

Endophytic Biofertilizer Approach for Sustainable Rice Production: A Systematic Review of Mechanisms, Climate Resilience, And Greenhouse Gas Mitigation Pathways

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ABSTRACT

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Climate change, soil degradation, and dependence on synthetic fertilizers increasingly threaten the productivity and sustainability of lowland rice farming in tropical Asia. Microbial endophytic biofertilizers, comprising beneficial bacteria and fungi that colonize internal plant tissues, offer a promising biological intervention to address these compounding challenges. This study employs a Systematic Literature Review using PRISMA methodology, complemented by bibliometric analysis via VOSviewer, to assess the multifunctional roles of microbial endophytic biofertilizers in enhancing soil and plant microbiome health, nutrient-use efficiency, abiotic stress tolerance, and potential greenhouse gas mitigation in rice-based agroecosystems. A total of 20 peer-reviewed studies meeting strict inclusion criteria related to rice-associated endophytic biofertilizers and climate-related outcomes published between 2015 and May 2026 were synthesized from Scopus and ScienceDirect databases. Bibliometric analysis identified four dominant research clusters: plant growth promotion and physiology, abiotic stress and climate resilience, microbiome and soil ecology, and microbial taxonomy and ecological diversity. The findings demonstrate that endophytic inoculation confers measurable benefits across major climate-related stressors, with yield improvements under saline conditions reaching 203.96%, cold stress survival rising from 22.67% to 66.67%, and nitrogen and phosphorus losses reduced by 24.59% and 17.46% per pot, respectively. Consortium-based formulations consistently outperformed single-strain inoculants, and endophytes function as microbiome engineers, reshaping rhizosphere and endosphere assembly. Multiple mechanistic pathways linking endophyte inoculation to reduced CH₄ and N₂O emissions were identified, though direct field-scale flux quantification remains absent and represents the most critical research gap. Future research should prioritize region-specific consortium development, omics-based field validation, and policy frameworks supporting endophyte-based biofertilizers within national low-emission rice farming strategies.

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1. INTRODUCTION

Climate change, characterized by rising temperatures, erratic rainfall, soil salinization, and declining land fertility, poses a significant threat to rice (*Oryza sativa* L.) production, which serves as the staple food for much of the global population, particularly across tropical Asia. In Asian rice systems, a 1 °C increase in mean temperature can reduce yields by 5–7% in the absence of adequate adaptation (Matthews et al., 1997; Nazarudin, 2024). Conventional agricultural practices dependent on synthetic fertilizers

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boost short-term yields but generate substantial ecological costs, including soil degradation, soil acidification, biodiversity loss, and elevated greenhouse gas emissions of CH₄ and N₂O (Kumar et al., 2022; Slameto et al., 2024). Globally, agricultural activities account for about 10–12% of total anthropogenic greenhouse gas emissions, while intensive flooded rice systems with high nitrogen inputs can emit several hundred kilograms of CO₂ equivalent per hectare per growing season (IPCC, 2007; Hanarisanty et al., 2022).

The soil and plant microbiome plays a central role in maintaining agroecosystem health, contributing to nutrient cycling, pathogen suppression, and stress resilience. Most terrestrial plants form functional associations with endophytic and rhizosphere microorganisms that influence growth, nutrient acquisition, and stress tolerance (Kandel et al., 2017; Tariq et al., 2025). In flooded rice systems, inoculation with nitrogen-fixing endophytes and phosphate-solubilizing bacteria markedly improves nutrient-use efficiency and yields; specific endophytic isolates increased plant nitrogen uptake by 55–80% (Zain et al., 2018), and multistrain consortia produced the highest grain yields in low-fertility Inceptisols (Wuriesyliane et al., 2013).

Endophytic biofertilizers are fertilizer formulations containing beneficial bacteria or fungi capable of colonizing internal plant tissues without inducing disease (Kandel et al., 2017; Tariq et al., 2025). Unlike rhizospheric microbes, endophytes form direct and stable associations within plant tissues, delivering more consistent improvements under field conditions. Endophytic biofertilizers can restore soil health, improve nutrient-use efficiency, and reduce environmental impacts of intensive cultivation (Kumar et al., 2021; Aishwarya et al., 2025), while microbial biofertilizers have been shown to suppress greenhouse gas emissions from rice paddy fields and support climate-adaptive rice farming (Sakoda et al., 2022; Rios-Ruiz et al., 2023). Endophytic microbes enhance nitrogen acquisition through biological nitrogen fixation, increase mineral availability, modulate phytohormone production, and reinforce stress responses (Aishwarya et al., 2025; Sahoo et al., 2025; Mani et al., 2023). Recent microcosm studies indicate that endophyte colonization can increase rice inorganic nitrogen use efficiency approximately twofold and reduce cumulative N₂O emissions by 13–21% in paddy soils through the dissimilatory nitrate reduction to ammonium (DNRA) pathway (Liu et al., 2025). Specific demonstrations in rice also include enhanced antioxidant enzyme activity and increased nitrogen, carbon, and chlorophyll content following endophyte colonization (Bianco et al., 2021), improved mineral nutrition, grain quality and yield via endophytic fungal inoculation (Tang et al., 2022), and inhibition of cadmium uptake by endophytic growth-promoting bacteria (Tian et al., 2022). These benefits collectively position endophytic biofertilizers as a promising biological strategy for reducing synthetic fertilizer dependence and supporting low-emission, climate-adaptive rice production.

Therefore, this review synthesizes current evidence on the mechanisms by which endophytic biofertilizers enhance rice productivity, improve soil and plant microbiome health, nitrogen-use efficiency, and greenhouse gas mitigation, while identifying challenges related to endophyte–host specificity, field-scale consistency, and integration with crop management practices. The novelty of this review lies in integrating endophyte-based biological interventions with climate resilience frameworks (Sena et al., 2024; Rudgers et al., 2020; Ahmed et al., 2022) and low-emission pathways relevant to tropical lowland rice systems in Indonesia and broader Southeast Asia (Slameto et al., 2024; Hanarisanty et al., 2022)

2. MATERIALS AND METHODS

2.1 Data Collection for Bibliometric Analysis

This study is based on a systematic literature review of peer-reviewed research articles published between 2015 and 2026. Relevant articles were identified through two major academic databases, namely Scopus and ScienceDirect. The search terms were constructed around five thematic dimensions: endophytic biofertilizers, nitrogen fixation, greenhouse gas mitigation, climate resilience, and soil microbiome health in rice farming systems. The search terms used included "endophytic biofertilizer," "endophyte," "rice," "nitrogen fixation," "methane," "greenhouse gas," "climate resilience," "soil microbiome," "stress tolerance," and "low emission."

Inclusion criteria focused on peer-reviewed English-language research articles examining the ecological, agronomic, and environmental roles of microbial endophytes in rice-based agroecosystems. Articles were excluded if they (1) were published outside the 2015 to 2026 period, (2) did not specifically address rice or endophytic microorganisms, (3) were not classified as original research articles, or (4) were not available in open access. Selected studies were then reviewed and categorized based on findings related to the agronomic functions of endophytic biofertilizers, abiotic stress tolerance mechanisms, greenhouse gas mitigation, and the health of soil and plant microbiomes. Data were synthesized and analyzed to identify research trends, knowledge gaps, and directions for future research. The search strategy and screening procedures used to identify relevant articles are summarized in Table 1.

2.2 Systematic Literature Review Using PRISMA

This systematic literature review followed the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines, complemented by bibliometric analysis using VOSviewer, to evaluate the multifunctional roles of microbial endophytic biofertilizers in enhancing soil and plant microbiome health for climate-resilient and low-emission rice farming. A comprehensive search and data extraction process was performed in the Scopus and ScienceDirect databases to ensure that high-quality and up-to-

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date findings were obtained. The entire review process, covering identification, screening, eligibility assessment, and inclusion of articles, is illustrated in Figure 1.

2.3 Data Analysis

Selected articles were systematically coded and analyzed using two complementary approaches: qualitative synthesis and bibliometric mapping. Qualitative analysis focused on categorizing findings into five main thematic areas: (1) the agronomic functions of endophytic biofertilizers as nutrient providers and phytohormone regulators; (2) abiotic stress tolerance mechanisms that support climate-resilient rice systems; (3) the potential of microbiome-based inoculants in reducing CH₄ and N₂O emissions; (4) contributions to the stability and health of soil and plant microbiomes; and (5) practical implications and adoption challenges at the field level.

Bibliometric analysis was performed using VOSviewer software to map co-occurrence networks of keywords, identify dominant research clusters, and visualize publication-year trends within the endophyte and rice research domain. A binary counting method was applied with a minimum keyword-occurrence threshold adjusted in line with the final VOSviewer output to produce a representative network of significant research terms. This dual-analytical approach allows comprehensive evaluation of the ecological, agronomic, and environmental dimensions of endophytic biofertilizer applications in rice-based farming systems.

Table 1. Search strategy used to identify relevant research articles

Search Strategy	Scopus	ScienceDirect
Endophytic biofertilizer AND rice AND nitrogen fixation	6	95
Endophyte AND rice AND greenhouse gas AND methane	0	8
Endophytic bacteria AND rice AND climate resilience AND stress	1	66
Soil microbiome AND rice AND endophyte AND sustainability	1	154
Rice AND endophyte AND low emission AND biofertilizer	0	23
Total	8	346

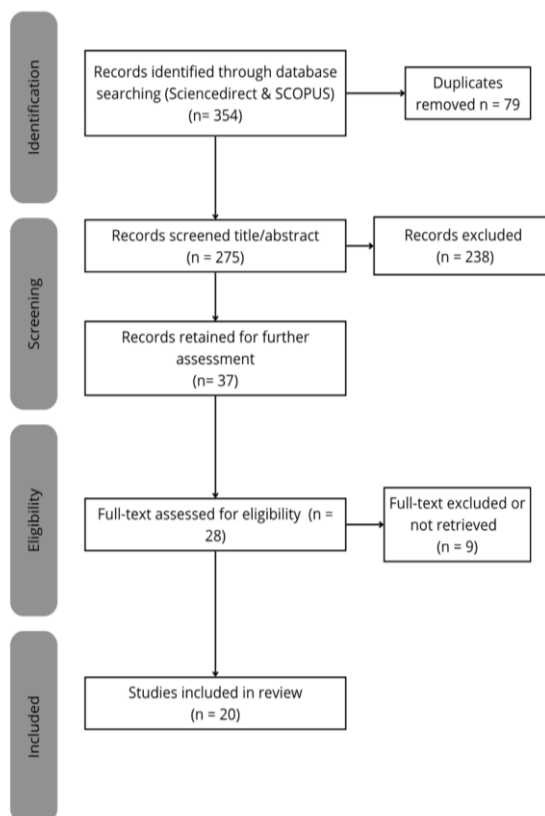


Figure. 1 PRISMA flow diagram illustrating the article selection process.

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3. RESULTS AND DISCUSSION

3.1 Bibliometric Analysis of Endophyte and Rice Research Trends

The bibliometric analysis was performed using VOSviewer to map the co-occurrence of keywords from the selected publications. A binary counting method was applied with an adjusted minimum-occurrence threshold to capture representative terms across the corpus. The resulting network reveals the principal research directions linking microbial endophytes with rice productivity, soil microbiome health, and climate resilience.

Although the analytical window emphasizes publications from 2019 to May 2026 and predominantly reflects research output from Asia, particularly China, India, and Southeast Asia, this regional concentration is itself an informative finding. It mirrors where rice agroecosystems face the strongest convergence of climate, soil-degradation, and food-security pressures, and where endophyte-based biofertilizer innovation is therefore advancing most rapidly. The keyword network captures the dominant themes in the field while providing a foundation that future studies can extend across longer time horizons.

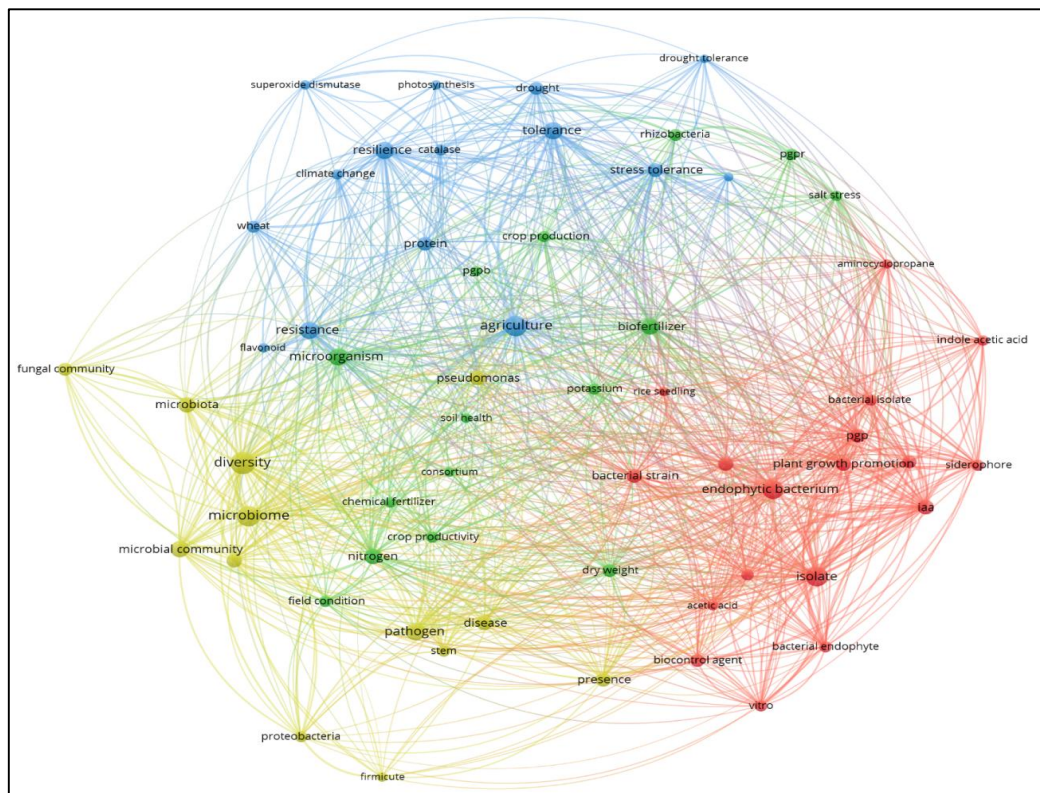


Figure 2. Network visualization of co-occurrence mapping in endophytic research

The VOSviewer network visualization (Figure 2) reveals four thematic clusters reflecting the multifunctional nature of endophyte and rice research. The first cluster centers on plant growth promotion and physiology, dominated by terms such as endophytic bacterium, plant growth promotion, PGP, IAA, indole acetic acid, siderophore, bacterial isolate, bacterial endophyte, biocontrol agent, and isolate. The second cluster emphasizes abiotic stress and climate resilience, with prominent keywords including tolerance, stress tolerance, resilience, drought, drought tolerance, climate change, catalase, photosynthesis, superoxide dismutase, salt stress, and PGPR. The third cluster reflects microbiome, soil ecology, and crop productivity, characterized by terms such as microbiome, microbial community, diversity, nitrogen, crop productivity, pathogen, field condition, chemical fertilizer, consortium, soil health, and stem. The fourth cluster captures microbial taxonomy and ecological diversity, represented by terms including fungal community, microbiota, proteobacteria, firmicute, Pseudomonas, microorganism, flavonoid, resistance, agriculture, and biofertilizer. The structural arrangement of these four clusters, summarized in Table 2, indicates that endophyte and rice research is no longer confined to single-strain functional screening but is converging toward integrated approaches that link microbial ecology, plant physiology, and sustainable agricultural intensification.

Table 2. A selection of terms organised into clusters according to the analysis of textual data

Cluster	Color	Research focus	Key keywords
Cluster 1	Red	Plant growth promotion and physiology	Endophytic bacterium, plant growth promotion, PGP, IAA, indole acetic acid, siderophore, bacterial isolate, bacterial endophyte, biocontrol agent, isolate

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Cluster 2	Blue	Abiotic stress and climate resilience	Tolerance, stress tolerance, resilience, drought, drought tolerance, climate change, catalase, photosynthesis, superoxide dismutase, salt stress, PGPR
Cluster 3	Green	Microbiome, soil ecology, and crop productivity	Microbiome, microbial community, diversity, nitrogen, crop productivity, pathogen, field condition, chemical fertilizer, consortium, soil health, stem
Cluster 4	Yellow	Microbial taxonomy and ecological diversity	Fungal community, microbiota, proteobacteria, firmicute, Pseudomonas, microorganism, flavonoid, resistance, agriculture, biofertilizer

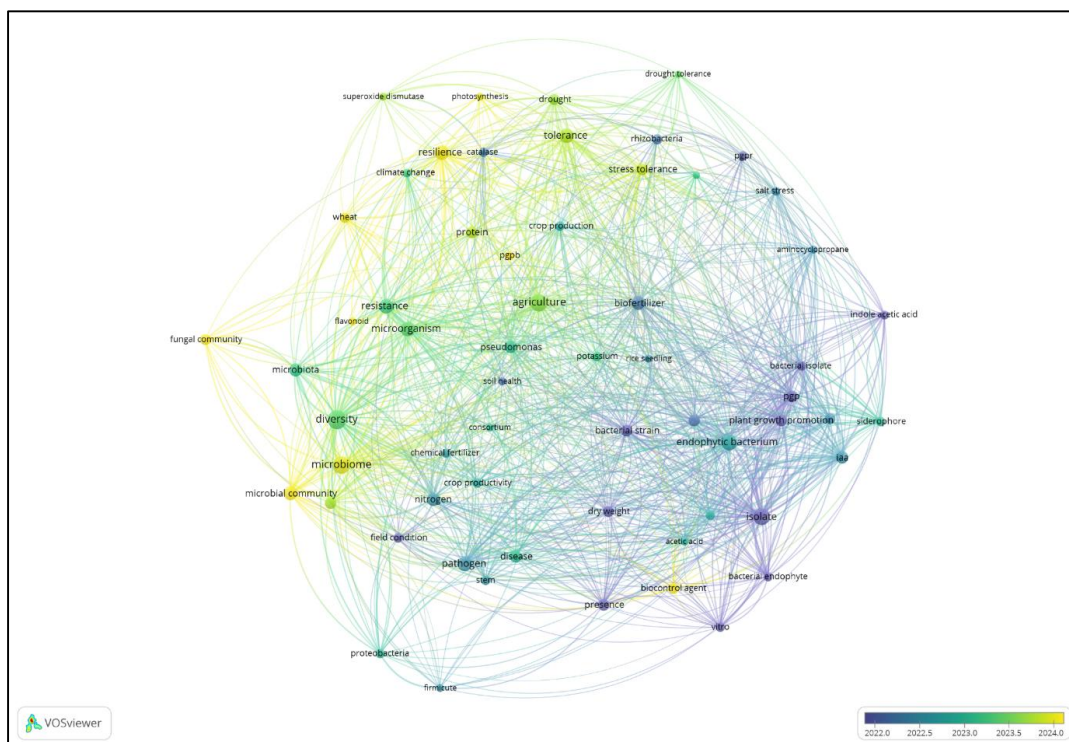


Figure. 3 Overlay visualization of publication year trends in endophytic research

The overlay visualization of publication years (Figure 3) reveals a clear temporal shift in research priorities. Earlier studies (2019 to 2021) primarily focused on classical plant growth-promoting (PGP) trait screening, bacterial endophyte characterization, and biocontrol activity against rice pathogens (Kumar et al., 2020; Krishnamoorthy et al., 2020; Soldan et al., 2019; Shen et al., 2019). From 2022 onward, the research front has moved toward microbiome-level analyses, holobiont concepts, abiotic-stress amelioration under climate change, and the use of mangrove- and wild-rice-derived endophytes as novel inoculant sources (Tian et al., 2024; Dai et al., 2025; Zeng et al., 2025; Alghamdi et al., 2025; Lal et al., 2026). This temporal trajectory indicates a maturation of the field from descriptive isolate-level studies to mechanistic and ecological frameworks that explicitly link endophyte inoculation with climate-adaptive rice production.

The density visualization (Figure 4) further confirms that the research field is currently concentrated around four high-density nodes: endophytic bacteria with PGP traits, abiotic stress tolerance (particularly salinity and cadmium), rice microbiome and soil ecology, and microbial taxonomic diversity. Notably, the keywords "low emission" and "greenhouse gas mitigation" remain relatively peripheral in the network, suggesting a research gap and an opportunity for future investigations to explicitly couple endophyte-based biofertilization with CH₄ and N₂O mitigation in flooded rice ecosystems.

Overall, the bibliometric mapping demonstrates that endophyte research in rice systems has evolved from isolated PGP-trait screening toward integrated microbiome-centered, climate-adaptive strategies. The convergence of plant physiology, microbial ecology, and sustainability themes positions microbial endophytic biofertilizers as a multifunctional tool capable of supporting climate-resilient, low-emission rice farming.

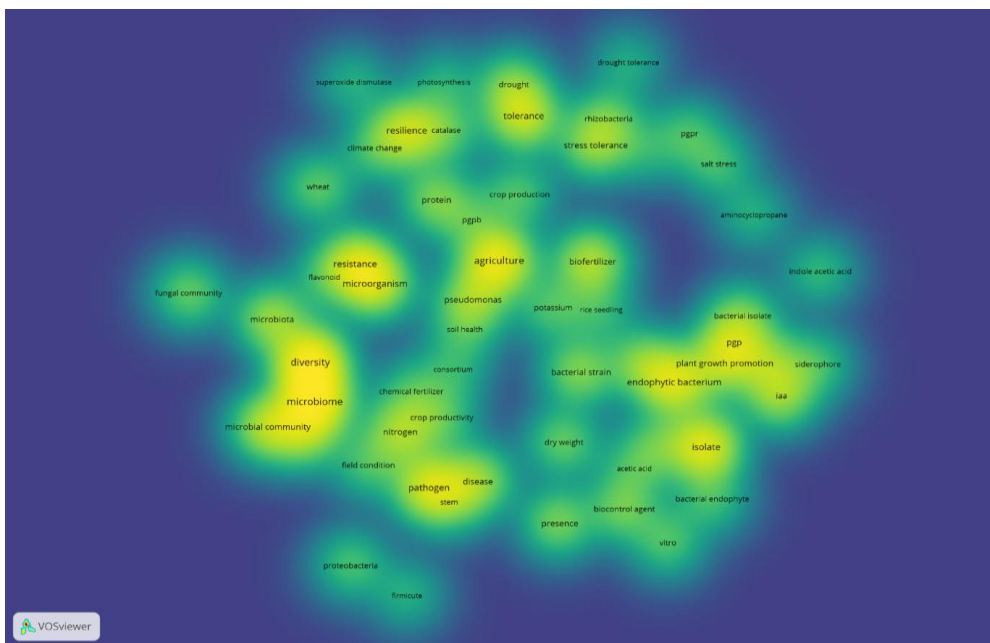


Figure 4. Density visualization of co-occurrence mapping for key keywords in endophytic research

3.2 Climate-Induced Constraints in Lowland Rice and the Role of Endophytic Biofertilizers in Mitigation

Climate change exerts cascading pressures on lowland rice systems through rising temperatures, irregular rainfall, flooding, soil salinization, drought, cold spells, and accumulation of heavy metals such as cadmium (Cd) in paddy soils. These stressors impair germination, reduce seedling vigor, disrupt nutrient uptake, increase oxidative damage, and ultimately compromise yield and quality (Zhao et al., 2024; Lal et al., 2026; Alghamdi et al., 2025). The conventional response—increased application of synthetic fertilizers and agrochemicals—exacerbates soil degradation, destabilizes the soil microbiome, and intensifies CH₄ and N₂O emissions from flooded paddies. Microbial endophytic biofertilizers offer a biologically grounded alternative: unlike rhizospheric microbes, endophytes colonize internal plant tissues (roots, stems, leaves, seeds), forming a direct and stable interface with plant metabolism (Tang et al., 2025; Wang et al., 2023; Zhao et al., 2024).

3.2.1 Salinity Stress

Salinity is one of the most pervasive climate-related stresses in coastal lowland rice systems. Endophytes from saline ecosystems—particularly mangrove propagules and halophytic wild rice—show exceptional capacity to confer salt tolerance to cultivated rice. Dai et al. (2025) showed that *Delftia tsuruhatensis* DYX29, isolated from *Kandelia obovata* mangrove propagules, tolerated 5% NaCl, produced siderophores (87.6% unit value), and exhibited ACC deaminase activity (29 U L⁻¹). Under salt stress, DYX29 increased rice biomass by 32.9%, soluble sugars by 23.1%, CAT by 37.8%, and POD by 88.2%; root IAA, brassinolide, ABA, and SA increased by 27.8%, 69.5%, 123.7%, and 28.6%, respectively. Soldan et al. (2019) reported *Gordonia terrae* KMP456-M40, also from mangrove propagules, increased rice biomass by 62% under axenic saline conditions and barley ear weight by 65% under non-axenic conditions.

Airin et al. (2023) extended this paradigm using endophytic fungi from the halophytic wild rice *Oryza coarctata*. *Aspergillus welwitschiae* AwOcstreb1 outperformed two *Talaromyces* strains at 900 mM salinity, conferred yield improvements of 125.16% (control) and 203.96% (saline), upregulated SOS1 1.6-fold, and reduced H₂O₂, electrolyte leakage, and Na⁺/K⁺ ratios. Alghamdi et al. (2025) demonstrated that mangrove-derived bacterial strains and their combinations enhanced flooding and salinity tolerance in *O. sativa* cv. Nipponbare via ABA signaling and lignin/suberin deposition. Salt-tolerance induction is therefore not driven by a single mechanism but by coordinated ACC deaminase activity, osmotic adjustment, antioxidant activation, ionic homeostasis, hormonal modulation, and structural cell-wall reinforcement.

3.2.2 Cold Stress

Zhao et al. (2024) demonstrated that *Microbacterium testaceum* M15, a seed endophyte from cold-tolerant cultivar JG117, enhanced cold tolerance in cold-sensitive CB9. M15 inoculation increased germination at 14 °C from 40% to 56.67% and survival at 4 °C from 22.67% to 66.67%, with chlorophyll increasing >30%, total protein 16.31%, CAT 26.15%, and MDA reduced by 37.76%. Shi et al. (2024) tested a consortium (PAB) of *Piriformospora indica*, *Agrobacterium rhizogenes*, and *Bacillus subtilis*: under cold stress at 4 °C, co-inoculation increased root length by 75.7%, enhanced photosynthesis, osmolytes, antioxidant enzymes, and upregulated cold-tolerance genes, while reducing MDA and electrolyte leakage. This indicates that synergistic consortia exceed the protective capacity of single-strain inoculants.

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3.2.3 Drought, Cadmium Toxicity, and Biotic Stresses

Lal et al. (2026) showed that *Fusarium incarnatum* K23 and *F. equiseti* SF5 restored root-to-shoot ratios by 10–11% under drought, with variety-specific reproductive enhancements. For cadmium toxicity, Tian et al. (2024) combined *Herbaspirillum* sp. R3 with Fe-Mn biochar, reducing Cd in roots, stems, and leaves by 49.28%, 29.31%, and 25.64%, while altering populations of Sideroxydans, Ideonella, and Geobacter. Xiang et al. (2024) showed the *Pseudomonas* 4N2 + *Bacillus* TB1 consortium reduced shoot Cd from 30% to 6% (cultivar 728B) and 31% to 13% (BB), while increasing POD by 7.37–18.18% and CAT by 13.65–30.72%.

On biotic stress and wind resistance, Tu et al. (2024) demonstrated that *Bacillus velezensis* LS123N seed-treatment controlled five rice diseases simultaneously and reduced lodging by 53–73%, with endophytic persistence of 78 days. Muthu Narayanan et al. (2024) showed mangrove endophytic fungi (MEFN02, MEFN06) reduced sheath blight (DSI 24–46%) and increased yield by $\geq 50\%$. A comprehensive summary of endophyte contributions across climate-related stressors is presented in Table 3.

Table 3. Contribution of microbial endophytic biofertilizers to rice resilience under climate-related stresses.

Stressor	Representative endophyte(s)	Key contribution	Reference
Salinity ($\leq 5\%$ NaCl)	<i>Delftia tsuruhatensis</i> DYX29	↑ Biomass 32.9%, soluble sugars 23.1%, CAT 37.8%, POD 88.2%; modulated IAA, BL, ABA, SA	Dai et al. (2025)
Salinity (axenic)	<i>Gordonia terrae</i> KMP456-M40	↑ Rice biomass 62% under salt stress; ↑ barley ear 65%	Soldan et al. (2019)
Salinity (900 mM)	<i>Aspergillus welwitschiae</i> AwOcostreb1	↑ Yield 125.16% (control), 203.96% (saline); ↑ <i>SOS1</i> 1.6-fold; ↓ H ₂ O ₂ , EL, Na ⁺ /K ⁺	Airin et al. (2023)
Salinity flooding +	Mangrove endophytic bacteria (KAUST strains)	↑ Growth, yield, grain quality of Nipponbare; ABA signaling, lignin/suberin deposition	Alghamdi et al. (2025)
Cold (4–14 °C)	<i>Microbacterium testaceum</i> M15	Germination 40→56.67% (14 °C); survival 22.67→66.67% (4 °C); chlorophyll +30%, MDA -37.76%	Zhao et al. (2024)
Cold (4 °C)	<i>P. indica</i> + <i>A. rhizogenes</i> + <i>B. subtilis</i> (PAB)	Root length +75.7%; ↑ photosynthesis, osmolytes, antioxidants; ↑ cold-tolerance gene expression	Shi et al. (2024)
Drought	<i>Fusarium incarnatum</i> K23, <i>F. equiseti</i> SF5	Restored root:shoot ratio 10–11%; ↑ panicle/grain weight; variety-specific efficacy	Lal et al. (2026)
Cd toxicity	<i>Herbaspirillum</i> sp. R3 + Fe-Mn biochar	↓ Cd in roots 49.28%, stems 29.31%, leaves 25.64%; altered key taxa	Tian et al. (2024)
Cd toxicity	<i>Pseudomonas</i> 4N2 + <i>Bacillus</i> TB1 consortium	↓ Shoot Cd 30→6% (728B), 31→13% (BB); ↑ POD 7.37–18.18%, CAT 13.65–30.72%	Xiang et al. (2024)
Multiple diseases + wind	<i>Bacillus velezensis</i> LS123N	↓ Blast severity (3.3→2.3); ↓ brown spot 34%; ↓ lodging 53–73%; persists 78 days	Tu et al. (2024)
Sheath blight (<i>R. solani</i>)	Mangrove endophytic fungi (MEFN02, MEFN06)	DSI 24–46%; ↑ growth 8–15%; ↑ yield $\geq 50\%$	Muthu Narayanan et al. (2024)

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3.3 Core Mechanisms of Endophytic Biofertilizers in Climate-Resilient Rice Systems

Synthesis of the 20 eligible studies reveals four interconnected core mechanisms: (i) biological nitrogen fixation, nutrient mobilization, and phytohormone signaling; (ii) ACC deaminase activity and oxidative-stress amelioration; (iii) induced systemic resistance and pathogen antagonism; and (iv) microbiome modulation in the rhizosphere and endosphere.

3.3.1 Nitrogen Fixation, Nutrient Mobilization, and Phytohormone Signaling

Rice tissues harbor a remarkable diversity of endophytes microorganisms capable of fixing atmospheric nitrogen, nutrient mobilization and phytohormone production. Roy et al. (2023) isolated 226 fungal endophytes from ten indigenous rice cultivars; of 26 PGP-screened isolates, 84.61% produced siderophores, 76.92% solubilized phosphate, 84.61% produced ammonia, and all grew on N-free Jensen's medium, with IAA production ranging from 1.52 to 43.89 mg mL⁻¹. Krishnamoorthy et al. (2020) identified nine seed-transmitted bacterial endophytes (PB001–PB009) exhibiting multiple PGP traits and seed priming with these isolates increased grain number per plant by up to a 182.87%. Kumar et al. (2020) isolated 32 bacterial endophytes from six rice varieties, with 53.1% producing IAA, 28.1% siderophores, and 56.2% solubilizing phosphate. Tang et al. (2025) isolated 163 endophytic strains from *Oryza longistaminata*, with ≥97% exhibiting one or more PGP traits and inoculation increasing rice height to 41.32 cm and N content to 13.15 g kg⁻¹. Tian et al. (2023) characterized 96 endophytic strains from *Oryza officinalis* with tissue-specific biomarkers and multiple PGP capacities including ACC deaminase activity.

A critical mechanistic study by Tang et al. (2019) used the endophytic fungus *Phomopsis liquidambari* to demonstrate that endophyte–rice symbiosis reduced nitrogen and phosphorus losses by 24.59% and 17.46% per pot, respectively, in nutrient-limited paddy soil. High-throughput sequencing and co-occurrence network analysis showed altered activation of N and P cycling functional genes and reshaped rhizosphere microbiota during the heading stage. Beyond nutrient supply, endophytes modulate plant hormonal balance: Dai et al. (2025) reported that *D. tsuruhatensis* DYX29 increased rice root IAA, brassinolide, abscisic acid (ABA), and salicylic acid (SA) by 27.8–123.7% under saline conditions. Shen et al. (2019) reported *Bacillus aryabhatai* MN1 produced IAA in a tryptophan-dose-dependent manner while tolerating two fungicides (etridiazole, metalaxyl), demonstrating compatibility with fungicide-intensive cultivation.

3.3.2 ACC Deaminase, Antioxidant Defense, and Osmoprotectants

ACC deaminase activity, which hydrolyzes the ethylene precursor 1-aminocyclopropane-1-carboxylate, is one of the most consistently reported abiotic-stress mitigation mechanisms. Dai et al. (2025) reported 29 U L⁻¹ ACC deaminase activity for DYX29; Tian et al. (2023) identified 96 endophytes with ACC deaminase activity; Airin et al. (2023) reported robust ACC deaminase activity in AwOstreb1, contributing to salt-stress amelioration. By reducing stress-induced ethylene, ACC deaminase prevents premature senescence and supports root elongation under salinity, drought, and flooding. Inoculation also activates plant antioxidant systems: Dai et al. (2025) showed CAT and POD activities increased by 37.8% and 88.2%; Xiang et al. (2024) showed the 4N2-TB1 consortium increased POD by 7.37–18.18% and CAT by 13.65–30.72% under Cd; Zhao et al. (2024) reported M15 decreased MDA by 37.76% and increased catalase by 26.15% under cold; Shi et al. (2024) confirmed the PAB consortium enhanced antioxidant enzymes and osmoregulators at 4 °C; and Roy et al. (2023) showed fungal consortia (AM34, AM10) elevated peroxidase, polyphenol oxidase, chitinase, and SOD activities.

3.3.3 Induced Systemic Resistance and Pathogen Antagonism

Endophytes contribute to disease management through direct antagonism, hydrolytic enzymes and antimicrobial metabolites, and induced systemic resistance. Kumar et al. (2020) identified *Bacillus subtilis* NIBSM_OsR10 carrying surfactin, iturin D, and bacillomycin D biosynthetic genes with activity against *Xanthomonas oryzae* pv. *oryzae*, *Rhizoctonia solani*, *Fusarium verticillioides*, and *Sclerotium rolfsii*. Tu et al. (2024) demonstrated *B. velezensis* LS123N controlled five rice diseases simultaneously through hydrolytic enzymes, siderophores, IAA, and phosphate solubilization, persisting 78 days post-treatment. Roy et al. (2023) found fungal consortia from indigenous rice cultivars exhibited antagonism against *Magnaporthe grisea* with elevated defense-enzyme production.

3.3.4 Microbiome Modulation: From Inoculant to Microbiome Engineer

An important emerging theme among the reviewed studies is the capacity of endophytes as microbiome modulators. Wang et al. (2023) inoculated tissue-cultured rice with the seed core endophyte *Xanthomonas sacchari* JR3-14 and tracked communities across 148 samples. Early inoculation enhanced α -diversity in root and stem endospheres, increased network complexity across growth stages, and co-enriched four beneficial taxa: *Bacillus*, *Azospira*, *Azospirillum*, and *Arthrobacter*. Phylogenetic-bin null model analysis showed drift dominated root compartments while deterministic assembly dominated stem compartments. Zeng et al. (2025) advanced the holobiont concept: *Acrocalymma vagum* A21 from wild rice *Oryza granulata* increased shoot height 44.41% and biomass 70.21%, released coumaric and trans-ferulic acid to recruit beneficial microbes, and engaged rice peroxidases (OsPRX70, OsPRX95)—CRISPR/Cas9 mutants of these genes abolished growth promotion. Four fungal genes (*AvGH3*, *AvGH7*, *AvMFS1*, *AvCBA*) were essential for colonization without pathogenicity. Tian et al. (2024) showed *Herbaspirillum* sp. R3 reshaped root communities, modulating *Sideroxydans*, *Ideonella*, and *Geobacter* abundances; Tang et al. (2019) showed *P. liquidambari* altered

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the rhizosphere bacterial network during heading. Together, these studies reposition endophytic biofertilizers from "single-strain inoculants" to "microbiome engineers" capable of long-term ecological intervention.

3.4 Greenhouse Gas Mitigation Pathways

The link between endophytic biofertilizers and greenhouse gas (GHG) mitigation in lowland rice farming represents one of the most consequential frontiers. Conventional flooded systems are major sources of CH₄ (via anaerobic decomposition by methanogens) and N₂O (via inefficient N-fertilizer use and denitrification). Although the eligible studies do not provide direct, isolated GHG flux quantification, multiple lines of evidence point to three convergent mitigation pathways.

First, reduction of nitrogen loss and N₂O precursors. Tang et al. (2019) showed *P. liquidambari* reduced N loss by 24.59% per pot, with altered activation of N functional genes (*nosZ*, *nifHDKD*). Because N₂O emissions are tightly coupled to surplus inorganic N, this represents direct molecular-level evidence that endophytes can reprogram the soil N cycle. Multiple N-fixing endophytes (Tang et al., 2025; Tian et al., 2023; Roy et al., 2023; Krishnamoorthy et al., 2020; Shen et al., 2019) reduce dependence on synthetic N fertilizers, representing an indirect but quantitatively important pathway.

Second, modulation of soil redox and methane oxidation. Endophyte-induced increases in root architecture (Shi et al., 2024; Tang et al., 2025) enhance oxygen transport via aerenchyma, supporting methane oxidation by methanotrophic bacteria. Tian et al. (2024) showed *Herbaspirillum* sp. R3 enriched *Sideroxydans*-related taxa involved in iron cycling, mechanistically linked to anaerobic methane oxidation in flooded soils. Third, microbiome restructuring as a climate-mitigation lever: Wang et al. (2023) demonstrated that *X. sacchari* JR3-14 enriched taxa (*Bacillus*, *Azospira*, *Azospirillum*, *Arthrobacter*) including strains with N₂O reductase (*nosZ*) capability, suggesting selective favoring of communities with lower net N₂O production.

Among the 20 eligible studies, none directly quantified CH₄ or N₂O fluxes in inoculated rice paddies under field conditions. This represents a critical priority for future research. Coupling endophyte inoculation with high-resolution GHG flux measurement (e.g., static-chamber CH₄/N₂O monitoring combined with metagenomic and metatranscriptomic profiling) will be essential to translate the mechanistic evidence into quantifiable, field-validated climate mitigation outcomes. A summary of mechanistic pathways is presented in Table 4.

Table 4. Mechanistic pathways linking microbial endophytic biofertilizers to GHG mitigation potential in lowland rice systems.

Mitigation pathway	Supporting evidence in this review	Expected effect on GHG
Reduced N loss and N ₂ O precursors	<i>P. liquidambari</i> ↓ N loss 24.59% per pot; altered N functional gene activation (Tang et al., 2019)	↓ N ₂ O emission potential
Reduced synthetic N fertilizer demand via BNF	Multiple endophytes with N-fix capacity (Tang et al., 2025; Tian et al., 2023; Roy et al., 2023; Krishnamoorthy et al., 2020; Shen et al., 2019)	↓ Indirect N ₂ O emissions
Enhanced root architecture and rhizosphere oxygenation	↑ Adventitious/lateral roots and root biomass (Shi et al., 2024; Tang et al., 2025)	Enhanced CH ₄ oxidation in rhizosphere
Microbiome restructuring favoring N ₂ O reducers and methanotrophs	Enrichment of <i>Bacillus</i> , <i>Azospira</i> , <i>Azospirillum</i> , <i>Arthrobacter</i> (Wang et al., 2023); <i>Sideroxydans</i> (Tian et al., 2024)	↓ Net CH ₄ and N ₂ O emissions
Improved nitrogen use efficiency (NUE)	Cross-cutting effect in nearly all studies	↓ Surplus N for denitrification/nitrification

3.5 Soil and Plant Microbiome Stability and Health

Endophytic biofertilizers do not act solely as plant-level inoculants but as systemic regulators of soil and plant microbiome health. Microbiome modulation operates at three nested scales. At the seed and seedling scale, Wang et al. (2023) demonstrated early *X. sacchari* JR3-14 inoculation durably restructured the rice microbiome trajectory. At the rhizosphere scale, Tang et al. (2019) showed *P. liquidambari* reshaped bacterial co-occurrence networks during heading, and Tian et al. (2024) showed *Herbaspirillum* sp. R3 altered core taxa (*Sideroxydans*, *Ideonella*, *Geobacter*) under Cd stress. At the holobiont scale, Zeng et al. (2025) provided molecular evidence that the *A. vagum*–rice holobiont releases coumaric and trans-ferulic acid to actively recruit beneficial microbes. Under stress, Xiang et al. (2024) reported the 4N2-TB1 consortium increased root bacterial richness and diversity under Cd, enriching Cd-binding taxa (*Bacillus*, *Leifsonia*). Soldan et al. (2019) and Dai et al. (2025) demonstrated mangrove-derived endophytes integrate with indigenous communities to maintain plant health under salinity. Endophytic biofertilizers thus contribute

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to microbiome health not merely by adding functional cells but by restoring microbial assembly processes disrupted by intensive cultivation, salinity, or contamination. A summary of impacts organized by species, consortium, and source of isolation is presented in Table 5.

Table 5. Summary of microbial endophytic biofertilizer impacts on rice agronomic traits, stress resilience, and microbiome health.

A. Single-Strain Endophytes

Species	Impact of endophytic application	Reference
<i>Bacillus</i> sp. TB1	Electron-dense structures in cell wall and cytoplasm associated with Cd(II) adsorption; Cd(II) removal rate 59.69% at 5 μ M exposure	Xiang et al. (2024)
<i>Pseudomonas</i> sp. 4N2	Strong Cd(II) sorption by cell wall; Cd(II) removal rate 41.45% at 5 μ M exposure	Xiang et al. (2024)
<i>Bacillus velezensis</i> LS123N	Seed-soaking enhanced rice seedling resistance to wind, reducing lodging by 53–73%; multifunctional traits (cellulase, protease, amylase, siderophore, phosphate solubilization, IAA)	Tu et al. (2024)
<i>Phomopsis liquidambari</i>	Enhanced growth and yield under N-limited conditions; reduced N loss by 24.59% and P loss by 17.46% per pot; reshaped paddy microbial communities	Tang et al. (2019)
<i>Herbaspirillum</i> sp. R3	↑ Dry matter of roots (20.27%), stem sheaths (17.56%), leaves (7.61%) at peak tillering; ↓ Cd content in roots, stems, leaves by 49.28%, 29.31%, 25.65%	Tian et al. (2024)
<i>Fusarium incarnatum</i> K23	Restored root:shoot ratio by 11% under drought; broader cross-variety efficacy in IR64, CR Dhan 307, Sahbhagi Dhan	Lal et al. (2026)
<i>Fusarium equiseti</i> SF5	Restored root:shoot ratio by 10% under drought; variety-specific reproductive enhancement in Sahbhagi Dhan	Lal et al. (2026)
<i>Delftia tsuruhatensis</i> DYX29	Salt tolerance to 5% NaCl; ACC deaminase 29 U L ⁻¹ ; ↑ biomass 32.9%, soluble sugar 23.1%, CAT 37.8%, POD 88.2% under salt stress; modulated IAA, BL, ABA, SA	Dai et al. (2025)
<i>Microbacterium testaceum</i> M15	Seed endophyte; germination at 14 °C from 40→56.67%; survival at 4 °C from 22.67→66.67%; ↑ chlorophyll >30%, protein 16.31%, CAT 26.15%; ↓ MDA 37.76%	Zhao et al. (2024)
<i>Xanthomonas sacchari</i> JR3-14	Early inoculation enhanced α -diversity in root/stem endospheres; co-enriched <i>Bacillus</i> , <i>Azospira</i> , <i>Azospirillum</i> , <i>Arthrobacter</i>	Wang et al. (2023)
<i>Bacillus aryabhatai</i> MN1	Root endophyte tolerant to etridiazole and metalaxyl; dose-dependent IAA; compatible with fungicide-intensive cultivation	Shen et al. (2019)
<i>Acrocalymma vagum</i> A21	Established holobiont with cultivated rice; ↑ shoot height 44.41%, biomass 70.21%; released coumaric and trans-ferulic acid; engaged OsPRX70, OsPRX95	Zeng et al. (2025)
<i>Aspergillus welwitschiae</i> AwOcestreb1	From halophytic <i>O. coarctata</i> ; robust ACC deaminase, IAA, siderophore, P/Zn solubilization, N fixation; ↑ yield 125.16% (no salt), 203.96% (45 mM); ↑ SOS1 1.6-fold	Airin et al. (2023)

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B. Endophyte Consortia and Co-Inoculants

Consortium	Impact of endophytic application	Reference
<i>Pseudomonas</i> sp. 4N2 + <i>Bacillus</i> sp. TB1	4N2-TB1 consortium immobilized Cd(II) in rice roots; ↓ shoot Cd from 30→6% (cv. 728B), 31→13% (cv. BB); ↑ POD 7.37–18.18%, CAT 13.65–30.72%; enriched <i>Bacillus</i> , <i>Leifsonia</i>	Xiang et al. (2024)
<i>Piriformospora indica</i> + <i>A. rhizogenes</i> + <i>B. subtilis</i> (PAB)	Co-inoculation at 4 °C cold stress ↑ root length 75.7%; ↑ photosynthesis, osmolytes, antioxidants; ↑ cold-tolerance gene expression; ↓ MDA, electrolyte leakage	Shi et al. (2024)
Mangrove-derived bacteria (KAUST strains)	Two-strain consortium enhanced flooding and salinity tolerance in <i>O. sativa</i> cv. Nipponbare; ABA signaling, lignin/suberin deposition; ↑ grain yield and quality	Alghamdi et al. (2025)
Fungal consortium AM34 + AM10	Inoculation enhanced peroxidase, polyphenol oxidase, chitinase, SOD in traditional rice; consortium BD+AM produced highest catalase activity	Roy et al. (2023)

C. Endophytes by Sources of Isolation

Source of isolation	Impact of endophytic application	Reference
Rice seed cultivars (Northeast India)	226 fungal endophytes; 26 PGP-screened: IAA 1.52–43.89 mg mL ⁻¹ ; P-solub index 1.58–3.72; 84.61% siderophore, 76.92% P-solub, 84.61% ammonia; isolates BD, KON, AM antifungal against <i>M. grisea</i>	Roy et al. (2023)
<i>Avicennia marina</i> mangrove propagules (KMP)	Mixed micro-colony formation on barley roots; ↑ barley ear DW 65% under salt; ≥80% isolates produced auxin; ↑ rice dry mass 62% under saline gnotobiotic conditions	Soldan et al. (2019)
<i>Kandelia obovata</i> mangrove propagules	Salinity-responsive endophytes identified; <i>D. tsuruhatensis</i> DYX29 transferred salt tolerance to cultivated rice with physiological, hormonal, and antioxidant modifications	Dai et al. (2025)
Wild halophytic rice <i>Oryza coarctata</i>	Three fungal endophytes; <i>T. adpressus</i> OPCRE2, <i>T. argentinensis</i> OPCRh1, novel <i>A. welwitschiae</i> AwOcastreb1; AwOcastreb1 conferred strongest salt tolerance and 203.96% yield improvement at 45 mM NaCl	Airin et al. (2023)
African wild rice <i>Oryza longistaminata</i>	163 endophytic bacterial strains; ≥97% with PGP traits; 11 strains (<i>E. cloacae</i> , <i>E. ludwigii</i> , <i>S. maltophilia</i> , <i>S. fonticola</i> , <i>B. velezensis</i>) with stable colonization on perennial rice	Tang et al. (2025)
Perennial wild rice <i>Oryza officinalis</i>	96 endophytic strains with multiple PGP traits; tissue-specific biomarkers: <i>Desulfomonile</i> , <i>Ruminiclostridium</i> (roots); <i>Lactobacillus</i> , <i>Acinetobacter</i> , <i>Dechloromonas</i> (stems); <i>Stenotrophomonas</i> , <i>Methylobacterium</i> (leaves)	Tian et al. (2023)
Wild rice <i>Oryza granulata</i>	Endophytic fungus <i>A. vagum</i> (A21); established mutualistic holobiont with CO-39, ZJ88, Japonica ZH11; recruited beneficial microbes via coumaric and trans-ferulic acid; engaged plant peroxidase machinery	Zeng et al. (2025)
Six rice varieties (central-eastern and northeastern India)	32 bacterial endophytes from four tissue compartments; 53.1% Gram-positive, 53.1% IAA, 28.1% siderophore, 56.2% P-solub; B.	Kumar et al. (2020)

	subtilis NIBSM_OsR10 with surfactin, iturin D, bacillomycin D antimicrobial genes	
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4. CHALLENGES AND FUTURE OPPORTUNITIES OF MICROBIAL ENDOPHYTIC BIOFERTILIZER UTILIZATION

Multiple eligible studies emphasize that seed-stage inoculation produces the most durable effects on rice physiology and the soil microbiome. Seed-soaking with *Bacillus velezensis* LS123N enabled endophytic persistence in rice tissues for at least 78 days post-planting in paddy, with total colonization reaching 99 days when the 21-day seedling tray stage is included, covering the most disease-vulnerable growth stages (Tu et al., 2024). Complementarily, early inoculation of seed core endophytes such as *Microbacterium testaceum* M15 and *Xanthomonas sacchari* JR3-14 has been shown to durably influence seedling vigor and restructure the rice-associated microbiome across subsequent growth stages (Zhao et al., 2024; Wang et al., 2023). Together, these findings support seed-coating formulations as a cost-effective, field-compatible delivery technology aligned with mechanized transplanting practices common in modern Indonesian rice production. Consortium-based formulations frequently outperform single-strain inoculants under multi-stress conditions, with the PAB consortium, the 4N2-TB1 consortium, the fungal AM34+AM10 consortium, and mangrove-derived two-strain consortia all demonstrating broader synergistic protection across cold, cadmium, pathogen, and salinity-flooding stress contexts (Shi et al., 2024; Xiang et al., 2024; Roy et al., 2023; Alghamdi et al., 2025).

Despite this strong foundation, several challenges constrain adoption. Limited farmer awareness and training remain the most immediate barriers in smallholder rice systems. Climatic and edaphic variability complicates adoption: many promising endophytes have been characterized predominantly under controlled greenhouse or laboratory conditions, with limited validation across diverse agroecological zones, soil types, and growing seasons. Scalability and quality control of bioformulations remain unresolved, including inoculant survival during storage, transportation, and field application. The absence of standardized regulatory frameworks for microbial bioproducts in many tropical countries, including Indonesia, adds institutional complexity that hinders commercialization and farmer access.

The most critical gap is the absence of direct field-scale quantification of greenhouse gas mitigation outcomes. Although multiple mechanistic pathways have been identified, no study to date has directly measured greenhouse gas fluxes in inoculated paddies under realistic field conditions. Closing this gap will require multidisciplinary field trials integrating controlled endophyte inoculation, GHG flux measurement, microbiome profiling, and concurrent yield assessments. Future research should prioritize region-specific endophyte consortia tailored to Indonesian agroecosystems—coastal saline lowlands, drought-prone uplands, and Cd-affected paddies—alongside omics-based field validation. Coupling endophyte inoculation with biochar, organic amendments, and improved water management could further strengthen mitigation outcomes. At the policy level, farmer training programs and quality-certification systems will be equally important to ensure scientific advances translate into genuine on-farm adoption.

5. CONCLUSION

Microbial endophytic biofertilizers represent a scientifically robust and multifunctional biological intervention for sustainable, climate-resilient, low-emission rice farming. Across the 20 eligible studies synthesized, four core contributions consistently emerge. First, endophytes enhance nutrient acquisition through biological nitrogen fixation, phosphate solubilization, and siderophore-mediated mineral mobilization, reducing N and P losses by up to 24.59% and 17.46% per pot while improving N uptake by 55–80%. Second, endophytes confer multi-mechanism stress tolerance through ACC deaminase activity, phytohormone modulation, antioxidant induction, and osmoprotectant accumulation, with yield improvements under saline conditions reaching 203.96% and cold-stress survival increasing from 22.67% to 66.67%. Third, consortium-based formulations consistently outperform single-strain inoculants under multi-stress conditions. Fourth, endophytic biofertilizers function as microbiome engineers, reshaping bacterial and fungal community assembly with long-term implications for nutrient cycling, soil health, and GHG mitigation.

Multiple mechanistic pathways linking endophyte inoculation to reduced CH₄ and N₂O emissions are identified, including reduced N loss, enhanced root architecture supporting rhizosphere oxygenation, and microbiome restructuring favoring N₂O-reducing and methanotrophic taxa. However, no eligible study directly quantified CH₄ or N₂O fluxes under field conditions—bridging this gap through multidisciplinary field trials integrating endophyte inoculation with high-resolution flux measurement and microbiome profiling represents the most urgent research priority. For Indonesian rice systems facing converging pressures from climate variability, soil degradation, and fertilizer dependency, endophytic biofertilizers offer a biologically grounded pathway toward sustainable intensification, contributing meaningfully to national and regional emissions-reduction commitments. Their capacity to enhance nutrient-use efficiency, strengthen climate resilience, and potentially reduce greenhouse gas emissions positions them as a promising component of future low-emission rice production systems in Indonesia and across tropical Asia.

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