth directly through phytohormone production (e.g., indole-3-acetic acid), phosphate solubilization, and nitrogen fixation and indirectly by producing siderophores, hydrolytic enzymes and antimicrobial metabolites (Santoyo et al., 2016; Zain et al. 2019). Additionally, many endophytes can induce systemic resistance (ISR) or systemic acquired resistance (SAR), priming the plant's immune system for more efficient pathogen defense (Pieterse et al., 2014).

In banana, beneficial endophytic bacteria from genera such as *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Stenotrophomonas* have been documented for their role in enhancing plant growth and suppressing Fusarium wilt (Kavino et al., 2010; Fan et al., 2023). For example, *Bacillus velezensis* strains have demonstrated potent antagonism against Foc, achieving significant reductions in disease incidence under greenhouse and field conditions (Fan et al., 2023), while *Pseudomonas aeruginosa* isolates produce phenazine derivatives and siderophores that inhibit multiple soilborne pathogens (Raaijmakers et al., 2010). However, the diversity and functional potential of endophytes are strongly influenced by host genotype, plant organ, developmental stage, and environmental conditions such as soil type and agro-ecological zone (Posada et al., 2024).

To accurately assess such diversity, morpho-molecular characterization provides a robust

framework that integrates classical and molecular methods. Morphological and biochemical traits including colony features, Gram reaction, cell morphology, and assays such as catalase, oxidase, citrate utilization, and starch hydrolysis offer preliminary taxonomic resolution (Cappuccino & Sherman, 2014). Molecular tools, particularly 16S rRNA gene sequencing, remain the standard for bacterial identification (Weisburg et al., 1991), while multilocus sequence analysis (MLSA) and next-generation sequencing (NGS) approaches provide higher phylogenetic resolution and insights into functional potential (Turner et al., 2013). Together, this integrative approach ensures reliable characterization of endophytic communities.

Although banana cultivation in Tamil Nadu spans a wide range of cultivars, soil types, and climates, systematic studies characterizing endophytic bacterial diversity across genome groups remain scarce. Most prior work in the region has focused either on a single cultivar or localized surveys without integrating morphological, biochemical, and molecular identification (Sharma et al., 2022). However, a few notable studies provide insights into banana endophytes in Tamil Nadu. For instance, Karthik et al. (2017) surveyed five cultivars (Rasthali, Hill Banana, Co1, Nattu Poovan, and Red Banana), isolating 352 bacterial endophytes across Actinobacteria, Firmicutes, and Proteobacteria, with several strains showing siderophore production, IAA synthesis, and plant growth–promoting effects. Ragavi et al. (2019) reported endophytes from the AAA cultivar Yangambi km5, identifying *Bacillus subtilis*, *Ochrobactrum daejeonense*, *Achromobacter xylosoxidans*, and *Pseudomonas aeruginosa*, which demonstrated antagonism against *Pectobacterium carotovorum*. Similarly, these studies highlight the richness of banana endophytic communities but also reveal that few investigations have employed integrative morpho-molecular characterization and comprehensive profiling of endophytic bacteria across major banana-growing districts in Tamil Nadu is therefore essential to uncover robust taxa with applications in sustainable crop production and disease management.

The present study aimed to (i) conduct a state-wide survey of banana cultivars across diverse agro-ecological regions of Tamil Nadu, (ii) isolate bacterial endophytes from pseudostem and root tissues, (iii) characterize them morphologically, biochemically, and through 16S rRNA gene sequencing, and (iv) document their taxonomic diversity as a basis for future research into their functional roles in plant growth promotion and disease suppression.

2. MATERIALS AND METHODS

2.1 Survey and Sample Collection

A field survey was conducted across major banana growing regions of Tamil Nadu to collect plant material for bacterial endophyte isolation. The locations were strategically selected to represent a wide range of agro-ecological conditions, including different soil types, cultivars, genome groups, and crop stages (Table 1). Sampling sites were georeferenced using a handheld GPS device (Garmin eTrex® 32x), and the latitude and longitude values were recorded in decimal degrees. Soil type was determined based on physical characteristics and cross-verified with the classification system of the Soil Survey and Land Use Organisation, Tamil Nadu. Information regarding cultivar, genome group, and crop age (in months) was gathered through field observation. At each site, three healthy, symptom free banana plants were randomly chosen from the central rows of the plantation to avoid border effects. Pseudo stem and root sections, measuring approximately 10–15 cm in length, were excised using sterile tools, placed in pre-labelled polyethylene bags, and stored in an insulated ice box to maintain low temperature during transportation.

2.2 Isolation of Bacterial Endophytes

Isolation of bacterial endophytes was performed within 24 hours of sample collection following a modified method of Ismail et al. (2022). Initially, plant tissues were washed under running tap water for 5–10 minutes to remove soil and debris. Surface sterilization was carried out by immersing the tissue segments (1–2 cm) in 70% ethanol for 1 minute, followed by 1% sodium hypochlorite for 30 seconds and finally rinsing them three times with sterile distilled water. The effectiveness of surface sterilization was confirmed by plating 100 µL of the final rinse water onto nutrient agar (NA) and incubating at 28 ± 2 °C for 48 hours; the absence of microbial growth indicated successful decontamination. Sterilized tissues were aseptically macerated in sterile phosphate-buffered saline (PBS, pH 7.2) using a pre-sterilized mortar and pestle. The homogenate was serially diluted up to 10^{-5}, and

100 µL from each dilution was spread evenly on NA plates. Plates were incubated at 28 ± 2 °C for 72 hours, after which morphologically distinct colonies were sub-cultured to obtain pure cultures. Isolates were designated as BBE (Banana Bacterial Endophytes), maintained on NA slants at 4 °C for short-term use, and preserved in 50% glycerol at −80 °C for long-term storage.

2.3 Morphological Characterization

The isolated bacterial endophytes from two different banana (*Musa* sp.) cultivars were subjected to preliminary morphological characterization. Colony morphology was examined on nutrient agar plates by observing characteristics such as size, shape, margin, elevation, surface texture, and pigmentation after incubation at 28 ± 2°C for 24–48 h. Cell shape (CS) was determined by preparing bacterial smears on clean glass slides, followed by heat fixation and observation under a light microscope (100× oil immersion). Gram staining (GS) was performed using the standard four step protocol: application of crystal violet (primary stain), Gram's iodine (mordant), 95% ethanol (decolouriser), and safranin (counterstain). Slides were examined microscopically to determine Gram reaction (positive or negative) and cell morphology (cocci, bacilli, or filamentous). Spore formation (SF) was assessed using Schaeffer Fulton spore staining method (Oktari et al. 2017), employing malachite green as the primary stain and safranin as the counterstain, followed by microscopic observation for endospore presence.

2.4 Biochemical Characterization

Biochemical profiling of the isolates was carried out following standard bacteriological protocols to aid in taxonomic identification. Starch hydrolysis (SH) was tested by inoculating the isolates onto starch agar plates, incubating at 28 ± 2 °C for 48 h and flooding the plates with Gram's iodine, clear halos around colonies indicated positive starch hydrolysis (Mamarasulov et al. 2022). Citrate utilization test (CUT) was performed on Simmons' citrate agar slants, where growth accompanied by a colour change from green to Prussian blue indicated positive utilization. Indole utilization test (IUT) was conducted using tryptone broth cultures incubated for 48 h, followed by the addition of Kovac's reagent, a red ring formation confirmed positive indole production. Catalase test (CT) was carried out by adding a drop of 3% hydrogen peroxide to a fresh culture smear, immediate bubble formation indicated catalase activity. Oxidase test (OT) was performed using oxidase reagent (tetramethyl-p-phenylenediamine), the appearance of a dark purple color within 30 seconds denoted a positive reaction. Methyl red test (MRT) was conducted in MR-VP broth incubated for 48 h, the addition of methyl red indicator producing a stable red color confirmed a positive result (Bulbul Roy et al. 2023).

2.5 Molecular Characterization

Genomic DNA was extracted from 24-hour-old bacterial cultures grown in nutrient broth using a modified cetyltrimethylammonium bromide (CTAB) protocol (Azeem et al. 2024). DNA concentration and purity were measured using a NanoDrop™ 2000 spectrophotometer (Thermo Scientific). The 16S rRNA gene was amplified using the universal primers 27F (5′-AGAGTTTGATCCTGGCTCAG-3′) and 1492R (5′-GGTTACCTTGTTACGACTT-3′). PCR was performed in a 25 µL reaction containing 12.5 µL of 2× PCR Master Mix (Promega), 0.5 µL of each primer (10 µM), 2 µL of template DNA, and 9.5 µL of nuclease-free water. The amplification was included an initial denaturation at 95 °C for 3 minutes, followed by 35 cycles of denaturation at 95 °C for 30 seconds, annealing at 55 °C for 30 seconds, extension at 72 °C for 90 seconds, and a final extension at 72 °C for 10 minutes. PCR products were analyzed by electrophoresis on 1% agarose gel stained with ethidium bromide and visualized under UV illumination. The amplicons (~1.5 kb) were purified using a QIAquick PCR Purification Kit (Qiagen) and sequenced bi-directionally by Eurofins Genomics (Bengaluru, India). The obtained sequences were assembled and edited using BioEdit v7.2 software, and their identities were determined by BLASTn search against the NCBI GenBank database. Phylogenetic analysis was performed in MEGA 11 using the Neighbor-Joining method with 1000 bootstrap replicates to assess branch reliability.

3. RESULTS AND DISCUSSION

3.1 Survey and Isolation of Bacterial Endophytes

A systematic survey across five major banana-growing districts of Tamil Nadu yielded 10 morphologically distinct bacterial endophyte isolates from different cultivars, genome groups, and soil types (Table 1). Sampling sites

encompassed diverse agro-ecological conditions, with soil textures ranging from sandy loam and alluvial to red loamy and clay soils. The cultivars represented included Ney Poovan (AB genome) and Red Banana (AAA genome) with crop stages varying from 7 to 9 months. Geographic coordinates of each site were recorded, confirming the wide distribution of the collected isolates across the state.

Similar patterns of endophyte diversity influenced by cultivar and environment have been reported, notably in Kenyan and global studies where sampling across soil types and developmental stages revealed rich microbial diversity (Posada et al., 2024). The presence of *Bacillus* and *Pseudomonas* as dominant endophytic genera has also been confirmed in multiple banana cultivars, including Rasthali, both through culture-dependent and -independent approaches (Santoyo et al., 2019; Sharma et al., 2022)

3.2 Morphological and Biochemical Characterization

All isolates were rod-shaped, with variation in Gram reaction, colony morphology, and biochemical profiles (Table 2). Among the isolates, BBE4, BBE31, and BBE13 were identified as Gram-positive, exhibiting red coloration, whereas the remaining isolates were Gram-negative, displaying a violet coloration. Colony morphology ranged from large, flat colonies with metallic sheen and pigmentation (BBE17, BBE48) to small, smooth, opaque colonies (BBE2, BBE39). Spore formation was detected in BBE4, BBE31, and BBE13.

In biochemical assays, all isolates were catalase positive except BBE4, BBE31, and BBE13, which showed negative reactions. Oxidase activity was observed in most isolates, with BBE4, BBE31, and BBE13 being oxidase negative. Starch hydrolysis was largely absent except in Gram-positive isolates (BBE4, BBE31, and BBE13) and citrate utilization varied among isolates. Methyl red and indole utilization tests also exhibited variable patterns, indicating metabolic diversity.

Morphological and biochemical diversity among Musa endophytes correlates with functional versatility, such as nutrient cycling and pathogen antagonism (Nguyen et al., 2023). In particular, such metabolic traits often unravels plant growth promotion and stress adaptation (Posada et al., 2024).

3.3 Molecular Identification

Partial 16S rRNA gene sequencing identified the isolates as belonging to diverse bacterial taxa (Table 3). *Pseudomonas aeruginosa* was represented by two isolates (BBE17, BBE48), while *Bacillus* sp. was identified in three isolates *B. thuringiensis* (BBE4, BBE31) and *B. velezensis* (BBE13). Other identified species included *Alcaligenes faecalis* (BBE2), *Alcaligenes* sp. (BBE39), *Myroides odoratimimus* (BBE6), *Stenotrophomonas maltophilia* (BBE9), and *Providencia stuartii* (BBE8). Amplicon sizes varied from 630 bp (BBE8) to 1,429 bp (BBE39). The molecular results confirmed the morphological and biochemical diversity observed among the isolates. Each isolates showed highest similarity and formed a close cluster related to respective groups in the Maximum likelihood phylogenetic tree analysis with a bootstrap value of 1000. The partial 16S rRNA gene sequences of the bacterial endophytes were subjected to BLAST analysis against the NCBI GenBank database. Isolate BBE17 (accession PV290431.1) showed 99% similarity with *Pseudomonas aeruginosa* strain C-1 (FJ972535.1), while BBE48 (PV290457.1) exhibited 99% similarity with *Pseudomonas aeruginosa* strain NO6 (FJ972534.1). Isolate BBE8 (PV290454.1) displayed 99% similarity with *Providencia stuartii* strain IRQDAS6 (HG427202.1). Isolate BBE9 (PV290456.1) was 98% similar to *Stenotrophomonas maltophilia* strain SWDDA-3 (FN569850.1). Isolate BBE6 (PV290455.1) showed 99% similarity with *Myroides odoratimimus* strain JRCGR-MO-1 174 (NZ_JANYMB010000174.1). Isolate BBE13 (PV290432.1) shared 99% similarity with *Bacillus velezensis* strain J50T55 (LC588630.1). Isolate BBE4 (PV290452.1) was 99% similar to *Bacillus thuringiensis* strain BTN 1254 (HF545005.1), while BBE31 (PV290453.1) exhibited 98% similarity with *Bacillus thuringiensis* strain RGT-11 (AB677944.1). Isolate BBE2 (PV290433.1) showed 99% similarity with *Alcaligenes faecalis* strain 9A4-13 (LR535791.1), and finally, isolate BBE39 (PV290449.1) shared 99% similarity with *Alcaligenes faecalis* strain MT1 (AM048879.1).

Table 1. Collection details of bacterial endophyte isolates from banana cultivars across different districts of Tamil Nadu

S.No	District	Isolate code	village	Latitude and Longitude	Soil type	Cultivar	Genome group	Crop Stage (Months)
1	Trichy	BBE17	Thottiyum	10.9833°N, 78.3333°E	Red loamy soil	Ney Poovan	AB	9
2		BBE2	Musiri	10.9333° N, 78.4500° E	Alluvial	Ney Poovan	AB	8
3		BBE4	Thuraiyur	11.1415°N, 78.5945°E	Sandy loam	Red Banana	AAA	9
4	Cuddalore	BBE6	Sivapuri	11.3728° N, 79.7134° E	Clay	Red Banana	AAA	7
5		BBE9	C. Mutlur	11.4476°N, 79.7102°E	Sandy clay	Red Banana	AAA	7
6		BBE39	Kamaya goundan Patti	9.7261°N, 77.3186°E	Red sandy loam	Red Banana	AAA	9
7	Theni	BBE31	Cumbum	9.7344°N, 77.2844°E	Red sandy loam	Red Banana	AAA	7
8	Coimbatore	BBE8	Avinashi	11.1929° N, 77.2686° E	Red loamy	Red Banana	AAA	9
9	Erode	BBE13	Sathiyamangalm	11.5048°N, 77.2384°E	Sandy loam	Ney Poovan	AB	8
10		BBE48	T.N. Palayam	11.5072° N,77.3850°E	Sandy loam	Red Banana	AAA	8

Table 2. Morphology and bio-chemical characteristics of banana bacterial endophytes

S. No.	Isolates	Colony morphology	Parameters								
			GS	CS	SF	SH	MRT	CUT	IUT	CT	OT
1	BBE17	Large, flat, metallic sheen, blue-green pigment	-	Rod	-	-	-	+	-	+	+
2	BBE2	Small, opaque, smooth	-	Rod	-	Variable	-	+	-	+	+
3	BBE4	Translucent, convex, smooth, non-pigmented	+	Rod	+	-	-	+	-	+	-
4	BBE6	Large, opaque, rough, irregular edge	-	Rod	-	Variable	-	+	Variable	+	+
5	BBE9	Smooth, glistening, yellowish, entire margins	-	Rod	-	Variable	Variable	+	-	+	Variable
6	BBE39	Small, opaque, smooth	-	Rod	-	Variable	-	+	-	+	+
7	BBE31	Translucent, convex, smooth, non-pigmented	+	Rod	+	-	-	+	-	+	-
8	BBE8	Moist, opaque, cream, smooth	-	Rod	-	-	+	+	+	+	+
9	BBE13	Cream, circular, slightly convex, rough with age	+	Rod	+	-	-	+	-	+	-
10	BBE48	Large, flat, metallic sheen, blue-green pigment	-	Rod	-	-	-	+	-	+	+

GS- Gram staining
CS- Cell shape
SF- Spore formation
SH- Starch hydrolysis
MRT- Methyl red test
CUT- Citrate utilization test
IUT- Indole utilization test
CT- Catalase test
OT- Oxidase test

Fig. 1. Axenic cultures of bacterial endophytes from two different banana cultivars

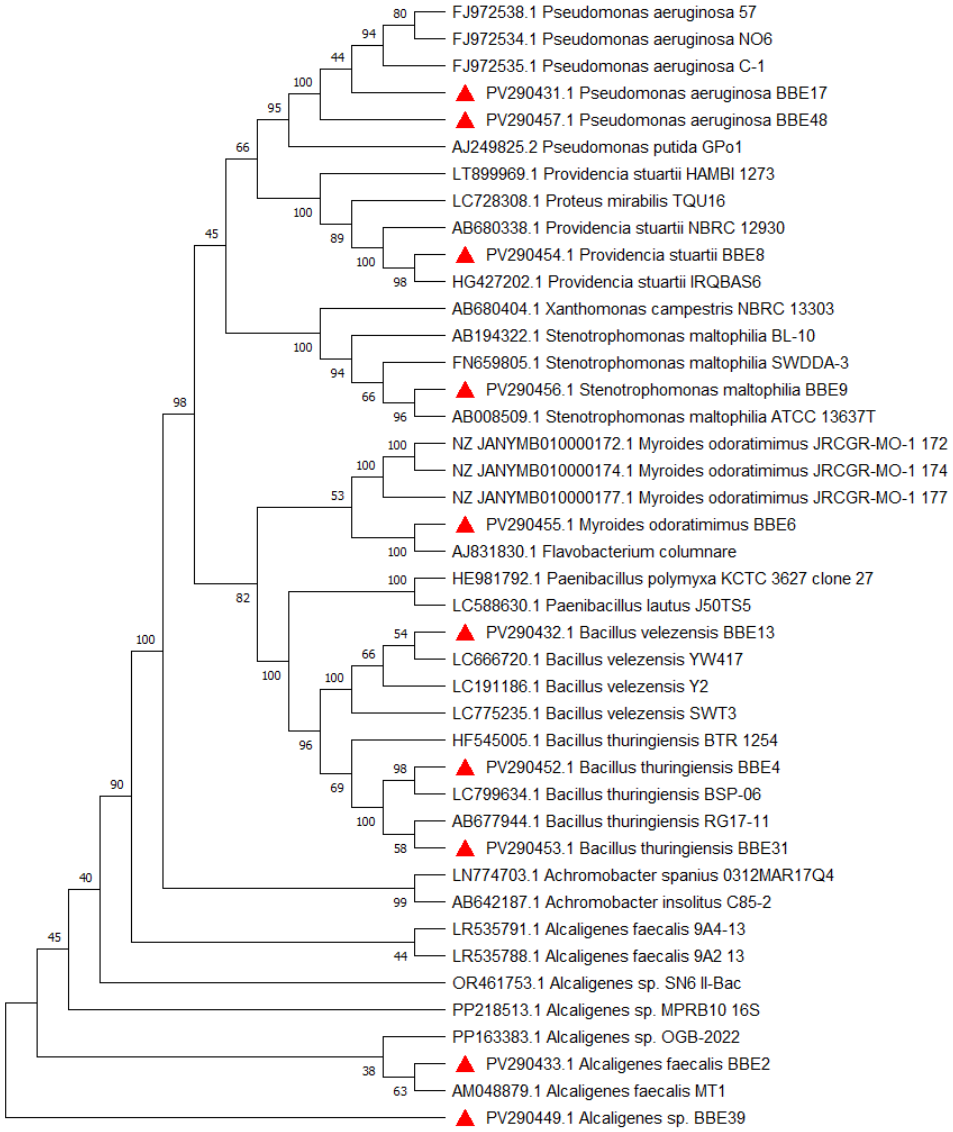

Fig. 2. Phylogenetic tree of banana bacterial endophytes based on 16S rRNA sequences. The tree was generated using the Neighbor-Joining method with 1,000 bootstrap replications

Table 3. Molecular characterization of banana bacterial endophytes

Isolate code	Organisms	Accession numbers	Amplicon size (bp)
BBE17	*Pseudomonas aeruginosa*	PV290431	972
BBE2	*Alcaligenes faecalis*	PV290433	838
BBE4	*Bacillus thuringiensis*	PV290452	840
BBE6	*Myroides odoretimimus*	PV290455	1412
BBE9	*Stnotrophomonas maltophilia*	PV290456	770
BBE39	*Alcaligenes sp.*	PV290449	1429
BBE31	*B. thuringiensis*	PV290453	769
BBE8	*Providencia stuartii*	PV290454	630
BBE13	*B. velezensis*	PV290432	839
BBE48	*Pseudomonas aeruginosa*	PV290457	978

The prevalence of *Bacillus* and *Pseudomonas* aligns with existing literature, where these genera are consistently predominant in banana endophyte communities and implicated in disease resistance (Santoyo et al., 2019; Fan et al., 2023). Notably, *B. velezensis* has been shown to suppress *Fusarium oxysporum* f. sp. *cubense* effectively achieving up to ~81% disease reduction in in vivo trials (Fan et al., 2023). The identification of less-reported genera such as *Alcaligenes*, *Myroides*, *Stenotrophomonas*, and *Providencia* enriches the known endophytic diversity in banana and suggests untapped functional potential (Posada et al., 2024).

4. CONCLUSION

The study revealed a diverse assemblage of bacterial endophytes inhabiting different banana (Musa spp.) cultivars across Tamil Nadu, encompassing both Gram-positive and Gram-negative taxa such as *Bacillus thuringiensis*, *B. velezensis*, *Pseudomonas aeruginosa*, *Stenotrophomonas maltophilia*, *Alcaligenes faecalis*, *Myroides odoratimimus*, and *Providencia stuartii*. Their morpho-biochemical and molecular diversity underscores the strong influence of cultivar and agro-ecological conditions on endophyte composition. The findings provide a foundational resource for functional validation and future integration of endophytes into sustainable crop health strategies.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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