Plants experience reduced a negative plant-soil feedback due to mycorrhizal fungi change with neighbors in a harsh environment

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Abstract

The fierce competition for limited nutrients, the dilution and activation of immunity to pathogens with the presence of other individuals could contribute to the lessening of negative plant-soil feedback (PSF). However, the relative contribution of these pathways to changes in negative PSF remains unknown in habitats with severe nutrient limitation. We conducted a PSF experiment on two common plant species in northwestern China's desertified soil. *Kalidium foliatum* and *Reaumuria songarica* were grown with or without intra- or interspecific neighbors. The PSF was separated into biological (B-PSF) and abiotic (A-PSF) components by adding a parallel treatment without any plant conditioning in the traditional soil sterilization processes to understand the effect of resource competition and microbial communities on the PSF changes. We found that the negative PSF of *R. songarica* were lifted with either intra or interspecific individuals; the negative PSF *K. foliatum* was only improved by the presence of interspecific neighbors. The decrease in negative PSF was mainly attributed to the decrease in negative B-PSF. The decrease in negative B-PSF was affected by mycorrhizal fungi and almost not by pathogens. Thus, at a low-density, plant individuals from harsh environments tend to facilitate each other, especially with the presence of interspecific species. This facilitation primarily occurs through enhanced cooperation with mycorrhizal fungi, thereby mitigating the negative PSF and improving coexistence of species.

Keywords: plant-soil feedback, plant-plant interaction, facilitation, coexistence, pathogens, ectomycorrhizal fungi.

Introduction

Plant-plant interaction (competition/facilitation) and plant-soil feedbacks (PSFs) are two mechanisms regulating community construction and diversity maintenance, with the interaction between them determining the spatial self-organization of a community (Bera et al. 2021; Momeni et al. 2013; Revilla et al. 2013; Verdú et al. 2009). The associations among plant-plant interactions, PSF and plant community dynamics are extensively studied (Casper and Castelli 2007; Crawford and Knight 2017; Klinerova and Dostal 2020). Stronger competitors are found to have more pronounced negative PSF compared to weaker competitors, indicating that PSF can hinder competitive advantages and facilitate coexistence (Chu et al. 2024; Dabu et al. 2024; Lekberg et al. 2018; Liu et al. 2023). Although facilitation and its relation to plant communities have been investigated in harsh environments and low-density communities (Chu et al. 2008; Yin et al. 2022; Zheng et al. 2024c), The intense competition for limited nutrients, along with the dilution and activation of immunity to pathogens with the presence of other individuals, may reduce the strength of negative plant-soil feedback (PSF) (Chu et al. 2008; Pelissier et al. 2021; Wang et al. 2023). However, the degree to which these mechanisms contribute to the mitigation of negative PSF remains uncertain in environments marked by severe nutrient limitation.

Plant-plant interactions influence PSFs in a complex way. According to negative density dependence theory, more individuals of the same species would accumulate more plant pathogens that specifically target them (Bagchi et al. 2014; Jevon et al. 2022; Mommer et al. 2018), resulting in a stronger negative biological PSF (B-PSF - PSF mediated by soil biotic properties, negative B-PSF is mainly driven by plant pathogens) (Bever et al. 2012; Dominguez-Begines et al. 2021; Laliberté et al. 2015). However, the presence of other individuals, either intra or interspecific, are also able to weaken the negative B-PSF (Bezemer et al. 2018; Shannon et al. 2014), especially in infertile habitats (Chu et al. 2008; Pan et al. 2024; Raynaud and Leadley 2004; Zhang and Tielborger 2020; Zheng et al. 2024b). Although other individuals in a community may bring higher abundance of soil pathogens (Bell et al. 2006), immunity could be triggered in neighboring plants through the secretion of allelochemicals (Keesing et al. 2006; Mapuranga et al. 2023; Mundt 2002; Pelissier et al. 2021; Rimbaud et al. 2018; Xu and Ridout 2000). Moreover, nutrient limitation in infertile habitats and the consequent low abundance of soil pathogens, may constrain the efficacy of dilution effect in mitigating the negative PSF (Ebeling et al. 2022; Seabloom et al. 2010). In addition, the presence of other individuals could also curb the spread of specialized pathogens (also known as the dilution effect) (Maron et al. 2011; Mikaberidze et al. 2015; Wang et al. 2023), thereby lessening the negative B-PSF.

The presence of other plant individuals could intensify nutrient constraints on plant growth, thus potentially aggravating negative abiotic PSF (A-PSF, PSF changes related to soil nutrient or structure etc.), especially in infertile habitats.

When facing severe limitation, plants will develop acquisitive traits, such as greater specific root length (SRL) (Bolte and Villanueva 2006; Kalliokoski et al. 2010; Wei et al. 2024) improved nutrient use efficiency (Bessler et al. 2012; Duan et al. 2014; Nunes et al. 2025; Xia et al. 2020; Yu et al. 2017), or form symbionts with beneficial microorganisms like mycorrhizal fungi (Liang et al. 2021; Nunes et al. 2025; Paul and Lade 2014; Song and Zhou 2021; van der Heijden et al. 2015; Yu et al. 2021), which could counteract the negative B-PSF. Changing towards acquisitive traits would make plants more prone to pathogen infection therefore result in aggravation of negative PSF (Dai et al. 2023; Kramer-Walter et al. 2016; Xi et al. 2021). Nevertheless, the formation of symbionts would reduce the impact of pathogens, thus contributing to the facilitation (Borowicz 2001; Chagnon and Bradley 2015). Yet, how the presence of other plants changes the negative PSF, and which mechanisms contribute to the alleviation of negative PSF remains largely uncertain in infertile habitat. Therefore, we hypothesized that 1) in infertile habitats, the presence of other plant individuals would reduce the intensity of the negative PSF caused by pathogens, and 2) this reduction is mediated by both the pathogen dilution effect and the nutrient limitation-utilization pathway, with the latter having a more prominent influence.

To elucidate the relationship between PSF and plant–plant interactions in nutrient-poor habitats and to verify our hypotheses, two species that are common in infertile habitat in northwest China, *Kalidium foliatum* and

Reaumuria songarica, were tested to investigate the impact of plant-plant interactions on PSF. The two species always coexist in their natural habitat (Liu Xiaokai et al. 2009). Partitioning PSF into B-PSF and A-PSF (Guo et al. 2025) was carried out to reveal how changes in root functional traits, soil fungi functional groups abundance or their interactions contribute to the changes in PSF in the presence of intra or interspecific plant individuals.

Materials and methods

Field conditions for collection of soil and plant seeds

The soil and seeds were collected in the lower reaches of Shiyang river, Wuwei City, China (38°58'42''N-39°15'52''N, 103°35'34''E-103°36'54''E, c.a 1300 m in altitude). The vegetation in the study area is mainly composed of *K. foliatum* (*Chenopodiaceae*) and *R. songarica* (*Tamaricaceae*), which are halophytes, with the two species coexisting in their natural habitat. The average annual precipitation and temperature of the sampling sites from 1953 to 2021 were 110.1 mm and 8.6 ℃ respectively.

Soil and seed collection

In March 2021, soil (c.a. 350 kg) was collected from 0-30 cm depth in naturally bare land (no plants in a 3-diameter circle for more than 10 years) from the field station, sieved (<10 mm) and homogenized. The main soil properties were: sand 55%; silt 37%; clay 8%; pH 8.5; organic C 1.44 g/kg; total N 0.17 g/kg; total P 0.15 g/kg; available N 9.46 mg/kg and available phosphorus 16.74 mg/kg

(Table S1). Seeds of *R. songarica* and *K. foliatum* were hand collected from nearby the field station in November 2020. All the seeds were immersed in water, and the ones that floated were removed with mesh. Then the seeds were air-dried and stored at room temperature till the experiment. A pre-experiment showed the germination rate of both species was more than 95%.

Plant-soil feedback experiment

Plant soil feedback experiments were conducted in a greenhouse in the Arid Land Salinization Research Station, Northwest Institute of Eco-environment and Resources, Chinese Academy of Sciences (Altitude 1330 m, 39°2'38' N,103°36'35'' E). The PSF experiment included two stages: the conditioning and the feedback stage (Fig.1). The conditioning stage lasted for 16 weeks (March 21st to July 11th, 2021) and was conducted in 1.5-gallon (21.3 cm in diameter and 20 cm in height) pots. Soil in these pots were watered 10 days prior to the sowing of the seeds. Seeds were soaked in water for 48 hours in advance and disinfected with 1% sodium hypochlorite solution for 1 minute, then cleaned with distilled water and planted in the middle of the pots. In this phase, 20 of the larger *R. songarica* seeds and 30 seeds of *K. foliatum* were planted in monoculture, respectively. Forty pots were planted per species. Additionally, 50 pots with no plants were set as the control. After two weeks of emergence, excessive seedlings were removed, leaving 2 seedlings per pot with the same spacing. During the growth period, 300 ml tap water was provided when the surface soil was dry. After 16 weeks, the aboveground biomass was collected, and the taproots were pulled out to prevent the plants from regenerating. Rhizosphere soils of both species were collected to investigate the fungal communities. The soil conditioned by plants in all pots were mixed for each treatment, respectively. Then half of each soil was steam sterilized twice (121℃, 30 min.) and allowed to cool.

The feedback stage lasted 14 weeks (July 15 to October 21, 2021). Seeds of *K. foliatum* and *R. songarica* were planted both in conditioned and unconditioned soils with sterilized and unsterilized groups. The two species were then planted using single seeding (one individual per pot), double seeding (two individuals of the same species per pot), and mixed seeding (two plants per pot, one for each species) methods, respectively. Thus, there were four soil types, and three seeding methods (Fig. 1). Each treatment had five replicate pots. Plant management protocols were the same as for the conditioning phase. On October 21, the aboveground and belowground biomass were collected. The collected roots were used to measure specific root length (SRL), root mean diameter (RAD) and tissue density (RTD) (Spitzer et al. 2021; Zhou et al. 2018). Simultaneously, rhizosphere soil was collected and stored at -20°C before being transported to Biomarker Technologies Co，LTD (Beijing, China) on dry ice after one week. Subsequently, amplicon sequencing of soil fungi was performed using the Illumina platform.

Calculation of plant-soil feedback, biological plant-soil feedback, and abiotic plant-soil feedback values

The conspecific PSF was quantified as the difference between plant biomass in conditioned-unsterilized (M_{NS}) and unconditioned-unsterilized soils (M_{CKN}) (Eq.1).

$$PSF = (M_{NS} - M_{CKN}) / \overline{M_{CKN}} \quad (1)$$

Biological plant-soil feedbacks (B-PSF) represents the plant growth change resulting from alterations in rhizosphere microorganisms mediated by plants (Bennett and Klironomos 2019; Bever 1994; Teste et al. 2017), which is often quantified by soil sterilization. However, soil sterilization results in bias in the B-PSF. We have therefore improved the method of quantifying B-PSF and validated its reliability (Guo et al. 2025). The specific calculation formula is presented below (Box. S1 and Fig. S1):

$$B\text{-}PSF = [(2M_{NS} - M_{CKS}) / \overline{M_{CKN}} - (M_S - M_{CKS})/\overline{M_{CKS}}]/2 \quad (2)$$

Where M_{NS} and M_S were the biomass of plants in unsterilized and sterilized soil conditioned by conspecific plants, respectively; M_{CKS} was the biomass of plants in unconditioned sterilized soil; $\overline{M_{CKN}}$ and $\overline{M_{CKS}}$ was the average biomass in unconditioned unsterilized and unconditioned sterilized soils, respectively (Fig. 1).

Similarly, the improved formula for A-PSF is as follows(Box. S1 and Fig. S1) (Guo et al. 2025):

$$A\text{-}PSF = [(M_S - M_{CKS})/\overline{M_{CKS}} - (M_{CKS} - M_S)/\overline{M_{CKN}}]/2 \quad (3)$$

Measurements of specific root length, root average diameter and root tissue density

The collected lateral roots were excised from the taproot and all roots were rinsed with deionized water to eliminate soil particles. Subsequently, the roots were arranged and scanned for each pot (Canon LiDE 220, Tokyo, Japan). After scanning, the samples were dried at 75℃ for 48 h before being weighed. The scanned root images were analyzed for total root length, root diameter and volume of roots using WinRHIZO (Regent Instruments Inc., Quebec City, QC, Canada). Specific root length was calculated as the ratio of total root length to dry mass; root tissue density was determined by dividing root mass by root volume.

Measurements of soil and plant properties

The soil pH was measured by using a portable pH meter (PHBJ-260, 0.01 resolution). Soil organic carbon (SOC) content was measured by the potassium dichromate external heating method (Bao 2000). The total nitrogen (TN) and total phosphorus (TP) were determined by continuous flow analysis (AutoAnalyzer 3, sensitivity 0.001 AUFS; Bran & Luebbe, GmbH, Norderstedt, Germany). The soil available nitrogen (AN) and available phosphorus (AP) were determined by alkaline hydrolysis diffusion and molybdenum antimony colorimetry, respectively (Bao 2000). The N content of plants was determined using a vario EL cube (Elementar, Germany). The N consumption of each plant was calculated by multiplying it's N content by its biomass; then, the total N consumption (TNC) was determined by summing the N consumption values of all plants within each pot.

Soil fungi functional groups

The TIANamp Soil DNA Kit (Tiangen BiotECH Co., Beijing, China) was used to extract the soil DNA from 0.25 g of fresh soil according to the guidelines. The composition and diversity of fungal communities were measured using ITS genes high-throughput sequencing (Li et al. 2020). ITS was amplified with broad-spectrum primers it1f (5'-CTTGGTCATTTAGAGGAAGTAA-3') (Gardes and Bruns 1993) and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3'). According to the standard protocol, Illumina MiSeq 250bp paired-ends (biomker Technologies, Beijing, China) was used for amplicon sequencing. Raw reads were firstly filtered by Trimmomatic v0.33 Then the primer sequences were identified and removed by cutadapt 1.9.1, which finally generated high-quality reads without primer sequences. Based on overlapping sequences, high-quality reads were assembled by FLASH v1.2.7, which generated clean reads. Chimeric sequences were identified and removed by UCHIME v4.2 (Li et al. 2013), generating effective reads. USEARCH was used to cluster labels with 97% similarity to obtain Amplicon Sequence Variants (ASVs) (Edgar 2013). OTUs were then classified and labeled based on UNITE (fungi) databases (Nilsson et al. 2019). Functional annotation of soil fungi was conducted using the Funguild database (Nguyen et al. 2016).

Statistical analysis

First, data sets were tested for homogeneity of variances using *Levene's* test and for normality using the *Shapiro–Wilk* test. Secondly, a one-sample *t-test* was conducted to determine whether the total PSF, abiotic, and biotic PSFs were different from zero (SPSS 22.0). The independent sample *t-test* was used to determine the significance of differences in PSF, root functional traits, leaf nitrogen content, total nitrogen consumption (TNC) and fungal functional group abundance among different seeding methods (SPSS 22.0). ANOVA analysis was carried out for the nitrogen consumption of *K. foliatum* and *R. songarica* between conditioned and unconditioned soils, respectively. To demonstrate which plants were more susceptible to nutrient limitation in conditioned soils, we analyzed the leaf nitrogen content and TNC in both conditioned and unconditioned soils. The variation of PSF, A-PSF, B-PSF, root functional traits and fungal functional group abundance under different seeding methods was calculated. The delta values of each parameter were differences in Double and Mix seeding relative to the Single seeding. Subsequently, the correlation coefficients (Spearman) between PSFs, soil physio-chemical properties, root traits and microbial functional groups between Single seeding and the other two seeding methods were analyzed using SPSS 22.0. The effects of changes in fungal functional groups, TNC and root traits on A-PSF and B-PSF variation in the presence of intraspecific/interspecific plant individuals were analyzed by Backward Elimination analysis (The MASS package in R). All Figure 2-5 were generated using Origin 2021, while Figure 1 and 6were created using FigDraw.

Results

Changes in PSF with the presence of other plant individuals

The biomass of *K. foliatum* and *R. songarica* was significantly lower in self-conditioned soil compared to unconditioned soils (Fig. S2), showing a negative conspecific PSF (Fig. 2a). Double seeding slightly moved the conspecific PSF of *K. foliatum* towards negative (Fig. 2a), with the A-PSF unchanged but the B-PSF becoming significantly negative (Fig. 2b, 2c). Double seedling of *R. songarica* marginally lifted its negative PSF (Fig. 2a), with opposite changes in the A-PSF and B-PSF. The magnitude of increase in the B-PSF was three times higher than the decrease in the A-PSF (Fig. 2b, 2c).

When the two species were planted in a mixture, their conspecific negative PSF was greater than in Single seeding (Fig. 2, bars in Mix comparing with Single). The conspecific PSF of *R.songarica* with the presence of *K. foliatum* even became positive (Fig. 2a). In contrast to the PSF, the A-PSF was more negative in Mix seeding. B-PSF showed a larger increase than PSF (Fig. 2). The percentage of the A-PSF to total the PSF significantly increased in Mix seeding compared to the other seeding methods (Fig. S3).

The conspecific PSFs of *K. foliatum* and *R. songarica* decreased by 43% and increased by 16% under Double seeding relative to the Single seeding, respectively. Under Mix seeding, the conspecific PSF of *K. foliatum* and *R. songarica* with the presence of other species' individuals increased by 30% and 116% respectively. Both A-PSF and B-PSF changes were more pronounced in *R. songarica* (121% and 145%) compared to *K. foliatum* (66% and 30%) with the presence of interspecific plants individuals (Fig. 2).

Changes in specific root length, root average diameter and root tissue density

The specific root length of *K. foliatum* and *R. songarica* significantly increased by 33% and 39% in the Mix planting relative to the Single seeding (Figs. 3a, 3b). The specific root length only increased with Double seeding for *R. songarica* (Figs. 3a, b). The root average diameter reduced either in Double or Mix seeding for both species (Figs. 3c, d). The root tissue density of *K. foliatum* increased significantly in Double seeding (Fig. 3e). In contrast, the root tissue density of *R. songarica* decreased in Double and Mix seeding, with the smallest root tissue density in Double seeding (Fig. 3f).

Nitrogen consumption in conspecific conditioned or unconditioned soils

The N content of *K. foliatum* decreased in the Double seeding in either conditioned or unconditioned soils. It also significantly increased in Mix seeding compared with Single seeding in unconditioned soils (Fig. 4a). The N content of *R. songarica* significantly decreased with the presence of either intraspecific or interspecific plant individuals both in unconditioned and conditioned soils (Fig. 4c). The total N consumption of *K. foliatum* in each pot was significantly higher under Double seeding and Mix seeding compared to Single seeding in unconditioned soils, with Mix seeding showing the highest total N consumption (Fig. 4b). In conditioned soils, it was significantly higher in Double and Mix seeding than in Single seeding (Fig. 4b). Averaged across the three seeding methods, the total N consumption of *K. foliatum* was significantly higher in unconditioned soils than in conditioned soils (Table. S2). In either unconditioned or conditioned soils, the total N consumption of *R. songarica* was significantly higher in Mix seeding than in Single and Double seeding (Fig. 4d). In conditioned soils, it was greater in Double seeding than in Single seeding (Fig. 4d). Averaged across the three seeding methods, it was significantly higher in unconditioned soils than in conditioned soils (Table. S2).

Changes in relative abundances of AMF, EcMF, and plant pathogens in rhizosphere soil

The relative abundance of AMF in the rhizosphere soils of *K. foliatum* remained unchanged regardless of the seeding method (Fig. 5a), while the abundance of EcMF increased under Mix seeding relative to the Single seeding (Fig. 5b). The abundance of both AMF and EcMF in the rhizosphere soils of *R. songarica* were higher in Double and Mix seeding relative to the Single seeding (Figs. 5d, 5e). The relative abundance of plant pathogens was enhanced in Double compared to the Single seeding (Figs. 5 c, f). When two individuals were presented, the relative abundance of plant pathogens in Double Seeding was lower than in Mix seeding for both species (Figs. 5c, 5f). The rhizosphere soils of the two species shared over 60% of the ASVs of plant pathogens (Fig. S4).

Relationship between changes in conspecific PSF，root traits and relative abundance of functional microorganisms

The △PSF positively correlated with △B-PSF ($r=0.86$, $P<0.001$) and negatively with △A-PSF ($r=-0.78$, $P<0.001$) (Table 1). There is a negative correlation between the △Pathogens and △EcMF (Table 1). In Double seeding, the △A-PSF was predominantly explained by the △Total N consumption (△TNC), △

Root average diameter (△RAD) and △EcMF, accounting for 40%, 22% and 14% of the observed differences, respectively (Table 2); the △B-PSF was primarily influenced by the △TNC (R^2=0.20) and △EcMF (R^2=0.70). Neither changes plant pathogens nor root functional traits explained the variation in B-PSF at a high rate (Table. 2). In Mix seeding, △TNC accounted for 59% of the variation in A-PSF, while △AMF (R^2=0.11, P=0.059) and △Specific root length (△SRL, R^2=0.11, P=0.057) also contributed to the variability in A-PSF; △EcMF, △SRL, △TNC and △Pathogens explained 47%, 24%, 9% and 7% of the variation in B-PSF, respectively (Table 2).

Discussion

Changes in PSF and its relation to abiotic and biotic PSF

The decrease in the A-PSF with the presence of either intra or interspecific plant individuals (Fig. 2b) supports the previous findings that competition for nutrients would move the PSF toward a negative interaction (Bennett and Klironomos 2019; Lekberg et al. 2018). However the increase in the conspecific PSF for both species, except the Double seeding of *K. foliatum* (Fig. 2a) shows that plant-plant interaction actually facilitates plant growth with a low plant-density in harsh environment (Chu et al. 2008; Lekberg et al. 2018; Wright et al. 2014; Yu et al. 2021; Zhu et al. 2023). This provides partial support for our first hypothesis. Although the positive/negative correlations between △PSF and △B-PSF/△A-PSF (Table 1) indicate that both biotic and abiotic pathways affect PSF, the lower correlation coefficient with △A-PSF (Table. 1) and the relatively smaller opposite change in the A-PSF (Fig. 2) reveal that the reduction in negative B-PSF mainly contributes to the increase of PSF. The higher R^2 of fungal functional groups with △PSF in stepwise linear regression model (Table. 2) also implies the more important role of the B-PSF in determining the PSF changes with the presence of other plant individuals. The trend of synchronous aggravation of negative PSF and B-PSF with Double seeding of *K. foliatum* (Figs, 2a, c) further corroborates the importance of the B-PSF. This result provides additional support to our first hypothesis.

The variation in root functional traits may change the resistance and infection of roots to pathogens, therefore impacting the PSF in the presence of other plant individuals (Homulle et al. 2022; Kramer-Walter et al. 2016; Laliberté et al. 2015). The increase in specific root length and decrease in root average diameter (Fig. 3) in both Double and Mix seeding for both species demonstrated that the changes in root traits facing plant-plant interaction induced changes in nutrient demand. The corresponding increase in root tissue density of *K. foliatum* should improve its resistance to soil-borne plant pathogens and thus counteract the negative B-PSF in both the Double and Mix seeding. The increase in the negative conspecific B-PSF of *K. foliatum* in the Mix seeding seems to support the relationship between root tissue density and plant resistance of plant pathogens (Kramer-Walter et al. 2016). However, the conspecific B-PSF of *K. foliatum* in Double seeding is more negative (Fig. 2c), which implies a minor contribution of increased root tissue density in resisting the negative effects of more pathogens. Decreased root tissue density (Fig. 3c) and more pathogens (Fig. 5f) should result in a more negative conspecific B-PSF for *R. songarica* in the Double seeding but in fact it increased (Fig. 2), which further proves there is little contribution of root traits to the conspecific B-PSF with just one species, when facing nutrient limitation induced by plant-plant interactions. When pooling the data from the Double and Mix seeding together, the marginal effect of △Root tissue density (△RTD) on △B-PSF (Tables. 1 and 2) also indicate a its minor impact on the alleviation in B-PSF.

Changes in A-PSF and B-PSF and the mechanisms within intraspecific plant individuals

The presence of individuals of the same species (Double seeding) depresses the growth of *K. foliatum* (Figs. 2a, c). More plant individuals bring about more plant pathogens (Bagchi et al. 2014; Jevon et al. 2022; Mommer et al. 2018). But pathogen damage to host plants will be diluted because of limited spread of pathogen in high-density community of fertile habitat (Liu et al. 2020; Mugabo et al. 2015; Thakur et al. 2021). In our study, the increase of relative abundance of plant pathogens in the rhizosphere of both species (Figs. 5c, f) suggests that the dilution effect may not be substantial in the Double seeding, which provides partial support for our second hypothesis. The increased relative abundance of plant pathogens in the rhizosphere of *R. songarica* (Fig. 5f) but no aggravation of its negative B-PSF (Fig. 2c) implies other mechanisms are regulating the alleviation of negative B-PSF in the Double seeding. More plant individuals could exacerbate the N limitation, evidenced by the reduction in N content of the plant tissues for both species in this study (Figs. 4a, c). Beside the adjustments in nutrient acquisition capacity and use efficiency to nutrient limitation, plants will also 1) develop symbiosis with EcM and AM and/or 2) reduce their nutrient demand to survive (Kitagawa et al. 2022; Zhu et al. 2020). More EcMF and AMF are conducive in improving the nutrient uptake as well as inhibiting the negative impact of plant pathogens, therefore, alleviating the negative PSF (Bennett et al. 2017; Chen et al. 2019; Kadowaki et al. 2018; Song and Zhou 2021; Tedersoo and Bahram 2019). In our study, when facing intensified nutrient limitation under Double seeding, *R. songarica* appeared to recruited more EcMF and AMF (Figs. 5d, e), which may help to improve plant nutrient uptake and potentially enhance resistance to pathogens, which could in turn contribute to the decrease in negative PSF (Fig. 2). In contrast, *K. foliatum* reduced its nutrient demand as evidenced by reduction in tissue N content (Figs, 4a) and did not recruit more beneficially microorganisms, resulting in a further increasing in the negative B-PSF, given the higher pathogens abundance. The contrast changes in beneficial fungi (Figs. 5 a, b, d, e) and the B-PSF (Fig. 2c) of the two species indicate the importance of beneficial fungi in the facilitation among plants when same species' individuals are presented (Fig. 6), which further support for our second hypothesis.

Changes in A-PSF and B-PSF and the mechanisms within interspecific plant individuals

The greater increase in total N consumption in the Mix seeding compared to Double seeding (Figs. 4b, d) indicates more severe competition for nutrients with individuals of the opposite species. This is also supported by the greater reduction of the A-PSF in Mix seeding compared with Double seeding (Fig. 2b). Faced with increased nutrient limitations, both plant species enhanced their specific root length and the abundance of rhizosphere mycorrhizal fungi to better adapt to nutrient limitation (Fig. 3 and 5). The increases in specific root length and rhizosphere mycorrhizal fungi abundance were more pronounced for *R. songarica* (Figs. 3b, 5d and 5e). More beneficial microorganisms could also antagonize the negative impact of pathogens (Laliberté et al. 2015; Tedersoo and Bahram 2019; Zheng et al. 2024a), thereby resulting in a larger magnitude of increase in the conspecific B-PSF of *R. songarica* (Fig. 2a). In addition, *K. foliatum* allocation of resources towards for defense (increase root tissue density, Fig. 3e) also could result in a weaker reduction in negative PSF. Notably, the increase in the conspecific B-PSF of *R. songarica's* was smaller than *K. foliatum's* (Fig. 2c) in the Mix seeding, which indicates that other mechanisms also contribute to the lift of negative B-PSF with the presence of interspecific species. Compared with the intraspecific interactions, interspecific plant individuals are more prone to bringing about the dilution effect because of the specificity of pathogens (Keesing and Ostfeld 2021; Liu et al. 2020; Vadell et al. 2020). The non-significant reduction in plant pathogens in the rhizosphere of both species in Mix seeding in contrast to the increase in Double seeding

(Figs. 5 c, f), and 35% difference in the ASVs of pathogens in the rhizosphere of the two species (Fig. S4) support a possible dilution effect under Mix seeding (Fig. 6). These results support the second hypothesis.

Conclusion

Low densities of plant individuals from harsh environments tend to facilitate each other, especially with the presence of individuals of a different species but not for resource-conservative individuals of the same species. Although the existence of other plant individuals resulted in intensified nutrient demand and aggravated the A-PSF, the increase in the B-PSF contributed to the overall increase of the PSF. Morphological changes in root traits are adjustments to the intensified nutrient limitation, but do not explain the changes in the PSF. With the intraspecific interactions, the improvement in beneficial fungi is mainly responsible for the alleviation of negative the conspecific B-PSF, whereas both the dilution of pathogens and the increase in the relative abundance of beneficial fungi could result in the lift of B-PSF when interspecific individuals are present. Our results elucidate how low-density plant interactions influence the performance of the PSF in infertile habitats. Future research should aim to identify the dynamic equations that describe how plant interactions modulate the PSF as plant density and environmental stress increase. Additionally, it is essential to assess how global change factors, such as climate warming and nitrogen deposition, affect this relationship to enhance our ability to predict the dynamics and successional trajectories of plant communities under future environmental conditions.

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Statements & Declarations

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All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Pinglin, Guo. The first draft of the manuscript was written by Pinglin, Guo and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. The datasets generated during and analysed during the current study are available from the corresponding author on reasonable request.