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Root exudate-driven mycorrhizal suppression underlies *Indocalamus tessellatus* invasion: Evidence from field and pot experiments

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ABSTRACT

Bamboo invasion into adjacent native forests poses significant threats to aboveground biodiversity and disrupts belowground soil processes. However, the ecological mechanisms driving *Indocalamus tessellatus* invasion are complex and remain poorly understood. This study combined field and controlled-environment experiments to investigate the effects of *I. tessellatus* invasion on plant communities, soil properties, and rhizosphere interactions. Field observations revealed that bamboo invasion significantly reduced shrub-layer diversity (Simpson and Pielou indices) in mixed coniferous-broadleaf forests, while arborous and herbaceous layers remained unaffected. Mycorrhizal colonization rates declined in five native species (*Pinus massoniana, Pteridium aquilinum, Eurya japonica, Symplocos stellaris*, and *Loropetalum chinense*), correlating with population declines in four species (*P. massoniana* excluded). Invasion also intensified soil acidification and altered nitrogen cycling, leading to decreased ammonium and nitrate levels. To examine potential allelopathic effects, we performed a pot experiment with *L. chinense* seedlings under simulated litter addition, root exudate addition, and combined treatments. Laboratory experiments demonstrated that *I. tessellatus* root exudates induced pronounced soil acidification, reducing *L. chinense* height gain by 25.40 % and mycorrhizal colonization by 48.73 %, whereas litter-mediated effects were less substantial. Although microbial α-diversity remained stable, root exudates reshaped bacterial and fungal community composition. Structural equation modeling identified root exudates as key drivers of growth inhibition via mycorrhizal suppression. These findings highlight the critical role of belowground mechanisms—root exudate-mediated soil acidification, mycorrhizal suppression, and microbial restructuring—in bamboo invasion. Understanding these processes provides actionable insights for managing invasive species and conserving biodiversity.

1. Introduction

Biodiversity serves as a foundational pillar of stable ecological communities, ensuring ecosystem balance and functionality (Barabás, 2021). High biodiversity enhances ecosystem resilience, buffering natural systems against environmental perturbations (Kazemi et al., 2018). However, this stability faces increasing challenges from biological invasions, which have emerged as a global crisis threatening biodiversity, ecosystem integrity, and socio-economic systems (Schaffner et al., 2020; Diagne et al., 2021). At local scales, invasive plants can competitively exclude native species, disrupt key ecosystem services, and hinder ecological restoration efforts (Hughes et al., 2020). The dual pressures of globalization and intensifying climate extremes are expected to exacerbate these impacts across diverse ecosystems (Li et al., 2025). Consequently, elucidating the mechanisms underpinning plant invasion and their cascading ecological effects remains a pressing research priority (Rezáčová et al., 2021).

Bamboos are among the most aggressive plant invaders, characterized by rapid clonal expansion and strong vegetative persistence (Xu et al., 2020). Their invasions span native habitats in China and Brazil, as well as introduced regions such as Japan and North America (Luan et al., 2021). In China alone, bamboo forests have expanded 1.5-fold over the past four decades, reaching more than 7.50 million hectares by 2021 (Feng and Li, 2023; Zeng et al., 2024). Although *Phyllostachys edulis*

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accounts for the majority of this coverage, the extensive use of *Indocalamus tessellatus* for food packaging, soil stabilization, ornamental planting, and understory greening has led to its increasingly widespread invasion (Qin et al., 2013). With short, densely clustered foliage and vigorous rhizomes, *I. tessellatus* establishes persistent understory layers that alter soil physicochemical properties and suppress native vegetation through belowground interference. These traits suggest a potentially strong ecological impact, underscoring the need to clarify its specific modes of invasion within forest ecosystems.

Many bamboo species exhibit common invasion strategies, including rapid clonal growth, high nutrient competitiveness, and aggressive rhizome expansion, which together enable them to dominate space and reshape soil nutrient dynamics across diverse forest ecosystems (Li et al., 2024a). However, such spatial and competitive mechanisms alone often fail to fully account for observed declines in native species richness and forest structural changes. Increasing attention has thus turned to chemically mediated plant–plant interactions (Xu et al., 2023). Notably, allelochemicals released through root exudates and litter play a crucial role in plant competition by inhibiting seed germination and suppressing seedling growth (Wang et al., 2024a; Zhao et al., 2022). *I. tessellatus,* although a dwarf bamboo species, appears to rely heavily on belowground strategies—particularly allelopathic interactions mediated through the rhizosphere and litter—to exert ecological influence (Rice, 1984; Fan et al., 2025). The production of allelopathic compounds likely plays a critical role in disrupting native plant growth and reshaping soil microbial communities, thereby facilitating the species' invasive success.

Bamboo litterfall induces significant ecosystem changes via three key pathways: modifying decomposer community diversity, accelerating nutrient cycling, and altering soil physicochemical properties (Tian et al., 2020; Wang et al., 2020; Luan et al., 2021). The leaching of secondary metabolites from fresh and decomposing litter facilitates chemical signaling that mediates belowground interspecific interactions. These biochemical processes act synergistically with bamboo's rhizome networks, which physically alter soil structure and impede native root development (Liu et al., 2019).

Building on the critical role of belowground processes, dwarf bamboo also responds to competitive pressures by reallocating resources, increasing investment in belowground structures (Winkler et al., 2016). This shift not only enhances belowground biomass but also intensifies the production and release of root exudates containing allelochemicals. In *I. tessellatus*, such allelopathic root exudates drive complex rhizospheric interactions with significant ecological consequences. Its root exudates contain diverse allelochemicals that exert dual-phase ecological effects (Wang et al., 2024a; Xia et al., 2023). The primary effects involve direct phytotoxicity, which inhibit seed germination and seedling growth through biochemical interference (Van Dam and Bouwmeester, 2016). The secondary effects occur via modulation of rhizosphere microbiota and plant–plant signaling, particularly by suppressing mycorrhizal symbioses (Ehlers et al., 2020). These microbial-mediated effects are critical, given the central role of mycorrhizal fungi in nutrient acquisition and stress tolerance for native plants (Tsunoda and van Dam, 2017).

Furthermore, the invasion success of *I. tessellatus* appears to be driven by a self-reinforcing microbial feedback loop: rhizosphere microbes capable of tolerating or detoxifying allelochemicals gain competitive advantage, thus facilitating bamboo establishment while suppressing native species (Li et al., 2015). Consequently, rhizosphere microbial responses significantly influence the performance of native vegetation in invaded habitats. However, key knowledge gaps remain regarding how allelochemicals regulate plant–microbe interactions and symbioses during *I. tessellatus* invasion. Understanding these biochemical–ecological linkages is essential for elucidating invasion dynamics and informing management strategies.

To address these gaps, this study aims to clarify the ecological impacts of *I. tessellatus* invasion on plant community composition, mycorrhizal colonization, soil chemical properties, and microbial community structure in subtropical coniferous–broadleaf mixed forests. We focus on belowground mechanisms, especially allelopathic effects that alter soil microbial communities and mediate plant interactions, driven by root exudates and litter inputs. We hypothesize that (1) *I. tessellatus* invasion reduces native plant diversity, alters soil chemical properties, and reshapes microbial community composition, and (2) Root exudates and leaf litter from *I. tessellatus* affect native plant growth and rhizospheric dynamics, with root exudates playing a dominant role by disrupting plant–mycorrhizal symbioses, reshaping microbial communities, and suppressing native species.

2. Materials and methods

2.1. The field study: study site description

The research was conducted at the International Bamboo and Rattan Center in Taiping City, Anhui Province, China (30.20°–30.25° N, 118.10°–118.15° E), within a subtropical monsoon humid climate zone. The region exhibits marked seasonal temperature variation, with mean temperatures of approximately 0 °C in January and 25 °C in July, and receives approximately 1600 mm of annual precipitation (Wang et al., 2024b).

The experimental site features a 20-degree slope with yellow and yellow-brown soils supporting a 40–50-year-old mixed coniferous-broadleaf forest. The canopy layer is dominated by *Pinus massoniana*, *Sassafras tzumu*, *Eurya japonica*, *Camellia japonica*, and *Lithocarpus glaber*. The understory comprises shrub species including *Loropetalum chinense*, *Symplocos stellaris*, and *Lindera aggregata*, while the herbaceous layer is characterized by representatives from the *Dicksoniaceae*, *Gleicheniaceae*, *Lygodiaceae*, and *Poaceae families*.

Over the past five years, *I. tessellatus* has been actively invading this forest ecosystem. We established sampling plots in three distinct forest types: (1) *I. tessellatus* pure forest (IF), (2) coniferous-broadleaf mixed forest with *I. tessellatus* invasion (IMF), and (3) uninvaded mixed coniferous-broadleaf forest (MF). The forest type classification was done based on the stem density of the invaded *I. tessellatus*: MF (control): no *I. tessellatus* present; IMF (invaded): 7 stems m^{-2} *I. tessellatus*; IF (fully invaded): 29 stems m^{-2} *I. tessellatus*, native tree species were replaced by *I. tessellatus*. Total woody plant density (DBH >5 cm) showed an inverse relationship with bamboo invasion intensity: MF, 1023 stems ha^{-1}; IMF, 815 stems ha^{-1}; and IF, 255 stems ha^{-1}.

2.2. Plant diversity survey in the field study

In the MF, IMF, and IF stands, we established 20 × 20 m plots (three replicates per stand) spaced 5 m apart along the direction of *I. tessellatus* invasion, which crossed MF, IMF, and IF sequentially. In October 2021, a comprehensive survey of all tree species (categorized into individuals with DBH ≥5 cm and those with DBH <5 cm) was conducted within each plot. Additionally, five randomly placed 2.5 × 2.5 m subplots were set up within each plot to record the composition and abundance of shrub and herbaceous plants. The Simpson index (D) and Pielou evenness index (J) were calculated as follows:

$$D = 1 - \sum_{i=1}^{s} \frac{n_i(n_i - 1)}{N(N - 1)}$$

$$J = \left[-\sum\nolimits_{i=1}^{s} P_i \text{InP}_i \right] \Big/ \text{InS}$$

Where S represents the number of species in the subplot, N represents the total number of all plant individuals, ni represents the total number of the i-th plant species, and Pi represents the proportion of the number of individuals of species i (ni) to the total number of plants in the community (N).

P. massoniana, *S. stellaris*, *E. japonica*, and *L. chinense* were present in both IMF and MF. In each subplot, fine roots (<2 mm diameter) of these four species along with those of *I. tessellatus* (in IF and IMF) were carefully excavated from the top 30 cm of soil in each of the four cardinal directions. After gently shaking off loose soil, the roots were transported to the laboratory, cleaned, and stored in sterile centrifuge tubes for mycorrhizal infection analysis.

Additionally, soil samples were collected from the top 30 cm layer in each subplot using an auger and combined into one composite sample per plot. In total, nine composite soil samples were obtained for chemical and microbial analysis.

2.3. Controlled environment study

Field observations revealed that *L. chinense* was the dominant species in both MF and IMF stands but exhibited the strongest suppression under *I. tessellatus* invasion. We initiated a controlled experiment in February 2022 to disentangle the relative contributions of *I. tessellatus* leaf litter and root exudates to this suppression, and to further elucidate the belowground interaction mechanisms potentially driving this invasion effect. Root exudates of *I. tessellatus* were collected biweekly following Phillips et al. (2008) with modification: In each plot, healthy individuals were selected, and a 30 cm-deep soil profile was excavated to expose intact rhizome–root systems. Fine lateral roots (15–20 cm length, <2 mm diameter) were gently cleaned with sterile deionized water and re-embedded in a sterilized soil–sand mixture (1:1, v/v) for 24 h acclimation under shade. Roots were then placed in 100 mL glass syringes moistened with sterile water and enclosed in a dual-layer buffer of aluminum foil and fresh bamboo litter to stabilize microclimatic conditions. Blank syringes without roots served as controls. After a 4-week equilibration in the field, exudates were collected biweekly by vacuum-flushing each syringe five times with sterile deionized water; the final eluate was retained, filtered (0.22 μm), and aliquoted for experimental application or stored at −80 °C for metabolomic analysis. Leaf litter was simultaneously collected from 1 × 1 m nylon nets (three per plot).

Metabolites from freeze-dried exudates and litter were extracted with pre-cooled methanol:water (7:3, v/v) containing internal standards, centrifuged, and filtered for analysis. Chromatographic separation was performed on a Waters ACQUITY UPLC® HSS T3 column (100 × 2.1 mm, 1.8 μm) using 0.1 % formic acid in water (A) and 0.1 % formic acid in acetonitrile (B) under a gradient of 5–95 % B over 22 min (flow rate 0.3 mL min^{-1}, column temperature 40 °C). Detection was via a QTRAP® 6500 Plus mass spectrometer (SCIEX, USA) with electrospray ionization (ESI) in both positive and negative modes; ion source temperature was 500 °C, ion spray voltage ±4500 V, curtain gas 20 psi, and GS1/GS2 both at 40 psi (Chen et al., 2017a). The remaining portions of litter and root exudates were reserved for the controlled growth experiment.

In March 2022, 60 one-year-old *L. chinense* seedlings of relatively uniform size were transplanted into individual basins (30 × 15 × 35 cm). Initial seedling height and root collar diameter (RCD) were measured before the application of the following treatments: *I. tessellatus* root exudates (R), fresh leaf litter (L), a combination of root exudates and leaf litter (RL), and control (no additives). Each treatment had three replicates, with five seedlings per replicate. Freshly collected litter (6 g) and root exudates (50 mL) were applied every two weeks.

After six months, all seedlings were measured (height and RCD) and harvested. Subsamples of roots were rinsed for mycorrhizal infection analysis, while the remaining plant material (roots, leaves, and stems) was oven-dried and separately ground for nutrient analysis (total phosphorus, nitrogen, potassium, calcium, and magnesium). Rhizosphere soil was collected by gentle root shaking for microbial and chemical characterization.

2.4. Determination of mycorrhizal infection rate

Root mycorrhizal colonization was evaluated following a modified trypan blue staining method (Peng et al., 2024). From each sample, 100 non-lignified root segments (0.5–1.0 cm in length) were randomly selected. The segments underwent sequential processing: rinsing with distilled water, clearing in 20 % KOH at 90°C, bleaching with alkaline H_2O_2, acidification in 5 % acetic acid, and staining with trypan blue solution at 66°C.

Following destaining in distilled water (≥12 h), five randomly selected segments per sample were mounted side by side on microscope slides. Colonization was assessed at 40 × magnification using a standardized grading system that quantified hyphal presence in 10 % increments (0–100 %) based on the proportion of colonized root length. For each seedling, the final colonization rate represented the mean value derived from systematic microscopic evaluation of multiple root segments.

2.5. Soil and plant chemical analysis

All soil analyses were performed immediately after sample collection. Gravimetric analysis was used to determine soil water content (SWC). Soil pH was measured with a calibrated FE28 pH meter (METTLER TOLEDO, Switzerland). Concentrations of ammonium (NH_4^+-N), nitrate nitrogen (NO_3^--N), and available phosphorus (AP) in soil, along with total phosphorus (TP) in plant tissue, were quantified using a flow injection analyzer (FIAstar 5000, Shimadzu, Japan).

Soil organic carbon (SOC) and total nitrogen (TN) were analyzed for both soil and plant samples using an elemental analyzer (EA3000, Euro Vector, Italy). Dissolved organic carbon (DOC) and nitrogen (DON) in soil were measured with a TOC-V analyzer (Shimadzu, Japan). Microbial biomass carbon (MBC) and nitrogen (MBN) were determined through chloroform fumigation followed by TOC-V analysis.

Plant tissue concentrations of potassium (K), calcium (Ca), and magnesium (Mg) were measured using flame atomic absorption spectrometry (PerkinElmer Inc., Waltham, USA).

2.6. Microbial community composition analysis

Genomic DNA was extracted from soil samples using a commercial kit. DNA purity and concentration were assessed by 1 % agarose gel electrophoresis and NanoDrop spectrophotometry, respectively. Bacterial 16S rRNA (V5-V7; primers 799 F/1193 R) and fungal ITS1–2 regions (primers ITS1/ITS2) were amplified with barcoded primers using Premix Taq polymerase. Amplicons were quantified, pooled equimolarly, purified, and used to construct libraries with the NEBNext® Ultra™ DNA Library Prep Kit. Sequencing was performed on an Illumina HiSeq platform (2 ×250 bp paired-end).

Raw reads were demultiplexed, quality-filtered, and clustered into OTUs at 97 % similarity after chimera removal. Representative sequences were taxonomically assigned against SILVA (bacteria) and UNITE (fungi) databases. Microbial community composition and diversity were analyzed based on OTU tables.

2.7. Statistical analyses

All statistical analyses were performed using IBM SPSS Statistics 20.0 (IBM Corp., USA). Data normality and homogeneity of variances were assessed using the Shapiro–Wilk and Levene's tests, respectively, prior to conducting parametric analyses. One-way ANOVA was used to evaluate the effects of *I. tessellatus* invasion on plant growth performance, microbial properties, and soil physicochemical properties. Two-way ANOVA was conducted to examine the main and interactive effects of *I. tessellatus* root exudates and leaf litter addition on soil chemical properties, plant growth parameters, microbial community composition, and mycorrhizal colonization rates. For variables showing significant differences ($P < 0.05$), post hoc comparisons were performed using Duncan's multiple range test. For datasets that did not meet the assumptions of normality or homogeneity, non-parametric tests were employed. To assess the individual and combined effects of root exudates and leaf litter on microbial community composition, principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarity matrices and permutational multivariate analysis of variance (PERMANOVA, 999 permutations) were conducted using the 'microeco' R package. General linear models (GLMs) and Pearson's correlation analyses (via the 'stats' package) were applied to evaluate relationships among plant growth parameters, microbial diversity indices, mycorrhizal colonization rates, soil chemical properties, and microbial community composition.

Piecewise structural equation modeling was conducted using the 'piecewiseSEM' R package to identify key causal pathways through which root exudates and leaf litter influence plant performance. Plant performance was represented by the first principal component (PC1) derived from a principal component analysis (PCA) based on RCD and net height growth.

3. Results

3.1. The field study: plant diversity and mycorrhizal colonization

Bamboo invasion showed no significant effects on plant diversity indices in either arborous or herbaceous layers (Fig. 1). However, it significantly reduced both the Simpson and Pielou indices in the shrub layer of mixed coniferous-broadleaf forests (MF) and *I. tessellatus*-coniferous-broadleaf mixed forests (IMF) ($P < 0.05$). Five species—*P. massoniana, Pteridium aquilinum, E. japonica, S. stellaris,* and *L. chinense*—were present across all three forest types.

Notably, bamboo invasion significantly decreased mycorrhizal colonization rates in all studied plant species except *E. japonica* (Fig. 2; $P < 0.05$). *I. tessellatus* maintained similar colonization rates, with no significant differences between pure bamboo stands (IF) and IMF. Among affected species, *P. aquilinum, E. japonica, S. stellaris, and L. chinense* exhibited particularly pronounced population declines following *I. tessellatus* invasion (Fig. S2).

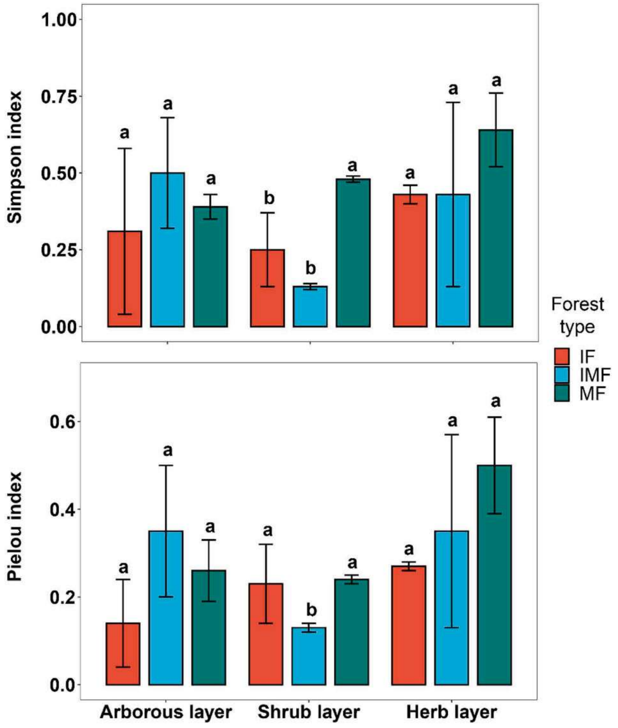

Fig. 1. Effects of bamboo invasion on the plant diversity. Different letters indicate significant differences between different stands based on Duncan's test at 0.05. IF, *I. tessellatus* pure forest; IMF, coniferous-broadleaf mixed forest with *I. tessellatus* invasion; MF, uninvaded mixed coniferous-broadleaf forest.

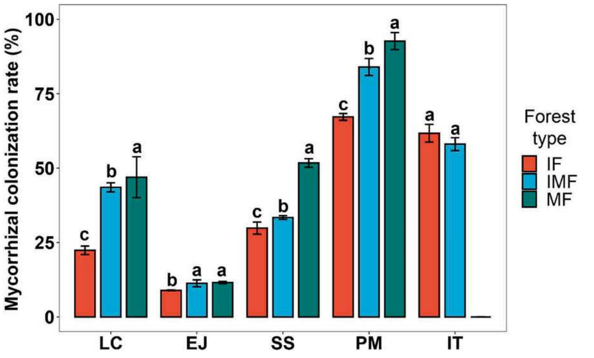

Fig. 2. Effects of bamboo (*Indocalamus tessellatus*) invasion on the mycorrhizal colonization rate of native species PM (*Pinus massoniana*), EJ (*Eurya japonica*), SS (*Symplocos stellaris*), and LC (*Loropetalum chinense*).

3.2. Effects of bamboo invasion on the soil chemical properties

Soil pH values were consistently acidic across all stands, ranging from 4.22 to 4.48 (Fig. 3). Mixed coniferous-broadleaf forests (MF) exhibited significantly higher pH values than pure bamboo stands (IF) ($P < 0.05$). We observed a clear gradient in soil nitrogen content, with TN following the pattern: IMF > MF > IF.

The concentrations MBN, DON, NH_4^+-N, and NO_3^--N were significantly lower in IF than MF and IMF stands ($P < 0.05$). While IF had the lowest SWC, differences among treatments were not statistically significant. Notably, bamboo invasion showed no significant effects on SOC, MBC, or DOC (Fig. 3).

3.3. The controlled-environment study: growth and mycorrhizal colonization of L. chinense

The net height growth of *L. chinense* seedlings exhibited significant variation among treatments, following the order: CK > L (litter addition) > RL (combined litter and root exudate addition) > R (root exudate addition) (Fig. 4a). Compared to CK, the R treatment alone reduced seedling height gain by 25.40 %, while the RL treatment resulted in a 21.69 % decrease. In contrast, none of the treatments significantly affected the RCD increment. Mycorrhizal colonization rates in *L. chinense* roots ranged from 11.84 % to 23.09 % across treatments. Both the R and RL treatments significantly suppressed colonization compared to CK ($P < 0.05$).

3.4. Soil chemical properties

Neither root exudate addition nor litter addition significantly affected SOC, TN, or NO_3^--N content (Fig. 5). However, R and L additions and their combination significantly reduced soil pH ($P < 0.05$) and the effect of R application was greater than L treatment (Fig. 5). Additionally, the R treatment significantly enhanced DON content ($P < 0.05$). Furthermore, the combined application of root exudates and litter significantly increased MBC and MBN contents relative to CK ($P < 0.05$).

3.5. Soil microbial properties

The addition of litter and root exudates did not significantly impact the microbial α-diversity in the rhizosphere soil (Fig. 6). However, these additions significantly altered the composition of both bacterial and fungal communities (Fig. 7). Notably, the fungal community structure demonstrated distinct clustering patterns in treatments where exudates

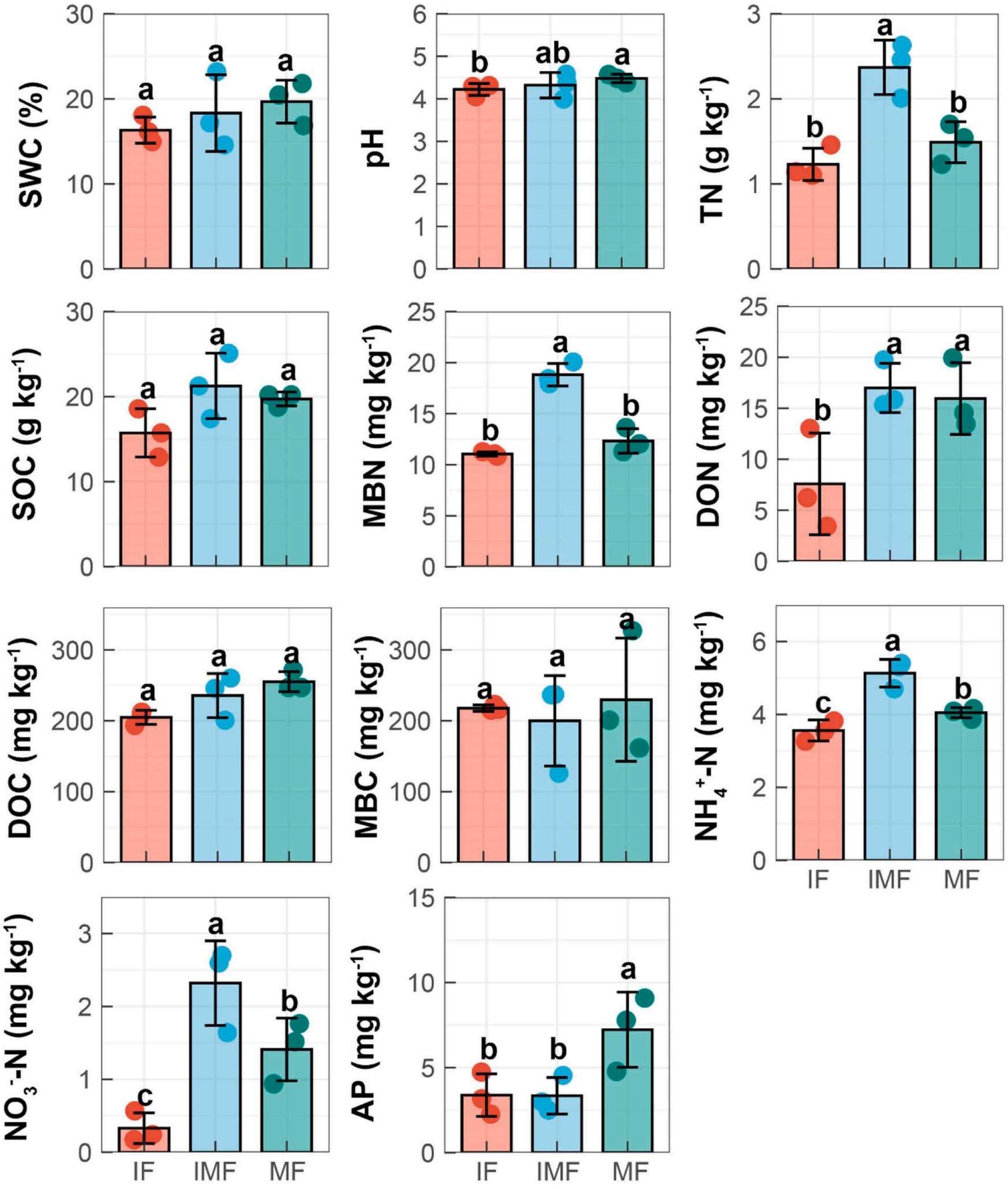

Fig. 3. Effects of bamboo invasion on the soil chemical properties: SWC (soil water content) NH_4^+-N (ammonium nitrogen), NO_3^--N (nitrate nitrogen), AP (available phosphorus), SOC (soil organic carbon), TN (total nitrogen), DOC (dissolved organic carbon), DON (dissolved organic nitrogen), MBC (microbial biomass carbon), MBN (microbial biomass nitrogen).

were applied alone or in combination with litter. In the rhizosphere soil of *L. Chinense*, the dominant fungal phyla included Ascomycota (38.28 %), Basidiomycota (36.68 %), unassigned fungi (21.86 %), Glomeromycota (1.32 %), Mortierellomycota (1.15 %), Rozellomycota (0.34 %), Mucoromycota (0.25 %), Chytridiomycota (0.06 %), Kickxellomycota (0.03 %), and Cercozoa (0.002 %). The top ten bacterial phyla in abundance were Proteobacteria (36.55 %), Acidobacteria (34.01 %), Actinobacteria (16.51 %), Chloroflexi (4.71 %), Verrucomicrobia (2.36 %), Bacteroidetes (1.57 %), Patescibacteria (1.27 %), Dependentiae (0.60 %), unassigned bacteria (0.58 %), and Planctomycetes (0.36 %). All treatments led to a significant reduction in the relative abundance of Proteobacteria and Actinobacteria when compared to CK (Table S1), while the L and R treatments significantly increased the relative abundance of Acidobacteria. R treatment showed a significantly higher relative abundance of Dependentiae, Patescibacteria, and Verrucomicrobia than CK ($P < 0.05$).

3.6. *Parameters affecting L. Chinense growth*

The piecewise SEM results indicated that the addition of root exudates significantly reduced mycorrhizal colonization rate, leading to slower *L. Chinense* growth (Fig. 8). The net height and RCD of *L. Chinense*, however, were not correlated to soil microbial diversity (Fig. 9a). Furthermore, height growth was positively associated with soil pH, but negatively associated with soil DON content (Fig. 9b), and mycorrhizal colonization rate was significantly correlated with soil AP

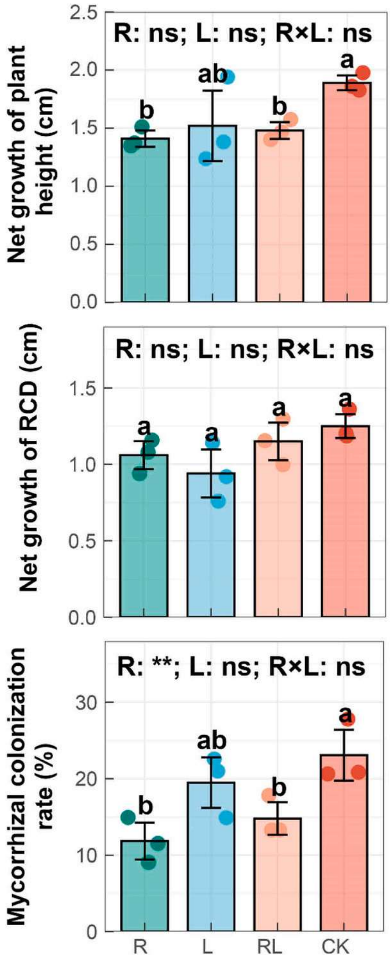

Fig. 4. Effects of litter and root exudate addition on the growth and mycorrhizal colonization f *L. chinense* seedlings. Note: RCD = root collar diameter. Different lowercase letters indicate statistically significant differences among treatments (Duncan's test, $P < 0.05$). R, root exudates addition; L, fresh leaf litter addition; RL, combined addition of root exudates and leaf litter; control, no substrate additions.

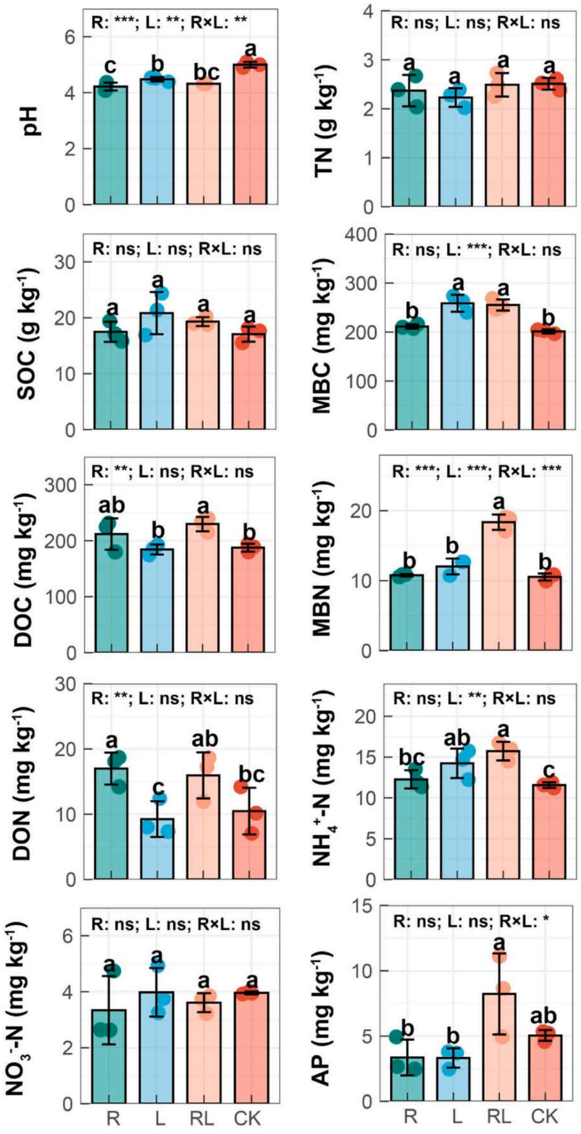

Fig. 5. Effects of litter and root exudate addition on the soil chemical properties. See Fig. 3 for other explanations.

content.

4. Discussion

4.1. Field evidence of ecological risks from I. tessellatus invasion

Plant diversity is a cornerstone of Earth's life-support systems, playing a vital role in sustaining ecosystem functions and ensuring community stability (Breitschopf and Bråthen, 2023). Our field observations demonstrate that the invasion of *I. tessellatus* leads to the complete disappearance of key species in coniferous-broadleaf mixed forests, including *Camellia japonica, Choerospondias axillaris, Lindera aggregata,* and *Hedera nepalensis* (Fig. S2). However, mature canopy species like *P. massoniana* seem resistant, likely due to established competitive dominance. These findings indicate that *I. tessellatus* predominantly affects plant growth and survival in the shrub layer. This pattern aligns with the observations of Kudo et al. (2017), who reported that dwarf bamboo suppresses native species diversity through aggressive growth and increasing density. Furthermore, the persistent spread of *I. tessellatus* may disrupt ecosystem processes and alter the growth dynamics of the arbor layer (Fortunel et al., 2009; Li et al., 2024b).

Plant diversity typically creates a variety of soil niches by generating diverse microhabitats, which in turn enhance soil microbial diversity and functionality (Zhou et al., 2024). In our study, although bacterial and fungal α-diversity and richness indices did not differ significantly between invaded and non-invaded forests, bamboo invasion induced pronounced shifts in microbial community composition. In particular, IMF exhibited a higher relative abundance of Acidobacteriota, coupled with notable declines in Basidiomycota and Actinobacteriota (Fig. S4). Such restructuring of microbial communities likely reflects functional alterations that could impair nutrient cycling and disrupt mutualistic symbioses. Consistent with this, mycorrhizal colonization rates decreased significantly in all native plant species after *I. tessellatus* invaision (Fig. 2). This reduction in mycorrhizal colonization may hinder nutrient and water acquisition, thus increasing the susceptibility of native species to competitive exclusion by *I. tessellatus*. Therefore, the concurrent decline in plant diversity and the restructuring of microbial community composition and function collectively altered soil physicochemical properties, supporting our first hypothesis. A global meta-analysis revealed that bamboo invasion generally increases soil pH in adjacent native forests, though this effect depends on the invasion stage and forest type (Wu et al., 2024). In contrast, our study demonstrates a marked decrease in soil pH with advancing *I. tessellatus* invasion. This acidification results not only from litter decomposition releasing organic acids but also from root exudates rich in low molecular

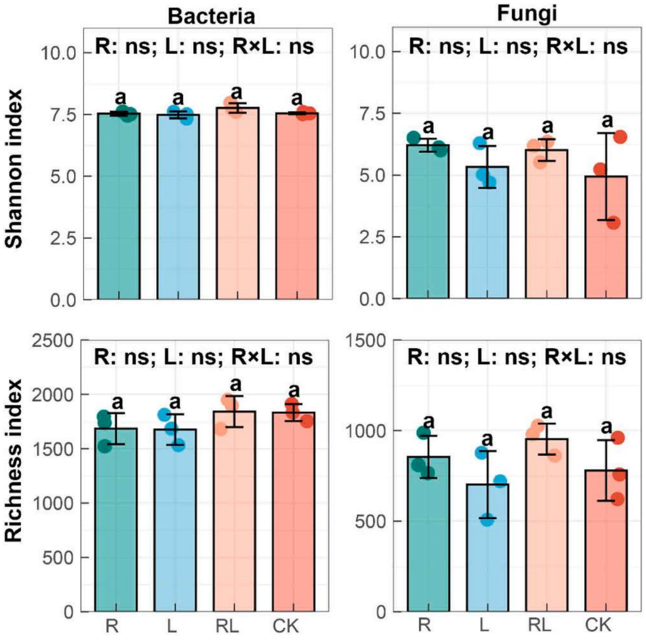

Fig. 6. Effects of litter and root exudate addition on the microbial α diversity of rhizosphere soil.

weight organic acids, phenolic compounds, and other allelochemicals (Fig. S7; Wang et al., 2016; Zhang et al., 2025). Additionally, the competitive strategy of dwarf bamboo, i.e., shifting resource allocation to belowground structures, may further alter soil pH (Vives-Peris et al., 2020; Winkler et al., 2016).

These changes are both a consequence of *I. tessellatus* invasion and a driver of disrupted soil nitrogen (N) cycling. In our study, IF exhibited

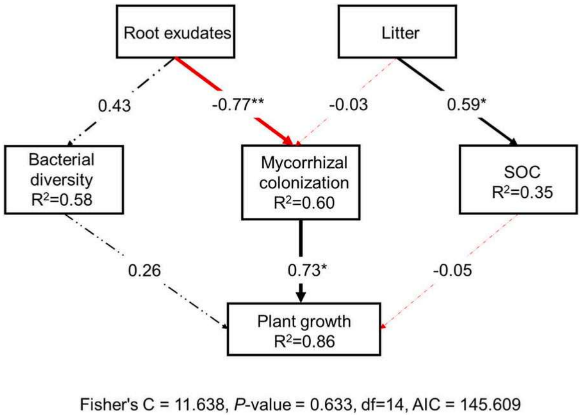

Fig. 8. SEM depicting the effects of root exudates and litter of *I. tessellatus* on *L. Chinense* growth. Note: * indicates $P < 0.05$, ** indicates $P < 0.01$.

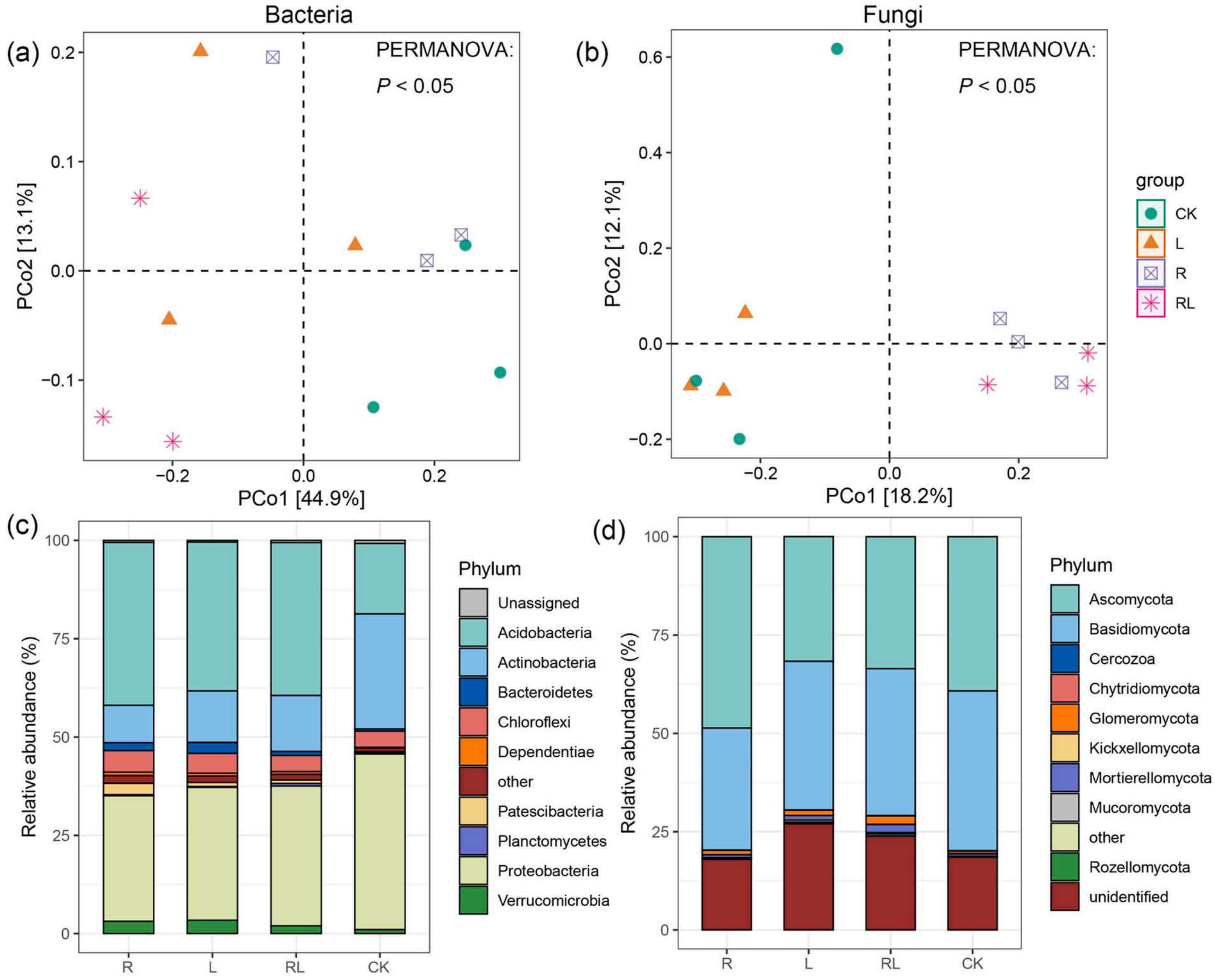

Fig. 7. Effects of litter and root exudate addition on the bacterial (a) and fungal (b) community structure and bacterial (c) and fungal (d) community composition of rhizosphere soil.

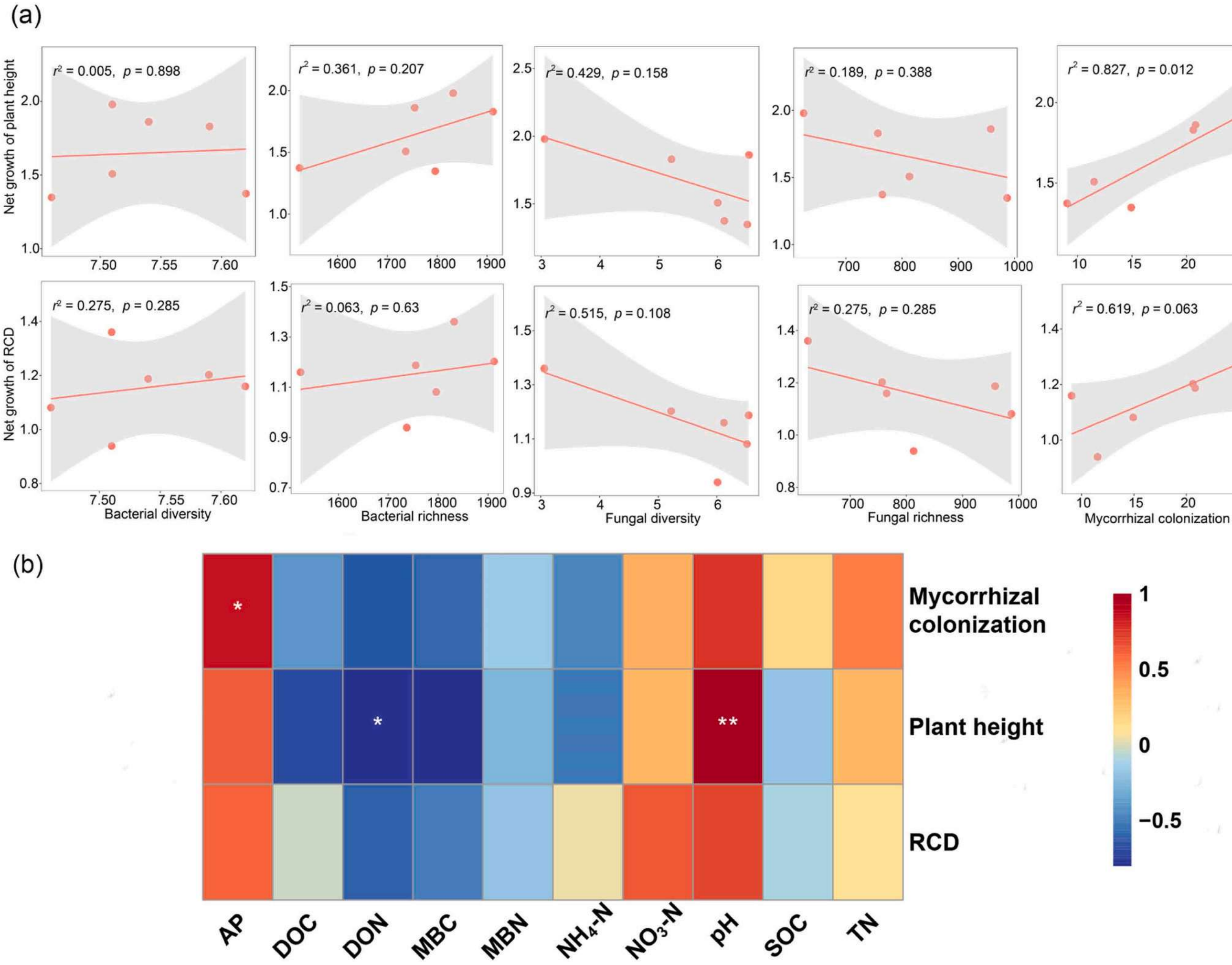

Fig. 9. Correlations between microbial diversity, mycorrhizal colonization, soil chemical properties and *L. Chinense* growth under the condition of root exudate addition.

the lowest levels of soil NH_4^+-N and NO_3^--N among all the forest types. Since bamboo preferentially absorbs NH_4^+-N (Zou et al., 2020), its invasion may reduce the abundance of ammonia-oxidizing bacteria and other nitrifying microorganisms (Luo et al., 2024), thereby suppressing N cycling. This aligns with findings by Song et al. (2016), who reported that moso bamboo invasion into evergreen broadleaf forests slows N mineralization and cycling. Furthermore, *I. tessellatus* invasion significantly decreased soil TN, likely due to poor litter quality and a decline in nitrogen-fixing bacteria (Xu et al., 2020). Collectively, our results highlight that *I. tessellatus* invasion poses two major ecological risks: (1) a decline in plant biodiversity and (2) the impairment of N fixation and cycling processes. Notably, the pronounced decline in mycorrhizal colonization, together with shifts in soil microbial communities observed in the field, indicates that belowground chemical interactions may be a key mechanism mediating these impacts on native species.

4.2. *Effects of I. tessellatus root exudates on L. chinense growth*

Allelopathy is a common adaptive strategy of successful invasive plants, enabling them to suppress native competitors and their symbiotic partners (Kalisz et al., 2021). *I. tessellatus* releases allelochemicals primarily through two pathways: litter deposition and root exudation. Our controlled experiment reveal that root exudates constitute the dominant pathway directly inhibiting *L. chinense* growth. Specifically, allelochemicals in the exudates reduce mycorrhizal colonization rates and alter rhizosphere nutrient dynamics, ultimately impairing *L. chinense* height growth, supporting our second hypothesis. This aligns with Abarca et al. (2021), who demonstrated that *Ligustrum lucidum* invasion disrupts mycorrhizal associations in *Celtis tala*, facilitating invader dominance.

Root exudates influenced multiple nutrient-related pathways. Firstly, the decline in mycorrhizal colonization limited *L. chinense*'s access to nutrient and water, thereby placing it at a competitive disadvantage relative to *I. tessellatus* (Hale et al., 2016). The observed positive correlation between soil AP and mycorrhizal colonization further indicates that reduced colonization directly impaired phosphorus uptake, restricting seedling growth (Fig. 9). Secondly, root exudates decreased concentrations of K, Ca, and Mg in *L. chinense* tissues (Figs. S5), likely reflecting diminished mycorrhizal-mediated nutrient acquisition. Thirdly, organic acids present in the root exudates acidified the rhizosphere, consistent with the soil acidification observed in our field study. This acidification likely increased the bioavailability of phytotoxic aluminium ions (Viet et al., 2013), inhibited fine root development and photosynthetic efficiency, and disrupted plant–arbuscular mycorrhizal fungi (AMF) symbioses, potentially enhancing DON leaching (Zhang et al., 2025).

These chemical alterations induced shifts in the rhizosphere microbiome, further amplifying the suppressive effects on *L. chinense* (McLaughlin et al., 2023; Yue et al., 2023). Consistent with field observations, the decline in soil pH favored Acidobacteria—an oligotrophic and pH-sensitive taxon (Liu et al., 2016)—while simultaneously reducing the abundance of Actinobacteria (Fig. S6). The increased dominance of Acidobacteria may lead to reduced nutrient mineralization rates (Kalam et al., 2020). Meanwhile, the loss of Actinobacteria, which play critical roles in antibiotic production, nitrogen fixation, and phosphorus solubilization (Palaniyandi et al., 2013), likely impairs pathogen suppression and nutrient cycling, particularly soil nitrogen transformations and plant phosphorus uptake. Collectively, these belowground microbial shifts establish a feedback loop that promotes *I. tessellatus* dominance and exacerbates the competitive disadvantage of native species.

4.3. Limitation, implications and future directions

Collectively, evidence from field surveys and controlled experiments points to a common mechanism: *I. tessellatus* invasion restructures plant and microbial communities, markedly reduces mycorrhizal colonization, and suppresses nitrogen cycling. Controlled experiments reveal that root exudate allelochemicals drive these changes by acidifying the rhizosphere, disrupting mycorrhizal symbioses, altering rhizosphere microbial composition, and limiting nutrient acquisition, thereby reinforcing the competitive dominance of *I. tessellatus* and hastening the decline of native species.

Given these findings, it is imperative to address *I. tessellatus* invasion through a long-term, ecologically grounded strategy that balances control efficacy with minimal ecosystem disturbance (Fernández et al., 2024). The findings of this study suggest that targeted belowground interventions, e.g., chemical treatments or severing bamboo rhizome networks (Chen et al., 2017b), are one of the most effective means of controlling *I. tessellatus* invasion. Furthermore, future afforestation and restoration planning should prioritize the selection of tree species that can coexist with or are most resistant to *I. tessellatus*, thereby enhancing long-term vegetation stability. Ultimately, the goal is not only to reduce *I. tessellatus* dominance, but also to restore native biodiversity and sustain forest ecosystem functions.

By isolating the effects of root exudates and litter inputs on *L. chinense* seedlings, this experiment highlights chemically mediated interactions as a key mechanism underlying the suppression of native species. However, further research is necessary to isolate and characterize the specific root-exuded compounds responsible for suppressing mycorrhizal symbiosis. We also acknowledge that this controlled experiment represents a simplified system that does not fully capture the ecological complexity of natural forest conditions. In natural ecosystems, the dominance of *I. tessellatus* likely results from multifaceted interactions, including competition for light and nutrients, modification of soil properties, suppression of understory regeneration, and potential feedbacks involving soil microbial communities (Xu et al., 2020). Furthermore, considering that allelopathic effects are context-dependent and influenced by experimental design (Zhang et al., 2021), future studies should incorporate additional species, aboveground-belowground interactions, and long-term feedbacks to more comprehensively elucidate how *I. tessellatus* shapes forest structure and function.

5. Conclusions

This study uses field and controlled experiments to evaluate the ecological impacts and belowground mechanisms of *I. tessellatus* invasion. We observed significant declines in shrub-layer plant diversity and disruptions to soil biogeochemical processes, including acidification and altered nitrogen cycling, alongside suppressed mycorrhizal colonization in native species. Our findings highlight the pivotal role of root exudates in mediating soil chemical changes, reshaping rhizosphere microbial community composition, and impairing native mycorrhizal associations. However, it is important to recognize that invasion dynamics are inherently multifactorial. Root exudates represent one of the key factors embedded within a complex interplay of processes that drive invasion success. Therefore, future research incorporating long-term and multitrophic field studies is essential to advance understanding of bamboo invasion ecology and to inform effective management strategies.

CRediT authorship contribution statement

Bo Deng: Writing – review & editing, Resources, Investigation, Funding acquisition, Conceptualization. **Gang Lei:** Resources, Investigation. **Lu Qiu:** Investigation, Formal analysis. **Qinglai Dang:** Writing – review & editing, Supervision. **Guorui Xie:** Writing – original draft, Software, Investigation, Conceptualization. **Zhuangzhuang Qian:** Writing – original draft, Visualization, Methodology, Funding acquisition, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123189.

Data availability

Data will be made available on request.

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