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Impacts of *Solidago canadensis* and *Erigeron canadensis* co-invasion on soil microbial communities

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Abstract

Invasive plants disrupt the structure and function of ecosystems, causing a decline in their diversity. The coexistence of *Solidago canadensis* and *Erigeron canadensis* within shared habitats is a common phenomenon, and the frequent occurrence of co-invasion has substantial implications for ecosystems. However, the effects of the co-invasion of two plants on the soil ecosystem across varying degrees of invasion remain uninvestigated. Therefore, we investigated how the co-invasion of *S. canadensis* and *E. canadensis* affects soil physiochemical properties and microorganisms across various degrees of invasion. The invaded regions exhibited significantly lower soil moisture content and pH values than those in the uninvaded areas ($p < .05$). Additionally, co-invasion resulted in higher soil organic matter (OM), total nitrogen (TN), total phosphorus (TP), and available phosphorus (AP) contents compared to single invasion by *E. canadensis*. Furthermore, the invaded regions exhibited a greater diversity of soil bacterial and fungal communities than the uninvaded regions. Under diverse invasion conditions, Actinobacteria and Ascomycota emerged as the predominant phyla of soil bacteria and fungi, respectively, leading to a shift in the soil microbial community structure. Moreover, homogenizing dispersal significantly influenced bacterial community succession, while ecological drift influenced the progression of fungal communities. Using structural equation modeling, this study established significant correlations between soil properties (pH, TN, and nitrate nitrogen) and bacterial interactions (diversity and community assembly) relative to microbial composition. This study revealed the influence of *S. canadensis* and *E. canadensis* co-invasion on soil microbial communities, thereby contributing a theoretical framework delineating the impact of these two invasive plant species.

KEYWORDS

bacterial interaction, co-invasion, fungal interaction, invasive plants, soil microorganisms

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1 | INTRODUCTION

The intensification of human activities, rise of economic globalization, and advancement of urbanization have collectively opened up greater opportunities for the successful colonization of alien organisms. Consequently, the threat to global biodiversity has grown significantly more severe (Hulme, 2009; Xu et al., 2019). Furthermore, invasive plants disrupt the structure and function of invaded ecosystems, leading to a decline in their diversity (Mollot et al., 2017; Pysek et al., 2020). Biological invasion has emerged as a fundamental concern in global change (Pysek et al., 2012). Previous studies primarily concentrated on individual invasive plant species (Liao et al., 2013; Rezacova et al., 2021; Wang, Jiang, et al., 2018) while ignoring instances of co-invasion.

Successful invasion of an invasive plant introduces a new structural component within the invaded ecosystem, elevating the potential for other invasive plants to establish themselves or exacerbate the impact on the ecological environment (Simberloff & Von Holle, 1999). This often results in the coexistence of various invasive plants within the same habitat, each exhibiting different degrees of invasion (Wang et al., 2020; Wang, Jiang, et al., 2018). Invasive plants possess the capability to alter the structure and function of local soil microbial communities. These alterations foster the growth of invasive plants, thereby expediting their invasion process (Castro-Diez et al., 2014; Rodrigues et al., 2015). The soil microbial modification by invasive plants is pivotal in hastening the invasion process. Therefore, exploring the effects of invasive plants on soil microorganisms is crucial in understanding the mechanisms facilitating successful plant invasion.

Invasive plants have a dual impact: they reduce the diversity of indigenous plants and soil microbes, in addition to disrupting the structure and function of invasive ecosystems (Mollot et al., 2017; Pysek et al., 2020). Soil microorganisms, acting as decomposers, play a pivotal role in supporting soil ecosystem functions and services, consequently attracting significant attention in research endeavors (Chen & Wen, 2021; Wardle et al., 2004). Invasive plants influence soil microbial diversity, community structure and assembly processes through litter decomposition and root exudates (Lin et al., 2022; Wei et al., 2020; Ye et al., 2023). For instance, the invasion of the Canadian herbaceous weeds *Solidago canadensis* and *Erigeron canadensis* in China results in an alteration of the soil microbial community structure, species composition, and their relative abundance (Wang et al., 2022). The assembly process of microbial communities stands as a pivotal focus in microbial ecology, involving varying proportions of deterministic and stochastic processes (Jiao et al., 2020; Zhou et al., 2021). Lin et al. (2022) observed that *Spartina alterniflora* invasion increased the significance of stochastic processes in this context. Hence, a thorough examination of microbial community responses aids in elucidating the interconnected effect of plants and microorganisms during the co-invasion process.

The Compositae is the largest family of invasive plants in China, accounting for 17.86% of the overall invasive plants. Within this family, *S. canadensis* and *E. canadensis* commonly coexist in shared habitats in North America (Lu et al., 2020). *Soldago canadensis*, a perennial herb, was introduced to Shanghai, China as an ornamental plant in the 1930s (Zhang et al., 2019). *E. canadensis*, an annual herbaceous plant, has proliferated across diverse habitats, including roadsides, farmlands, forests, and nature reserves. When an invasive plant successfully colonizes an area, its occurrence creates a new habitat, elevating the possibility of subsequent invasive plants settling in the same environment. This often leads to the coexistence of multiple invasive plants within a single habitat. Hence, investigating the effect of co-invasion by two distinctively invasive plants on soil microorganisms is crucial. Such exploration provides a theoretical basis for formulating strategies aimed at preventing and managing invasive plant species.

Therefore, this study aimed to investigate how the soil ecosystem is influenced by the co-invasion of *S. canadensis* and *E. canadensis*, and how it affects soil physiochemical properties and microorganisms across various degrees of invasion (i.e., coverage). Our hypotheses included the following: (1) invasion would induce changes in the physicochemical properties of soil in invaded regions, potentially leading to increased soil fertility; (2) it would prompt alterations in the community structure and species composition of soil microorganisms; (3) it would modify the relative proportions of different processes involved in assembling microbial communities; and (4) soil physicochemical properties would influence the composition and structure of microbial communities by impacting the assembly process and co-occurrence network of soil microorganisms.

2 | MATERIALS AND METHODS

2.1 | Study design

Sample plots were selected and arranged during the second half of 2021. Subsequently, in July 2022, a randomized survey was performed in Chaohu, Anhui Province, China, encompassing communities affected by *S. canadensis* and *E. canadensis* invasion, along with adjacent uninvaded indigenous communities. The

sampling area had a subtropical humid monsoon climate, with an average annual temperature of 16°C and rainfall of approximately 1100 mm, mainly concentrated between May and August. The land-use type within the sampling area was classified as abandoned land. The plant community composition is dominated by herbaceous plants such as *Setaria viridis*, *Echinochloa crusgalli*, *Vicia unijuga* and *Glycine soja*, and the prevalent soil type was brown soil. The following five treatments were employed in this study: (1) CK: no exotic invasive plants; (2) T1: single invasion of *S. canadensis*; (3) T2: co-invasion of both invasive plants, with heavy *S. canadensis* coverage (>75%) and light *E. canadensis* coverage (<35%); (4) T3: co-invasion of both invasive plants, with light *S. canadensis* coverage (<35%) and heavy *E. canadensis* coverage (>75%); and (5) T4: single invasion of *E. canadensis*. The invasion degrees of the two invaders were divided into light (<35%) and heavy (>75%) on the basis of their coverage in the same sampling ecosystems (Wang et al., 2020; Wang, Jiang, et al., 2018; Wang, Zhou, et al., 2018). For each treatment, five 1 m × 1 m quadrats were randomly selected for analysis and positioned 10 m apart, resulting in 25 quadrats overall.

2.2 | Collection of soil samples

In each quadrat, three soil subsamples (depth of 0–15 cm) were randomly collected. These samples were mixed thoroughly to form the soil sample representing the quadrat. A portion of this soil was stored as bulk soil at −80°C for high-throughput sequencing analysis. Overall, 25 soil samples numbered CK, T1-B, T2-B, T3-B, and T4-B, were air dried and then analyzed.

In addition, when the rhizosphere soil of invasive plants was collected, companion plants were initially removed. Subsequently, the entire invasive plant was excavated. Following the removal of the large soil attached to the roots, the soil attached to each root was gently brushed using a sterilized brush to extract the rhizosphere soil of the plant (Tang et al., 2020). Three invasive plants were selected from each sample, and a rhizosphere soil sample was obtained after thorough mixing. The 30 soil samples were labeled as follows to indicate the treatment, plant species, and rhizosphere: T1-SC-R, T2-SC-R, T2-EC-R, T3-SC-R, T3-EC-R, and T4-EC-R. A portion of rhizosphere soil samples was stored at −80°C for high-throughput sequencing of rhizosphere soil microorganisms. Another portion was used to assess soil physicochemical properties after air-drying, and the data (Table S1) were used to fit the correlation between microbial diversity, microbial community, and environmental factors.

2.3 | Soil physicochemical characteristics

All soil samples were mixed using a 1 mm aperture sieve and divided into two parts. One was used to assess soil moisture content (SM), pH value, electrical conductivity (EC), ammonium nitrogen (AN), nitrate nitrogen (NN), and available phosphorus (AP). The second sample was ground through a 0.149 mm (100 mesh) aperture sieve to evaluate soil organic matter (OM), total nitrogen (TN), total phosphorus (TP), and total potassium (TK).

SM content was assessed using the drying method. Soil pH (water–soil ratio 1:2.5) and EC (water–soil ratio 1:5) were measured using a pH meter (PHS-3E) and a conductivity meter (DDS-11A), respectively (Meng et al., 2019). Soil OM was measured using the external heating potassium dichromate volumetric method (Wu et al., 2022). Soil TN was analyzed using the semi-micro Kjeldahl method; soil TP and TK were determined using the NaOH melting method. AN and NN in the soil were determined using the 2 mol L^{-1} KCl extraction-flow analyzer method. Lastly, soil AP content was measured via the Olsen method (Ren et al., 2021).

2.4 | High-throughput sequencing of soil microorganisms

A total of 55 samples of bulk and rhizosphere soil were analyzed. The OMEGA soil DNA extraction kit (MP Biomedicals, USA) was used to extract genomic DNA from the soil samples. The DNA extract was examined on a 1% agarose gel, and DNA concentration and purity was determined using a NanoDrop 2000 (Thermo Scientific, Wilmington, USA). The V3–V4 region of the bacterial 16sRNA gene was amplified using primers 338F (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) via ABI GeneAmp®9700 (ABI, CA, USA). For the fungal ITS region, amplification was performed with primers ITS1F (5′-CTT GGTCATTTAGAGGAAGTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′).

The PCR amplification of the 16S RNA gene was performed as follows: initial denaturation at 95°C for 3 min, followed by 27 cycles of denaturing at 95°C for 30 s, annealing at 55°C for 30 s and extension at 72°C for 45 s, and then a single extension at 72°C for 10 min, ending at 10°C. Similarly, PCR amplification of the fungal ITS region was only 35 cycles, with parameters were consistent with the PCR amplification program of 16 s RNA. The PCR reaction mixture contained Takara rTaq DNA polymerase in a 20 μL reaction system with 2 μL of 10× buffer, 2 μL of 2.5 mM dNTPs, 0.8 μL forward primer

(5 μM), 0.8 μL reverse primer (5 μM), 0.2 μL rTaq polymerase, 0.2 μL BSA, 10 ng Template DNA, and supplemented with ddH2O to 20 μL. The PCR products of the same sample were mixed and detected using 2% agarose gel electrophoresis. The PCR product was recovered using the AxyPrepDNA gel Recovery Kit (AXYGEN company), and detected and quantified using the QuantiFluor™—ST blue fluorescence quantitative system (Promega, USA). Sequencing was carried out on the Illumina MiSeq PE300 platform.

2.5 | Statistical analysis

A one-way ANOVA was used to analyze the differences in soil physicochemical properties between different treatments, while the Turkey test was employed for post-hoc multiple comparisons. Microbial data were normalized using OTU based on the minimum number of sample sequences. The Mothur software (Version 1.30.20) was utilized to calculate alpha diversity indexes (Shannon, Simpson, Chao1, and ACE).

A Circos plot was constructed to visualize microbial community composition across different treatments using Circos v.0.67-7. Subsequently, Qiime software (Version 2020.2.0) was used to calculate the Bray-Curtis distance, and the WGCNA, stats, and ggplot2 packages of the R v.3.3.1 were used to draw PCoA diagrams (Shen et al., 2022). Additionally, ANOSIM comparative analysis of similarities in soil microbial communities under different treatments was performed using Vegan package of R v.3.3.1 (Shen et al., 2022). The network was visualized using Gephi software (v. 0.9.2). βNTI, an index to measure changes in diversity during community construction, was used to describe diversity differences at various distributions. RCbray was used to compare differences in microbial composition between different communities. Picante package of R v.3.3.1 was utilized to calculate the βNTI/RCbray values to explore the randomness and certainty within microbial communities (Stegen et al., 2013). $|\beta NTI| > 2$ indicates dominance in the deterministic process, where $\beta NTI > 2$ refers to heterogeneous selection, and $\beta NTI < -2$ denotes the homogeneous selection. $|\beta NTI| < 2$ indicates dominance in the stochastic process, which can be further divided based on RCbray. RCbray >0.95 indicates dispersal limitation, RCbray < -0.95 denotes homogenizing dispersal, $|RCbray| \leq 0.95$ represents Ecological drift (Zhou & Ning, 2017).

Pearson's correlation analysis was used to identify correlations between microbial diversity, network properties, assembly processes, and environmental factors using SPSS 22. A correlation heat map was employed to depict the relationship between microorganisms and environmental factors using the pheatmap package of R v.3.3.1 (Zhou et al., 2017). Structural equation modeling (SEM) revealed the interplay between soil microbial diversity, network properties, assembly processes, microbial composition, and soil properties. Soil microbial diversity describes microbial richness (Shannon index). Network properties indicate invasion extent. Assembly processes are captured in the βNTI index. Microbial composition is indicated by Bray–Curtis dissimilarity. Soil properties include SM, pH, EC, OM, TN, TP, and NN. SEM analysis was performed using SPSS AMOS (v. 28.0). First, we imported these data into AMOS software. Second, we construct the path and adjusted the layout. Finally, the initial model was obtained by data operation. Chi-square testing ($p > .05$, $X^2/df < 3$) and the comparative fit index (CFI ≥ 0.95) were used to determine whether the model was suitable for continuous adjustment. All figures were generated using QriginPro 2023b.

3 | RESULTS

3.1 | Effects of *S. canadensis* and *E. canadensis* invasion on soil physicochemical properties

Compared to the control, the SM content and pH values under the invasive treatments decreased significantly ($p < .05$), whereas the alteration in EC varied. The single invasion of *S. canadensis* decreased soil EC by 45.80%. In contrast, the co-invasion of *S. canadensis* and *E. canadensis* did not show a significant effect on the EC of the soil (Table 1). The invasion of *S. canadensis* and *E. canadensis* significantly affected the chemical properties of the soil (Table 1). Compared to the control, invasive treatments significantly increased the soil TN, TP, and AP contents ($p < .05$). Moreover, compared to the single invasion of *E. canadensis*, co-invasion resulted in increased soil OM content ($p > .05$), while showing similar trends in TN ($p > .05$), TP ($p > .05$), and TK ($p > .05$).

3.2 | Effects of *S. canadensis* and *E. canadensis* invasion on soil microbial community diversity

The invasion of *S. canadensis* and *E. canadensis* significantly affected soil microbial diversity (Table 2). For bacteria, compared to the control, the single invasion of *S. canadensis* and co-invasion increased the ACE and Chao1 indices ($p < .05$), but reduced the Simpson index ($p < .05$). Compared to the single invasion of

TABLE 1 Effects of *Solidago canadensis* and *Erigeron canadensis* invasion on soil physicochemical properties.

	CK	T1	T2	T3	T4
SM (%)	3.81 ± 0.03a	3.22 ± 0.02b	2.98 ± 0.02c	2.72 ± 0.02d	2.94 ± 0.02c
pH	6.54 ± 0.12a	6.28 ± 0.06ab	5.50 ± 0.04c	5.99 ± 0.06b	5.85 ± 0.04b
EC (μS/cm)	28.10 ± 3.41a	15.22 ± 0.80b	32.94 ± 1.37a	28.66 ± 2.88a	27.00 ± 0.22a
OM (g/kg)	10.96 ± 1.50b	22.93 ± 1.90a	18.92 ± 2.17ab	17.61 ± 2.56ab	9.57 ± 2.33b
TN (g/kg)	0.64 ± 0.07c	1.28 ± 0.02a	1.15 ± 0.01a	0.97 ± 0.02b	0.90 ± 0.01b
TP (g/kg)	0.076 ± 0.004c	0.132 ± 0.004a	0.136 ± 0.002a	0.115 ± 0.003b	0.113 ± 0.003b
TK (g/kg)	12.73 ± 0.27a	12.72 ± 0.70a	14.05 ± 0.49a	13.97 ± 0.26a	12.46 ± 0.26a
AP (mg/kg)	1.83 ± 0.28b	6.63 ± 0.35a	9.51 ± 0.97a	8.41 ± 1.22a	6.49 ± 1.10a
AN (mg/kg)	8.86 ± 0.73a	12.04 ± 1.41a	9.60b ± 1.17a	8.56 ± 0.50a	8.94 ± 0.49a
NN (mg/kg)	7.84 ± 0.12b	8.00 ± 0.10b	8.44 ± 0.11ab	8.15 ± 0.08b	8.79 ± 0.13a

Note: Data are the average values ± standard error. Different letters in the same row indicate significant differences among the different treatments ($p < .05$).

TABLE 2 Effects of *Solidago canadensis* and *Erigeron canadensis* invasion on soil microbial diversity.

	Community diversity index		Community richness index	
	Shannon	Simpson	ACE	Chao1
Bacterial				
CK	6.45 ± 0.02c	0.0055 ± 0.0002b	3689.07 ± 85.58d	3640.04 ± 82.97d
T1-B	6.74 ± 0.02a	0.0032 ± 0.0001de	4606.68 ± 18.87a	4629.03 ± 28.41a
T1-SC-R	6.63 ± 0.03b	0.0038 ± 0.0002d	4459.72 ± 26.57a	4291.34 ± 115.00b
T2-B	6.63 ± 0.02b	0.0037 ± 0.0001de	4184.93 ± 143.51b	4014.69 ± 56.66c
T2-SC-R	6.57 ± 0.05bc	0.0041 ± 0.0003 cd	3918.65 ± 75.80 cd	3915.03 ± 88.92c
T2-EC-R	6.59 ± 0.02b	0.0038 ± 0.0001d	4032.21 ± 26.55bc	4027.06 ± 37.13c
T3-B	6.80 ± 0.02a	0.0030 ± 0.0001e	4693.27 ± 28.56a	4698.25 ± 50.00a
T3-SC-R	6.50 ± 0.03c	0.0042 ± 0.0002 cd	4068.85 ± 84.99bc	4039.04 ± 84.93c
T3-EC-R	6.43 ± 0.06 cd	0.0047 ± 0.0004c	4099.97 ± 100.68bc	4071.04 ± 110.65bc
T4-B	6.34 ± 0.02d	0.0070 ± 0.0002a	3941.48 ± 45.34c	3897.12 ± 51.69c
T4-EC-R	6.23 ± 0.04e	0.0074 ± 0.0005a	3682.15 ± 138.14d	3629.85 ± 134.31d
Fungal				
CK	4.21 ± 0.14b	0.039 ± 0.009ab	535.60 ± 35.12e	538.29 ± 35.87e
T1-B	4.75 ± 0.04a	0.023 ± 0.002ab	1326.20 ± 23.71a	1330.20 ± 27.07a
T1-SC-R	4.76 ± 0.05a	0.024 ± 0.001ab	1341.10 ± 35.37a	1346.92 ± 39.72a
T2-B	4.72 ± 0.32a	0.048 ± 0.031a	1305.00 ± 46.74a	1284.20 ± 49.28a
T2-SC-R	4.97 ± 0.04a	0.017 ± 0.002b	1329.78 ± 21.97a	1327.33 ± 21.72a
T2-EC-R	4.98 ± 0.03a	0.018 ± 0.0010b	1172.92 ± 33.37b	1163.71 ± 32.10b
T3-B	4.80 ± 0.06a	0.021 ± 0.002ab	1095.81 ± 32.01bc	1088.05 ± 33.90bc
T3-SC-R	4.86 ± 0.03a	0.020 ± 0.001b	1093.25 ± 38.00bc	1110.64 ± 42.84bc
T3-EC-R	4.82 ± 0.04a	0.022 ± 0.001ab	1086.42 ± 31.16bc	1088.58 ± 28.47bc
T4-B	4.84 ± 0.03a	0.022 ± 0.001ab	1048.70 ± 53.81c	1052.38 ± 55.33c
T4-EC-R	4.80 ± 0.02a	0.025 ± 0.001ab	837.39 ± 39.53d	849.61 ± 38.96d

Note: Bulk soil: T1-B, T2-B, T3-B, and T4-B; Rhizosphere soil: T1-SC-R, T2-SC-R, T2-EC-R, T3-SC-R, T3-EC-R, and T4-EC-R. Data are expressed as mean ± standard error. Different letters in the same row indicate significant differences among the different treatments ($p < .05$).

E. canadensis, the co-invasion increased the Shannon, ACE, and Chao1 indexes of bulk and rhizosphere soil bacteria but decreased the Simpson index ($p < .05$). Compared to the single invasion of *S. canadensis*, co-invasion decreased the Shannon, ACE, and Chao1 indexes of the rhizosphere soil bacteria, showcasing an inverse trend with the Simpson index ($p > .05$) (Table 2). The Shannon and ACE indexes of bulk soil bacteria were higher than those of rhizosphere soil bacteria, regardless of single or co-invasion, showing an inverse trend to the Simpson index (Table 2).

For fungi, the invasion of *S. canadensis* and *E. canadensis* significantly increased the Shannon, ACE, and Chao1 indexes compared to the control ($p < .05$). However, the Simpson index did not change significantly. Co-invasion decreased the ACE and Chao1 indices of the rhizosphere soil fungi more than the single invasion of *S. canadensis* ($p > .05$). Co-invasion increased the ACE and Chao1 indices of the rhizosphere soil fungi more than the single invasion of *E. canadensis* ($p < .05$) (Table 2).

3.3 | Effects of *S. canadensis* and *E. canadensis* invasion on soil microbial community composition and structure

Under various invasion conditions, Actinobacteria emerged as the dominant phylum among the soil bacteria. Furthermore, Actinobacteriota, Proteobacteria, Chloroflexi, Acidobacteria, and Firmicutes accounted for approximately 80% of the total bacteria (Figure 1a). However, the relative abundances of these five bacterial phyla varied significantly among the different treatments ($p < .01$) (Figure S1). Under various invasive conditions, the dominant phylum of soil fungi was Ascomycota, which together with Basidiomycota accounted for approximately 80% of the bacterial communities (Figure 1b). Significant differences were observed in the relative abundances of these fungal communities in the soil following *S. canadensis* and *E. canadensis* invasion ($p < .001$) (Figure S2). PCoA revealed a significant disparity between the microbial communities in the invaded and uninvaded regions (Figure 2a,b), indicating that invasion changed the structure of the microbial community (Figures S3 and S4).

3.4 | Microbial network among *S. canadensis* and *E. canadensis* invasion

The relationship between soil microorganisms under the co-invasion of *S. canadensis* and *E. canadensis* was investigated using a correlation network diagram (Figure 3). For bacteria, the OTU-level correlation network diagram revealed significant interactions between different OTUs of soil bacteria under the co-invasion of *S. canadensis* and *E. canadensis*. At the OTU level, the positive correlation accounted for 57.19%, higher than the negative correlation. Among them, Actinobacteria had the strongest correlations with other phyla, whereas Cyanobacteria exhibited the weakest relationships with other phyla (Figure 3a). For fungi, the OTU-level correlation network diagram revealed a significant interaction between different OTUs during the co-invasion by *S. canadensis* and *E. canadensis*. At the OTU level, the positive correlation accounted for 68.86%, higher than the negative correlation. Among them, Ascomycota exhibited the closest connections with other phyla, while Mortierellomycota was the most distinct (Figure 3b).

3.5 | Assembly processes of soil microbial communities under *S. canadensis* and *E. canadensis* invasion

The assembly process of the microbial community under various degrees of invasion was evaluated by calculating the βNTI value (Figure 4). Since most of the βNTI values of samples were between −2 and 2, the stochastic process was the main factor affecting the assembly of soil bacterial and fungal communities (Figure 4a,c). A combination of weighted βNTI and Bray–Curtis-based RCbray was used to evaluate the relative contribution of different assembly processes under various invasion degrees. The most important ecological process of bacteria in all treatments was homogenizing dispersal, which accounted for 40%–67% of community succession, and ecological drift in each treatment accounted for 33%–40% of community succession. This finding indicates that each ecological process played a crucial role in soil bacterial community succession (Figure 4b). Each treatment exhibited ecological drift for fungi, accounting for 33%–100% of the community succession. Only the soil fungal community assembly under the single invasion of *S. canadensis* exhibited homogeneous selection (Figure 4d).

3.6 | Potential key factors influencing microbial community assembly in *S. canadensis* and *E. canadensis* invaded regions

Correlation analysis among soil microbial diversity, network properties, assembly processes, and soil properties demonstrated that soil OM, TN, and TP were significantly positively correlated with the bacterial Shannon,

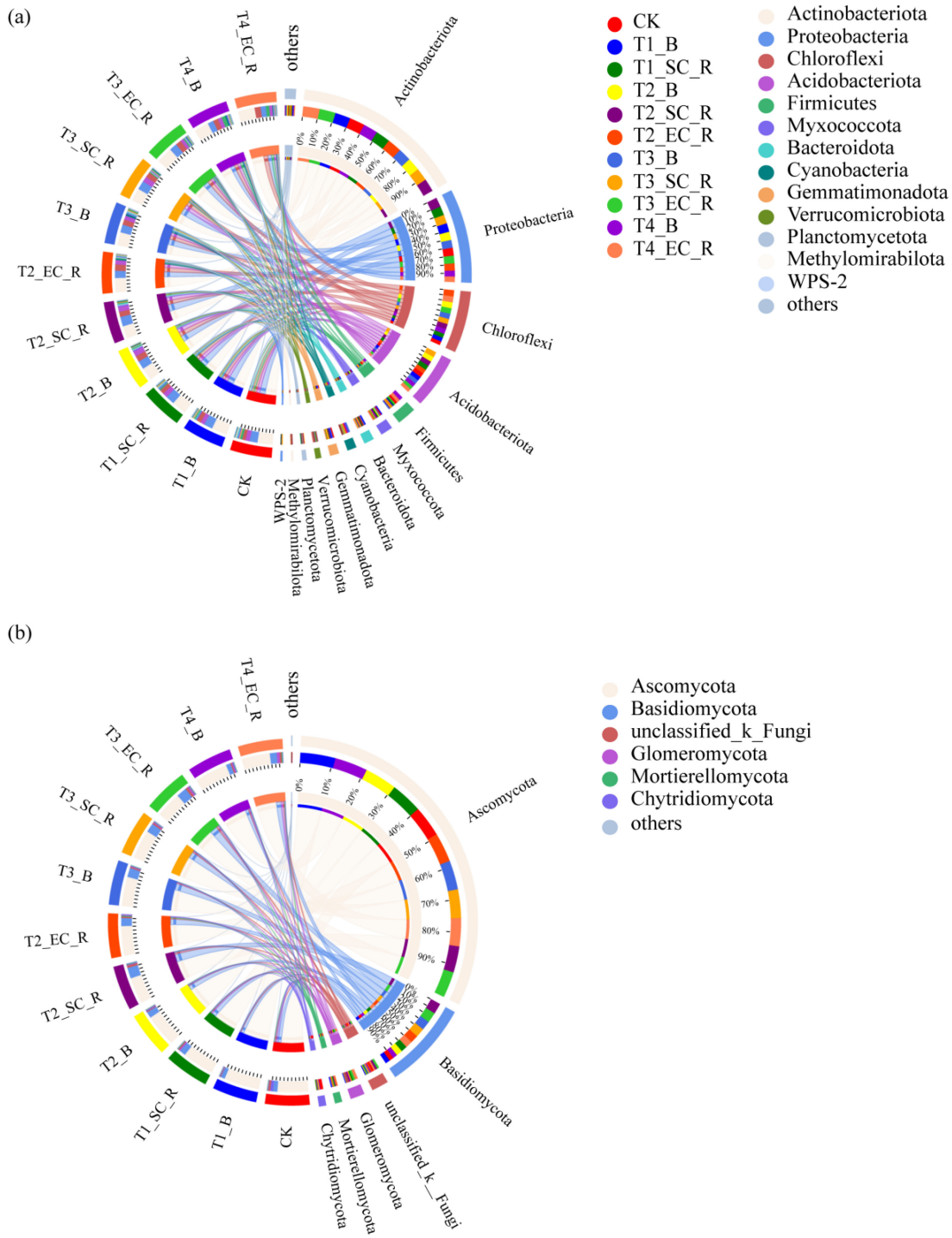

FIGURE 1 Effects of *Solidago canadensis* and *Erigeron canadensis* invasion on the composition and relative abundance of soil microbial phylum level. (a) Bacterial phyla. (b) Fungal phyla. The width of the bars for each phylum indicates the relative abundance of that phylum in the sample.

ACE, and Chao1 indexes ($p < .05$). Moreover, the correlation with βNTI was comparable (Table 3). A significant negative correlation was observed between NN and the bacterial Shannon and Chao1 indexes ($p < .05$). Further, the correlation between betweenness centrality and βNTI was comparable. The fungal ACE and Chao1 indexes were significantly positively correlated with soil OM, TN, TP, AP, and AN ($p < .05$). However, they exhibited an inverse correlation with soil pH ($p < .01$) (Table 3). Additionally, degree and closeness centrality exhibited a significant positive correlation with soil SM ($p < .05$), but were negatively correlated with NN ($p < .05$). The pH exhibited a significant negative correlation with βNTI ($p < .05$).

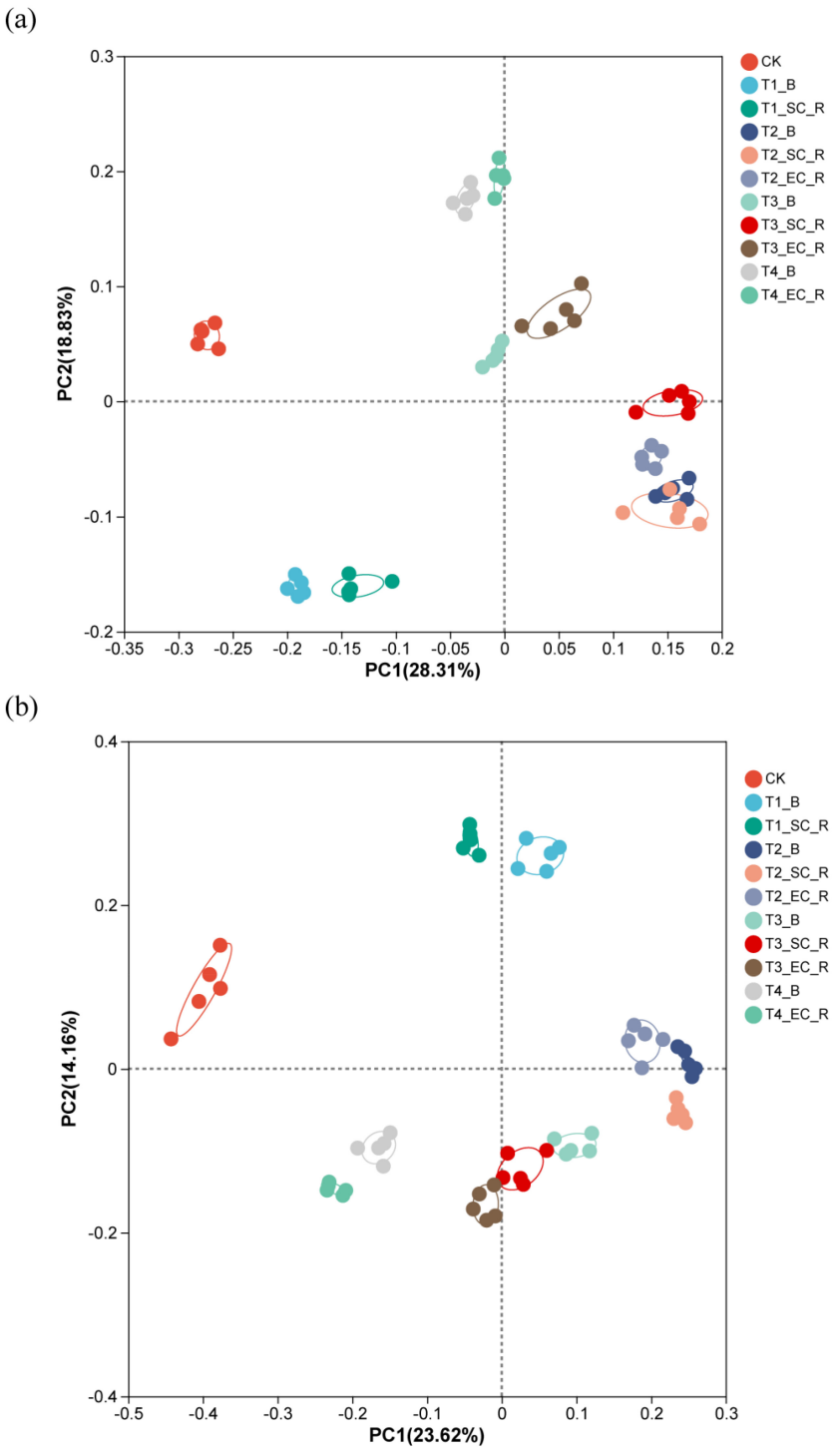

FIGURE 2 Differences in microbial communities under *Solidago canadensis* and *Erigeron canadensis* invasions of different degrees. Principal coordinate analysis illustrating soil microbial community composition at the OTU level during *S. canadensis* and *E. canadensis* invasion, based on Bray–Curtis distances. (a) Bacterial community. The first and second axes account for 28.31% and 18.83% of the total variation, respectively. (b) Fungal community. The first and second axes represent 23.62% and 14.16% of the total variation, respectively.

Additionally, the correlation heatmap showed that soil OM was significantly positively correlated with Myxococcota and Bacteroidota ($p < .05$), but significantly negatively correlated with Firmicutes ($p < .01$) (Figure S5). Soil TN and TP were positively correlated with Proteobacteria, Acidobacteriota, Myxococcota, and Bacteroidota ($p < .05$). The correlation heatmap indicated significant positive correlations between Ascomycota and TN, TP, and SM ($p < .01$), whereas Basidiomycota showed a negative correlation with soil pH and SM ($p < .01$) (Figure S6).

The structure equation modeling (SEM) was employed to assess how alterations in soil properties caused by alien plants directly or indirectly influenced soil microbial diversity, network properties, assembly processes, and microbial composition (Figure 5). For bacteria, soil OM, TN, and NN were not only directly associated with bacterial diversity, but also indirectly linked to

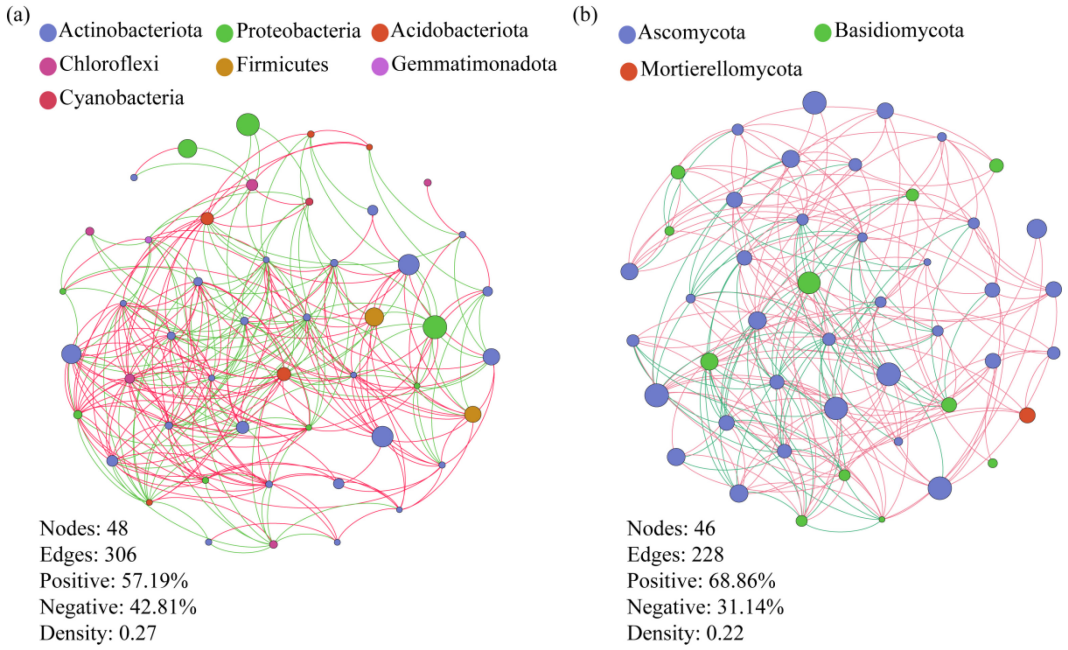

FIGURE 3 Networks depicting soil microbial communities during *Solidago canadensis* and *Erigeron canadensis* invasions. Each node represents an operational taxonomical unit (OTU). Node size (OTU) corresponds to species abundance. The red and green colors of connecting lines denote positive and negative correlations, respectively.

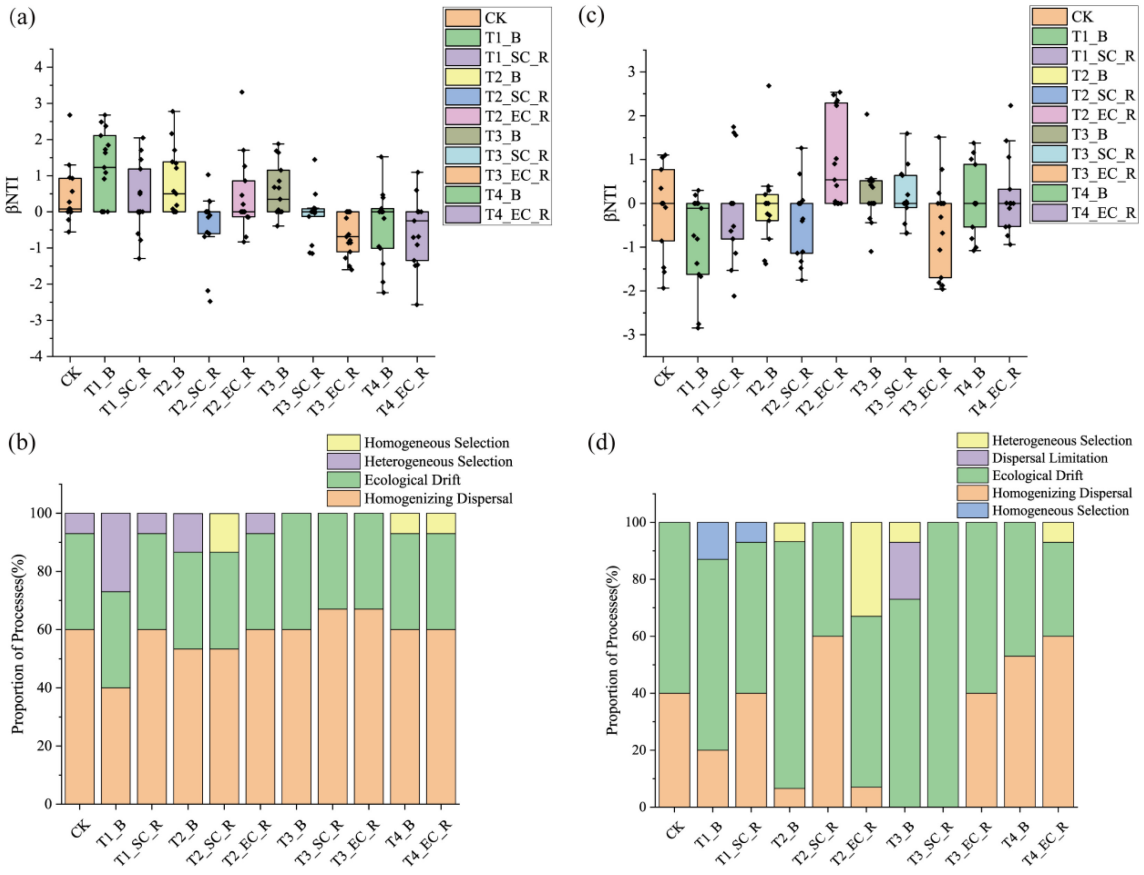

FIGURE 4 Assembly process of soil microbial communities under *Solidago canadensis* and *Erigeron canadensis* invasion. (a) βNTI value of bacteria. (b) Proportions of each processes in bacterial community. (c) βNTI value of fungi. (d) Proportions of each processes in fungal community.

TABLE 3 Correlation analysis among soil microbial diversity, network properties, assembly processes, and soil properties.

	Correlation value								
Parameter	**pH**	**EC**	**OM**	**TN**	**TP**	**TK**	**AP**	**AN**	**NN**
Bacterial									
Shannon	−0.007	−0.263	0.493**	0.469**	0.404**	0.237	0.024	0.134	−0.336*
Simpson	0.143	0.169	−0.496**	−0.490**	−0.379**	−0.148	−0.159	−0.169	0.209
ACE	0.069	−0.292*	0.441**	0.507**	0.454**	0.241	0.131	0.082	−0.264
Chao1	0.073	−0.341*	0.397**	0.430**	0.339*	0.194	0.064	0.050	−0.278*
Degree	−0.045	0.152	0.179	0.116**	0.043	0.041	0.223	0.062	−0.129
Closeness centrality	−0.024	0.174	0.189	0.147	0.068	0.081	0.159	0.051	−0.176
Betweeness centrality	0.088	−0.086	0.197	0.066	−0.050	0.067	0.092	0.042	−0.316*
βNTI	−0.014	−0.114	0.287*	0.367**	0.407**	0.251	−0.007	−0.101	−0.349**
Fungal									
Shannon	−0.455**	0.065	0.077	0.191	0.090	−0.234	0.323*	0.101	0.285*
Simpson	0.056	0.063	−0.019	−0.019	0.051	0.274*	−0.066	−0.030	−0.130
ACE	−0.489**	−0.027	0.319*	0.714**	0.592**	0.015	0.369**	0.270*	0.075
Chao1	−0.478**	−0.017	0.300*	0.711**	0.578**	−0.005	0.373**	0.274*	0.082
Degree	0.248	−0.127	0.131	0.214	0.162	−0.089	−0.086	−0.002	−0.353*
Closeness centrality	0.302*	−0.162	0.147	0.214	0.143	−0.016	−0.163	0.048	−0.416**
Betweeness centrality	0.140	0.044	0.068	0.302*	0.248	−0.132	0.148	−0.044	−0.178
βNTI	−0.293*	0.112	0.007	0.152	0.172	−0.191	0.119	−0.087	0.170

Note: Soil microbial diversity included Shannon, Simpson, ACE, and Chao1 indices. Network properties included Degree, Closeness Centrality, and Betweeness Centrality. Assembly processes included βNTI index. Soil properties included pH value (pH), electrical conductivity (EC), organic matter (OM), total nitrogen (TN), total phosphorus (TP), total potassium (TK), available phosphorus (AP), ammonium nitrogen (AN), and nitrate nitrogen (NN).
*$p < .05$.**$p < .01$.

community assembly and network properties via their influence on bacterial diversity. Soil SM exhibited a significant positive relationship with community assembly and bacterial composition. Additionally, soil SM exhibited a direct correlation with bacterial composition and indirectly affected bacterial composition through its influence on community assembly (Figure 5a). For fungi, soil TN exhibited a significantly positive relationship with network properties. Soil NN demonstrated a significant negative correlation with network properties. Additionally, soil pH was directly correlated with fungal composition, and indirectly influenced community assembly and fungal composition through its association with fungal diversity (Figure 5b).

4 | DISCUSSION

4.1 | Effects of *S. canadensis* and *E. canadensis* invasion on soil physicochemical properties

Environmental factors significantly impact the composition and structure of soil microbial communities, with pH recognized as a primary influencing factor (Wang et al., 2022; Wang, Zhou, et al., 2018; Wei et al., 2020). Research indicates that invasive plants possess a strong ability to absorb soil nitrogen, resulting in the tendency to increase the pH value of the soil (Fan et al., 2010; Kuebbing et al., 2014). However, the outcome of our study demonstrated a significant reduction in soil pH ($p < .05$) due to single- and co-invasion. This alteration might be attributed to the secretion of acidic allelochemicals into the soil by *S. canadensis*, including phenolic compounds, and flavonoids, leading to soil acidification (Abhilasha et al., 2008; Kato-Noguchi & Kato, 2022). Additionally, *E. canadensis* contributes to this process by secreting phenols and phenolic acids into the soil (Djurdjevic et al., 2011, 2012).

Soil nutrients play a crucial role in sustaining plant growth. Variations in their structures and elemental compositions cause plants to absorb nutrients with varying contents and ratios of each element (Wang et al., 2022). Various plants exert distinct effects on soil properties through root exudates and litter decomposition. Previous studies have demonstrated that invasive plants alter the physicochemical properties of the soil by selecting soil nutrients or through allelopathic

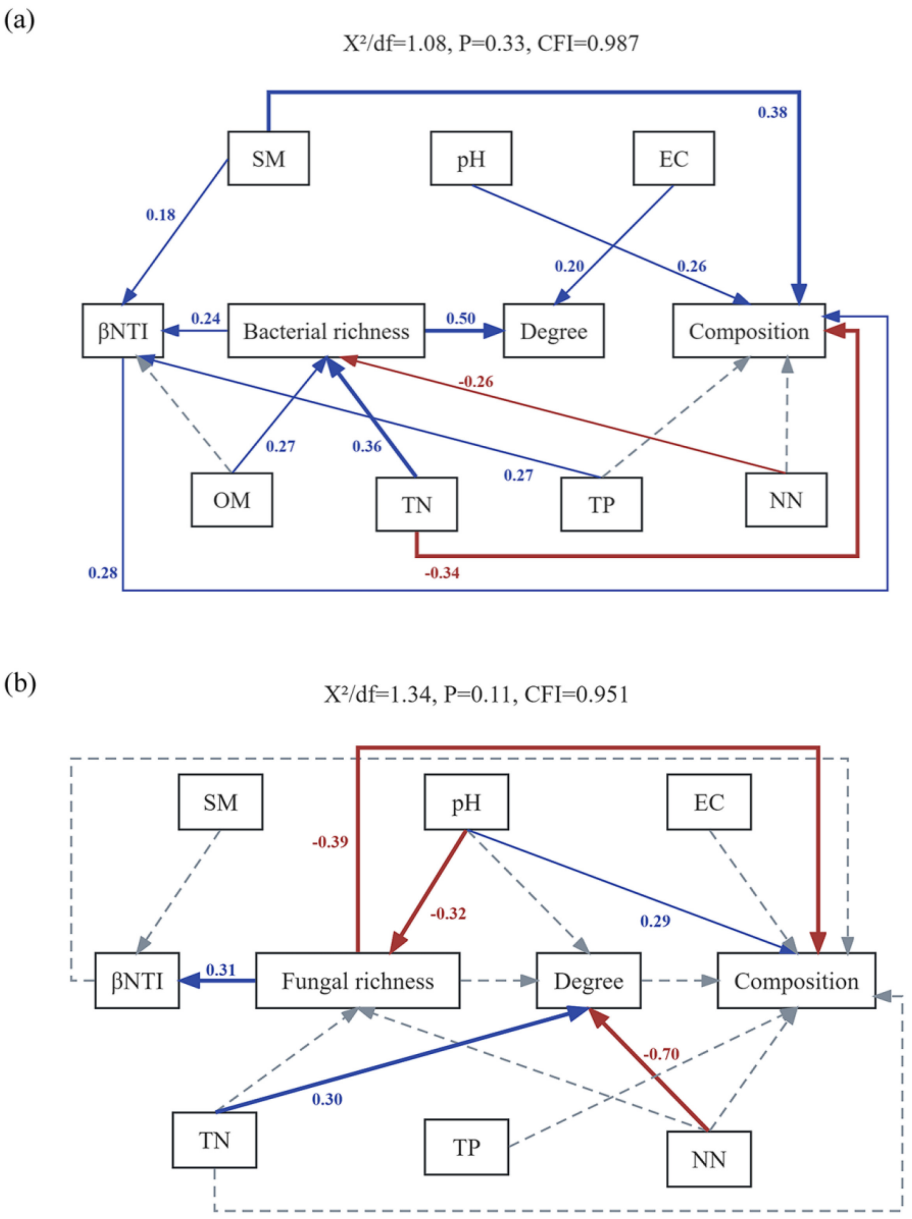

FIGURE 5 The structure equation modeling diagram illustrates the relationship among soil microbial diversity, network properties, assembly processes, microbial composition, and soil properties. The blue and red lines indicate positive and negative effects, respectively. The width of the arrows indicates the strength of significant standardized path coefficients. The gray lines depict paths with non-significant coefficients. Soil microbial diversity indicates microbial richness (Shannon index). Network properties indicate degree. Assembly processes denote βNTI index. Microbial composition indicates Bray–Curtis dissimilarity. Soil properties include soil moisture content (SM), pH value (pH), electrical conductivity (EC), organic matter (OM), total nitrogen (TN), total phosphorus (TP), and nitrate nitrogen (NN).

interactions (Dassonville et al., 2008; Fan et al., 2010; Yang et al., 2016). These mechanisms promote invasive plant growth and modify soil properties through co-invasion (Wang, Zhou, et al., 2018; Wei et al., 2020). In this study, single- and co-invasion increased soil TN, AP, and NN contents. This increase may be attributed to the larger litter produced by invasive plants, stemming from their higher biomass than native plants. Consequently, the soil in the invaded regions potentially harbors a higher soil element content, influencing an uptick in soil nutrients and alterations in the soil nutrient cycle (Liao et al., 2008; Zukswert & Prescott, 2017). Compared to the single invasion of *E. canadensis*, reducing *E. canadensis* coverage when co-invading with *S. canadensis* increased the soil OM, TN, TP, TK, and AP content. This indicates that the co-invasion of *S. canadensis* and *E. canadensis* enhances soil nutrient levels.

4.2 | Effects of *S. canadensis* and *E. canadensis* invasion on soil bacterial community

Soil microorganisms, exhibiting the highest biodiversity in terrestrial ecosystems, support ecosystem functions and stability (Crowther et al., 2019; Mason-Jones et al., 2022; Yang et al., 2023). Previous studies have indicated that high aboveground biodiversity plays a role in maintaining belowground microbial diversity, attributed largely to the varied secretions introduced into the soil (Upton et al., 2019). Our results partially supported our

findings that compared with the uninvaded region, a single invasion of *E. canadensis* exhibited reduced soil bacterial diversity and richness. However, diversity increased during the sole invasion of *S. canadensis*, showing a distinct pattern to that of *E. canadensis*. This variation might be attributed to the interplay between microbial diversity and plant species, considering factors such as root exudate type and quantity. Furthermore, our results indicate that co-invasion treatments with *S. canadensis* increased the diversity and richness within the soil bacterial community. Compared to single invasion, co-invasion reduced diversity and richness in bacterial communities within the rhizosphere soil of *S. canadensis*, while increasing these aspects in the rhizosphere soil of *E. canadensis*. This aligns with the relationship between vegetation type and observed patterns. Therefore, this study shows that the diversity and richness of rhizosphere bacterial communities undergo alterations based on the coverage of invasive plants, displaying distinct changes between *S. canadensis* and *E. canadensis*.

Soil microbial diversity is widely acknowledged to be influenced by numerous environmental factors, with soil physicochemical properties being the most pivotal (Kourtev et al., 2002). In this study, positive correlations were observed between soil OM, TN, and TP with the Shannon, ACE, and Chao1 indexes of soil bacteria. These findings suggest that invasive plants may augment soil bacterial diversity by increasing soil nutrient content (Jaroslav et al., 2022; McLeod et al., 2021). Additionally, it was observed that irrespective of the degree of invasion, the Shannon, ACE, and Chao1 indexes of bulk soil bacteria associated with *S. canadensis* or *E. canadensis* exceeded those of rhizosphere bacteria. This observation indicates a higher diversity and richness of bulk soil microbial communities associated with these two invasive plants. This discrepancy might arise from the superior impact of allelochemicals secreted by plant roots on the proliferation of rhizosphere soil bacteria compared to that of bulk soil bacteria.

Simultaneously, the invasion of *S. canadensis* and *E. canadensis* alters the structure, species composition, and relative abundance of the soil microbial community (Wang et al., 2022). Actinobacteria were found to be the dominant phylum of soil bacteria in the invaded regions of *S. canadensis* and *E. canadensis*. However, while the dominant phyla in the rhizosphere and bulk soil remain the same, their relative abundances differ significantly (Wang, Zhou, et al., 2018). Compared with the uninvaded region, co-invasion decreased the relative abundance of Actinobacteria while increasing the relative abundances of Proteobacteria and Chloroflexi in the rhizosphere soil of *S. canadensis*. Across each treatment, Actinobacteria exhibited a higher relative abundance in the bulk soil of *S. canadensis* than the rhizosphere soil, whereas *E. canadensis* demonstrated the reverse trend. These observations underscore differences in bacterial richness concerning invasive plant species across rhizosphere and bulk soil (Kamutando et al., 2017). This study revealed significant positive correlations between soil pH, Actinobacteria, and Firmicutes while exhibiting a significant negative correlation with Chloroflexi. Consequently, plant invasion alters the relative abundance of certain bacteria, forming a conducive soil microenvironment.

Additionally, a single invasion of *S. canadensis* increased the relative abundances of Actinobacteria, Proteobacteria, and Chloroflexi. In contrast, a single invasion of *E. canadensis* decreased the relative abundances of Actinobacteria, Proteobacteria, and Acidobacteria in the bulk soil. This shows that the roots of distinct invasive plants create varying soil microenvironments to adapt to them (He et al., 2022). Following invasion by invasive plants, the structure and species composition of the soil microbial community tend to undergo alterations (Rezacova et al., 2021; Yang et al., 2019). This study revealed that within the invaded region, the assembly process of the soil bacterial community is influenced by stochastic and deterministic processes. However, the proportions of these processes varied across different invasion conditions. In the case of bacteria, stochastic processes accounted for 60% and 100% of the assembly. In this study, bacterial diversity influenced the bacterial assembly process, while soil OM, TN, and NN showed an indirect relationship with the assembly process and network properties through bacterial diversity. Furthermore, the inter-relationship among bacterial phyla was mainly positive, suggesting a mutualistic interaction among soil bacteria in the presence of *S. canadensis* and *E. canadensis*. Research indicates that increased bacterial community diversity tends to shift the assembly process towards stochastic processes. Conversely, lower bacterial diversity leans towards deterministic assembly processes (Xun et al., 2019). Additionally, the invaded region exhibits high soil bacterial diversity and richness, enhancing its environmental tolerance and metabolic adaptability, thereby reducing susceptibility to environmental factors (Lin et al., 2022). Consequently, stochastic processes gain prominence in the bacterial assembly process, as observed in the *Spartina alterniflora* invaded region, as described by Chen and Wen (2021).

4.3 | Effects of *S. canadensis* and *E. canadensis* invasion on soil fungal community

Besides the impact of soil physicochemical properties on soil bacterial diversity and species composition, it is

worth noting that the diversity and composition of soil fungal communities are also affected, although the nature of this effect might differ (Kourtev et al., 2002). This study demonstrated that the invasion of *S. canadensis* and *E. canadensis* led to increased Shannon, ACE, and Chao1 indexes of fungi in bulk soil and rhizosphere soil compared to uninvaded regions. These findings suggest that the invasion by *S. canadensis* and *E. canadensis* enhanced the diversity and richness of soil fungal communities, aligning with previous research outcomes (Wang, Zhou, et al., 2018). However, in contrast to a single invasion, co-invasion reduced the richness of the fungal community in the rhizosphere soil of *S. canadensis*, while increasing the fungal community diversity and richness in the rhizosphere soil of *E. canadensis*. Therefore, this study illustrates that varying coverage levels of invasive plants not only influence the diversity and richness of rhizosphere bacterial communities but also significantly affect the diversity and richness of fungal communities, displaying distinct variations between *S. canadensis* and *E. canadensis* (Wang, Zhou, et al., 2018). The invasion of *S. canadensis* and *E. canadensis* amplified the soil TN, TP, and AP contents, correlating positively with the ACE and Chao1 indexes. Therefore, the invasion of these plants might foster increased diversity within the soil fungal community by increasing soil nutrient content. This suggests a potential enhancement in soil functionality and nutrient uptake mechanism employed by invasive plants (Chen & Wen, 2021).

Soil fungi play a crucial role in facilitating the growth of invasive plants (Gaggini et al., 2018). Invasion of these plants has resulted in alterations in the richness of specific groups within the soil fungal community of the invaded region (Rezacova et al., 2021). This study reveals that the dominant phylum of soil fungi in the invaded regions was Ascomycota. However, there were significant differences in the relative abundances of these phyla among the various treatments. Additionally, differences were observed in the relative abundance of the predominant fungal phyla between the rhizosphere and bulk soils. Therefore, *S. canadensis* and *E. canadensis* potentially facilitate more conducive soil fungal communities, thereby enhancing their invasion (Wang, Zhou, et al., 2018).

Our findings revealed a significant positive correlation between Ascomycota, TN, and TP, along with increased TN content in the soil from co-invasion. This could be attributed to the role of Ascomycota as saprophytic bacteria, pivotal in decomposing litter, promoting nutrient cycling and energy flow within the soil. In summary, a single invasion or co-invasion alters the community structure and species composition of soil fungi to adapt to the new environment (Ye et al., 2023). Furthermore, the relationship between fungal phyla was predominantly positive, indicating mutualistic interactions among soil fungi in the presence of *S. canadensis* and *E. canadensis*, aligning with the bacterial relationships observed. In this study, the dominance of stochastic processes, accounting for 67%–100% of fungi, may be attributed to increased nutrient release from the litter of invasive plants, supporting greater diversity in soil fungi. Additionally, soil pH potentially influences the microbial assembly process. Structural equation modeling indicated that soil pH indirectly relates to the assembly process through bacterial diversity. However, Zhuang et al. (2020) discovered that heterogeneous selection contributed to >40% of the fungal community assembly in mangrove rhizosphere soil, which is inconsistent with the findings of this study. The discrepancy may potentially stem from variations in research subjects and scales. The assembly process of soil fungal communities under certain invasion conditions involves dispersal limitations compared to the bacterial community. This divergence may be attributed to the size and lifestyle disparities between fungi and bacteria. Soil bacteria, characterized as single-celled organisms, are generally smaller than most fungi (Powell et al., 2015), potentially influencing their dispersion and spatial aggregation (Zheng et al., 2021).

In conclusion, this study revealed that compared to the uninvaded region, both single- or co-invasion of *S. canadensis* and *E. canadensis* enhanced the contents of TN, TP, AP, and NN in the soil. These increments promoted vegetative growth and facilitated the establishment of a predominant population. Additionally, the invasion by *S. canadensis* and *E. canadensis* increased the diversity and richness of bulk soil microbial communities. As the coverage of invasive plants varied, alterations in the diversity and richness of rhizosphere microbial communities ensued, displaying distinct patterns between *S. canadensis* and *E. canadensis*. The dominant phyla in the bulk and rhizospheric soils were identical, but their relative abundances varied. As such, single- and co-invasion of these plants induce alterations in the community structure and species composition of soil microorganisms, enabling them to adapt to a new environment more effectively. Furthermore, the microbial assembly process was primarily steered by stochastic processes. Homogenizing dispersal and ecological drift emerged as the principal factors influencing the succession of bacterial and fungal communities, respectively. Structural equation modeling revealed a significant relationship between soil properties (pH, TN, and NN) and bacterial interactions (diversity and community assembly) concerning microbial composition. This study offers

a building block towards the fuller understanding of whether or how, plant invasions should be controlled.

AUTHOR CONTRIBUTIONS

Mengying He: Conceptualization, Methodology, Formal analysis, Investigation, Writing—Original Draft. Tingting Liu: Resources, Investigation. Yaqi Liu: Resources, Investigation. Yiyi Long: Resources, Investigation. Yue Li: Writing—Review & Editing, Investigation. Qingsong Xie: Resources, Investigation. Zhen Zhang: Conceptualization, Methodology, Writing—Review & Editing.

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CONFLICT OF INTEREST STATEMENT

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.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in NCBI (PRJNA997630).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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