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Research Article

Shift in the effects of invasive soil legacy on subsequent native and invasive trees driven by nitrogen deposition

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Abstract

Invasive plants can interact with soil microbes to enhance their own performance. Such interactive effects may persist and later affect plant performance and their population dynamics. Such 'invasive soil legacy' is the specific plant–soil feedback that can affect future invasions, while it is not clear how nitrogen deposition and interspecific competition influence invasive soil legacy. Thus, we collected field soil and conducted a greenhouse experiment to investigate the effects of soil legacy of the invasive tree *Rhus typhina* on the performance, functional traits and soil microbial communities of *R. typhina* and the native tree *Ailanthus altissima* under three nitrogen levels with and without interspecific competition. The experiment revealed that the outcomes of invasive soil legacies were context-specific and depended on local soil nutrient levels and species competition. Specifically, nitrogen addition changed the negative conspecific soil legacy on subsequent *R. typhina* to a positive effect, while it became negative in *A. altissima*. The invasive soil legacy promoted the transpirational rate of *R. typhina* and *A. altissima* in monoculture, but inhibited it in a mixture under nitrogen deposition. Nitrogen deposition reduced bacteria and fungi biomass of *A. altissima* in monocultures and mixtures. In contrast, nitrogen deposition decreased bacterial and fungal biomass of *R. typhina* in monocultures, but enhanced them in mixtures. Therefore, changes in plant growth, transpiration rate and soil microbial biomass might contribute to the different responses of invasive and native plants to invasive soil legacies. Nitrogen deposition and interspecific competition promote the viability of invasive plants from plant–soil feedback and indicate that ranges of subsequent plants might further expand through below-ground process under nitrogen deposition in the future.

Key words: Functional traits, interspecific competition, nitrogen deposition, plant–soil feedback, soil microbes

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Introduction

Feedback interactions between plants and soil microbes have been shown to influence both plant and soil community composition (Van Breemen and Finzi 1998; Bever 2003; Semchenko et al. 2022). By interacting with soil microbes, invasive plants are able to promote their establishment and growth (van der Putten et al. 2007; Tian et al. 2021; Xu et al. 2024). Furthermore, microbes involved in these interactions may persist in the soil even after the removal of invasive plants and this phenomenon is called 'soil legacy' (Crawford and Hawkes 2020). Soil legacies of invasive plants determine their further success and re-establishment of native plants and, thus, influence the population dynamics of the invaded community (Gioria and Pyšek 2016; Heinen et al. 2020; Chen et al. 2024). Positive soil legacies that benefit invasive plants or are more advantageous to them than to native plants, could exacerbate the spread of invasives, thereby threatening the biodiversity of native habitats. If the soil legacy of invasive plants has positive effects on invasive plants or more positive ones on invasive than native plants, the expansion of the invasives would be enhanced (Ahmad et al. 2021). However, mechanisms underlying the differences in soil legacy effects of invasive plants on themselves versus native plants are still unclear (Chen et al. 2021).

Plant can adjust their functional traits to increase absorption of light and nutrients in response to the soil legacy of invasive plants (Hannula et al. 2021; Xu et al. 2021). For example, plants can increase their chlorophyll content, specific leaf area (SLA) and photosynthetic rate or increase allocation to roots to enhance the absorption of soil nutrients (Hannula et al. 2021). Plants can secrete root exudates that enrich soil microbial communities, potentially aiding the decomposition of allelochemicals released by invasive plants into the soil (Xu et al. 2022), while others manipulate soil microbes that increase soil nutrient concentrations (Jongen et al. 2021). However, the varying responses of invasive and native plants to invasive soil legacies, as mediated by their functional traits and soil microbes, remain inadequately studied.

Invasive plants, soil microbes and interactions between them are affected by environmental factors (Enders et al. 2020). Given widespread nitrogen fertilisation and atmospheric nitrogen deposition, soil nitrogen is gradually increasing and can affect conspecific relationships and the success of plant invasion (Li et al. 2022). Thus, the response of invasive and native plants to invasive soil legacies might be nitrogen-dependent (Chen et al. 2021). Nitrogen deposition can promote the chlorophyll content and photosynthetic rate of invasive plants (Liu et al. 2017; Valliere et al. 2017), perhaps enabling them to release more resources for use by soil microbes, which might contribute to the acclimatisation of subsequent plants to the soil legacy. Recent studies, however, found that nitrogen deposition inhibits the soil microbes and weakens the relationships between host plants and soil microbes (Xu et al. 2021). Still, whether nitrogen deposition can promote or inhibit the responses of subsequent plants to the soil legacies of invasive plants remains unclear.

The response of subsequent plants to soil legacy by invasive plants via trait plasticity and manipulation of soil microbes, might also be influenced by biotic factors, such as competition with native plants species when a target plant competes for soil water and nutrients and for light with its neighbours (Robakowski et al. 2018). This could inhibit or even offset the response of subsequent plants to a soil legacy (Crawford and Knight 2017). Neighbouring plants might affect a target plant's capacity to interact with soil microbes and adjust to soil legacies through their own root exudates (Huang et al. 2021). The interspecific competition could change the responses of invasive and native plants to soil legacy and, in turn, change the competitive advantage (Buerdsell et al. 2021). Nitrogen addition can alleviate the interspecific competition between neighbouring and target plants, thus providing more resources for subsequent plants to adapt to invasive soil legacies. Yet it is not known whether the impact of increased nitrogen on the responses of subsequent plants to the invasive soil legacies differs depending on interspecific competition.

Here, we explore the effects of simulated nitrogen deposition on the soil legacy of the invasive tree *Rhus typhina* on other individuals of the same species and on the native tree *Ailanthus altissima*. *Rhus typhina* is native to North America and recently invasive in north China where it has expanded into native communities displacing species due to altering composition and structure of the native soil microbial communities (Zhu et al. 2020). *Ailanthus altissima*, native to north China, is generally used for vegetation restoration, while its habitats are encroached by *R. typhina*. Our recent study found that *R. typhina* can generate a soil legacy that reduces the growth of *A. altissima* by both changing soil microbes and releasing allelopathic compounds via root exudates (Xu et al. 2021). We conducted a greenhouse experiment to explore the response of plant performance (represented by total biomass), functional traits, soil properties and soil microbes of invasive *R. typhina* and native *A. altissima* to test invasive soil legacy of *R. typhina* under three nitrogen levels in monoculture or interspecific mixture. This research addresses two topics:

1. Does nitrogen addition change the responses of subsequent *R. typhina* and *A. altissima* to the soil legacy of the invasive plant? – We hypothesised that nitrogen deposition promotes the positive effects of *R. typhina*'s soil legacy on its conspecific plant, but intensifies its negative effects on *A. altissima*.
2. Is the effect of nitrogen addition on the soil legacy of *R. typhina* the same with interspecific competition compared to a monoculture? – We hypothesised that interspecific competition changes the effects of nitrogen deposition on invasive soil legacy on *R. typhina* and *A. altissima*.

Materials and methods

Soil collection and plant material

We collected the soil in the Zhenshan Mountains, Shandong Province, China (37°31'28"N, 121°21'8"E). In these places, *R. typhina* was introduced and has expanded for more than 30 years. The density of invasive *R. typhina* was almost 20 stems per m^2 and with just a scattered few shrubs and herbs present in the invaded sites. We collected soil at five randomly-selected sampling sites of *R. typhina* > 50 m apart. At each sampling site, a 10 m × 10 m plot was established and samples were taken from the corners and from the centre. We collected almost 10 kg soil from the top 5–30 cm of soil by alcohol-sterilised shovels. The five soil samples were combined to create a single composite sample for each plot. Control soil samples were collected from a native community about 100 m away from the invasive sites at similar elevation to minimise variation in abiotic soil factors (Huangfu et al. 2019). There were no visible signs of *R. typhina* presence in the native sampling sites. Thus, we obtained two kinds of soil samples, one had a soil legacy of the invasive species ('invasive soil legacy') and the other one had a soil legacy of the native species ('native soil legacy'). The soil samples were sieved < 2.5 mm to remove stones and litter and stored in a low temperature soil storage cabinet at 4 °C.

The seeds of *R. typhina* and *A. altissima* were bought from the Dacheng Seed Company (Suqian, China), which had collected the seeds in Shandong Province. The seeds of the two species were collected from 6–10 years old trees in more than three mountains and the seeds were mixed before planting. Then, 1 kg seeds per species were disinfected with 3% hydrogen peroxide (H_2O_2) for 10 min, rinsed with demineralised water and planted in peat substrate sterilised by steam of 121 °C for 30 min. In April 2020, seeds were planted in small plastic pots (5 cm diameter, 10 cm height) in a greenhouse (Fig. 1), with one seed per pot buried at a depth of 1 cm.

Experimental design

The invasive or native soil collected from the field was mixed with sterilised soil (2.7 kg of peat substrate and 3.7 kg soil from the Shandong University Garden, which was sieved (2.5 mm) to remove coarse litter and stones and then sterilised (121 °C, 30 min) with a field-soil mass ratio of 8%, to reduce the bias from differential soil abiotic properties (Crawford and Hawkes 2020). The soil nitrogen concentration of the mixed soil was 50 mg N kg^{-1}. The mixture was filled into large plastic pots (32 cm diameter and 28 cm height). After 15 days, the seedlings were transplanted into large plastics pots. The seedlings of the two species were

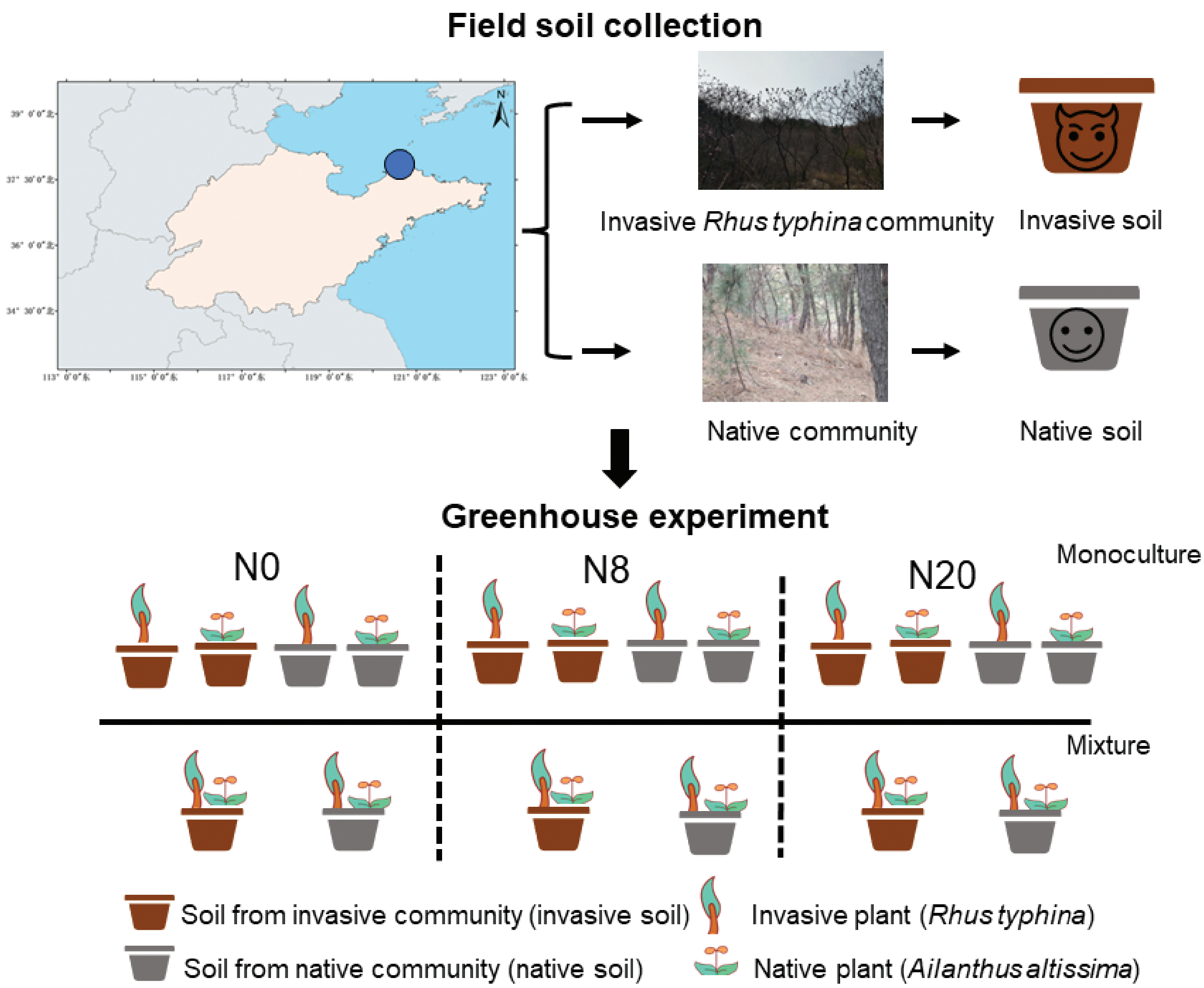

Figure 1. Experimental design to explore effects soil legacy and nitrogen on *Rhus typhina* and *Ailanthus altissima* in monoculture and mixture. The experiment had two parts: one was a field soil collection and the other one a greenhouse experiment. The soil samples were collected in Zhenshan Mountains, Shandong Province, China (37°31'28"N, 121°21'8"E). The two soil samples included one where invasive *R. typhina* had grown and the other without this species. The brown pots represented the soil inoculated soil from *R. typhina* community. The grey pots represented the soil inoculated soil from *R. typhina* community. N0: no nitrogen addition; N8: moderate nitrogen addition (8 N m^{-2} $year^{-1}$); and N20: high nitrogen addition (20 N m^{-2} $year^{-1}$).

randomly allocated to the pots with invasive or native soil, using one seedling per pot ('monoculture treatment'). Conversely, one seedling of *R. typhina* and one *A. altissima* were planted in the same pot type with invasive or native soil as interspecific pair ('mixture treatment'). In the monoculture, the seedlings were placed centrally within the pot, whereas in the mixture, one seedling of each species was planted at two equidistant points along the pot's diameter. To avoid the effects of plant density upon soil legacy, we explored the soil legacy of the native community or the invasive *R. typhina* on itself and on native *A. altissima* in monoculture and mixture separately. Seedlings that died within 15 days after transplantation were substituted with seedlings of the same age.

To explore how simulated nitrogen deposition affects soil legacy, three fertilisation treatments were applied: N0 (control), N8 (8 g N m^{-2} $year^{-1}$) and N20 (20 g N m^{-2} $year^{-1}$) to either soil legacy treatment (invasive or native) in each monoculture or mixture treatment condition (Fig. 1). The N8 (moderate nitrogen addition level) is the current average nitrogen atmospheric deposition rate for northern China and N20 (high nitrogen level) is the average nitrogen deposition predicted for the region in the coming decades (Luo et al. 2014). As the experiment lasted less than a year, the amount of nitrogen was equivalent to 70% of the annual nitrogen deposition (including N8 and N20) (Luo et al. 2016; Xu et al. 2021). Each nitrogen addition was achieved by adding an ammonium nitrate (NH_4NO_3) solution (0, 0.085 g, 0.213 g NH_4NO_3 dissolved in 100 ml distilled H_2O for the N0, N8 or N20 treatments, respectively) once a week, for a total of 10 times. Nitrogen addition began 1 month after transplanting the seedlings into large plastic pots. Once transplanted, the seedlings were provided with demineralised water every 2 days to keep the soil moist. Each treatment had six replicates ('pots'). There were two soil legacies (invasive or native soil legacy) × two plant species (*R. typhina* and *A. altissima*) × three nitrogen addition levels (N0, N8 or N20) × six replicates in each monoculture or mixture treatment condition (Fig. 1). The experiment was carried out in a greenhouse with daily mean temperature of 30 °C and air humidity maintained at about 85% by a ventilating fan throughout the experimental period lasting 28 weeks, from April to harvesting at the end of October.

Measurements of functional traits, soil properties and soil microbes

We measured functional plant traits, including total biomass, height, crown area, net photosynthetic rate (A_{net}), transpiration rate (E), total chlorophyll, leaf nitrogen and leaf phosphorus. We measured soil properties, including soil nitrogen and soil phosphorus. We measured gram–positive bacteria, gram–negative bacteria and fungi; total bacteria to fungi ratio following phosphorus lipid fatty acid analysis (PLFA; cf. Suppl. material 1).

Statistical analysis

To calculate the invasive soil legacy, we used a metric for the latter, as follows:

$$\text{Invasive soil legacy index} = \ln\,[(\text{total biomass}_{\text{invasive soil}})/(\text{total biomass}_{\text{native soil}})\}$$

The total $\text{biomass}_{\text{invasive}}$ was the total biomass of target with invasive soil legacy and total $\text{biomass}_{\text{native}}$ was that with native soil legacy. If the metric had a positive value, it implied the invasive soil legacy promoted plant performance and vice versa.

To assess the effect of the invasive soil legacy on the functional traits, soil properties and microbial biomass, we calculated the response index in monoculture and mixture of *R. typhina* and *A. altissima*, as follows:

$$\text{Response index} = \ln\left[(X_{\text{invasive soil}})/(X_{\text{native soil}})\right]$$

The $X_{\text{invasive soil}}$ was the functional traits, soil properties and soil microbes of native vs. invasive soil legacy and total $\text{biomass}_{\text{native}}$ was the one with native soil legacy. If the response index was > 0, it meant that the invasive soil legacy promoted this parameter and vice versa.

We used one-way ANOVA to assess the effect of nitrogen addition on the invasive soil legacy index and response index of *R. typhina* or *A. altissima* in monoculture and mixture. Post-hoc testing (Tukey HSD test) was used to compare the pairwise differences in invasive soil legacy index and response index amongst three nitrogen addition treatments of *R. typhina* and *A. altissima* in monoculture and mixture. The data were tested for normality and homogeneity of variance before fitting the ANOVAs. Missing values were ignored by the "*na.rm*" function. All statistical analyses were implemented in R v.4.1.2 software (R Core Team 2022).

Results

Nitrogen addition enhanced invasive soil legacy on *Rhus typhina*, but reduced its effects on *A. altissima* in monoculture

Nitrogen addition modulated the invasive soil legacy effect on both *R. typhina* ($F = 11.6$, $P < 0.001$) and *A. altissima* in monoculture ($F = 23.0$, $P < 0.001$; Fig. 2a). The invasive soil legacy index of *R. typhina* was lower in N8 than in the N0 treatment, while it was higher in the N20 treatment. The invasive soil legacy index of *A. altissima* in the N8 and N20 treatment were 421% and 215% lower than in the N0 treatment, respectively.

Nitrogen addition had negative effects on height, crown area, specific leaf area and leaf nitrogen, but positive effects on photosynthesis rate and transpiration rate of *R. typhina* to invasive soil legacy (all $P < 0.003$; Fig. 3a). Nitrogen addition had negative effects on the response index of height and crown area, but positive effects on the transpiration rate, total chlorophyll and leaf nitrogen of *A. altissima* to invasive soil legacy (all $P < 0.001$; Fig. 3b). Besides, nitrogen addition had negative effects on the response index of gram-positive bacteria, bacteria, fungi, bacteria to fungi ratio, but positive effects on soil nitrogen and soil phosphorus of *R. typhina* to invasive soil legacy (all $P < 0.036$; Fig. 3a). Nitrogen addition had negative effects on the response index of soil nitrogen, gram–positive and gram–negative bacteria, fungi and bacteria–fungi ratio, but positive effects on soil phosphorus of *A. altissima* to invasive soil legacy (all $P < 0.036$; Fig. 3a). The detailed response index of functional traits, soil properties and soil microbes of *R. typhina* and *A. altissima* in monoculture under three nitrogen deposition levels is shown in the Suppl. material 1.

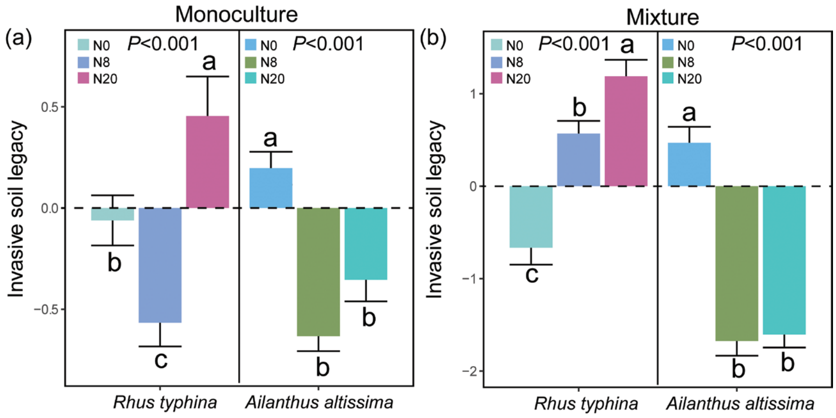

Figure 2. Invasive soil legacy index (mean ± SE) of *Rhus typhina* and *Ailanthus altissima* under three nitrogen addition levels in a monoculture (**a**) and mixture (**b**). Differing lowercase letters indicate significant differences according to post-hoc Tukey's HSD test. The *P* values represented the result of one-way ANOVA of nitrogen deposition on invasive soil legacy index of invasive *R. typhina* and native *A. altissima*. N0: no nitrogen addition; N8: moderate nitrogen addition (8 N m^{-2} year^{-1}); and N20: high nitrogen addition (20 N m^{-2} year^{-1}). The colours of the bars represent the nitrogen addition treatments of *R. typhina* and *A. altissima*.

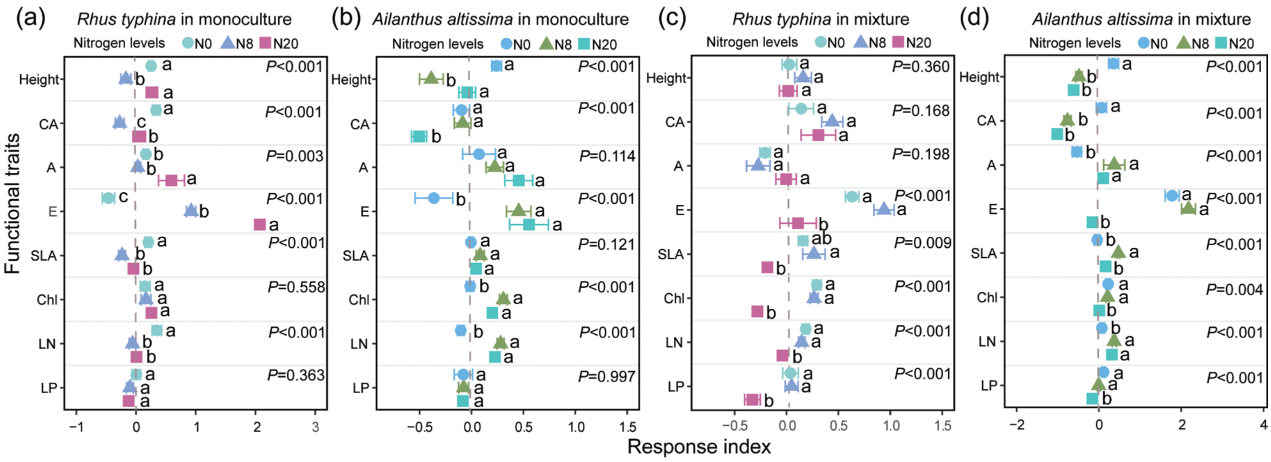

Figure 3. Response index (mean ± SE) of functional traits of *Rhus typhina* in monoculture (**a**) and mixture (**b**) and *Ailanthus altissima* in monoculture (**b**) and mixture (**d**) under three nitrogen addition levels. Differing lowercase letters indicated significant differences according to post-hoc Tukey's HSD test. P values represented the result of one-way ANOVA of nitrogen deposition on invasive soil legacy index of invasive *R. typhina* and native *A. altissima*. CA: crown area; A: photosynthetic rate; E: transpiration rate; SLA: specific leaf area; Chl: total chlorophyll; LN: leaf nitrogen; and LP: leaf phosphorus. N0: no nitrogen addition; N8: moderate nitrogen addition (8 N m^{-2} year^{-1}); and N20: high nitrogen addition (20 N m^{-2} year^{-1}). The colours of the bars represent the nitrogen addition treatments of *R. typhina* and *A. altissima*.

Nitrogen addition shifted the response of *R. typhina* and *A. altissima* to invasive soil legacy in mixture

Nitrogen addition changed the invasive soil legacy effect on both *R. typhina* (F = 31.6, $P < 0.001$) and *A. altissima* in mixture (F = 59.0, $P < 0.001$; Fig. 2a). The invasive soil legacy index of *R. typhina* in N8 and N20 treatment were 186% and 279% higher than in N0, respectively, while the index of *A. altissima* in N8 and N20 treatment was 186% and 279% lower than in N0, respectively.

Nitrogen addition had negative effects on the response index of transpiration, specific leaf area, total chlorophyll, leaf nitrogen and phosphorus of *R. typhina* to invasive soil legacy (all $P < 0.009$; Fig. 3c). Nitrogen addition had negative effects on the response index of height, crown area, transpiration, total chlorophyll and leaf phosphorus, but positive effects on the photosynthetic rate, specific leaf area and leaf nitrogen of *A. altissima* to invasive soil legacy (all $P < 0.004$; Fig. 3d). Moreover, nitrogen addition had positive effects on the response index of soil nitrogen and phosphorus, gram-positive and gram-negative bacteria and fungi of *R. typhina* (all $P < 0.011$; Fig. 4c). Moreover, nitrogen addition had positive effects on the response index of soil phosphorus, but negative effects on soil nitrogen, gram-positive and gram-negative bacteria and fungi of *A. altissima* (all $P < 0.005$; Fig. 4d). The detailed response index of functional traits, soil properties and soil microbes of *R. typhina* and *A. altissima* in a mixture under three nitrogen deposition levels is showed in the Suppl. material 1.

Discussion

Nitrogen deposition changes the negative effects of invasive soil legacy on invasive *R. typhina* into positive effects

Our study confirmed that nitrogen addition altered the effects of the invasive soil legacy of *R. typhina* on subsequent generations of the same species, which supports hypothesis 1. Specifically, although the soil legacy of invasive *R. typhina* was negative towards itself without extra nitrogen, nitrogen deposition reversed this effect. Without extra nitrogen, negative effects of the invasive soil legacy on subsequent invasive plants might be due to the fact that invasive plants could accumulate pathogenic microbes in the rhizosphere during long-term field colonisation and generate negative plant–soil feedback (Flory et al. 2013; Stricker et al. 2016; Goss et al. 2020). Under nitrogen deposition, invasive plants might absorb more nutrients (Fig. 4), which could promote rapid growth (Valliere et al. 2017). Besides, nitrogen deposition promoted carbon assimilation (Fig. 3), which could increase the resistance of invasive plants to

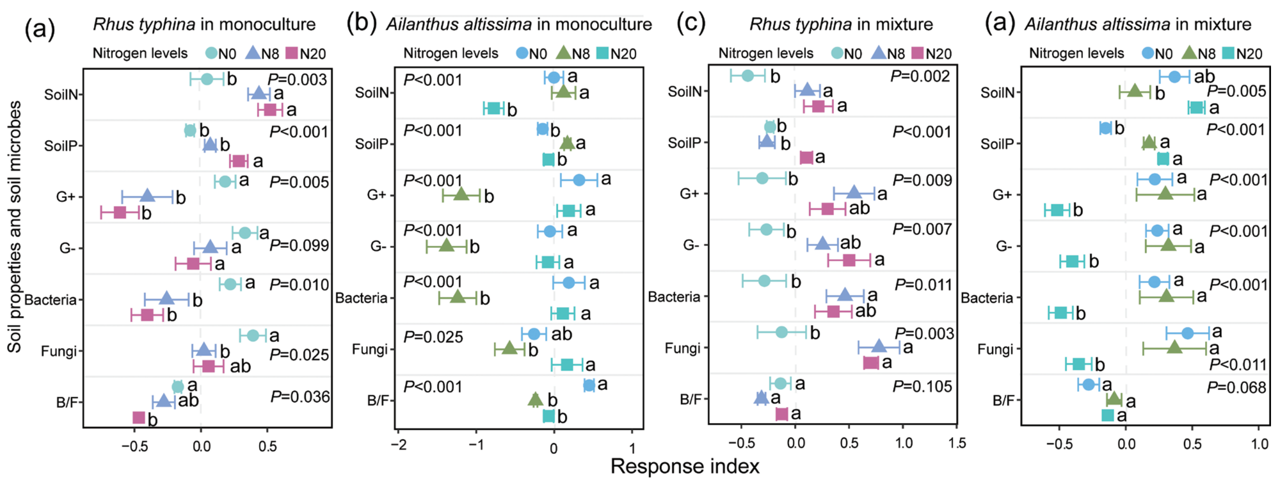

Figure 4. Response index (mean ± SE) of soil properties and microbes of *Rhus typhina* in monoculture (**a**) and mixture (**b**) and *Ailanthus altissima* in monoculture (**b**) and mixture (**d**) under three nitrogen addition levels. Differing lowercase letters indicated significant differences according to post-hoc Tukey's HSD test. P values represented the result of one-way ANOVA of nitrogen deposition on invasive soil legacy index of invasive *R. typhina* and native *A. altissima*. SN: soil nitrogen; SP: soil phosphorus; G+: gram-positive bacteria; G-: gram-negative bacteria; and B/F: bacteria to fungi ratio. N0: no nitrogen addition; N8: moderate nitrogen addition (8 N m^{-2} $year^{-1}$); and N20: high nitrogen addition (20 N m^{-2} $year^{-1}$). The bar colours represent the nitrogen addition treatments of *R. typhina* and *A. altissima*.

pathogens with more resource reserve (Cappelli et al. 2020). Moreover, the nitrogen addition promoted the transpiration rate of *R. typhina* under the invasive soil legacy, which should promote nutrient uptake by the increases of transpirational pull (Wu et al. 2019). This is consistent with seedlings of the invasive *Prunus serotina* (Black cherry) having negative soil legacy effects on low-fertile soil, but positive effects on high-fertile soil (McCarthy-Neumann and Kobe 2019). Therefore, the soil nitrogen should be given special attention in the invasive range of *R. typhina* and disrupting microbial communities and artificial defoliation might be potential ways to control the invasive plants, especially in areas with high soil nitrogen.

Nitrogen deposition changes the positive effects of invasive soil legacy on native *A. altissima* into negative effects

The soil legacy of invasive *R. typhina* had a positive impact on native *A. altissima* without additional nitrogen, yet nitrogen addition resulted in a negative outcome (Fig. 2), also supporting hypothesis 1. The contrasting effects of nitrogen deposition on invasive and native plants indicated that natives might have a different response to invasive soil legacy. Without nitrogen deposition, invasive *R. typhina* had positive effects on the native *A. altissima*, which was consistent with the results that invasive *Eragrostis lehmanniana* (Lehman lovegrass) had positive plant–soil feedbacks on the growth of *Bouteloua gracilis* (Mosquito grass), but remains the superior competitor (Buerdsell et al. 2021). With nitrogen addition, the abundance of gram-positive and gram-negative bacteria associated with *A. altissima* under invasive soil legacy was reduced compared to soil from native communities (Fig. 4), possibly attributable to the absence of a shared evolutionary history between native plants and invasive soils (Fitzpatrick et al. 2017). Bacteria play a role in degrading allelochemicals produced by invasive species (Xu et al. 2021) and reductions of bacteria might explain the negative soil legacy of invasive plants on native plants with extra nitrogen addition. Besides, the invasive soil legacy of *R. typhina* decreased the height and crown area of subsequent native *A. altissima*, which will reduce carbon assimilation.

Interspecific competition changes the effects of invasive soil legacy on invasive *R. typhina* under moderate nitrogen deposition

Invasive soil legacy was negative on the invasive *R. typhina* in monoculture, but positive in a mixture under moderate nitrogen deposition (N8), which indicated invasive soil legacy is affected not only by abiotic factors, but also certain biotic factors, such as interspecific competition (Huangfu et al. 2019), supporting hypothesis 2. It might be due to the fact that, with nitrogen deposition, neighbouring plants can release more root exudates to promote target plants to enrich bacteria and fungi (Bais et al. 2004; Zhang et al. 2022), which might assist the invasive target plant to absorb nutrients and defend pathogen microbes (Yu et al. 2022). This was consistent with our results that bacteria and fungi of *R. typhina* with a soil legacy of invasive plants increased in monoculture, but decreased in mixture with moderate nitrogen. The study of Xu et al. (2021) also showed root exudates released by native *A. altissima* into soil can promote invasive *R. typhina* to manipulate soil microbes.

Conclusion

Invasive soil legacy is a specific plant–soil feedback that can affect re-establishment and management of ecosystems invaded by introduced plants. Our research indicates that nitrogen deposition can shift the direction of soil legacy effects and plant–soil feedback on subsequent invasive vs. native plants, a potential mechanism by which nitrogen deposition disproportionately benefits invasive species. Nitrogen deposition turns the effects of conspecific soil legacy on invasive plants from negative to positive, which might be due to nitrogen deposition promoting growth and transpiration of invasive plants. However, the effects of soil legacy of invasive plants upon native plants shift from positive to negative following nitrogen addition, which might be due to nitrogen inhibiting the response of growth and crown expansion of native plants to invasive soil legacies. Interspecific competition intensifies the effects of nitrogen on the outcome of soil legacy of invasive plants by increasing the biomass of bacterial and fungal community. Overall, our study highlights the critical roles of nitrogen and competition in plant–soil feedback processes, with implications for the restoration of habitats compromised by invasive species.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Z.W. Xu, X. Guo and W.H. Guo conceived the study; Z.W. Xu, Y. Hu and J.F Wang performed the greenhouse experiments and Z.W. Xu carried out the data analysis. Z.W. Xu, M.Y. Li and X. Guo wrote the initial manuscript. H. Skálová and Z.W. Xu edited the manuscript. All authors commented on drafts of the manuscript and approved the final version.

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Data availability

Data are not currently provided; upon acceptance, all data will be provided in Figshare: https://doi.org/10.6084/m9.figshare.21293373.

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Supplementary material 1

Supplement of methods of results

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Data type: docx

Explanation note: The supplement includes the measurements and results of functional traits and soil properties.

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