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Acaricidal activity of symbiotic bacteria associated with entomopathogenic nematodes against the red palm mite *Raoiella indica* Hirst (Acari: Tenuipalpidae)

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ABSTRACT: The red palm mite *Raoiella indica* Hirst, 1924 (Acari: Tenuipalpidae) is an important invasive pest affecting tropical crops, particularly coconut and banana, in several countries. In Brazil, pest management is limited by the reduced availability of registered chemical control products, which may favor the selection of resistant populations. Symbiotic bacteria of entomopathogenic nematodes (EPNs), such as *Xenorhabdus* (Thomas and Poinar, 1979) and *Photorhabdus* (Boemare and Akhurst 2006), are known to produce metabolites with insecticidal and acaricidal activity, but their activity against *R. indica* has not been evaluated yet. In this study, an exploratory laboratory bioassay was conducted to assess the acaricidal activity of 15 bacterial isolates of *Xenorhabdus* and *Photorhabdus* through topical application to adult females of R. indica. Mortality was recorded over a six-day period and compared with water and culture-medium controls. Several isolates induced mortality rates exceeding 95%, and two isolates resulted in complete adult mortality. In addition, oviposition was strongly reduced by specific isolates. Females exposed to isolates CER144 and CER09 laid on average 0.03 and 0.15 eggs per alive female per day, respectively, compared with approximately 0.85 eggs per alive female per day in both controls, indicating a reduction of over 80% in egg production. Although preliminary, these findings provide the first evidence that EPN-symbiotic bacteria represent a promising and underexplored source of compounds for the biological control of *R. indica*, opening perspectives for sustainable pest management in tropical and subtropical systems.

Key words: biological control, *Xenorhabdus*, *Photorhabdus*, invasive mite.

INTRODUCTION

The red palm mite (RPM) *Raoiella indica* Hirst, 1924 (Acari: Tenuipalpidae) is a phytophagous species native to Asia that has expanded its distribution across several continents. Outside its native range, it is considered an invasive pest, causing significant economic losses to major crops such as coconut and banana (Kane and Ochoa 2006, Kane et al. 2012). This mite was originally described in 1924 from specimens collected on coconut trees in Coimbatore, Tamil Nadu, India (Mesa et al. 2009, Senasica 2015). Since then, its presence has been reported on palm species throughout the Eastern Hemisphere, including Pakistan (Chaudhri 1974), Israel (Gerson et al. 1983), and African countries such as Sudan (Pritchard and Baker 1958) and Egypt (Sayed 1942). In 2004, *R. indica* was found for the first time in the Americas on the Caribbean island of Martinique (Flechtmann and Etienne 2004), from where it rapidly spread to several neighboring countries (Kane et al. 2012, Vasquez and Moraes, 2012).

In Brazil, where the RPM was first recorded in 2009 (Navia et al. 2011), the availability of suitable habitats and the diversity of host plants provide optimal conditions for its establishment and population growth (Amaro et al. 2023). An assessment of its potential economic risk estimated that more than 10% of Brazilian banana-growing areas and nearly 10% of coconut-growing areas are classified as at high or very high risk (Amaro et al. 2021), highlighting the pest's potential to cause significant economic and social losses. Chemical control is limited by operational constraints, such as the height of many adult coconut trees (Kane et al. 2012), as well as by sustainability concerns, including resistance development, non-target effects, high production costs, and environmental restrictions (Assis et al. 2013, Lankinen et al. 2024). In addition, regulatory limitations further restrict chemical control options, as only abamectin and fenpyroximate are currently registered for *R. indica* control in Brazil (MAPA 2025), which may favor the selection of pesticide-resistant populations. Collectively, these constraints reinforce the need to diversify management strategies and identify bioactive sources compatible with integrated pest management.

An effective alternative to the limitations of chemical control is biological control based on the use of microbial organisms. Entomopathogenic nematodes (EPNs) represent a particularly promising group due to their specificity toward arthropods, adaptability to diverse environments, tolerance to agrochemicals, safety for humans and the environment, and compatibility with other control strategies (Sanchez and Rodriguez 2007, Aponte and Olivares 2008, Lopez 2008). Among the eight recognized families, Steinernematidae and Heterorhabditidae stand out because of their ease of mass production and their highly efficient mutualistic association with bacteria of the family Enterobacteriaceae (Lopez 2008). These symbiotic bacteria, mainly *Xenorhabdus* (Thomas and Poinar, 1979) and *Photorhabdus* (Boemare and Akhurst 2006), are released into the host hemocoel and produce a wide range of bioactive metabolites with insecticidal, acaricidal, nematicidal, and antimicrobial activities (Grewal et al. 1993, Webster et al. 1998, Subramanian and Muthulakshmi 2016, Gaugler and Kaya 2018).

These symbiotic bacteria can be isolated for direct application against target organisms, making them attractive candidates for biological pest control, including the RPM. Evidence of their acaricidal potential is emerging. Eroglu et al. (2019) demonstrated that bacterial isolates associated with entomopathogenic nematodes caused 92–100% mortality in adults of *Tetranychus urticae* Koch (Acari: Tetranychidae). However, the potential of entomopathogenic nematodes and their symbiotic bacteria as bio-inputs for the integrated management of pest mites remains largely unexplored, particularly against *R. indica*.

Therefore, the objective of this study was to conduct a laboratory screening of 15 symbiotic bacterial isolates against adult female *R. indica*, quantifying mite mortality and oviposition using both water and culture-medium controls to contextualize baseline mortality. This work is framed as a prospecting and isolate-prioritization study, providing initial evidence to guide subsequent investigations on metabolite profiling and evaluation across additional life stages.

MATERIALS AND METHODS

Adult females of *R. indica* used in the experiments were obtained from colonies maintained *in vivo* on coconut plants (*Cocos nucifera* L.) cultivated in pots under controlled greenhouse conditions at the Acarology Laboratory, Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo (ESALQ-USP).

Fifteen bacterial strains of the genera *Xenorhabdus* and *Photorhabdus* (Table 1), symbiotically associated with entomopathogenic nematodes (*Steinernema* Travassos and *Heterorhabditis* Poinar), were obtained from the entomopathogen collection "Oldemar Cardim Abreu," which houses various nematode isolates from different biomes. The nematodes are maintained in aqueous suspension at 15°C, and their associated bacteria are preserved for long-term storage at -80°C in tryptic soy broth (TSB; pancreatic digest of casein, 17 $g{\cdot}L^{-1}$; papaic digest of soybean, 3 $g{\cdot}L^{-1}$; sodium chloride, 5 $g{\cdot}L^{-1}$; dipotassium hydrogen phosphate, 2.5 $g{\cdot}L^{-1}$; and glucose monohydrate, 2.5 $g{\cdot}L^{-1}$; pH 7.3) supplemented with 20% glycerol. The bacterial strains used in this study were originally isolated from last instars of *Galleria mellonella* L. (Lepidoptera: Pyralidae) previously infected with their respective entomopathogenic nematodes, following the methodology described by Akhurst (1980).

To confirm the presence of phase I (blue colonies), the bacteria were streaked onto NBTA medium (nutrient agar supplemented with bromothymol blue, 0.025 g·L^{-1}, and triphenyl tetrazolium chloride, 0.04 g·L^{-1}) and incubated at 27°C in the dark. For the bioassays, bacterial colonies were transferred to TSB medium and incubated under agitation (150 rpm) at 27°C for six days, a period selected to allow adequate growth and accumulation of secondary metabolites, as reported for these bacterial genera (Furgani et al. 2008, Chacón-Orozco et al. 2020, Gulsen et al. 2022). The concentration of each broth culture was determined by plating on NBTA medium for colony-forming unit (CFU) counts, and the suspensions used in the bioassays ranged from 1×10^7 to 2.1×10^7 CFU mL^{-1}.

Table 1. Symbiotic bacteria and their associated entomopathogenic nematodes used in this study.

Isolate	Nematode	Bacteria species	Soil source
AM163	*Steinernema diaprepesi*	*Xenorhabdus doucetiae*	Sinop (MT), Brazil
CER09	*Steinernema puertoricense*	*Xenorhabdus romanii*	Rio Verde (GO), Brazil
CER129	*Steinernema puertoricense*	*Xenorhabdus romanii*	Rio Verde (GO), Brazil
CER140	*Steinernema puertoricense*	*Xenorhabdus romanii*	Rio Verde (GO), Brazil
CER144	*Steinernema* sp.	*Xenorhabdus* sp.	Rio Verde (GO), Brazil
CER21	*Steinernema* sp.	*Xenorhabdus* sp.	Rio Verde (GO), Brazil
HBEN01	*Heterorhabditis bacteriophora*	*Photorhabdus luminescens*	Germany
IBCB06	*Steinernema brazilense*	*Xenorhabdus* sp.	Porto Murtinho (MS), Brazil
IBCB47	*Steinernema feltiae*	*Xenorhabdus bovienii*	Germany
IBCB48	*Steinernema* sp.	*Xenorhabdus* sp.	Itapetininga (SP), Brazil
IC1	*Steinernema* sp.	*Xenorhabdus* sp.	São João da Boa Vista (SP), Brazil
IL2	*Steinernema carpocapsae*	*Xenorhabdus nematophila*	São João da Boa Vista (SP), Brazil
PAM25	*Steinernema rarum*	*Xenorhabdus szentirmaii*	Bagé (RS), Brazil
PONTO2C	*Steinernema brazilense*	*Xenorhabdus* sp.	Porto Murtinho (MS), Brazil
T12	*Heterorhabditis* sp.	*Photorhabdus* sp.	São João da Boa Vista (SP), Brazil

Each experimental unit consisted of a 9-cm Petri dish containing hydrophilic cotton moistened with distilled water and a banana leaf section (4 × 5 cm) placed with the abaxial surface upward. A moistened cotton strip was placed at the leaf margin to maintain turgidity and reduce mite escape; dishes were rehydrated as needed. This detached-leaf system was used for all treatments and controls, thereby standardizing any effect of leaf detachment on mite survival across experimental units.

The mites used in the tests were collected from colonies established from a few mated females, transferred from older stock colonies four or five weeks before the experiment, to ensure that these units predominantly contained newly emerged adults, considering an average egg-to-adult period of 25 days (3.6 weeks) at 24°C (Fidelis et al. 2019). In each experimental unit, 20 adult females of *R. indica* were introduced. Females were selected based on morphological characteristics of the adult stage, including oval and flattened body shape, bright red coloration, and body length of approximately 230–320 µm. Then, 900 µL of the bacterial broth culture (live bacterial cells + metabolites present in the culture medium) was applied into each unit with a Potter spray tower calibrated at 15 PSI (1 bar). Under these conditions, the 900-µL aliquot resulted in an average wet residue deposition of 0.72 mg·cm^{-2} on the arena surface, corresponding to an estimated application rate of 72 L·ha^{-1}. Prior to application, each Falcon tube containing the bacterial suspension was gently homogenized by inverting it several times to ensure even distribution, avoiding vigorous agitation. A total of 10 units were used per treatment. Besides the 15 bacterial treatments, two control treatments were included (TSB medium alone and distilled water) to distinguish effects of the culture medium from those of the bacterial isolates. The experimental units were maintained in a climatic chamber under controlled conditions of 25 ± 2°C, 75 ± 10% relative humidity, and a 12:12 h (light:dark) photoperiod. The number of surviving adult females and the oviposition of *R. indica* were recorded at two, four, and six days after treatment. This bioassay was repeated twice.

All analyses were conducted in R (v4.3.2; R Core Team). Mortality was assessed at days 2, 4, and 6 using cumulative dead counts per dish. For visualization of mortality over time, survival curves were estimated per isolate using an interval-censored nonparametric estimator (package *survival*), treating deaths as occurring between consecutive observation times; these curves were interpreted as descriptive time-course summaries given dish-level grouping.

To quantify treatment effects on mortality at the end of the bioassay, analyses were conducted using the cumulative counts recorded at day 6 for each experimental unit. Final mortality was analyzed by fitting the paired counts of dead and alive as a beta-binomial generalized linear mixed model (GLMM) with a logit link and assay as a random intercept to account for among-assay variability. The beta-binomial family was selected to accommodate extra-binomial variation (overdispersion). Treatments in which all experimental units showed 100% mortality were excluded from model fitting because the absence of within-treatment variance caused complete separation under the logit link, yielding non-estimable coefficients. However, these treatments were retained in the descriptive results and were interpreted as causing complete mortality. Water control was used as the reference level, and estimated marginal means were obtained with *emmeans* and backtransformed to mortality probabilities. Treatment contrasts versus the water control were performed using Dunnett-adjusted comparisons.

Oviposition was analyzed as an egg-laying rate standardized by survival at the end of the assay. To express egg output on a per-day basis, the total oviposition of each unit was divided by assay duration, and the resulting value was then standardized by the number of living females recorded at day 6 (egg/alive female/day). Treatment effects on egg rate were tested using GLMM as a fixed effect and assay as a random. Because egg rate was non-negative, continuous, and included zeros, a Tweedie distribution with a log link was used. Replicates with no surviving females at day 6 were excluded to avoid undefined rates. Water control was used as the reference level. Treatment contrasts versus the water control were performed using Dunnett-adjusted comparisons.

RESULTS

Descriptive survival curves supported the endpoint analysis (Fig. 1), with high survival (maintained above 70%) in both controls and rapid declines under all bacterial treatments (all below 35%), several reaching near-zero survival by days 4–6. Two isolates (IBCB06 and IL2) consistently produced complete adult mortality (100%) across evaluation times and were therefore not included in the fitted GLMMs due to complete separation.

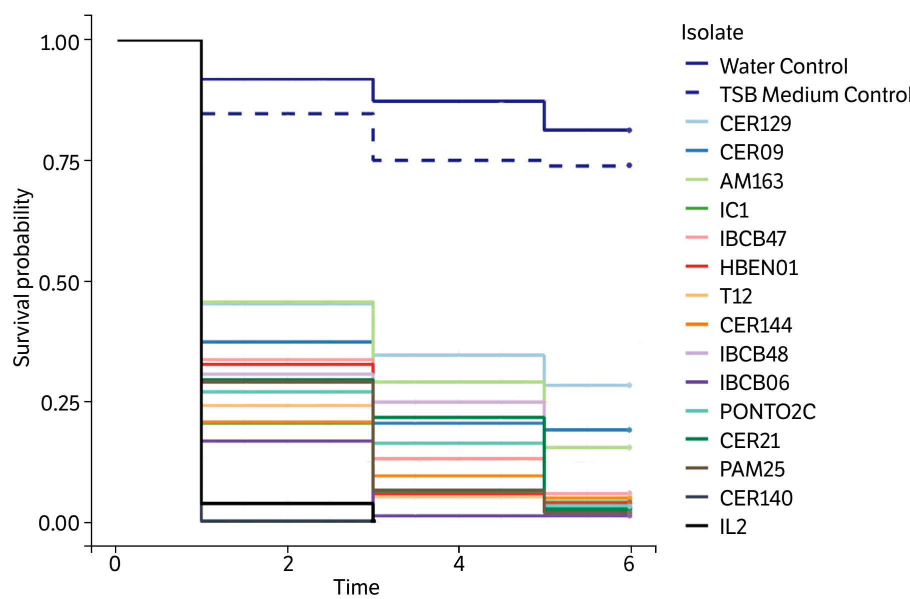
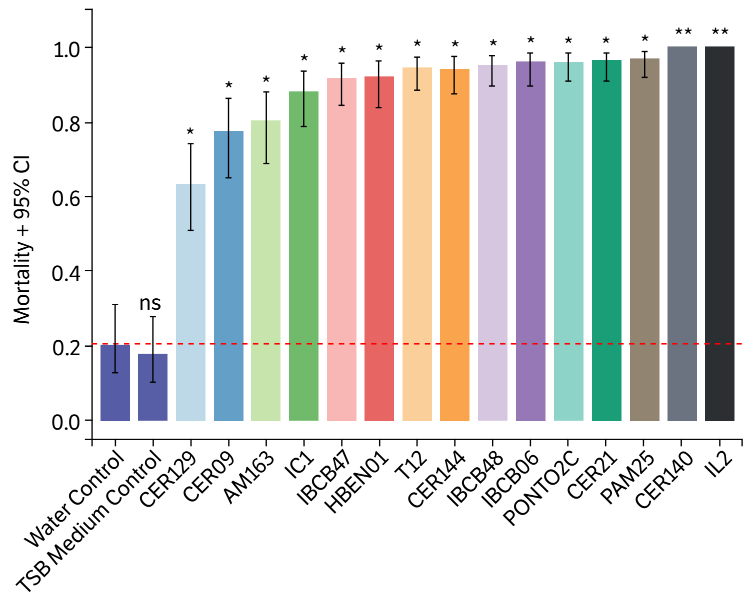


Figure 1. Descriptive interval-censored survival curves of adult females of *Raoiella indica* exposed to bacterial isolates. Survival probability over time (days 2, 4, and 6).

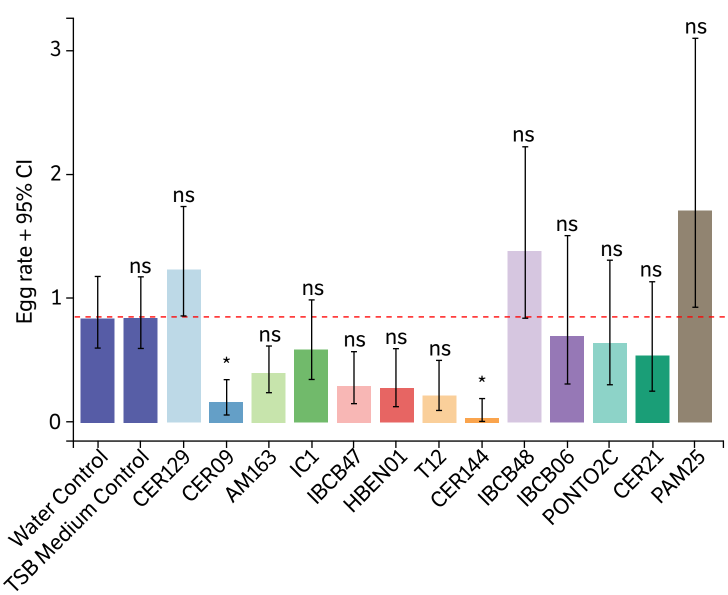
For the remaining isolates, treatment had a significant effect on mean mortality ($\chi^2(14) = 247.93$, $p < 0.0001$) (Fig. 2), but mortality levels also varied between the two independent assay runs (χ^2 (1) = 66.85, $p < 0.0001$). Despite this between-assay variation, all bacterial treatments differed from the controls (Dunnett-adjusted $p < 0.0001$). The two controls (water and TSB medium) did not differ from each other ($p = 0.99$) and exhibited similarly low mortality (20.3 and 17.4%). In terms of isolate ranking, CER129 and CER09 (both identified as *Xenorhabdus romanii* Tailliez et al. 2006) showed the lowest mean mortality (63.3 and 77.3%), while all other isolates exceeded 80% mortality.



ns: not significantly different; *significantly different; **total mortality (not included in the model-based contrasts).

Figure 2. Mortality of adult female of *Raoiella indica* exposed to bacterial isolates. Bars show model-estimated marginal means (mortality probability at day 6) from generalized linear mixed model; error bars are 95% confidence intervals. The dashed horizontal line indicates the model-estimated mean mortality of the water control.

Oviposition (egg rates) was also affected by the treatments ($\chi^2(14) = 71.67$, $p < 0.0001$) (Fig. 3), whereas variation between assay runs was negligible ($\chi^2(1) \approx 0.00$, $p \approx 1.00$). None of the two controls (water and TSB medium) differed from each other ($p = 0.99$), with 0.85 and 0.84 eggs/alive female/day, respectively. Mites exposed to isolates CER144 and CER09 presented the significantly reduced oviposition with means of 0.03 ($p = 0.010$) and 0.15 ($p = 0.021$) eggs/alive female/day, while other isolates did not differ from water control, despite varying means.



ns: not significantly different; *significantly different; **total mortality (not included in the model-based contrasts); 95%CI: 95% confidence interval.

Figure 3. Oviposition (egg rate) of adult female of *Raoiella indica* exposed to bacterial isolates. Bars show model-estimated marginal means (eggs per alive female per day) from generalized linear mixed model; error bars are 95% confidence intervals. The dashed horizontal line indicates the model-estimated mean egg rate of the water control.

DISCUSSION

This study provides evidence that symbiotic bacteria associated with *Xenorhabdus* spp. from *Steinernema* spp. and *Photorhabdus* spp. from *Heterorhabditis* spp. can induce high mortality in adult females of *R. indica* under laboratory conditions. Notably, several isolates consistently caused very high mortality, and IL2 (*Xenorhabdus nematophila*) and IBCB06 (*Xenorhabdus* sp.) produced complete adult mortality across all evaluation times.

Our findings are consistent with previous reports showing that EPN-symbiont bacteria and their products can be highly active against phytophagous mites. Eroglu et al. (2019) reported over 90% mortality in mobile stages of *T. urticae* following exposure to cell-free supernatants of *Xenorhabdus szentirmaii* and *X. nematophila*. Similarly, Cevizci et al. (2020) observed high mortality in *T. urticae* (86.5–89%) when mite cuticles were fully exposed to bacterial metabolites, whereas partial contact resulted in much lower mortality (25–34%), demonstrating the role of exposure route and surface coverage in contact-based assays. Hsieh et al. (2023) further demonstrated that *Photorhabdus luminescens* (0805-P2R) caused substantial mortality in *T. urticae* and *Tetranychus kanzawai* Kishida 1927 (Acari: Tetranychidae), and documented tissue alterations in the midgut and silk glands. Collectively, these studies support the hypothesis that EPN-symbiont bacteria can affect mites through multiple pathways, including cuticular contact and internal physiological disruption, thereby placing our results on *R. indica* within an established and expanding body of evidence identifying these bacteria as promising sources of acaricidal bioactive compounds (Eroglu et al. 2019, Cevizci et al. 2020, Hsieh et al. 2023).

Although this study focused on adult mortality endpoints, reductions in oviposition (when detected) are also relevant, as they represent biologically meaningful sublethal effects capable of slowing population growth even when mortality is incomplete. Cevizci et al. (2020) reported reduced egg laying in *T. urticae* following exposure to bacterial metabolites. Tissue-level damage (Hsieh et al. 2023) and reduced oviposition (Cevizci et al. 2020) provide plausible mechanistic links between exposure and reproductive impairment, potentially mediated by bacterial secondary metabolites such as xenocoumacins and other bioactive compounds (Sajnaga et al. 2024).

For *R. indica*, the combination of lethal and reproductive effects would increase the value of candidate isolates for future development. Nonetheless, non-target safety and compatibility with natural enemies are central considerations for progressing from screening to application. Cevizci et al. (2020) observed low ovicidal activity and only mild effects on mobile stages of predatory mites—*Phytoseiulus persimilis* (Athias-Henriot 1957) and *Neoseiulus californicus* (McGregor 1954) (Acari: Phytoseiidae)— suggesting that selectivity may be achievable, although this must be evaluated for key predators associated with RPM. Additionally, bacterial products from other genera, such as *Serratia ureilytica*, have shown efficacy against phytophagous mites and compatibility with predatory mites (Wong-Villareal et al. 2025), supporting the broader potential of bacterial bioactives within integrated pest management frameworks.

As an initial study, the present work highlights the need for further investigations, particularly those focused on species-level characterization of the most promising nematode isolates. The most efficient isolates should be prioritized for taxonomic identification and metabolite characterization (*e.g.*, liquid chromatography coupled with mass spectrometry profiling and/or genomic analysis of biosynthetic gene clusters), as proposed for advancing from phenotype-based evaluations toward a mechanistic understanding of the observed effects (Shi et al. 2022). Key next steps include:

- Characterization of the active metabolites;
- Dose–response and persistence assays on foliage;
- Evaluation of eggs and immature stages;
- Expansion of temporal replication;
- Assessment of non-target effects and phytotoxicity under more realistic exposure conditions.

In a subsequent stage, field-based evaluations will be necessary to validate the efficacy of the most promising treatments under realistic agricultural conditions. Overall, the results obtained provide relevant information for the development of management strategies for *R. indica* in agricultural systems and reinforce the potential of entomopathogenic nematodes as valuable tools in integrated pest management programs.

CONCLUSION

This study provides experimental evidence supporting EPN symbiont bacteria as a promising source of acaricidal agents against *R. indica*, demonstrating through laboratory screening their high pathogenic potential against adult females. Two isolates (IBCB06 and IL2) consistently caused 100% adult mortality, while most of the remaining isolates induced mortality levels exceeding 80%, differing from the controls. In addition, some isolates reduced oviposition, suggesting potential effects on population dynamics beyond direct adult mortality. Overall, these findings fulfill the objective of prospecting and prioritizing bacterial isolates, thereby contributing to the development of management strategies for *R. indica* in agricultural systems.

CONFLICT OF INTEREST

Nothing to declare.

AUTHORS' CONTRIBUTION

Conceptualization: González-Cano, L. M., Chacon-Orozco, J. G., Leite, L. G., Moraes, G. J. and Sato, M. E. **Methodology:** González-Cano, L. M., Chacon-Orozco, J. G. and Leite, L. G. **Investigation:** González-Cano, L. M. and Godoy, L. L. **Writing – Original Draft:** González-Cano, L. M. and Godoy, L. L. **Writing – Review and Editing:** Chacon-Orozco, J. G., Leite, L. G., Moraes, G. J. and Sato, M. E. **Funding Acquisition:** Sato, M. E. **Final approval:** Sato, M. E.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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DECLARATION OF USE OF ARTIFICIAL INTELLIGENCE TOOLS

The authors declare that artificial intelligence tools were used exclusively to improve the English language and clarity of the manuscript. All scientific content, data analysis, interpretation, and conclusions were performed and verified by the authors.

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