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Impact of *Parthenium hysterophorus* L. invasion on soil fungal communities in the Yellow River Delta

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Abstract

Purpose As an invasive plant, *Parthenium hysterophorus* severely impacts the ecological environment of the Yellow River Delta and reduces biodiversity in the invaded areas. The effects of *P. hysterophorus* invasion on the local environment became increasingly critical, while few information was available for the effects of *P. hysterophorus* invasion on soil bacteria. The present study aimed to reveal the impacts of hysterophorus on the fungal communities in the Yellow River Delta.

Methods Sixteen soil samples including four groups (ROOT group, YRR group, YNR group, and GBS group) were collected. High-throughput methods were used to explore the fungal composition of the *P. hysterophorus*-invaded surrounding environment and native plant-growed environment.

Results Our results showed that the ACE (351.97) and Chao1 (351.95) values of the rhizosphere soils of *P. hysterophorus* (YRR group) were the highest among the four groups, whereas the non-rhizosphere soil samples of *P. hysterophorus* (YNR group) had the highest Shannon (7.188) and Simpson (0.984) values. The total number of operational taxonomic units (OTUs) obtained from the four groups was 1965, with 161 common OTUs among different groups. At the phylum level, both Ascomycota and Basidiomycota were the dominant fungi, with Ascomycota having the highest abundance. At the genus level, except for the endophytic fungi of *P. hysterophorus* roots (ROOT group), *Fusarium*, *Mortierella*, *Comoclathris*, and *Cladosporium* were the dominant fungi in three groups. The fungal communities within the roots of *P. hysterophorus* were distant from other groups, indicating that the composition of the fungal communities within the roots had a low degree of similarity to the other three groups. LEfSe analysis showed that Ascomycota at the phylum level and *Cladosporium*, *Curvularia*, and *Alternaria* at the genus level play essential roles in the ROOT group, and *Comoclathris* plays a vital role in the YNR group.

Conclusions This study explored the effects of *P. hysterophorus* invasion on the local soil fungal communities by analyzing the fungal communities in *P. hysterophorus roots*, rhizosphere soil, non-rhizosphere soil, and rhizosphere soil of native plants. Generally, *P. hysterophorus* rhizosphere fungi specifically affect the surrounding environment.

Keywords Root, Soil, Microorganism, Invasive plants

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Introduction

The globalization of the economy has led to an increase in trade volume among countries, resulting in the introduction of more alien species to meet various domestic needs. As a result, the phenomenon of alien biological invasion has intensified and attracted significant attention both domestically and abroad (Dutta 2018). This invasion of alien species can cause a reduction in biodiversity and disrupt the balance of the ecosystem (Courchamp et al. 2017). The competitive ability of alien species often surpasses that of native species, leading to a loss of dominance by the latter and the eventual destruction of the local ecosystem. Given their crucial role in the biogeochemical cycle, soil microorganisms are indispensable to the wetland ecosystem (Trap et al. 2016). The microbial community in rhizosphere soil plays varying ecological roles during different stages of plant growth. Studies have shown that rhizosphere microorganisms can assist plants in absorbing soil nutrients, improving plant resistance, and protecting plants from pathogens. A favorable soil microbial composition is essential for the formation of good soil structure, ecosystem function, and material cycle (Wang et al. 2017). Invasion of exotic plants results in changes in the soil microbial community and physical and chemical properties (Shang et al. 2023), which impacts the competitive relationship between exotic and native species and further contributes to the invasion of alien plants (Shang et al. 2022a). For instance, when alien species invade new habitats, their rhizosphere probiotic communities dominate the habitats, accelerating the host's adaptation to the environment to a certain extent (Zhang et al. 2020).

The Yellow River Delta (YRD) is recognized as one of China's significant estuarine deltas (Zhang et al. 2016) and is renowned for its highly diverse coastal wetland ecosystem (Yu et al. 2012). However, the YRD's ecological balance is threatened by the invasion of invasive species such as *Spartina alterniflora* (Shang et al. 2022b). The adaptability, reproduction, and competitive ability of invasive species negatively impact native plants, soil microbial communities, and physical and chemical properties of the local environment (Zheng and Liao 2017). *Parthenium hysterophorus* L., a plant species from the family Asteraceae with an erect stem and main root, is an annual plant native to the USA and northern Mexico (Batish et al. 2002). *P. hysterophorus* L. is known for its strong reproductive capacity via sexual or asexual reproduction, with its pollen potentially causing allergic reactions and other diseases. This invasive species can also affect the growth of other species, alter the physical and chemical properties of soil, and disrupt the ecological balance of the invaded area, subsequently reducing local biodiversity and impeding economic development. After being identified in Yunnan Province, China, *P. hysterophorus* rapidly spread south of the Yangtze River, and it was found in Shandong Province in 2004, inflicting damage to local crops and the environment. We investigated the bacterial relationship between the *P. hysterophorus* community and the native community. However, the relationship between the rhizosphere soil and the soil fungal community of *P. hysterophorus* is unclear. Therefore, we selected four types of micro-habitats, including the *P. hysterophorus* roots, *P. hysterophorus* rhizosphere soil, *P. hysterophorus* non-rhizosphere soil, and native plant-growed soil, and studied related soil physical and chemical properties (pH, EC, and total organic carbon [TOC]). Furthermore, we used high-throughput sequencing techniques conducted to analyze the fungi in these habitats. In this study, the differences in soil fungal communities and soil physical and chemical properties between invaded areas and native plant communities were compared to understand the diversity of soil fungi and the effects of *P. hysterophorus* invasion on soil physical and chemical properties and the fungi community. This research provides a theoretical basis for better control of the *P. hysterophorus* wetland ecosystem invasion.

Materials and methods

Sample site

Soil samples were collected from the vicinity of Siyuan Lake in the YRD of Binzhou (37°16′ N–38°16′ N, 118°20′ E–119°20′ E), which is situated in a warm temperate monsoon climate zone with distinct continental meteorological features and significant seasonal variations. The average annual temperature of the region is 18.3 °C. The land severely invaded by *P. hysterophorus* was selected as the sample site, where it formed a single community. The density of the *P. hysterophorus* in the plot is 58, sporadically accompanied by *Setaria viridis* (L.) Beauv (Shang et al. 2023).

Sample collection and determination of soil physical and chemical properties

In the sample plots, root, rhizosphere soil, and non-rhizosphere soil of *P. hysterophorus* and rhizosphere soil of *S. viridis* were collected. A rhizosphere/non-rhizosphere soil sample was mixed with five sub-samples collected. The soil samples were then divided into two parts. One part was used to determine the physical and chemical properties of the soil, whereas the other part was immediately transferred to a low-temperature refrigerator (− 80 °C) for subsequent sequencing of fungal communities. The root tissue of *P. hysterophorus* was also collected aseptically and a low-temperature refrigerator (− 80 °C) for subsequent sequencing of fungal communities.

The pH of the soil sample was determined using a pH meter in the supernatant of the soil–water mixture with a water/soil ratio of 5:1 (Shang et al. 2023). The EC of the sample was measured using an electrical conductivity meter in the supernatant of a soil–water mixture with a water/soil ratio of 5:1 (Shang et al. 2023). The TOC in the soil samples was determined by the volumetric potassium dichromate external heating method, as described in a previous study (Shang et al. 2023).

High-throughput sequencing of soil microbes

The soil samples stored at − 80 °C were dispensed into 1.5-ml centrifuge tubes and placed on an ultra-clean workbench. Each treatment was repeated four times. The endophytic fungi of *P. hysterophorus* roots were labeled as ROOT (ROOT1, ROOT2, ROOT3, and ROOT4), the fungi in the rhizosphere soil of *P. hysterophorus* were labeled as YRR (YRR1, YRR2, YRR3, and YRR4), the non-rhizosphere soil samples of *P. hysterophorus* were labeled as YNR (YNR1, YNR2, YNR3, and YNR4), and the rhizosphere soil of native plants was labeled as GBS (GBS1, GBS2, GBS3, and GBS4).

The DNA of the soil was extracted by using the soil DNA kit. PCR amplification of ITS1F and ITS2R (ITS1F: 5′-CTTGGTCATTTAGAGGAAGTAA-3′; ITS2R: 5′-GCTGCGTTCTTCATCGATGC-3′) was performed using universal primers for PCR amplification of the fungal ITS region (Cui et al. 2019). The PCR products from the same sample were mixed and used AxyPrep DNA Gel Extraction Kit recycle product purification. Furthermore, the NEXTFLEX Rapid DNA-Seq Kit was used to build the library. The library was sequenced using Illumina's NovaSeq 6000.

Data analysis

The alpha diversity index was calculated using the Qiime software (version 2.0) and SPSS 23.0 Student's *t* test (IBM SPSS Inc., USA) (Bolyen 2019), and dilution curves and PCoA graphs were generated using R package ggplot (version 3.4.4) (McMurdie and Holmes 2013). The sequencing data obtained in this study are available at NCBI (accession number: PRJNA956238).

Results

Alpha diversity analysis

Alpha diversity is used to measure the species abundance and diversity of individual samples, and there are various measuring indices, including Chao1, ACE, Shannon, and Simpson (Fig. 1). Chao1 and ACE indices were used to estimate species abundance, whereas Shannon's and Simpson's indices were used to measure diversity of species abundance and community evenness. The YRR group had the highest ACE (351.97) and Chao1 (351.95) indices among the four groups, indicating that the abundance of the rhizosphere soil fungal communities of *P. hysterophorus* was higher than that of the other three groups. The YNR group had the second-highest ACE (339.33) and Chao1 (335.75) indices.

The YNR group showed the highest Shannon index (7.188) and Simpson index (0.984) among the four groups, indicating a higher diversity of fungal communities in the non-rhizosphere soil of *P. hysterophor*us. The Chao1 (277.25), ACE (278.30), Shannon (5.947), and Simpson (0.944) indices of the ROOT group were the lowest among the four groups, indicating the lowest abundance and diversity of fungal communities in the roots of *P. hysterophorus*.

OTU abundance analysis

In our study, we identified 967 OTUs in the YRR group, 943 OTUs in the YNR group, 787 OTUs in the GBS group, and 835 OTUs in the ROOT group (Fig. 2). The total number of OTUs obtained from different groups was 1965, with 161 common OTUs found between the four groups. Specifically, 448 OTUs were shared between the YNR and YRR groups, 425 between the YRR and GBS groups, and 368 between the YNR and GBS groups. The number of OTUs in the rhizosphere and non-rhizosphere soils of *P. hysterophorus* was higher than that in *P. hysterophorus* roots.

Soil microbial community structure analysis

Based on species annotation results, the top 10 species ranked by richness at the phylum level (excluding "others") were used to generate a column accumulation map, as shown in Fig. 3. At the phylum level, the dominant fungi in the rhizosphere and non-rhizosphere of *P. hysterophorus* were Ascomycota, Basidiomycota, and Mortierellomycota, with a total relative abundance of 83.8% and 85.8%, respectively. The dominant fungi within the *P. hysterophorus* roots were Ascomycota and Basidiomycota, with a total relative abundance of 88.1%. In the rhizosphere soil of the native plants, the dominant fungi were Ascomycota, Basidiomycota, and Glomeromycota, with a total relative abundance of 85.1%. Ascomycota and Basidiomycota were also dominant in all four groups, with Ascomycota having the highest abundance at 54.7% (YRR), 64.9% (YNR), 78.1% (GBS), and 56.5% (ROOT).

The top 10 genera ranked in abundance, except for unclassified species, were selected to generate a column accumulation map, as shown in Fig. 4. At the genus level, the dominant fungi were *Fusarium*, *Mortierella*, *Comoclathris*, and *Cladosporium* in three groups. In the *P. hysterophorus* root, the dominant fungi were *Fusarium*, *Comoclathris*, *Cladosporium*, and *Alternaria*, with a total relative abundance of 41.7%.

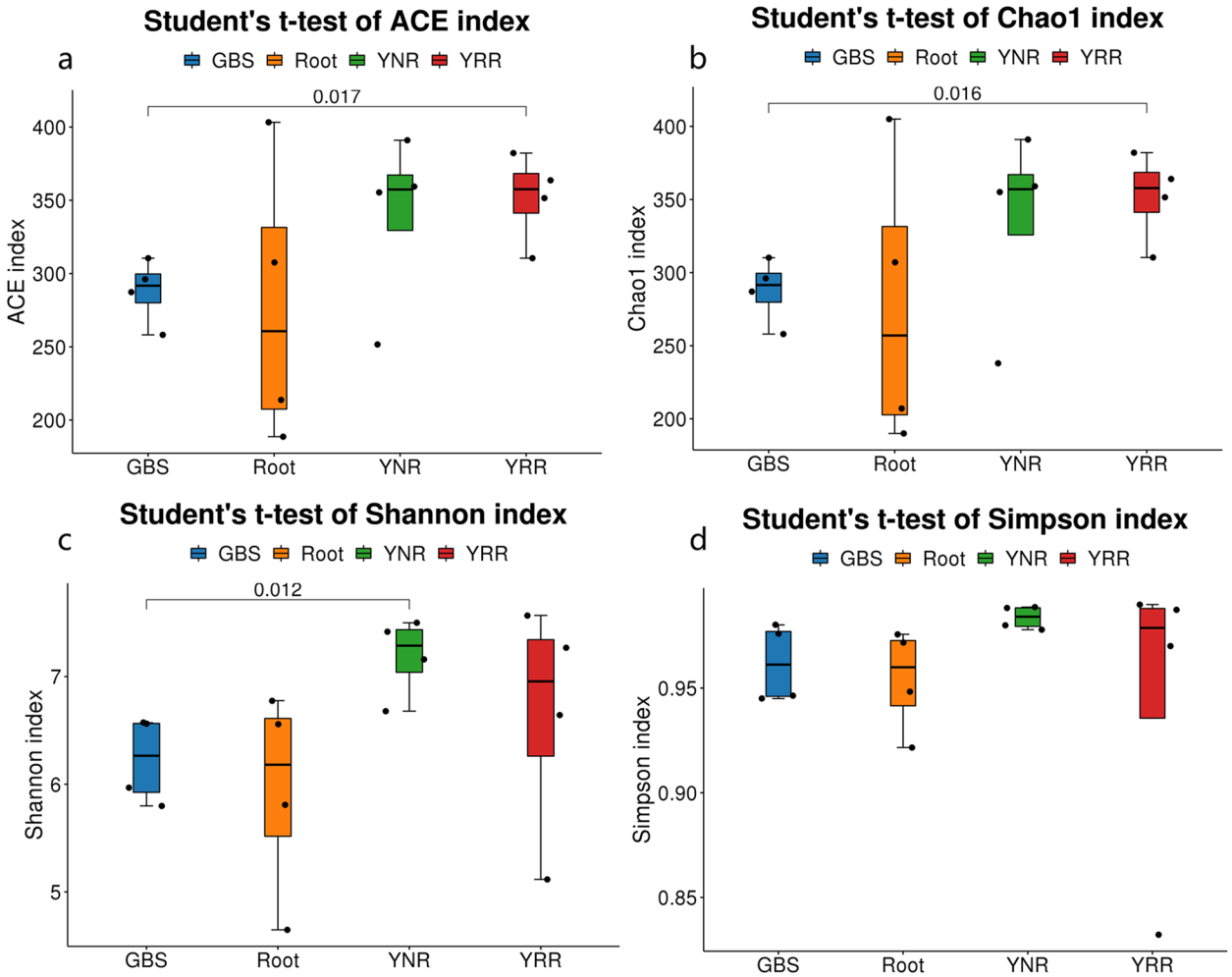

Fig. 1 Alpha diversity indices of fungi among different groups. **a** ACE index. **b** Chao1 index. **c** Shannon index. **d** Simpson index. GBS, rhizosphere soil of native plants (*S. viridi*); Root, endophytic fungi of *P. hysterophorus* roots; YNR, non-rhizosphere soil samples of *P. hysterophorus*; YRR, fungi in the rhizosphere soil of *P. hysterophorus*. The number on the line between the columns is the *P* value of the *T* test (if the *P value* > *0.05*, the *P value* is not displayed by default)

PCoA analysis

PCoA analysis can be used to visualize the differences or similarities between different groups and compare the variability of fungal communities among samples. Our results showed that the contributions of PC1 and PC2 were 10.12% and 8.82%, respectively (Fig. 5). The fungal communities of *P. hysterophorus* were similar in composition to those of the rhizosphere soil of native plants, as they were close in distance. Conversely, the fungal communities within the roots of *P. hysterophorus* were distant from the other groups, indicating that the composition of the fungal communities within the roots had a low degree of similarity to the other three groups.

LEfSe analysis

LEfSe analysis can identify species with significant differences between different groups. In the ROOT group, *Ascomycota* at the phylum level and *Cladosporium*, *Curvularia*, *and Alternaria* at the genus level play important roles. In contrast, *Comoclathris* plays a crucial role in the YNR group (Fig. 6).

Correlation between soil fungal species and soil physicochemical properties

The clustered heat map displays the effects of different environmental factors on soil microorganisms. Our results indicated that Olpidiomycota and Mucoromycota are correlated with pH, whereas Ascomycota is associated with EC. Additionally, Mucoromycota and Mortierellomycota are related to TOC levels (Fig. 7). The pH, EC, and TOC data were submitted as a supplement (Table S1).

Anosim (analysis of similarities), also known as similarity analysis, is a statistical method primarily used to

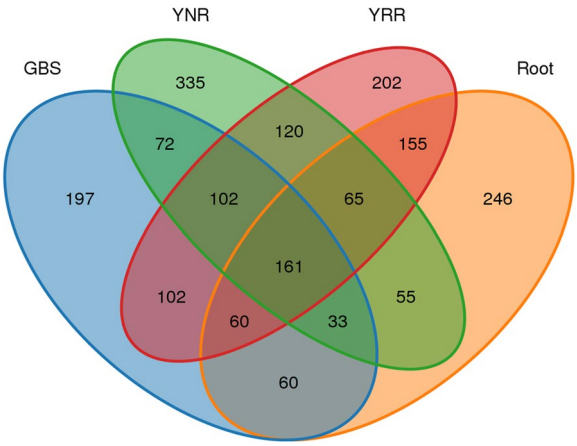

Fig. 2 Venn diagram showing the number of shared and unique OTUs among different groups. Different colors mean different groups. GBS, rhizosphere soil of native plants (*S. viridi*); Root, endophytic fungi of *P. hysterophorus* roots; YNR, non-rhizosphere soil samples of *P. hysterophorus*; YRR, fungi in the rhizosphere soil of *P. hysterophorus*

analyze the similarity between groups of multidimensional data. The Binary–Jaccard algorithm is used to calculate the inter-sample distance, and both the *R* value and *P* value are calculated. A higher *R* value indicates that the difference between groups is more significant than the difference within groups. Conversely, a smaller *R* value suggests no significant difference between or within groups. In this study, the *R* value was 0.292 (*P value* = *0.002*), indicating that the difference between groups is significant and substantial (Fig. 8).

Discussion

Previous studies have shown that plant invasion can significantly increase the pH of invaded soils (Dzurendova et al. 2020). However, in the present study, we found that the pH of the rhizosphere soil of *P. hysterophorus* did not differ significantly from that of the non-rhizosphere soil, and the TOC content was significantly lower than that of the non-rhizosphere soil. The dominant flora is a crucial factor in maintaining the stability of microbial communities and can significantly influence the composition and structure of such communities. In this study, the dominant phyla found in the soil samples were *Ascomycota* and *Basidiomycota*, which was consistent with the previously reported dominant fungal taxa in soil (Deveau et al. 2018). Interestingly, during the invasion of *P. hysterophorus*, the phylum *Glomeromycota*, which was the dominant fungal group in the rhizosphere soil of native plants, was gradually replaced by the saprophytic fungus *Mortierellomycota*. *Mortierellomycota* can decompose lignin and other difficult-to-decompose substances, thereby accelerating soil nutrient circulation and improving soil quality (Landinez-Torres et al. 2020). We speculate that the

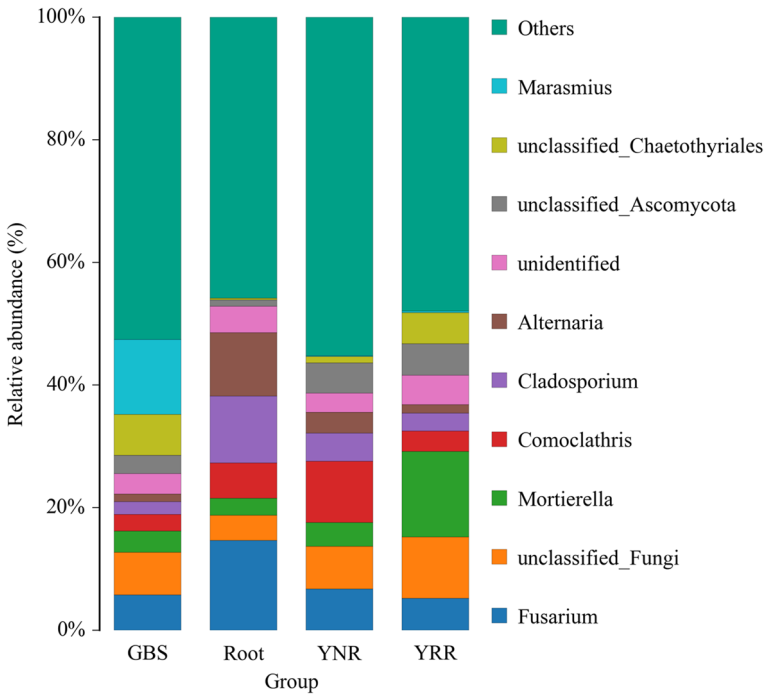

Fig. 3 Community structure of four groups at the phylum level. GBS, rhizosphere soil of native plants (*S. viridi*); Root, endophytic fungi of *P. hysterophorus* roots; YNR, non-rhizosphere soil samples of *P. hysterophorus*; YRR, fungi in the rhizosphere soil of *P. hysterophorus*

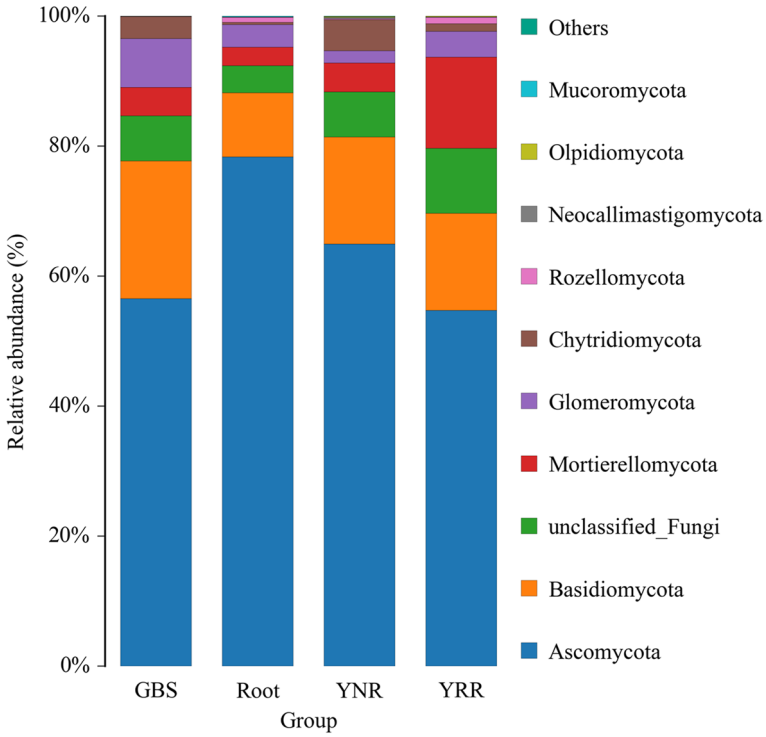

Fig. 4 Community structure of four groups at the genus level. GBS, rhizosphere soil of native plants (*S. viridi*); Root, endophytic fungi of *P. hysterophorus* roots; YNR, non-rhizosphere soil samples of *P. hysterophorus*; YRR, fungi in the rhizosphere soil of *P. hysterophorus*

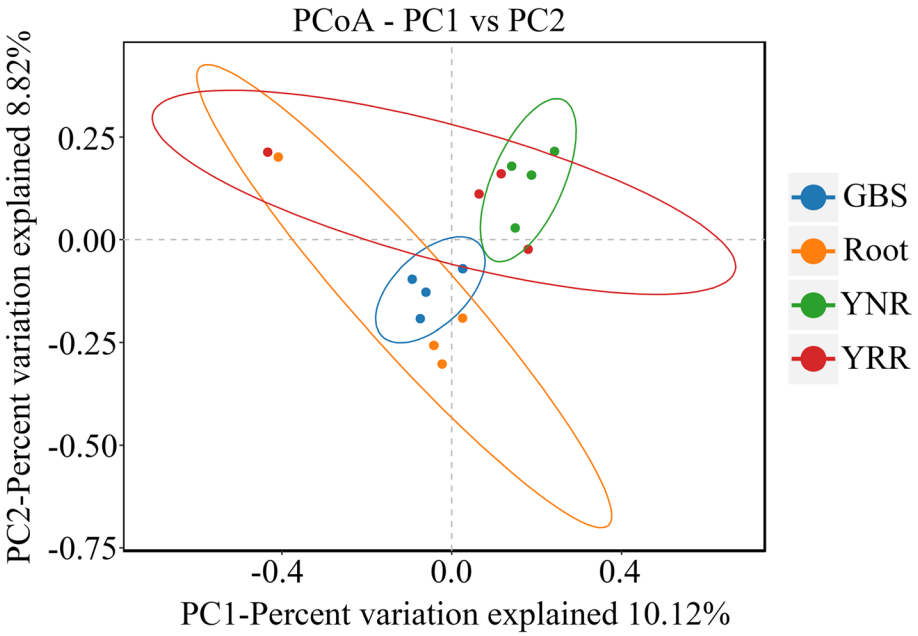

Fig. 5 The PCoA based on the Bray–Curtis distance shows the variation in bacterial community structure.GBS, rhizosphere soil of native plants (*S. viridi*); Root, endophytic fungi of *P. hysterophorus* roots; YNR, non-rhizosphere soil samples of *P. hysterophorus*; YRR, fungi in the rhizosphere soil of *P. hysterophorus*

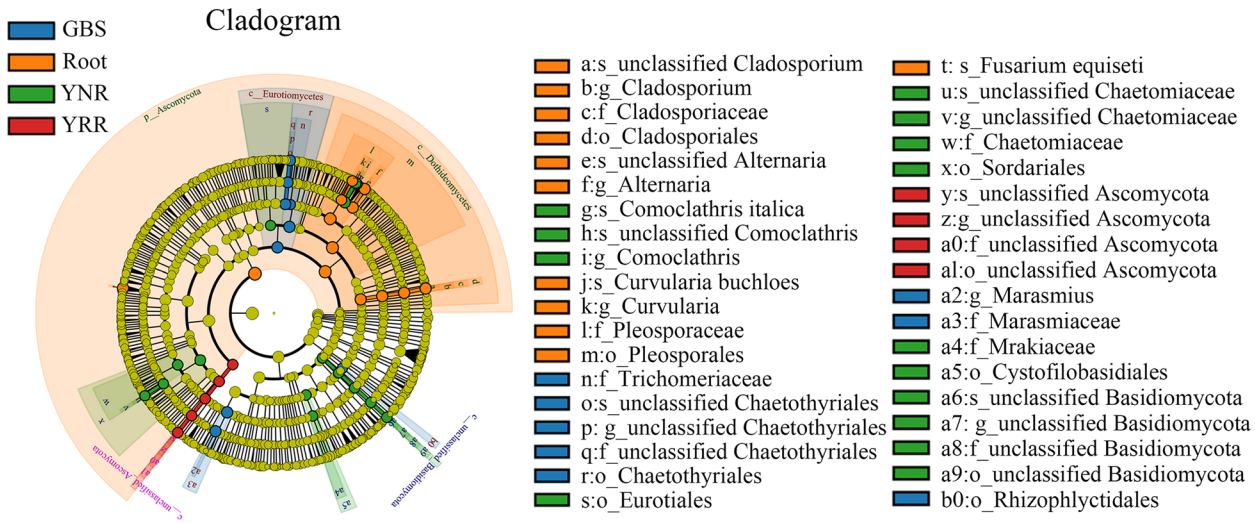

Fig. 6 LEfSe analysis at different fungal taxonomic levels among different groups. Different colored dots mean the taxa with significant differences among different samples. GBS, rhizosphere soil of native plants (*S. viridi*); Root, endophytic fungi of *P. hysterophorus* roots; YNR, non-rhizosphere soil samples of *P. hysterophorus*; YRR, fungi in the rhizosphere soil of *P. hysterophorus*

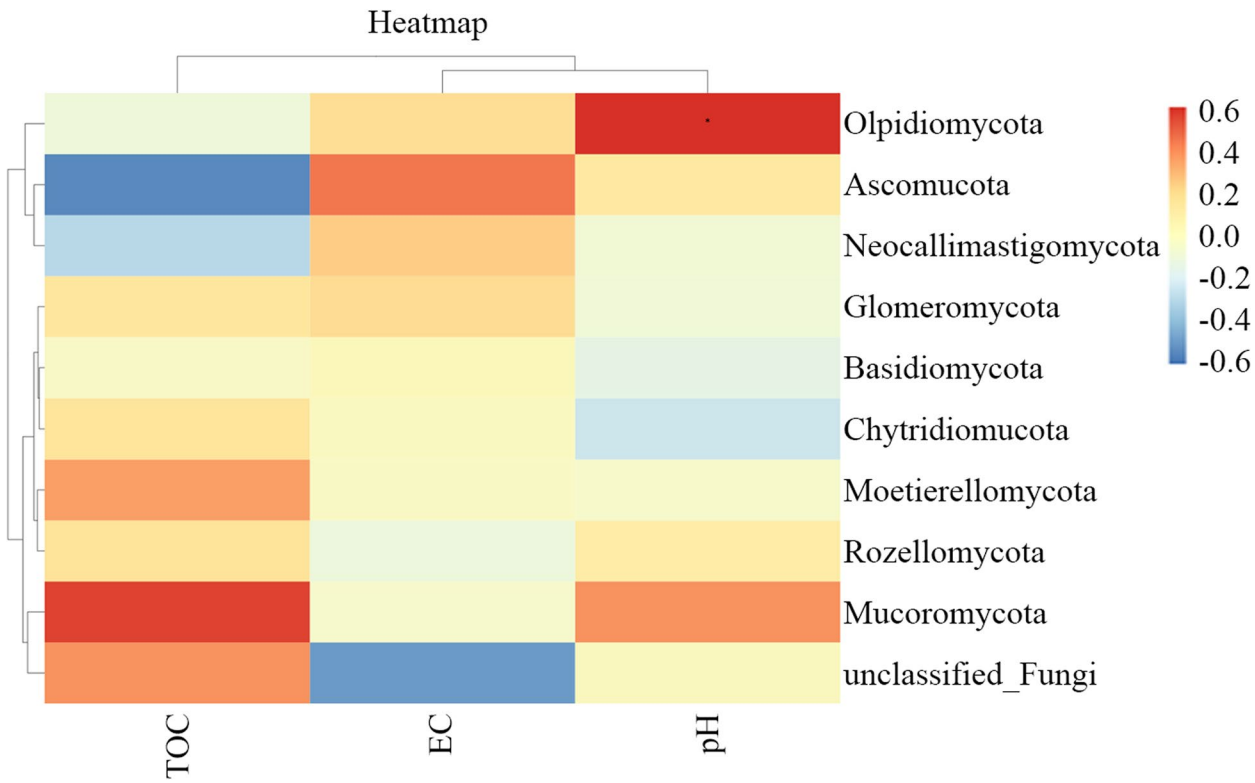

Fig. 7 Cluster heat map of the relationship between the soil's physicochemical properties and the fungal community. * means significant at 0.05 level

rhizosphere soil microorganisms of *P. hysterophorus* may be responsible for accelerating the decomposition of soil organics. At the genus level, the content of *Mortierella* in the rhizosphere soil of *P. hysterophorus* was higher than that of the native plants. *Mortierella* is known to produce polyunsaturated fatty acids and has been reported to act as a beneficial flora, inhibiting the growth of pathogenic bacteria in some crops (Sun et al. 2013). In our study,

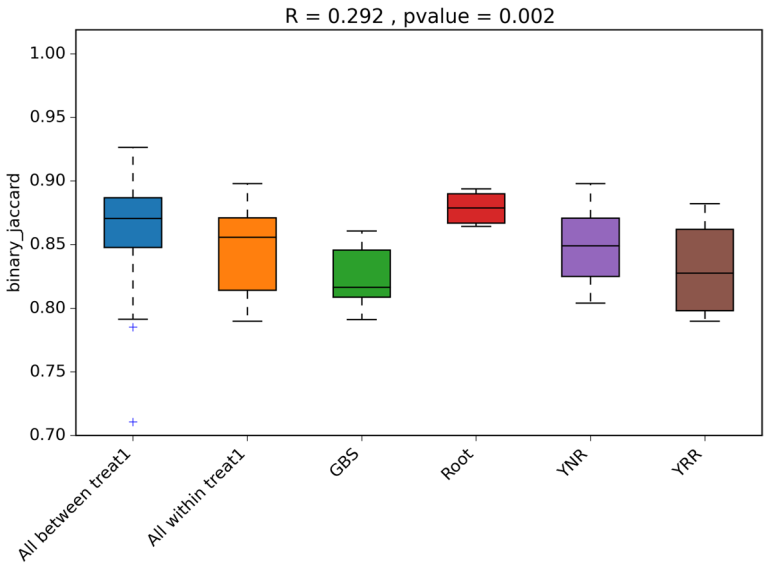

Fig. 8 Anosim analysis of different groups. GBS, rhizosphere soil of native plants (*S. viridi*); Root, endophytic fungi of *P. hysterophorus* roots; YNR, non-rhizosphere soil samples of *P. hysterophorus*; YRR, fungi in the rhizosphere soil of *P. hysterophorus*

we investigated the endophytic fungi in the roots of *P. hysterophorus*. Endophytic fungi have been reported as significant contributors to the competitiveness of exotic plants, and their high diversity indicates that they possess complex and versatile functional characteristics. Our previous study found that only 377 OTUs were identified in the Root group (Shang et al. 2023), while 835 OTUs of the ROOT group were identified in the present study. We speculated that compared with endophytic bacteria, the endophytic fungi might have more important functions in the root of *P. hysterophorus*. Ultimately, we found that Alternaria was the dominant group of root endophytes and a potentially pathogenic fungus at the genus level. Further analysis using LEfSe showed that *Alternaria* plays an essential role within the roots of *P. hysterophorus*. Thus, Alternaria in the roots of *P. hysterophorus* may indirectly serve as a weapon to invade in the proper direction. Our previous study found that the Acidobacteriota might be necessary for *P. hysterophorus* invasion (Shang et al. 2023). In general, the invasion strategy of *P. hysterophorus* was not only reflected at the bacterial level, but also at the fungal level.

There are some disparities in microbial diversity and richness between the rhizosphere soil and non-rhizosphere soil of *P. hysterophorus*. In the present study, the diversity of rhizosphere soil fungi is lower than that of non-rhizosphere soil. Whereas for the bacterial diversity in our previous study, the richness is higher than that of non-rhizosphere soil (Shang et al. 2023). Exotic plants can alter the soil microbial diversity and community structure at the invasion site during the invasion process. This enhances their ability to adapt to the environment and facilitates their invasion and growth (Sun et al. 2013). Soil fungi play a crucial role in the ecosystem as decomposers, contributing to the degradation of organic matter and the conversion of soil nutrients (Frac et al. 2018). The results showed that the invasion of *P. hysterophorus* caused changes in soil microbial composition and structure, which, in turn, affected the physical and chemical properties of the soil. This favored the growth of *P. hysterophorus*, allowing it to form a dominant community and impacting the changes in plant community diversity at the invaded site. Finally, High-throughput sequencing technology helps us better understand the impacts of plant invasions on the surrounding environment. Previous studies found that the sequencing alone could not adequately assess population size and dynamics (Beule et al. 2021). Thus, we need to increase the number of samples and detection frequency in subsequent experiments.

Conclusions

This study explored the effects of *P. hysterophorus* invasion on the local soil fungal communities by analyzing the fungal communities in *P. hysterophorus roots*, rhizosphere soil, non-rhizosphere soil, and rhizosphere soil of native plants. Ascomycota at the phylum level and *Cladosporium*, *Curvularia*, and *Alternaria* at the genus level play essential roles in the ROOT group, and *Comoclathris* plays a vital role in the YNR group. Generally, *P. hysterophorus* rhizosphere fungi specifically affect the surrounding environment.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13213-023-01735-6.

Additional file 1: Table S1. Soil physical and chemical property data.

Informed consent

Not applicable.

Author contributions

Methodology, L.G. and X.X.; Software, W.S.; Writing—original draft preparation, L.G., X.X. and S.S.; writing—review and editing, Z.Z. and J.Z. All authors have read and agreed to the published version of the manuscript.

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Availability of data and materials

The obtained sequencing data was available in NCBI (accession numbers PRJNA956238).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All the agreed to publish.

Competing interests

The authors declare that they have no competing interests.

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