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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Mixed evidence for plant–soil feedbacks in forest invasions

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Abstract
Plant–soil feedbacks (PSFs) are plant-mediated changes to soil properties that ultimately influence plant performance, and can, thus, determine plant diversity, succession, and invasion. We hypothesized that PSFs influence invasion processes and that PSF mechanisms are largely driven by changes in soil properties produced by specific plant species. To test these hypotheses, we studied the effects of different soils collected from under common plant species on the growth of the invasive plant *Phytolacca americana*. We found that PSFs may interfere with invasion resistance because *P. americana* seedlings showed reduced growth (lower biomass) in soils collected from underneath some native species compared with soils collected from underneath *P. americana* and two non-native plants. We then selected eight co-occurring native and non-native plant species, and examined PSF dynamics and mechanisms in a pairwise conditioned soil greenhouse experiment. Plant species-specific conditioning effects regarding soil nutrients and enzyme activities were observed. *Phytolacca americana* had a high ability to use soil N, which may be related to its high invasion ability. Soil P was significantly lower in *Quercus acutissima*-conditioned soil, indicating that low *P* availability in *Q. acutissima* forests may enhance resistance to plant invasion. However, surprisingly, some native plants did not produce PSF effects that decreased the relative performance of invasive plants, nor did the invasive plants produce PSF effects that increased their own performance. We speculate that these PSF findings from greenhouse experiments cannot be extrapolated to field conditions because the litter and allelochemicals of some plants may be important for invasion resistance.

Keywords Allelochemicals · Invasion resistance · Native species · Plant–soil feedback · Species trait

Introduction

Biological invasion can potentially reduce biodiversity and alter species composition, structures, processes, and functions of recipient ecosystems (Vitousek et al. 1997; Ehrenfeld 2010; Ricciardi et al. 2017) and is, thus, an important component of the ongoing global environmental change. Invasion resistance is thought to constrain the spread and impact of invaders (Levine et al. 2004); therefore, there is a growing interest in the mechanisms involved in invasion resistance, i.e., to understand what makes plant communities more susceptible or resistant to invasions (Davis et al. 2000; Fridley et al. 2007; Pearson et al. 2018). An understanding of these mechanisms is essential for designing appropriate control measures and may aid biodiversity conservation efforts (Middleton et al. 2010; Yu et al. 2018).

Plant–soil feedbacks (PSFs) are plant-mediated changes to soil properties that ultimately influence the performance of the same or other plant species (van der Putten et al. 2013). PSFs are important and increasingly recognized

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aspects of aboveground–belowground linkages in plant ecology that influence plant diversity, succession, and invasion (Kulmatiski et al. 2008; Perkins and Nowak 2013). Invasive plants can rapidly alter recipient communities, and associated PSFs can contribute to invasion success (Klironomos 2002; Levine et al. 2006; Suding et al. 2013). Perkins and Nowak (2013) found that invasive species tended to produce PSFs that were more beneficial to themselves than other species, suggesting that PSFs may be a mechanism by which some non-native species increase their invasive potential. Morris et al. (2016) provided the first evidence for the underlying mechanism by which the invasive annual cheatgrass increases N availability and establishes positive PSFs that promote its success in western rangelands. Dostálek et al. (2016) revealed a strong negative feedback effect as a consequence of soil conditioning by *Rorippa austriaca* from the native range. In contrast, a negative feedback effect was not observed for *R. austriaca* in the invasive range of this species. Dostálek et al. (2016) indicated that the loss of the negative intraspecific PSF and the increased growth of the invasive population might contribute to a successful range expansion of *R. austriaca*. Although PSFs have been suggested as a mechanism that drives the success of invasive plants (Pfennigwerth et al. 2018), few studies have investigated the influence of PSFs on the vulnerability of a site to invasion. Such knowledge is important as it can further our understanding of the mechanisms responsible for invasion resistance.

PSFs have become an important concept to explain vegetation dynamics (Van der Putten et al. 2013); however, the mechanism underlying these feedbacks is still poorly understood (Kardol et al. 2015). PSFs can be driven by a wide range of biotic and abiotic factors, ranging from soil microbial feedbacks mediated by pathogens and mutualists that accumulate in the rhizosphere to nutrient feedbacks driven by the differential use of nutrient pools by different plant species (Smith-Ramesh and Reynolds 2017). Moreover, a broad and diversified group of secondary chemicals that act as allelochemicals are known to govern species interactions in ecosystems and are key drivers of soil and ecosystem functioning (Chomel et al. 2016). Understanding PSFs and their underlying mechanisms will improve our ability to predict the consequences of these interactions for plant community composition and productivity under a variety of conditions (van der Putten et al. 2013; Bailey and Schweitzer 2016; van Nuland et al. 2016; van der Putten et al. 2016; Dong et al. 2017). Specifically, the examination of PSF dynamics and the underlying mechanisms among invasive and native species may improve our understanding of vegetation dynamics and plant invasion processes. Moreover, such examinations may improve our understanding of the essential factors that regulate invasion resistance.

The objective of the present study was to test whether PSFs play a role in changing the relative performance of invasive species and if they influence invasion resistance. We conducted an experiment to study the effects of different soils from under common plant species on the growth of an invasive plant species. We then selected eight common co-occurring plant species that are native and non-native to Asia and performed a pairwise conditioned soil greenhouse experiment that was comprised of two phases: a soil-conditioning phase and a bioassay generation, to examine the PSF dynamics and explore the PSF mechanisms. Our previous studies indicated that invasive plant species vary in their ability to spread into different communities and that the allelopathy of resident trees in the soil may contribute to invasion resistance to some extent both in warm temperate forests and in lower subtropical China (Hou et al. 2011; Chen et al. 2019). Based on the findings of these aforementioned studies, we hypothesized that: (1) PSFs influence invasion processes, whereby the PSFs of invasive plants may facilitate their invasion success but the PSFs of some native plants may contribute to invasion resistance; and (2) PSF mechanisms are largely driven by changes in soil properties, including soil microbial communities, nutrients, and allelochemicals, which are produced by specific plant species.

Materials and methods

Study site and plant species

Zhenshan Mountain (Yantai, Shandong; N37°30′–37°32′, E121°19′–121°21′; 230–250 m a.s.l.) is located along the coast of the Yellow Sea, on the Northern Shandong Peninsula, China. The area is characterized by continental monsoon climate with a mean annual rainfall of 740.3 mm and a daily mean annual temperature of 12 °C. Frequent human activity has resulted in a shift in the vegetation types from primary vegetation to mainly secondary vegetation. The dominant tree species are *Robinia pseudoacacia* L., *Quercus acutissima* Carruth, *Pinus thunbergii* Parlat., and *Pinus densiflora* Siebold and Zucc. (Hou et al. 2013), and the common deciduous shrubs are *Amorpha fruticosa* L. and *Rhus chinensis* Mill. Among these species, *Q. acutissima*, *P. thunbergii*, *P. densiflora*, and *R. chinensis* are native to Asia; whereas, *R. pseudoacacia* and *A. fruticosa* are non-native species that originated from North America.

Phytolacca americana L. is a perennial herb that is native to North America and was introduced to China in 1935 (Fu et al. 2012). This species severely invaded shelter forests in hilly areas along the coastal regions and has become widely distributed in China, posing a serious threat to the biodiversity of invaded forests (Fu et al. 2012). The China Forestry Administration listed *P. americana* as an invasive plant in

2009. *Rhus typhina* L. is a deciduous, large shrub or small tree native to eastern North America. It was introduced in China in 1959 to rehabilitate the degraded mountain areas in northern China because of its high reproduction and spread rate (Wang et al. 2008). Despite being a good pioneer species in bare hills, its aggressive growth strategy results in the suppression of other species (Wang et al. 2013); therefore, *R. typhina* is sometimes considered to be an invasive species in China (Weber et al. 2008).

Effect of different soils under common plant species on the growth of *Phytolacca americana*

To determine the role of PSF in invasion resistance, we collected different soils under common plant species with different origins to test their influence on the growth of the herbaceous invasive *P. americana*. Soil samples were collected in the field on Zhenshan Mountain in July 2016 from the top 10 cm of the soil under some common plant species (four species native to Asia: *Q. acutissima*, *P. thunbergii*, *P. densiflora*, and *R. chinensis*, and two non-native species that originated from North America: *R. pseudoacacia*, and *A. fruticosa*) and under *P. americana* grown in the area. Soil samples were collected under six scattered plants of each species, and were fully mixed and sieved (1 cm mesh). Soil samples were then placed into small pots (diameter: 6 cm, height: 8 cm). Similarly, the top 10 cm of soils were collected from interspace areas (non-forested land where only grass grows), and used as the control.

Phytolacca americana seeds (soaked in 15% H_2O_2 for 7 h to break dormancy) were sown in a seed bed. Uniform seedlings (~ 3 cm high) were then selected and transplanted at one seedling per pot containing the above-mentioned soil samples. Each treatment had six replicates. The positions of the pots were randomized twice a week to compensate for any environmental variation, and plants were watered daily. Aboveground biomass of *P. americana* was harvested after 30 days, at which time we observed significant differences in plant growth. The aboveground biomass was dried for 72 h at 60 °C and then weighed.

Two-phase greenhouse experiment

For this experiment, we selected eight plant species that were common in the Shandong Peninsula, China: four species native to Asia—*Q. acutissima* (QA), *P. thunbergii* (PT), *P. densiflora* (PD), and *R. chinensis* (RC)—and four non-native species that originated from North America—two non-invasive species *R. pseudoacacia* (RP) and *A. fruticosa* (AF), and two invasive species *P. americana* (PA) and *R. typhina* (RT). A pairwise conditioned soil experiment was designed in two phases: soil conditioning phase and bioassay generation, in a greenhouse in Yantai, Shandong, China to examine the PSF mechanisms and PSF types of the aforementioned eight plant species.

The eight species used in the soil conditioning phase were subsequently replanted in the bioassay generation, except one unplanted control (CK). In March 2017, the top 20 cm of soils from the interspace areas on the Zhenshan Mountain was collected. The collected soil was stored for 14 days, and then fully mixed and sieved (1 cm mesh) before being transferred to pots (diameter: 20 cm, height: 25 cm). Each pot was randomly assigned a plant species or unplanted control. Some plant seeds required dormancy breaking (Table S1). Plant seeds were sown in a seedling bed. Uniform seedlings (~ 3 cm high) were then selected and transplanted at one seedling per pot. The greenhouse was maintained with ambient light and temperature, and plants were watered daily. The positions of the pots in the greenhouse were randomized once a week to compensate for any environmental variation. Potted treatments for the eight species and the unplanted control were each replicated 64 times, resulting in 576 pots in the soil conditioning phase. This phase comprised 75 days of growth (i.e., until the roots were about to extend beyond the bottom of the pots), after which all plant individuals were removed from the pots. For each plant species and the unplanted control treatment, the 64 replicates were randomly assigned to eight groups (eight pots per group), and soils from these eight pots within a group were homogenized and sampled (100 g) for soil property analyses.

Conditioned soils within a group were homogenized and repotted, and the bioassay generation was planted. All bioassay species were sown in (1) soil conditioned by the same species, (2) soil conditioned by all the other species, and (3) soil that was unplanted in the conditioning phase. These treatment combinations (i.e., 9 soil origins × 8 replanting species = 72 pots per replicate) were replicated 8 times, resulting in 576 pots. To observe the comprehensive effects of the soils on plant performance in the bioassay generation, two to five seeds were directly planted in each pot but only the first emergent was allowed to grow. This phase comprised 70 days of growth (which was enough time to observe significant differences in plant growth). Plants were grown under similar conditions to those described in the conditioning phase. At harvest, the roots of plants were rinsed gently with water to remove the adhering soil, and the whole plant individuals were dried at 60 °C for 72 h and weighed. Because of the low survival rate in this second phase, effective biomass data for *P. thunbergii*, *P. densiflora*, and *R. chinensis* seedlings are not available.

Soil nutrients and soil enzyme activities analysis

All fresh (4 °C in a refrigerator) and air-dried (room temperature) soil samples were stored separately. Fresh samples were used to determine soil NH_4^+ and NO_3^-, and air-dried samples were sieved (2 mm mesh) to determine other soil chemical properties.

Soil pH was measured using an electrode pH meter in 1:2.5 (w/v) soil water suspensions. Soil total C and N were determined by dry combustion with an elemental analyzer (Elementar Analysensysteme GmbH Vario EL, Elementar, Germany). Subsamples (10 g) were extracted with 50 mL of 2 mol L^{-1} KCl to determine the NO_3^- and NH_4^+ contents, which were measured using a spectrophotometer. Total P and total K contents in the soil were first melted with NaOH, and then determined using a spectrophotometer and a flame photometry detector, respectively. To determine soil available P, 5-g soil samples were extracted using 25 mL of 0.05 mol L^{-1} HCl–0.025 mol L^{-1} (1/2 H_2SO_4), and the P concentration of the extracts was determined using a spectrophotometer. To obtain soil available K content, 5-g soil samples were extracted using 50 mL of 1 mol L^{-1} NH_4OAc, and the K concentration of the extracts was determined using a flame photometry detector. All chemical analyses were performed following Bao (2000).

Soil enzymes affect soil nutrient cycling and are often related to soil microbial metabolism. Soil enzyme activity is, therefore, often used to assess soil nutrient availability and microbial activity (Alkorta et al. 2003; Cui et al. 2019). The enzyme activities in the soil samples were assayed following Guan et al. (1986), as follows. Urease activity was assayed using the indophenol blue colorimetric method and expressed as the amount (mg) of NH_3–N/g of dried soil produced during a 24-h incubation period at 37 °C. Sucrase activity was assayed with 3,5-dinitrosalicylic acid colorimetry and expressed as the amount (mg) of glucose produced during a 24 h incubation period at 37 °C. Phosphatase activity was assayed using the alkaline phosphatase colorimetric method and expressed as the amount (mg) of phenol produced per gram of dried soil within a 24-h incubation period at 37 °C (Quan and Liang 2017).

Data analysis

The response index (RI) was calculated to evaluate the effect of different soils on the aboveground biomass of *P. americana*. RI was calculated as follows: $(\text{Variable}_{\text{treatments}}–\text{Variable}_{\text{control}})/\text{Variable}_{\text{control}}$, where $\text{Variable}_{\text{control}}$ represents the mean value of the six replicates from the control soil. The absolute value of the RI indicates the intensity of the effect, whereby RI values > 0 indicate a positive effect, RI values < 0 indicate an inhibitory effect, and RI values = 0 indicate no effect.

The relative response (RR) index of bioassay species performance was calculated to evaluate the cumulative effects of the soil conditioning species on bioassay generation performance. RR values were then used to determine the PSF type (details in Perkins and Nowak 2013). The following equations were used:

$$\begin{aligned}\mathrm{RR}_{x,x} = {} & \left[(\text{biomass of species x in soil x}) - (\text{biomass of species x in other soils})\right] / \\ & \left[(\text{biomass of species x in soil x}) + (\text{biomass of species x in all other soils})\right],\end{aligned}$$

$$\begin{aligned}\mathrm{RR}_{\text{others},x} = {} & \left[(\text{biomass of other species in soil x}) - (\text{biomass of other species in other soils})\right] / \\ & \left[(\text{biomass of other species in soil x}) + (\text{biomass of other species in other soils})\right].\end{aligned}$$

Differences in pH, soil nutrients, and soil enzyme activities, among soil conditioning species (identity of the species in the first generation), between conditioning species native status (all native versus all non-native), and between invasive status (all invasive versus all non-invasive) were, respectively, compared using a multivariate analysis of variance (MANOVA) with Wilks' lambda criterion to determine the *F* value for soil conditioning species and Hotelling's trace to determine the *F* value for the native status and invasive status. Follow-up analyses of the between-subject effects were conducted using univariate tests.

To evaluate the potential PSF mechanisms, soil factors that significantly affected the biomass of each species were selected using the stepwise multiple regression method. The measured values of soil nutrients and soil enzyme activities were used as the soil factor group. The soil factors pH (X_1), total C (X_2), total N (X_3), total P (X_4), total K (X_5), NH_4^+–N (X_6), NO_3^-–N (X_7), available P (X_8), available K (X_9), urease (X_{10}), phosphatase (X_{11}), and sucrase (X_{12}) were used as independent variables of the soil factor group. The biomass (Y) of the different plant species was used as the dependent variable.

A one-way analysis of variance (ANOVA) was conducted to test the effect of soil origin on the aboveground biomass of *P. americana*, the effect of soil conditioning species on soil nutrients and soil enzymes activities, and the effect of soil conditioning species on bioassay generation performance. A Student–Newman–Keuls multiple range test was used to identify statistically significant differences at $p < 0.05$. The key soil factors (soil nutrients and soil enzyme activities) that influenced plant biomass were determined using multiple regression analysis (a stepwise method). T-tests were used to determine if RR values were different from zero and if there were differences between $\mathrm{RR}_{x,x}$ and $\mathrm{RR}_{\text{others},x}$ for each soil conditioning species. All statistical analyses were performed using IBM SPSS statistics 24 (IBM Inc., USA). All plots were constructed using SigmaPlot 10 (Systat Software Inc., Poland).

Results

Effect of different soils under common plant species on the growth of *Phytolacca americana*

Soils from different plant species had different effects on the biomass accumulation of *P. americana* ($p < 0.001$, Fig. 1). Compared to the non-forested land soil, soils from the non-native species *P. americana*, *R. pseudoacacia*, and *A. fruticosa* increased the aboveground biomass of *P. americana* by 40.21%, 32.41%, and 37.54%, respectively. In contrast, soils from the native species *Q. acutissima*, *P. thunbergii, P. densiflora*, and *R. chinensis* reduced the aboveground biomass of *P. americana* by 10.22%, 51.67%, 43.48%, and 33.50%, respectively (Fig. 1).

Soil nutrients and soil enzyme activities

Soil conditioning species and native status had significant overall effects (Table 1), whereas invasive status did not produce any significant effects. Follow-up univariate between-subject tests indicated that soil conditioning species influenced most of the soil nutrients and soil enzyme activities, and native status influenced soil NO_3^-–N, available K, and the urease and sucrase activities (Table 1).

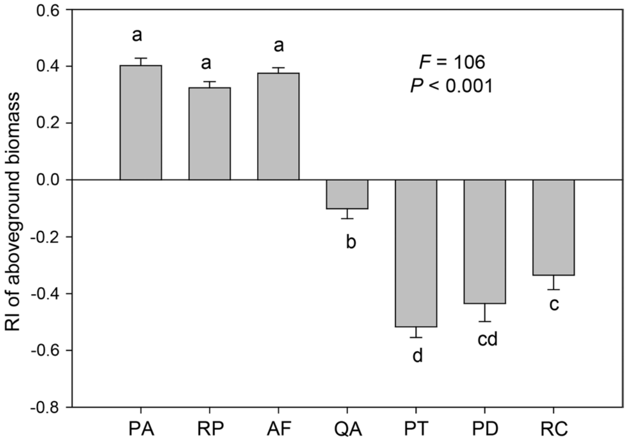

Fig. 1 Effect of different soils (0–10 cm) collected from under common plant species on the aboveground biomass of *Phytolacca americana*. The response index (RI, means ± standard errors of the mean) was calculated to evaluate the effect of the different soils on the aboveground biomass of *P. americana*. The absolute value of RI indicates the intensity of the effect, whereby RI values > 0 indicate a positive effect; RI values < 0 indicate an inhibitory effect; and RI values = 0 indicate no effect. Non-native species that originated from North America are *Phytolacca americana* (PA), *Robinia pseudoacacia* (RP), and *Amorpha fruticosa* (AF). Native species from Asia are *Quercus acutissima* (QA), *Pinus thunbergii* (PT), *Pinus densiflora* (PD), and *Rhus chinensis* (RC). Differences in RI between soils were tested and different letters indicate significant differences between treatments

Table 1 Comparison of the overall and between-subject effects of soil conditioning species (identity of the species in the first generation), native status (all native vs all non-native), and invasive status (all invasive vs all non- invasive) on pH and soil nutrients and soil enzyme activities using a multivariate analysis of variance (MANOVA) and univariate analysis

	Conditioning species		Native		Invasive	
	F(df)	*P*	*F(df)*	*P*	*F(df)*	*P*
Overall						
MANOVA	$4.449_{(104,59)}$	< 0.001	$4.882_{(13,11)}$	0.006	$247.021_{(11,1)}$	0.050
Univariate tests						
pH and soil nutrients						
pH	$6.770_{(8)}$	< 0.001	$0.931_{(1)}$	0.345		
Total C	$35.872_{(8)}$	< 0.001	$0.436_{(1)}$	0.516		
Total N	$3.076_{(8)}$	0.021	$0.181_{(1)}$	0.675		
Total P	$2.311_{(8)}$	0.064	$2.847_{(1)}$	0.105		
Total K	$7.873_{(8)}$	< 0.001	$0.083_{(1)}$	0.776		
NH_4^+–N	$1.840_{(8)}$	0.131	$2.342_{(1)}$	0.140		
NO_3^-–N	$8.121_{(8)}$	< 0.001	$19.176_{(1)}$	< 0.001		
Available P	$9.595_{(8)}$	< 0.001	$1.295_{(1)}$	0.267		
Available K	$1.707_{(8)}$	0.161	$4.880_{(1)}$	0.037		
Soil enzyme activities						
Urease	$15.918_{(8)}$	< 0.001	$6.057_{(1)}$	0.022		
Phosphatase	$10.487_{(8)}$	< 0.001	$1.165_{(1)}$	0.292		
Sucrase	$5.246_{(8)}$	0.001	$24.738_{(1)}$	< 0.001		

Univariate tests for invasive status were not conducted because the overall MANOVA was not significant

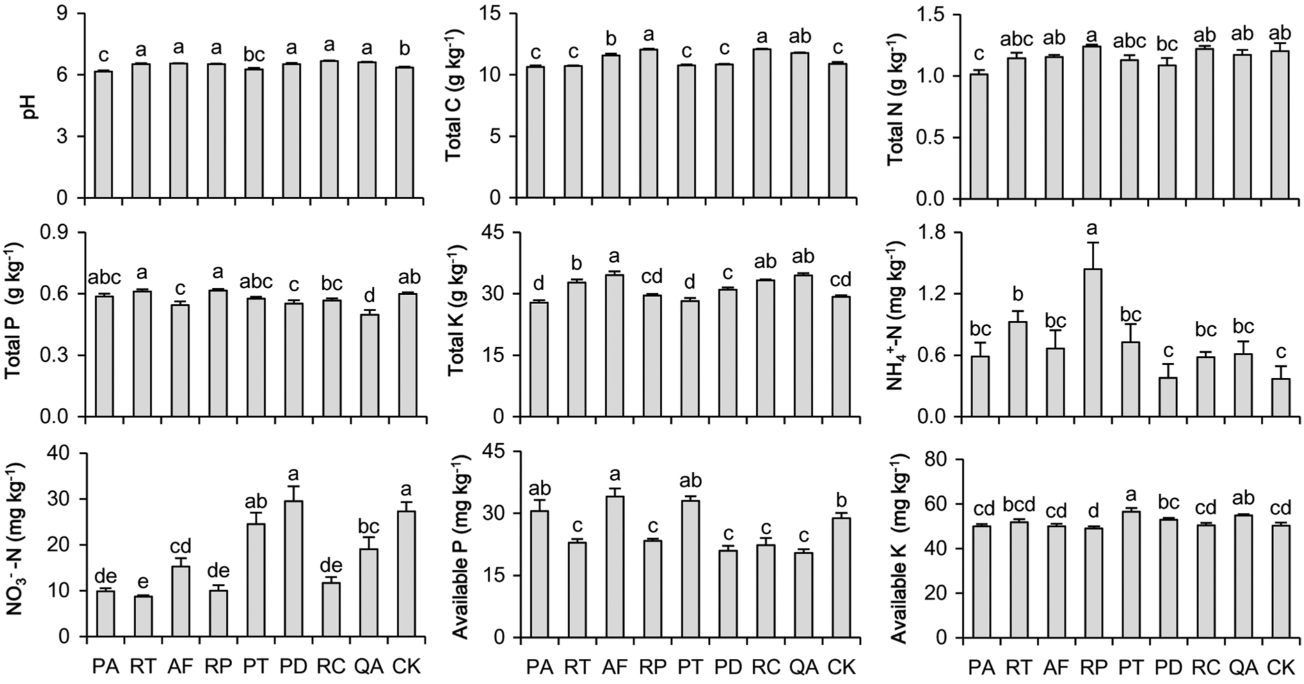

Fig. 2 pH and soil nutrients after conditioning generation by different plant species. Non-native species that originated from North America are *Phytolacca americana* (PA), *Rhus typhina* (RT), *Amorpha fruticosa* (AF), and *Robinia pseudoacacia* (RP). Native species from Asia are *Pinus thunbergii* (PT), *Pinus densiflora* (PD), *Rhus chinensis* (RC), and *Quercus acutissima* (QA). CK represents the unplanted control. Data represent means ± standard errors of the mean (SEM)

After soil conditioning by the first plant generation, soil pH and most of the soil nutrients differed significantly among species (Fig. 2), indicating species-specific soil conditioning effects. Soil pH was significantly lower in the *P. americana*-conditioned soil compared with the soils of other species (except of *P. thunbergii*) and with the blank control (− 3.30%). Compared with the blank control, soil total N (− 15.83%) and NO_3^-–N (− 63.78%) were significantly lower in the *P. americana*-conditioned soil. Compared with the blank control, soil pH (+ 2.52%), total K (+ 11.81%), and NH_4^+–N (+ 151.35%) were significantly higher in the *R. typhina*-conditioned soil; but the NO_3^-–N (− 68.04%) and available P (− 20.69%) were significantly lower in this conditioned soil. Compared with the blank control, soil pH (+ 3.93%), total C (+ 8.09%), total K (+ 17.68%), and available K (+ 9.00%) were significantly higher in the *Q. acutissima*-conditioned soil; but the total P (− 16.67%), NO_3^-–N (− 30.13%), and available P (− 29.22%) were significantly lower in this conditioned soil.

Similarly, species-specific effects were found for most soil enzyme activities (Fig. 3). Urease activity was highest in the *Q. acutissima*-conditioned soil. Phosphatase activity was highest in the *R. chinensis*- and *Q.*

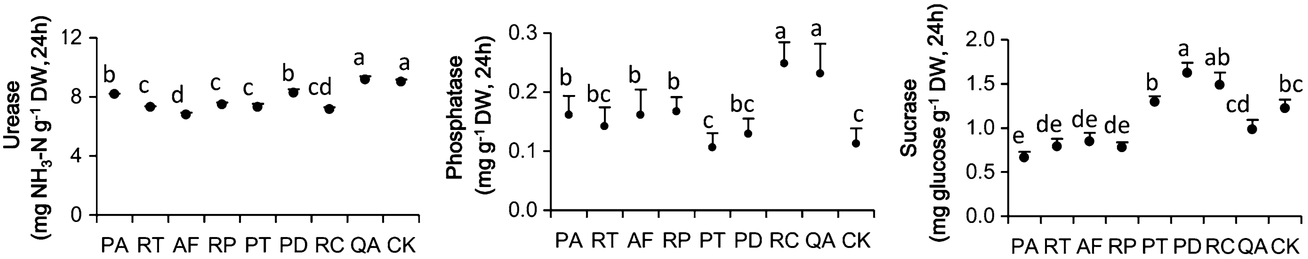

Fig. 3 Soil enzyme activities after conditioning by different plant species. Non-native species that originated from North America are *Phytolacca americana* (PA), *Rhus typhina* (RT), *Amorpha fruticosa* (AF), and *Robinia pseudoacacia* (RP). Native species from Asia are *Pinus thunbergii* (PT), *Pinus densiflora* (PD), *Rhus chinensis* (RC), and *Quercus acutissima* (QA). CK represents the unplanted control. Data represent means ± standard errors of the mean (SEM)

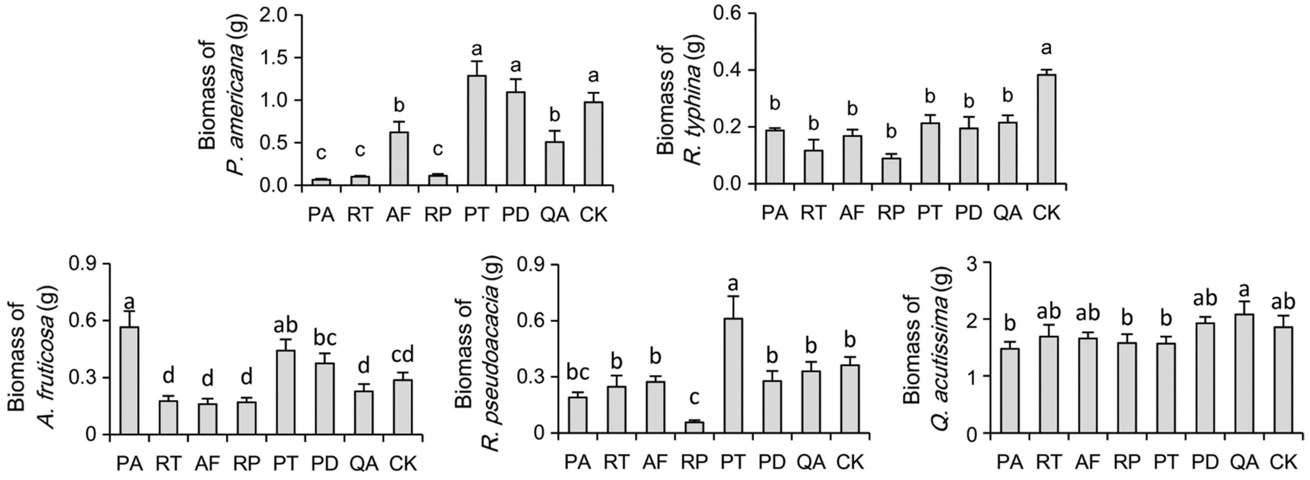

Fig. 4 Effects of soils conditioned by different plant species on the biomass of the bioassay generation of plants. Non-native species that originated from North America are *Phytolacca americana* (PA), *Rhus typhina* (RT), *Amorpha fruticosa* (AF), and *Robinia pseudoacacia* (RP). Native species from Asia are *Pinus thunbergii* (PT), *Pinus densiflora* (PD), and *Quercus acutissima* (QA). CK represents the unplanted control. Because of the low survival rate of *Rhus chinensis* seedlings, we were not able to obtain enough *R. chinensis*-conditioned soil for the bioassay phase of the experiment. Because of the low survival rate in the bioassay phase, effective biomass data of *P. thunbergii*, *P. densiflora*, and *R. chinensis* seedlings are not available. Data represent means ± standard errors of the mean (SEM)

acutissima-conditioned soils. Sucrase activity was highest in the *P. densiflora*-, *R. chinensis*-, and *P. thunbergii*-conditioned soils.

PSF mechanisms

Different types of cultivation soil had different impacts on the biomass accumulation of the subsequent plants (Fig. 4). For *P. americana*, biomass performances were significantly decreased by 93.13%, 89.64%, 36.00%, 88.41%, and 47.69% when grown in *P. americana*-, *R. typhina*-, *A. fruticosa*-, *R. pseudoacacia*-, and *Q. acutissima*-conditioned soils, respectively, as compared to its performance in the CK soil. The differences in these biomass performances among *P. thunbergii*- and *P. densiflora*-conditioned soils and the CK soil were not statistically significant ($p > 0.05$). For *R. typhina*, biomass performances were significantly decreased in all of the other species-conditioned soils, compared to its performance in the CK soil (in which the species showed the highest performance). For *A. fruticosa*, biomass performances were significantly increased by 97.21% and 54.01% in *P. americana*- and *P. thunbergii*-conditioned soils, respectively, as compared to its performance in the CK soil. The differences in the biomass performances among the conditioned soils from the other species and the CK soil were not statistically significant ($p > 0.05$). For *R. pseudoacacia*, biomass performances were significantly increased by 68.78% in *P. thunbergii*-conditioned soil and decreased by 84.25% in *R. pseudoacacia*-conditioned soil, compared to its performance in the CK soil. The differences in the biomass

Table 2 Significant effects of various soil parameters (NO_3–N, available P, and available K, NH_4^+–N, Total N, Total K, Urease) on aboveground biomass of five plant species using stepwise multiple regression analysis

Species	Model statistics			Significant variable statistics			
	F	*P*	R^2	Variable	Standardized coefficients	*t*	*P*
Phytolacca americana	25.380	< 0.01	0.65	NO_3–N	0.665	6.954	< 0.01
				Available P	0.310	3.352	< 0.01
				Available K	0.233	2.432	0.019
Rhus typhina	5.767	0.021	0.13	NH_4^+–N	0.395	− 2.401	0.021
Amorpha fruticosa	26.870	< 0.01	0.54	Total N	0.434	− 4.284	< 0.01
				Total K	0.552	− 5.451	< 0.01
Robinia pseudoacacia	6.979	< 0.01	0.30	NO_3–N	0.345	2.765	< 0.01
				Available P	0.264	2.215	0.031
				Available K	0.258	2.065	0.044
Quercus acutissima	5.848	0.019	0.10	Urease	0.318	2.418	0.019

performances among the conditioned soils from other species and the CK soil were not statistically significant ($p > 0.05$). For *Q. acutissima*, biomass performances were significantly decreased by 28.86%, 24.19%, and 24.68% in *P. americana*-, *R. pseudoacacia*-, and *P. thunbergii*-conditioned soils, respectively, as compared to its performance in *Q. acutissima*-conditioned soil (in which the species showed the highest performance). The biomass performance of *Q. acutissima* in the conditioned soils from all species and in the CK soil was not significantly different ($p > 0.05$).

The significant soil factors for the biomass of each species were selected to evaluate PSF mechanisms, using the stepwise multiple regression method (Table 2). The significant soil factors influencing *P. americana* biomass and *R. pseudoacacia* biomass were NO_3^-–N (X_7), available P (X_8), and available K (X_9); the significant soil factor influencing *R. typhina* biomass was NH_4^+–N (X_6); the significant soil factors influencing *A. fruticosa* biomass were total N (X_3) and total K(X_5); the significant soil factor influencing *Q. acutissima* biomass was urease (X_{10}) (Table 2). Thus, the stepwise multiple regression analysis indicated the soil factors that significantly influenced the biomass of different plant species. Moreover, different soil factors significantly influenced the biomass of different plant species, which indicated species-specific effects.

PSF types

We examined the $RR_{x,x}$ and $RR_{others,x}$ values to determine the specific type of PSF generated by each soil conditioning species (Table 3). *P. americana* generated a conspecific negative feedback. *P. americana* conditioned the soil in a manner that decreased the subsequent growth of specimens of the same species (indicated by negative $RR_{x,x}$ values −0.191). *Q. acutissima* generated a heterospecific positive feedback and conditioned the soil in a manner that benefited the subsequent growth of plants of the same species (indicated by positive $RR_{x,x}$ values 0.056). However, other species tended to respond more strongly (i.e., had a larger relative increase in biomass; $RR_{others,x} = 0.487 > RR_{x,x} = 0.056$) compared to *Q. acutissima*. $RR_{x,x}$ and $RR_{others,x}$ values generated by *R. typhina*, *A. fruticose*, and *R. pseudoacacia* were not different from zero, which indicated that these three species produced neutral feedbacks.

Discussion

Effect of different soils under common plant species on the growth of *Phytolacca americana*

Field investigations in the hilly habitats of the Shandong Peninsula have revealed that communities dominated by the non-native species *R. pseudoacacia* or *A. fruticosa* were more vulnerable to invasions by invasive plants, such as *P. americana* and *R. typhina*, than those dominated by the native species *Q. acutissima* (Hou et al. 2013; Wei et al. 2017). In this study, we revealed that the soil samples taken from the top 10 cm of the soil profile of some common plant species grown in the field had significantly different effects on the biomass accumulation of the invasive species *P. americana*. Soils from the non-native species increased the aboveground biomass of *P. americana*; while, the soils from the other four species native to Asia inhibited the growth of *P. americana*. PSFs may provide insights into the fundamental questions of biological invasion processes, such as: why and how do some species resist plant invasion while others do not? The results of the present study, coupled with our previous field observations and studies (Hou et al. 2011; Chen et al. 2019), support the hypothesis that some native plant species tend to have higher resistance to plant invasions than non-native species, and that soil, as an important component of the ecosystem, plays a crucial role in invasion resistance. Previous studies have also provided some experimental evidences in support of this hypothesis, although investigations in this subject area are rare (Liu et al. 2017; Hulvey and Teller 2018).

Table 3 Summary of species responses to own ($RR_{x,x}$) or other ($RR_{others,x}$); values are soil feedback-type categorization determined by the differences between $RR_{x,x}$, $RR_{others,x}$, and zero

Soil conditioning species	$RR_{x,x}$	$RR_{other,x}$	Plant–soil feedback type
Phytolacca americana	**−0.19 (0.10)**^{a}	0.29 (0.17)^b	Conspecific negative
Rhus typhina	−0.06 (0.04)	0.19 (0.16)	Neutral
Amorpha fruticosa	−0.10 (0.07)	0.38 (0.21)	Neutral
Robinia pseudoacacia	−0.19 (0.03)	0.00 (0.09)	Neutral
Quercus acutissima	**0.06 (0.01)**	**0.49 (0.15)**	Heterospecific positive

Because of the low survival rate in the second phase, effective biomass data of *Pinus thunbergii, Pinus densiflora*, and *Rhus chinensis* seedlings are not available. Bold values are significantly different from zero, values marked with different letters indicate that $RR_{x,x}$ and $RR_{others,x}$ are significantly different from each other. A negative RR value indicates that a species performed worse in that conditioned soil than in other soils, a positive RR value indicates that a species performed better in that soil than in the other soils. Exotic species: *P. americana*, *R. typhina*, *A. fruticosa*, and *R. pseudoacacia*. Native species: *Q. acutissima*

PSFs influence the invasion process

PSFs influence individual plant performance and, thus, plant-community composition (van der Putten et al. 2013; Kardol et al. 2015). In the present study, we found that the selected species produced species-specific effects on the soil properties and on the biomass accumulations of most of the plant species. Contrary to expectations, some native plants did not produce PSF effects that decreased the relative performance of invasive plants, nor did the invasive plants produce PSF effects that increased their own relative performance. For example, we found that the native species *Q. acutissima* produced PSF effects that increased its own relative performance as well as that of the other species; while, the invasive species *P. americana* produced PSF effects that decreased its own relative performance.

As plants grow, they modify their soil environment, including nutrient availability and soil microbial activities (Bennett et al. 2017; Fujii et al. 2018). In this study, we found species-specific soil conditioning effects on soil nutrients and soil enzyme activities (which are mainly regulated by soil microbes) caused by plants. For example, *P. americana*-conditioned soil showed a significant decrease in pH and soil nutrients (e.g., total N and NO_3^-–N); while, *Q. acutissima*-conditioned soil showed improvements in the soil pH and soil nutrients (e.g., total C, total K, and available K). *R. typhina*-conditioned soil showed an increase in the pH, total K, and NH_4^+–N, and a decrease in NO_3^-–N and available P. Some native species, especially *Q. acutissima*, had high soil enzyme activities, such as urease and phosphatase activities. Stepwise regression showed that the subsequent plant growth was positively correlated with these soil properties. Therefore, the changes in soil nutrients and soil enzyme activities after plant growth may have affected the biomass of subsequent plant species, providing a partial explanation for the PSF results we observed.

Previous studies have indicated that PSFs influence the establishment and spread of invasive plant species (Kourtev et al. 2002; Perkins and Nowak 2013; Chiuffo et al. 2015; Dostálek et al. 2016). Soil N cycling is a process of particular interest because N is a critical limiting nutrient for plant growth (Vitousek and Howarth 1991). Soil N was significantly lower in the *P. americana*-conditioned soil, indicating that the invasive species had a high ability to use soil N. While it is well known that species vary in their ability to acquire, utilize, and compete for available N, our results seem to support the argument that the higher ability to use soil N of some exotic plant species is usually related to their higher ability to invade (Liao et al. 2008; Morris et al. 2016).

Additionally, soil P was significantly lower in the *Q. acutissima*-conditioned soil indicating that the species had a higher ability to use soil P. Phosphorus is an essential macromineral for plants, and the ability of a species to invade new communities is often influenced by the P availability of the resident community (Brewer and Cralle 2003; Wolf et al. 2004; Chen et al. 2019). *Centaurea diffusa*, for example, is an invader of North American grasslands and has been shown to lose its competitive advantage in soils with low P levels (Suding et al. 2004). Our findings indicated that the high ability of *Q. acutissima* to acquire and utilize soil P may be a potentially important restriction factor in *Q. acutissima* forests, and which improves its resistance to plant invasion. However, this particular hypothesis remains to be experimentally tested in future studies.

Extension and outlook

PSFs can be driven by a wide range of abiotic and biotic factors (Pfennigwerth et al. 2018; Png et al. 2018). Besides nutrient availability and soil biota, secondary chemicals also influence PSF processes (Smith-Ramesh and Reynolds 2017; Bennett and Klironomos 2019). Secondary chemicals that act as allelochemicals, released directly into the soil in the form of root exudates or cycled into the soil from decomposing litter, can affect plant and microbial growth (Stinson et al. 2006; Callaway et al. 2008; Smith-Ramesh and Reynolds 2017). Our previous studies, both in warm temperate forests and in lower subtropical China, have indicated that the allelopathy of resident trees in soil contributes to the invasion resistance and that plant litter—as an important component of soils—from different forests differentially confer invasion resistance and affect the performance of invasive plants (Hou et al. 2011; Chen et al. 2019). The PSFs in our experiments mostly lacked litter-based loops because we used plant seedlings to conduct greenhouse experiments and the period of interaction with the soil was limited. The seedlings produced little litter, which can reduce the decomposition and slow the subsequent release of available N and allelochemicals into the soil. This potentially contributed to the differences in the PSFs between the greenhouse and field conditions. Some studies have reported that PSFs may be differently mediated by root- and litter-based loops (Ke et al. 2015; Zhang et al. 2019). For example, Elgersma et al. (2011) revealed that the litter and rhizosphere of some plant species differ, with contrasting effects on specific species or trophic groups of soil biota. Similar, to the findings in the present study, other recent studies have also demonstrated differences in the PSFs between greenhouse and field conditions (Heinze et al. 2016; Dong et al. 2017). Therefore, we speculate that the differences in PSFs between the greenhouse and field conditions observed in the present study may suggest that litter and allelochemicals of some native plants play an important role in the formation of invasion resistance. This topic requires investigation in future studies.

There has been recent debate in PSF literature concerning the adequacy of soil mixing in PSF experiments [e.g., Rinella and Reinhart (2018, 2019), Teste et al. (2019)], which is relevant to this study. In the first experiment, for instance, to test whether the soil under plant species of different origins differentially affect invasive plant growth, we collected soils from under six scattered individuals of each species and mixed these samples to test the average effects of soil from each species. We believe this is a valid means to achieve the purpose of the experiment herein proposed; however, attention should be paid to establishing a more rigorous sampling procedure in further investigations.

Conclusions

We investigated the relative importance of PSF as a mechanism that drives the change of invasion resistance and the role of the feedback of invasive species with soil in successful invasions. Our results indicated that PSFs may play a role in invasion processes and that PSF dynamics are largely driven by changes in soil properties, which are produced by specific plant species and their associated microbial communities. We encourage further investigations on this topic as they may identify native plant species that are significantly resistant to invasive plants, and which can, thus, be used to construct highly resistant plant communities or develop green herbicides to ecologically prevent and control plant invasions.

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Author contribution statement YPH and QQH conceived and designed the study. WW and PZ performed the experiments and collected the data. WW, PZ, and YPH wrote the manuscript. WW, PDC, YPH, and XFB designed and performed the data analyses. QQH and GYN reviewed and improved the manuscript. All authors participated in the data interpretation and revised the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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