

Research Article

Solidago canadensis modifies microbial community and soil physicochemical properties through litter leachates and root exudates

Yanwen Bo^{1,2}, Yali Liao¹, Mark Pawlett^{2, ID}, Rasheed Akbar^{1,3, ID}, Nickolas Girkin^{2,4}, Jianfan Sun^{1,5,*}, Amjad Ali⁶, Naushad Ahmad⁷, Wei Liu⁸, Xiaoyan Wang⁸, and Daolin Du⁹

¹Institute of Environment and Ecology, School of Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China,

²Faculty of Engineering and Bioscience, Cranfield University, Bedfordshire MK43 0AL, UK, ³Department of Entomology, Faculty of Physical and Applied Sciences, The University of Haripur, Haripur 22062, Pakistan, ⁴School of Biosciences, University of Nottingham, Loughborough LE12 5RD, UK, ⁵Jiangsu Collaborative Innovation Center of Technology and Material of Water Treatment, Suzhou University of Science and Technology, Suzhou 215009, China, ⁶School of Material Science & Engineering, Jiangsu University, Zhenjiang 212013, China, ⁷Department of Chemistry, College of Science, King Saud University, Riyadh 11451, Saudi Arabia, ⁸College of Optical, Mechanical and Electrical Engineering, Zhejiang A&F University, Hangzhou 311300, China, ⁹Jingjiang College, Institute of Environment and Ecology, School of Emergency Management, School of Environment and Safety Engineering, School of Agricultural Engineering, Jiangsu University, Zhenjiang 212013, China

*Corresponding author. E-mail: zxsjf@ujs.edu.cn

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Abstract

Invasive plants alter soil microbial communities and physicochemical properties through chemical inputs from litter, root exudates and leachate, impacting a range of soil processes, but precise effects are poorly understood. We investigated the little effects of *Solidago canadensis*, a common invasive species in China, on soil microbial communities under natural conditions. Experimental treatments included *S. canadensis* seedling density (1 and 2 plants/pot) and litter quantity (10 and 20 g/pot), with control groups containing no plants or litter. After 120 days, soil samples were analyzed for physico-chemical properties, GC–MS chemical composition, and bacterial community composition using high-throughput sequencing. Results showed that *S. canadensis* seedlings and litter inputs significantly increased soil pH, soil organic matter (SOM), and total nitrogen (TN), while phosphorus and potassium remained unchanged. We identified 66 chemical compounds, predominantly ketones, alcohol, aldehyde, hydrocarbon, ester, acid, terpenoids and alkaloids, associated with the presence of *S. canadensis*, alongside shifts in dominant bacterial genera including *Sphingomonas*, *Acidobacteriales* and *Gemmatimonas*. Rarer genera under the invasive treatment species, such as *Candidatus*, *Rhodoplanes* and *Novosphingobium*, were positively correlated with soil TN, pH, and SOM. Collectively, these findings demonstrate that allelochemical inputs from *S. canadensis* litter and root exudates significantly reshape soil properties and microbial communities, with potential implications for ecosystem dynamics and invasion success.

Keywords: allelopathy, invasive plant, litter effects, root exudates, soil microbial communities, high-throughput sequencing

加拿大一枝黄花通过凋落物渗滤液和根分泌物改变土壤微生物群落和理化性质

摘要：外来植物通过凋落物、根系分泌物和渗滤液中的化学物质改变土壤微生物群落和理化性质，影响一系列土壤过程，但其具体机制仍不清楚。本研究以中国广泛分布的入侵植物——加拿大一枝黄花 (*Solidago canadensis*) 为对象，探讨其在自然条件下对土壤微生物群落和理化性质的影响。实验处理包括加拿大一枝黄花幼苗密度 (每盆1和2株) 和凋落物量 (每盆10和20g)，并设置了不含植物或凋落物的对照组。实验处理120天后，采集土壤样品，分析其理化性质、GC-MS化学成分，并基于高通量测序测定了细菌群落组成。结果表明，加拿大一枝黄花幼苗和凋落物输入显著增加了土壤的pH、有机质 (SOM) 和总氮 (TN)，而磷和钾则未发生变化。我们识别出66种化学物质，主要包括酮类、醇类、醛类、烃类、酯类、酸类、萜类和生物碱，这些物质与加拿大一枝黄花的存在相关。此外，*Sphingomonas*、*Acidobacteriales* 和 *Gemmatimonas* 等优势细菌属发生了显著变化，而 *Candidatus*、*Rhodoplanes* 和 *Novosphingobium* 等稀有细菌属与土壤TN、pH和SOM呈正相关。上述研究结果表明，加拿大一枝黄花凋落物和根系分泌物中的化学物质增加显著影响了土壤性质和细菌群落，这可能会对生态系统动态和入侵成功产生重要影响。

关键词：化感作用，外来植物，凋落物效应，根分泌物，土壤微生物群落，高通量测序

INTRODUCTION

Invasive species pose significant threats to ecosystem dynamics by affecting ecological structure and community function. *Solidago canadensis*, an invasive plant, significantly impacts soil ecosystems through its litter and rhizosphere inputs (Qiao *et al.* 2024). Litter originating from *S. canadensis* can increase soil bacterial biomass, detritivores and microbivores abundance while concurrently, reducing bacterial biomass, abundance of herbivores, predators in the rhizosphere (Zhang *et al.* 2019). The exudates secreted by invasive plants can alter the abundance and diversity of soil fungi and microbial populations, thereby creating specific chemical niches within the rhizosphere that facilitate microbial colonization (Gioria *et al.* 2023; Pan *et al.* 2023). Understanding these plant–soil microbe interactions is crucial for determining the competitive dynamics of plant community structures and ultimately for identifying future sustainable opportunities for invasive species management and remediation (Akbar *et al.* 2024a; Bever 2003; Zhou *et al.* 2021).

Beyond the rhizosphere, the broader soil environment can also be affected by invasive plants through non-biological inputs, particularly plant litter. The deposition of chemically distinctive litter can differentially affect microbial community development, including by influencing nutrient availability and cycling processes (Dassonville *et*

al. 2011; Liao *et al.* 2008; Tamura and Tharayil 2014; Tharayil *et al.* 2013). Organic matter inputs from litter can significantly increase the activity (respiration) of heterotrophic soil organisms and alter the proportions of different bacterial groups, including Gram-negative bacteria (e.g. bacteroidetes and proteobacteria) (Farrer *et al.* 2021; Nemergut *et al.* 2011). Furthermore, it has been suggested that invasive plants may exhibit allelopathic effects, whereby secondary metabolites in root exudates or from plant litter can modify the soil chemistry of invaded sites (Adomako *et al.* 2019; Akbar *et al.* 2024b; Torres *et al.* 2021). Identifying the causal relationships between soil microbial community composition and the diversity of compounds present in root exudates and litter is essential for understanding how these changes affect ecosystem functions, such as nutrient cycling and plant–soil feedback mechanisms. This understanding can inform management strategies aimed at controlling invasive species and restoring native plant communities.

Solidago canadensis benefits from associations with arbuscular mycorrhizal fungi, which can enhance nutrient uptake and alter litter quality, and contribute to its relative success as an invasive species (Adomako *et al.* 2021; Qi *et al.* 2022). *Solidago canadensis* can release various allelopathic compounds, including phenolics and flavones, which can impact the broader microbial community (Kato-Noguchi and Kato 2022; Yuan *et*

al. 2013). The combined effects of these inputs on soil microbial community composition and soil chemical properties remain an important area of investigation, as understanding these interactions is crucial for developing effective management practices to mitigate the impacts of invasive species on native ecosystems. At present, however, the comprehensive impacts of such effects, particularly on soil systems, are poorly understood.

Previous attempts to correlate plant invasion with changes in the composition of soil microbial communities have yielded mixed results (Khan *et al.* 2024; Liu *et al.* 2019; Lu *et al.* 2020), most likely due to the diversity of compounds present in exudates and plant litter, and their varied impacts and interactions. Here, we aimed to elucidate the effects of *S. canadensis* and its litter on soil microbial communities by quantifying the variations in soil physical and chemical properties, chemical composition, and bacterial community composition in response to invasion. Specifically, we investigated how the concentration of *S. canadensis* litter and different planting densities (root input levels) interactively and individually alter soil physicochemical properties and chemical diversity. Furthermore, we explored the implications of these changes on the diversity and composition of soil bacterial communities. By addressing these questions, we sought to contribute to the broader understanding of how invasive plants influence soil nutrient dynamics and microbial ecology.

MATERIALS AND METHODS

Soil sample and *S. canadensis* L. litter

Soil was collected from three sites devoid of *S. canadensis* located near Jiangsu University, Zhenjiang City, Jiangsu province, China (32°12' N, 119°27' E). The soil texture was loamy sand (82.63 ± 0.20% sand, 15.12 ± 0.07% silt, and 2.25 ± 0.03% clay, pH was 6.58 ± 0.05, the cation exchange rate was 6.2 ± 0.02 cmol kg⁻¹, and organic matter was 5.37 ± 0.52 g/kg. Three nearby sites devoid of *S. canadensis* were selected for soil collection due to their accessibility and historical diversity of plant communities. The top layer of soil (0–10 cm) was collected using a spade, mixed thoroughly, and transported promptly to the laboratory. The soil was then air-dried and sieved (2 mm) to remove visible coarse plant material and stones. Plant litter was collected from an abandoned field (32°12' N, 119°27' E) with a high density of *S. canadensis* near Jiangsu University. The collected litter was transported to the

laboratory where it was manually sorted to remove large debris and non-plant material, then filtered through a coarse mesh to remove smaller impurities. The litter was subsequently oven-dried at 65 °C for 24 h, crushed, and sieved (2 mm).

Experimental design

We incorporated a multi-factorial design to quantify both the impacts of both *S. canadensis* seed density (0, 1, 2 seedlings/pot) and *S. canadensis* plant litter concentrations (0, 10 and 20 g/pot, equivalent to 0, 33, 50 g/kg soil). Each experimental pot was rectangular with dimensions of 120 mm × 108 mm × 90 mm, holding approximately 800 g of soil. The treatments were as follows: NZ (no litter, no seedlings), NO (no litter, 1 seedling), NT (no litter, 2 seedlings), LZ (10 g litter/pot, no seedlings), LO (10 g litter/pot, 1 seedling), LT (10 g litter/pot, 2 seedlings), HZ (20 g litter/pot, no seedlings), HO (20 g litter/pot, 1 seedling), HT (20 g litter/pot, 2 seedlings), with five replicates of each treatment. After blending the litter and soil sample, *S. canadensis* seedlings, grown to a height of 8–10 cm, were transplanted into pots. The experiment was conducted in a greenhouse with a mean daytime temperature of 30 °C and a nighttime temperature of 25 °C, under a light/dark photoperiod of 10 h light and 14 h darkness. Soil moisture was monitored using a soil moisture probe (GEMHO RJ45), and irrigation was adjusted to maintain soil moisture at an optimal level for plant growth (45%–55% field capacity). Pots were arranged randomly within the glasshouse. *S. canadensis* was harvested after 120 days, at which point rhizosphere soil samples were collected and immediately stored at –80 °C for molecular analysis. Rhizosphere soil was sampled by collecting three random soil cores from each pot, at a depth of 0–5 cm, ensuring each core was separated from the others by 2–3 cm. Samples were subsequently mixed to create a composite for each pot, resulting in a total of five replicate samples for each treatment. Each sample was divided into two portions: one was air-dried at room temperature and then sieved 2 mm for soil chemical analysis, while the other was stored at –20 °C for composition analysis by GC–MS.

Soil pH was evaluated using a pH meter after shaking the soil water (1:2.5 w/v) suspension for 30 min (Nelson *et al.* 1982). Soil organic matter (SOM) was analyzed by the potassium dichromate volumetric method (Nelson *et al.* 1982). Total nitrogen (TN) and total phosphorus (TP) were assayed using the Kjeldahl method and Mo–Sb colorimetric methods, respectively (Zhang *et al.* 2024). Total

potassium (TK) content was assessed by digesting soil samples in $\text{HF-HClO}_4\text{-HNO}_3$ acid mixture following the flame photometry method (Lan *et al.* 2024).

Soil samples GC–MS analysis

The collected soil samples were dried at room temperature and then stored at -20°C until extraction and analysis. Soil samples were crushed and sieved (2 mm) to remove root residues. The sieved sample (5 g) was extracted using ultra sonication three times for 30 min each with 20 mL of methanol in a sonic bath. After extraction, the mixture was filtered through two layers of filter paper, and the resulting filtrate was centrifuged at 4000 rpm for 15 min. The supernatant was concentrated under a vacuum at 40°C to near dryness on a rotary evaporator. The dry residue from the evaporation was redissolved in 100% methanol and passed through a $0.45\ \mu\text{m}$ membrane before GC–MS analysis (Ren *et al.* 2015).

The gas chromatograph (GC; Agilent 7890A), was equipped with a fused silica capillary column (HP-5, 30 m $0.25\ \text{mm}$; film thickness $0.25\ \mu\text{m}$). The oven temperature was held at 60°C for 2 min before increasing from 60 to 180°C at a rate of 3°C min^{-1} over 5 min, and then from 180 to 230°C at a rate of 6°C min^{-1} with helium as the carrier gas (flow rate of $1.0\ \text{mL min}^{-1}$). The injector temperature was 200°C , and injection volume was $0.1\ \mu\text{L}$. Mass spectra were assessed at 70 eV (EI) using a mass scan range of m/z 30–500 amu with a mass scan time of 4 s. Relative quantities of individual components were calculated based on GC peak areas. Peaks were identified by comparing their mass spectra and retention indices with the National Institute of Standards and Technology (NIST) 08 spectral databases (Cumeras *et al.* 2023; Huang *et al.* 2013).

Soil DNA extraction and amplification

DNA was extracted from soil samples (0.5 g wet weight) using E.Z.N.A Soil DNA Kit (OMEGA, USA) according to the manufacturer protocol. Extracted DNA was diluted in TE buffer (10 mM Tris–HCl, 1 mM EDTA, pH 8.0) and stored at -20°C until use. The extraction, purification and sequencing of genomic DNA were performed at Biomarker Technologies Co., Ltd. (Beijing, China). The V3–V4 region of the 16S rRNA was PCR amplified from microbial genomic DNA. The forward primer was 338 F: 5′-ACTCCTACGGGAGGCAGCA-3′, and the reverse primer was 806 R: 5′-ATGACGGGACTACHVGGTWTCTAAT-3′ under a PCR of one pre-denaturation cycle at 95°C for

5 min, 25 cycles of denaturation at 95°C for 30 s, annealing at 50°C for 30 s, and elongation at 72°C for 30 s, and one post-elongation cycle at 72°C for 5 min. The PCR-amplified products were separated into 0.8% agarose gels and extracted from the gels (Pal *et al.* 2024).

Illumina MiSeq sequencing and processing of sequencing data

V3–V4 amplicons were sequenced using the Illumina MiSeq pair-end method with a 6-cycle index read. The average sequence read length was 450 base pairs. Sequence reads were filtered so that their average Phred quality score was greater than 20 and their length was greater than 200 bp. After trimming, readings were assembled by Flash software, and unassembled reads discarded. The sequence data was sorted and analyzed using the Quantitative Insights into Microbial Ecology (QIIME) suite of analysis tools. Sequences were assigned to operational taxonomical units (OTUs) with a pair-wise identity threshold of 97% and then classified taxonomically using Ribosomal Database Project (RDP) classifiers (Cui *et al.* 2023; Xue *et al.* 2024).

We estimated the relative abundance of individual taxa within each community by comparing the number of sequences ascribed to a particular taxon to the total number of sequences obtained for each sample. In addition, we conducted Alpha Diversity and Beta Diversity analyses. The Chao1, Abundance-based Coverage Estimator (ACE, Kang *et al.* 2024), Shannon, and Simpson indices were utilized in the alpha diversity analysis, with Shannon and Simpson indices specifically determining community diversity. Chao1 and ACE were utilized to calculate community richness. The links between the bacterial populations and chemical characteristics in the various treatments were clarified using redundancy analysis (RDA) (Liu *et al.* 2014; Zhou *et al.* 2020).

Statistical analysis

Statistical analysis was carried out using IBM SPSS Statistics 24.0. Data were analyzed using a two-way analysis of variance (ANOVA) considering seed density and litter quantity as factors. Post-hoc mean comparisons were performed using SNK (Student–Newman–Keuls) and the Duncan multiple range test at a significance level of $P < 0.05$. Linear Discriminant Analysis Effect Size (LEfSe) was utilized to determine the statistical significance and biological relevance of various taxa abundantly present in each treatment (Fig. 2). The LEfSe was used to detect bacterial

community features (i.e. bacterial richness and diversity) with significantly different abundances (Shen *et al.* 2010). This analysis visually represents differences through color coding, with Linear Discriminant Analysis (LDA) scores indicating the extent of consistent differences in relative abundance among the analyzed bacterial communities across different treatments.

RESULTS

Soil physicochemical properties

Soil pH ranged between 6.55 and 7.34 throughout, with an increasing trend in response to escalating quantities of *S. canadensis* litter and seedlings ($P < 0.05$, Table 1). TN content exhibited a marked increase from 0.21 to 0.51 g ($P < 0.05$). Conversely, SOM and TP levels did not show significant differences across the treatments, with their values ranging from 5.37 to 7.43 g/kg and 0.66 to 0.69 g/kg, respectively ($P > 0.05$). There was also no significant in TK content between treatments ($P > 0.05$).

Chemical composition of soil samples

We identified a total of 66 chemical compounds across all treatments (Supplementary Table S1). These compounds included ketones, alcohols, aldehydes, hydrocarbons, esters, acids, ethers, phenols, terpenoids and alkaloids (Supplementary Table S2). The distribution and relative concentration of these compounds varied among the treatments,

as follows: NZ (22 compounds, 70.39% of total), NO (31, 71.79% of total), NT (28, 75.24% of total), LZ (26, 71.54% of total), LO (34, 73.77% of total), LT (35, 81.43% of total), HZ (30, 72.14% of total), HO (34, 71.35% of total) and HT (34, 72.74% of total). Notably, eight compounds, 2-pentanone, 2-butanamine, methyl(1s*,2s*,5R*)-1,5-dimethyl-2-ethenyl-cyclohexane-1-carboxylate, 2-methyl undecanal, 2-(2-ethoxyethoxy) ethanol, 1, 4, 7, 10, 13, 16-hexaoxacyclooctadecane, phytol and nonahexacontanoic acid, were consistently present across all treatments.

A significant increase in both the number and relative concentrations of these chemical compounds was observed with the addition of *S. canadensis* litter and seedlings, compared to the control treatment (NZ) ($P < 0.05$, Supplementary Table S2). The number and concentration of ketone compounds remained relatively unchanged across all treatments. However, the quantities of alcohols, aldehydes, hydrocarbons, esters and terpenoids increased with higher abundance/number of *S. canadensis* litter and seedlings, while their relative concentrations tended to decrease in treatments with higher abundance. Acidic compounds comprised the highest relative content (31.24%), with no alkaloids detected in the control treatment (NZ). As the concentration of acidic compounds decreased, the presence of alkaloids gradually increased in comparison to the control treatment. These variations in soil chemistry can impact the soil microbial community, leading to changes in the types and content of compounds and,

Table 1: Soil physicochemical properties

Sample	pH	SOM (g/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)
NZ	6.58 ± 0.08d	5.37 ± 0.05a	0.21 ± 0.06e	0.66 ± 0.09bc	12.81 ± 0.05a
NO	6.77 ± 0.08c	5.92 ± 0.07a	0.29 ± 0.07de	0.65 ± 0.10abc	12.49 ± 0.07a
NT	6.55 ± 0.10d	6.05 ± 0.09a	0.33 ± 0.09cd	0.66 ± 0.10abc	13.29 ± 0.06a
LZ	6.75 ± 0.07c	5.64 ± 0.09a	0.26 ± 0.10c	0.67 ± 0.08abc	12.97 ± 0.08a
LO	6.84 ± 0.05c	6.60 ± 0.07a	0.40 ± 0.05b	0.69 ± 0.08ab	12.98 ± 0.06a
LT	6.87 ± 0.08c	7.57 ± 0.06a	0.42 ± 0.11b	0.68 ± 0.09ab	12.53 ± 0.09a
HZ	7.10 ± 0.06b	6.47 ± 0.10a	0.39 ± 0.11b	0.69 ± 0.09ab	12.82 ± 0.05a
HO	7.21 ± 0.09ab	6.88 ± 0.07a	0.49 ± 0.11a	0.68 ± 0.10a	11.66 ± 0.06b
HT	7.34 ± 0.10a	7.43 ± 0.06a	0.51 ± 0.06a	0.69 ± 0.09a	12.46 ± 0.08a

Note: SOM = soil organic matter, TN = total nitrogen, TP = total phosphorus, TK = total potassium. Different lowercase letters indicate significant differences between means within a row according to Duncan's multiple range tests at ($P < 0.05$) level after ANOVA, $n = 5$.

consequently, affecting soil properties and function. For example, hexadecanoic acid was exclusive to the NZ treatment, whereas its methyl ester derivative, rather than hexadecanoic acid itself, appeared in the other treatments.

Bacterial richness and diversity

A total of 1,777,980 valid sequences were acquired, with an average read length of 458 bp. These sequences were clustered into OTUs, ranging from 1236 to 1432 at a 97% similarity threshold (Table 2). Our analysis revealed that the soil samples from both high (H) and low (L) *S. canadensis* treatment groups (Z, O, T) significantly influenced the bacterial OTU count ($P < 0.05$). Species richness, assessed using Chao1 and ACE indices, were notably higher in the HT (high treatment) soil compared to others ($P < 0.05$). However, no substantial difference in species richness was observed between the high and low treatment groups. Furthermore, an increasing trend in the Shannon index and a decrease in the Simpson index suggested that the addition of *S. canadensis* litter and seedlings contributed to enhanced bacterial diversity in the soil.

Bacterial community composition

We performed phylogenetic analyses at the genus level, identifying 21 distinct bacterial genera in soil samples. Among these, three genera *Sphingomonas*, *Acidobacteriales* and *Gemmatimonas* emerged as the most prevalent across all treatments (Fig. 1). In the control group (NZ), these genera had relative abundances of 21%, 4% and 10%, respectively.

However, with the introduction of increasing abundance of *S. canadensis* litter and seedlings, a significant decrease in the relative abundance of these genera was observed ($P < 0.05$).

In contrast, *Methylobacillus*, *Rhizomicrobium*, *Novosphingobium* and *Bradyrhizobium* were absent in the control group (NZ), but their presence and relative abundance progressively increased in both low (L) and high (H) seed density treatment groups. It is notable that while the litter concentration remained constant, the increasing presence of *S. canadensis* seedlings was not associated with any significant shifts in the overall abundance of the soil bacterial communities.

Linear discriminant effect size analysis

LEfSe (Fig. 2) revealed significant changes in certain bacterial taxa due to the litter treatments. Specifically, the abundances of *Sphingobacteria*, *Anaerolineae*, *Deltaproteobacteria* and *Rhizobiales* were altered in these treatments. In contrast, *Gemmatimonas* was identified as the most abundant genus in the control group. The LDA scores for *Rhizobiales* and *Deltaproteobacteria* were above 4, indicating that these taxa exhibited significant differential abundance primarily in the HZ and HO treatment groups.

Redundancy analysis

In the RDA (Fig. 3), the presented indices accounted for 72.5% and 4.2% of the variance observed in soil properties and the bacterial community. Analysis indicated that soil TN, pH, and SOM were correlated with microbial communities in the LZ, HZ, HO, and HT

Table 2: Comparison of the estimated OTU richness and diversity indices for clustering at 97% similarity, as obtained from the pyrosequencing analysis

Sample	Reads	OTUs	ACE	Chao 1	Shannon	Simpson
NZ	219266 ± 0.13a	1236 ± 0.08c	1276 ± 0.10c	1310 ± 0.11b	4.40 ± 0.11b	0.08 ± 0.04a
NO	212377 ± 0.10a	1273 ± 0.11c	1289 ± 0.08c	1312 ± 0.12b	4.53 ± 0.12b	0.03 ± 0.05ab
NT	224280 ± 0.09a	1254 ± 0.09c	1316 ± 0.12bc	1327 ± 0.10b	4.64 ± 0.10b	0.03 ± 0.04ab
LZ	175990 ± 0.09a	1373 ± 0.06b	1403 ± 0.11b	1416 ± 0.10a	5.65 ± 0.09ab	0.01 ± 0.03c
LO	189387 ± 0.12a	1409 ± 0.06ab	1423 ± 0.09ab	1427 ± 0.11a	5.76 ± 0.12ab	0.02 ± 0.03c
LT	187190 ± 0.11a	1410 ± 0.07ab	1424 ± 0.13ab	1432 ± 0.11a	5.84 ± 0.11a	0.02 ± 0.05c
HZ	197527 ± 0.11a	1402 ± 0.07ab	1421 ± 0.02ab	1428 ± 0.11a	5.74 ± 0.13ab	0.01 ± 0.05c
HO	16893 ± 0.12a	1410 ± 0.10ab	1426 ± 0.10ab	1440 ± 0.10a	5.90 ± 0.09a	0.01 ± 0.03c
HT	203032 ± 0.13a	1432 ± 0.05a	1441 ± 0.09a	1449 ± 0.11a	5.91 ± 0.10a	0.01 ± 0.06c

Note: N = normal, 0 g litter/pot; L = low, 10 g litter/pot; H = high, 20 g litter/pot; Z: 0 seedling; O = 1 seedling; T: 2 seedlings. Different letters indicate statistically different numbers between treatments ($P < 0.05$).

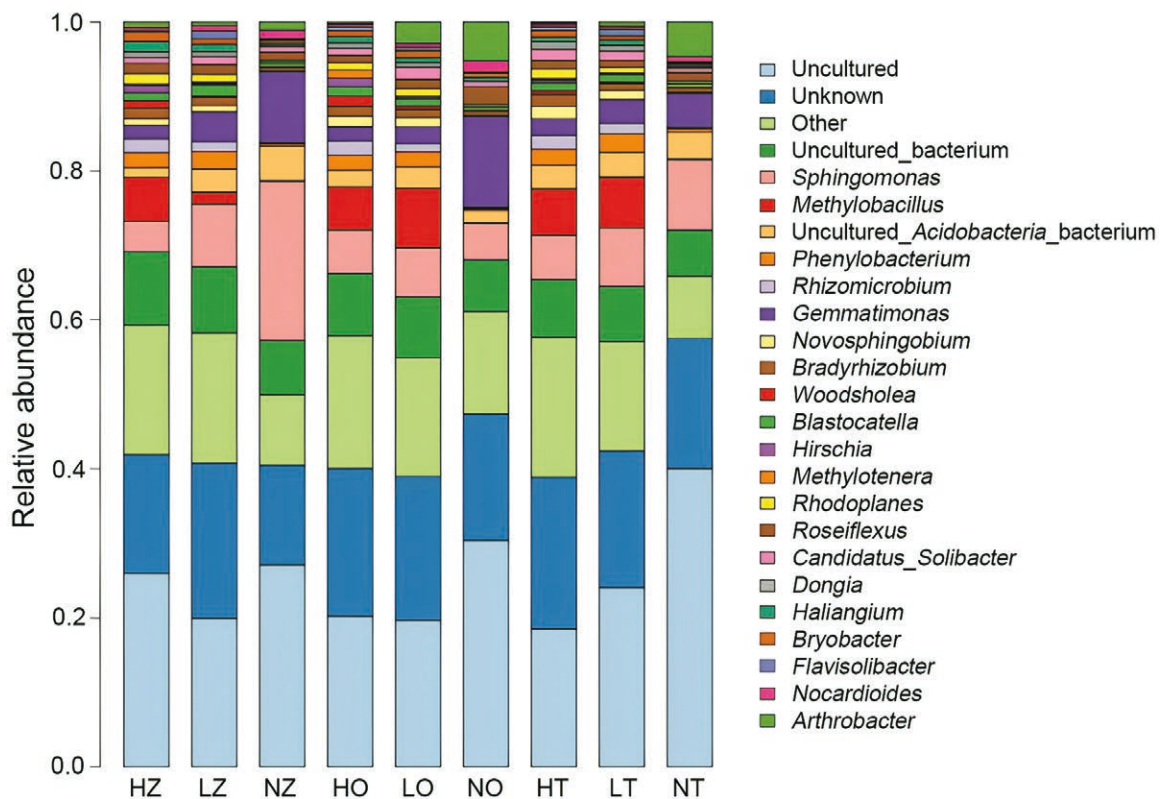


Figure 1: Bacterial community composition at the genus level. Relative abundances of the dominant bacterial (genus level) groups were chosen for each having greater than 1% relative abundance. Relative abundances were estimated based on the frequency of occurrence of sequences classified to each taxonomic group.

samples. Conversely, TP and TK demonstrated negative correlations with the control and other treatments (NZ, NO, NT, LT). All soil properties, except for pH, exhibited positive correlations with the HO treatment group.

A significant correlation was identified between soil pH, SOM, and TN and the prevalence of 15 out of the 20 analyzed bacterial genera. Specifically, the genera *Novosphingobium* and *Bradyrhizobium* showed positive associations with these soil properties. In contrast, the genera *Sphingomonas*, *Acidobacteria* and *Gemmatimonas* displayed negative correlations, indicating a varied response of bacterial genera to changes in soil chemical properties.

DISCUSSION

Effect of soil physicochemical properties

Our results underscore the significant impact of *S. canadensis* seedlings and litter on soil physicochemical properties, particularly pH and TN. These changes arise from a complex interplay of biological and chemical processes, primarily driven by the metabolites released through root exudation and the

decomposition of litter. Root exudates, which include a variety of organic compounds such as sugars, organic acids, amino acids, peptides and enzymes can alter soil pH by enhancing the availability of nutrients and affecting microbial activity. The decomposition of litter further contributes to nutrient cycling, releasing essential elements into the soil matrix and thus impacting chemical composition. Our observations align with prior research, which emphasize the role of plants in modifying the rhizosphere and their indirect effects on the carbon cycle through interactions with decomposer communities (Biswas and Kole 2017; Cesco *et al.* 2012).

The presence of *S. canadensis* not only alters soil chemistry but also can modify the community structure of microorganisms and soil fauna (Wang *et al.* 2023). Shifts in microbial dynamics can enhance decomposition rates and nutrient mineralization, facilitating a more efficient nutrient cycling process (Wu *et al.* 2023). The intricate relationships between plant roots and soil microorganisms are crucial for maintaining soil health and productivity, which are essential for ecosystem stability (Bhaduri *et al.* 2022). Furthermore, soil organic matter is vital as it serves as

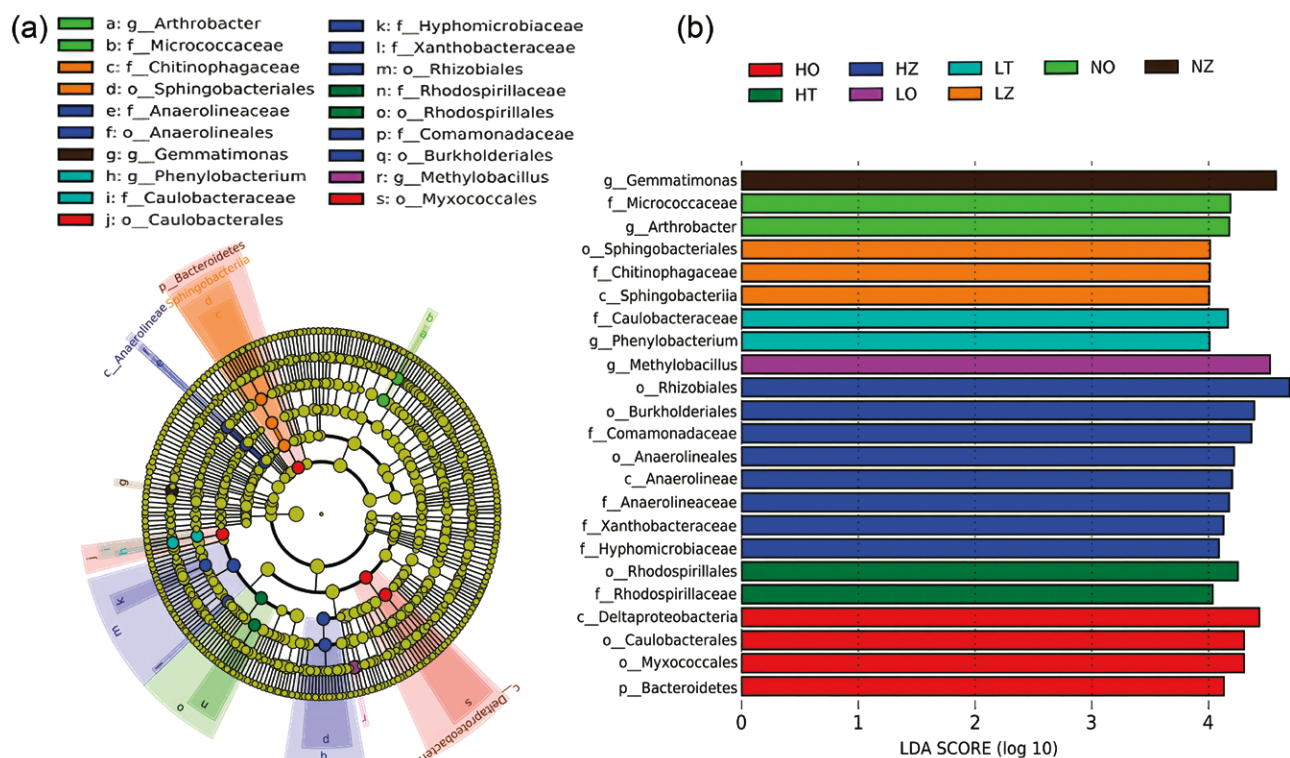


Figure 2: A LefSe method identifies the abundant taxa significantly different across all treatments. The taxa with significantly distinct abundances between treatments are represented by colored dots, which, from the center outward, represent the kingdom, phylum, class, order, family, and genus levels, respectively. The diameter of each circle is proportional to the taxon's abundance (a). The colored silhouettes represent the trends of the taxa that differ significantly. Each luminance dot has an effect size LDA score and only taxa with an LDA significance threshold of >2 is displayed (b). There was no difference between the NT treatment and the control.

a primary reservoir for carbon and a diverse range of essential nutrients, including nitrogen, phosphorus and several micronutrients (Waqas *et al.* 2020). The accumulation of organic matter is vital for improving soil structure, enhancing water retention, and fostering a favorable environment for root growth (Védère *et al.* 2020). This organic matter significantly contributes to overall soil fertility and ecosystem health by supporting diverse biological communities and promoting resilience against environmental stressors. Understanding the mechanisms by which *S. canadensis* and similar plants influence soil properties can inform land management strategies designed to enhancing soil quality and sustainability.

Significant changes in compounds

Our analysis revealed a diverse array of chemical compounds across all treatment soils, with variations in both type and concentration influenced by specific environmental conditions. This observation is consistent with findings by Cesco *et al.* (2010) and Bag *et al.* (2022), who documented the significant effects of plant species and environmental factors on soil

chemical composition. The inherent complexity of soil heterogeneity poses challenges for understanding the interactions of biotic and abiotic components, as variations in soil pH, redox potential and the presence of reactive mineral surfaces can markedly influence chemical dynamics (Alford *et al.* 2007; Barto and Cipollini 2009; Baveye *et al.* 2018). These factors are critical in mediating essential soil processes including organic matter decomposition, nutrient cycling and enzyme activity (Dick *et al.* 2000; Khan *et al.* 2023). Flavonoids are particularly noteworthy due to their dual and often contrasting roles in soil ecosystems, with both positive and negative feedback loops (Wang *et al.* 2004). Specifically, flavonoids have been shown to inhibit the activity tyrosine kinase and topoisomerase, which play vital roles in cellular signaling and DNA replication, respectively. This inhibition can alter the turnover of phosphorylated compounds, thereby affecting nutrient availability and microbial function. The interactions between these chemical compounds and soil microorganisms are complex, ultimately determining the diversity and concentration of compounds within the soil matrix.

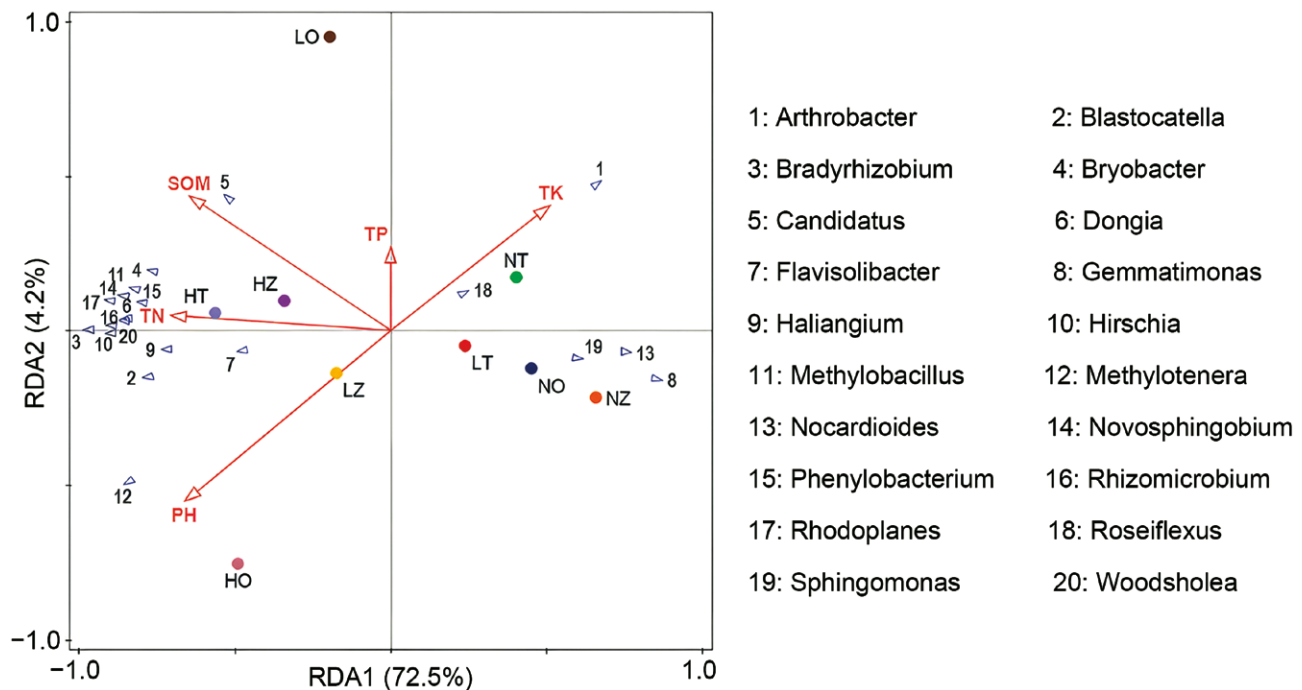


Figure 3: RDA displays correlations between the bacterial community and soil properties. The arrows represent the correlations between the lengths and angles.

In the rhizosphere, flavonoids released by plant roots can enhance microbial growth and activity, promoting a positive feedback loop. For instance, compounds such as quercetin can stimulate the proliferation of specific bacterial populations, which may facilitate further flavonoid exudation (Hartwig and Da 1991; Ren *et al.* 2024; Shah and Smith 2020). This microbial response can increase the concentration of flavonoids in the rhizosphere, thereby amplifying their effects on soil chemical properties (Mashabela *et al.* 2022; Narayanan and Glick 2022). The interplay among these factors is crucial as it determines the type and quantity of chemical compounds present; this also influences broader soil health, fertility, and ecosystem functioning.

Bacterial diversity and community composition

We demonstrated that the addition of *S. canadensis* litter and seedlings significantly increased bacterial richness and diversity. Notably, genera such as *Sphingomonas*, *Acidobacteriales* and *Gemmatimonas* were consistently detected across all soil samples, though their relative abundances varied compared to the control treatment (NZ). The genus *Sphingomonas* contains environmental isolates that play important roles in the bioremediation and biodegradation of organic pollutants (Gatheru Waigi *et al.* 2017). *Sphingomonas* can degrade a wide range of polycyclic

aromatic hydrocarbons (naphthalene, phenanthrene and pyrene), suggesting that the presence of *S. canadensis* may impact these processes (Premnath *et al.* 2021; Zhou *et al.* 2022). Some genera of Acidobacteria were ubiquitous and present in lower depths where roots are most abundant, as were fungal saprophytes and chemoorganoheterotrophic bacteria (Conradie and Jacobs 2020). The biological functions of Acidobacteria are not well known because most microorganisms of this group have not been cultured (Kalam *et al.* 2020). Interestingly, the Acidobacteria can colonize these habitats, likely due to their capability to degrade plant recalcitrant organic compounds (Štursová *et al.* 2012). *Gemmatimonas* has broad physiological potential (Mujakic *et al.* 2022; Zeng *et al.* 2014, 2020), with representatives of the phylum also reported in alpine and arid environments (Debruyne *et al.* 2011; Ruan *et al.* 2020) and agricultural soils (Chaudhry *et al.* 2012; Pascual *et al.* 2018). However, their ecological functions are poorly understood because they have rarely been cultured (Chee-Sanford *et al.* 2019; Debruyne *et al.* 2013). The decreased abundance of *Gemmatimonas*, *Acidobacteria* and *Sphingomonas* was attributed to their preferred niches (Fierer *et al.* 2007). *Gemmatimonas* is a saprotrophic bacterium that grows slowly under low nutrient conditions, while *Acidobacteria* has an improved tolerance/preference for acidic conditions.

We observed a significantly greater abundance of bacterial communities in response to increasing *S. canadensis* litter, including *Methylobacterium*, *Rhizomicrobium*, *Novosphingobium* and *Bradyrhizobium*. *Methylobacterium* is widespread in soil, air and water (Gamit and Amaresan 2022; Lidstrom 2005; Szwetkowski and Falkinham 2020). *Methylobacterium* can utilize multiple simple organic substrates (excluding methane), including methanol, a major volatile organic compound emitted by plants (Green and Ardley 2018; Bijlani *et al.* 2021).

The genus *Novosphingobium* belongs to the class *Alphaproteobacteria*, order *Sphingomonadales*, and family *Sphingomonadaceae*, has been isolated from diverse habitats, including soil, coastal and freshwater sediments, and hexachlorocyclohexane (HCH)—contaminated soil (Liu *et al.* 2005; Niharika *et al.* 2012). Previous research has shown that *Novosphingobium* can degrade aromatic compounds, polycyclic aromatic hydrocarbon and HCH (Yuan *et al.* 2009). The cyanobacteria of the genera *Rhizobium*, *Bradyrhizobium* and *Azorhizobium* are symbiotic nitrogen-fixing, suggesting potential implications for plant–soil nitrogen cycling arising from the presence of *S. canadensis* (Bottomley and Maggard 1990; Hayat *et al.* 2010). *Sphingomonas* decreased in abundance, whereas *Bradyrhizobium* and *Rhizomicrobium* increased. This result can be explained the promotion of N-fixing bacterial groups (*Bradyrhizobium* and *Rhizomicrobium*) but not aromatic compound degrading genera (Ngoc-Lan *et al.* 2016). The most abundant genera identified in litter included Bacteroidetes and Proteobacteria have previously been shown to include *Bradyrhizobium*, *Rhizomicrobium*, *Rhodanobacter*, *Burkholderia*, *Sphingobacteria* and *Novosphingobium* (López-Mondéjar *et al.* 2015). LEfSe analysis (Fig. 2), indicated that *S. canadensis* litter addition had a significant effect on bacteria community structure, most likely mediated through the release of litter nutrients impacting chemistry and substrate availability for microbial communities (Baldrian *et al.* 2013; Chen *et al.* 2015).

Moreover, the microbial community associated with litter undergoes successional changes due to variations in the decomposition dynamics of the litter components (Lee *et al.* 2020; Matulich *et al.* 2015; Snajdr *et al.* 2011; Voříšková and Baldrian 2013). Previously, enzymes with the greatest activity in litter (e.g. β -glucosidase, endocellulase and endoxylanase) were accompanied by a high abundance of bacteria from the genera *Mucilaginibacter*, *Ferruginibacter*, *Pedobacter* and *Collimonas* (Štursová *et al.* 2012; Zhang

et al. 2020). These observations suggest that litter may be the most influential factor in determining the bacterial community composition of the soil.

CONCLUSIONS

Our study highlights the significant impact of *S. canadensis* on soil ecosystems. The litter and seedlings of *S. canadensis* release chemical compounds that notably alter soil properties, including pH, SOM, TN, TP, and TK. These changes are closely linked to variations in soil bacterial communities, specifically increasing the richness and diversity of bacteria, and elevating the abundance of genera such as *Methylobacillus*, *Rhizomicrobium*, *Novosphingobium* and *Bradyrhizobium*. Our findings emphasize on the intricate relationship between the chemical composition of *S. canadensis* and its influence on soil microbial dynamics, offering new perspectives on the mechanisms of plant invasion and its ecological consequences. Understanding the specific soil properties and microbial communities that favor *S. canadensis* can aid in designing soil amendments or treatments that make the soil less suitable for this, and potentially other, invasive species, supporting sustainable ecosystem management in the future.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Chemical composition of *S. canadensis* litter mixed with soil for 4 months.

Table S2: Composition of relative contents (RC) and number (*n*) of compounds from all treatments.

Authors' Contributions

Yanwen Bo (Conceptualization, Data curation, Investigation, Methodology, Software, Writing—review & editing), Yali Liao (Resources, Software, Validation, Writing—review & editing), Mark Pawlett (Formal analysis, Methodology, Project administration, Writing—original draft), Rasheed Akbar (Conceptualization, Investigation, Methodology, Writing—original draft, Writing—review & editing), Nickolas Girkin (Funding acquisition, Resources, Visualization, Writing—review & editing), JIANFAN SUN (Conceptualization, Methodology, Project administration, Supervision, Writing—original draft), Amjad Ali (Data curation, Funding acquisition, Resources, Software), Naushad Ahmad (Funding acquisition, Resources, Software, Validation), Wei Liu (Funding acquisition, Methodology, Project administration, Visualization),

Xiaoyan Wang (Data curation, Formal analysis, Funding acquisition, Visualization), and Daolin Du (Supervision, Validation, Visualization, Writing—original draft)

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Conflicts of interest statement. The authors declare that they have no conflict of interest.

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Bo, Yanwen; Liao, Yali; Pawlett, Mark; Akbar, Rasheed; Girkin, Nicholas T. ...

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