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Research Article

Soil abiotic and microbial legacies jointly contribute to growth of invasive *Solidago canadensis*

Summary

The invasion success of exotic plants strongly depends on soil properties of new ranges, however, little is known about the joint contribution of soil abiotic and biotic legacies to this success. To address the role of soil abiotic and microbial properties in plant invasions and associated mechanisms, we conducted two complementary experiments. In the first experiment, we grew invasive *Solidago canadensis* in regular soils from its different invasion stages and measured plant growth to address the joint contribution of soil abiotic and microbial properties. In a second experiment, we set up four sterilization × three sites treatments and measured plant growth to address the influence of different soil microbes on *S. canadensis*. The growth of *S. canadensis* was constrained by soil N and bacteria, and was positively correlated to its leaf area and root area, but not its leaf chlorophyll contents and root hydraulic conductivity. Bactericide had no effects on *S. canadensis* growth, and the decreased growth was greater in the presence of bactericide and fungicide together than in the presence of fungicide alone. The effects of microbial removal varied with microbial groups and sites. These results suggest that soil abiotic and biotic legacies may jointly contribute to plant invasions.

Introduction

The successful invasion of exotic plants can be ascribed to multiple possible mechanisms [1,2]. Of all the mechanisms, the properties of soils alone (e.g. nutrient availability and enemies) and plant-soil interactions (e.g. positive or negative feedback) have been increasingly recognized as key mechanisms determining invasion success [2-7]. In other words, the initial regimes of soil abiotic and biotic properties and their changes induced by invader-soil interactions play a crucial role in plant invasions (see below). Accordingly, increasing attention focusing on plant invasions has been paid to soil legacy effects [8-10].

The importance of soil abiotic properties (i.e. soil abiotic legacy) in plant invasions at least encompasses two mechanisms: resources and conditions. For example, soil nitrogen (N) and phosphorus (P) determine the growth of invasive plants because they usually grow rapidly and thus need large quantities of soil N and P [1,2,11], soil pH, as a condition, influences soil nutrient availability and soil microbial composition and structure [12,13]. The importance of soil microbes (i.e. soil microbial legacy) in plant invasions also at least covers two mechanisms: beneficial and detrimental effects. For example, the releases of soil-borne enemies or enhanced mutualisms benefit invasive plants whereas accumulated pathogens harm native plants [3,4,6,14,15]. However, it should be noted that invasive plants commonly interact with their surrounding soils [16,17]. This interaction can dramatically alter soil abiotic and biotic legacies, thereby influencing the performance of invasive plants (Gaggini et al. 2017).

To date, we know less about the joint role of soil abiotic and biotic legacies in plant invasions than we do about the individual role of soil abiotic or biotic legacies, particularly in the context of long-term plant-soil interactions. Additionally, soil abiotic and biotic legacies may differentially influence invasive plants because their influencing mechanisms are different [1,2,7]. Addressing the coupled contributions of soil abiotic and microbial legacies, which are influenced by long-term invader-soil interactions, in plant invasions needs a series of invasion stages [7,18]. The Chongming Island in China provides an ideal platform for understanding this question because there are distinctly different stages invaded by *Solidago canadensis* on there [19].

Our central hypothesis was that soil abiotic and microbial legacies, as modified by long-term *S. canadensis*–soil interactions, can jointly influence its subsequent growth. Our second hypothesis was that soil bacteria and fungi may exhibit

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additive effects on the growth of *S. canadensis* if they are crucial for its invasion success. Additionally, we hypothesized that soil legacies affect the growth of *S. canadensis* through changing its root and leaf performance at the same time. We tested these hypotheses by conducting two complementary experiments and measuring whole-plant biomass, and leaf and root functional traits.

Methods

Plant material and samples sites

Solidago canadensis is native to North America, and an exceptionally successful worldwide invader in Europe, large parts of Asia, Australia, and New Zealand [20]. *S. canadensis* was introduced into China in 1935, and is now a most noxious invasive forb in China [21,22]. This invader is perennial and characterized by having fast growth, strongly influencing its surrounding soil, and forming dense mono-dominant stands [21-24].

The Chongming Island, with an area of 1267 km^2, is the third largest island in China. Since 1968 a few artificial dikes have been constructed over there [19]. Three dikes, which were constructed in 1968, 1990, and 1998, were selected in our study. Accordingly, mono-dominant stands of *S. canadensis* on these dikes roughly represent different invasions stages [19].

Experiment 1: plant growth under different soil regimes

We sampled soils from mono-dominant stands of *S. canadensis* on the three dikes. On each dike we collected ten soil samples from the upper 10 cm of the profile at 10 locations, which were at least 5 m apart from each other. Prior to experiment, the abiotic and biotic properties of each soil sample were measured. Soil pH was measured with a pH meter (HI 99121, HANNA Instruments), soil organic matter (SOM) was measured by the dichromate oxidation and titration methods, soil available nitrogen (N, the sum of nitrate and ammonium) was determined using the Kjeldahl method, soil available phosphorus (P) was determined with a UV-visible spectrophotometer.

Soil microbes were assessed using phospholipid fatty acid (PLFA) profiles. PLFAs were extracted, fractionated, quantified and analyzed in the amount of fresh soil equivalent to 8 g of dry soil as described by Bossio & Scow [25]. From these samples, fatty acid methyl esters (FAMEs) were identified using the MIDI Sherlock Microbial Identification System 6.0 (MIDI, Inc.125, Newark, DE19713). A total of 77 different PLFAs were detected and identified in the different soil samples. The fatty acids chosen to represent bacteria were i14:0, 14:0, i15:0, a15:0, 15:0, a16:0, i16:0, 16:1ω7c, 16:1ω9c, 15:0 2OH, i15:0 3OH, 16:1 2OH, i17:0, a17:0, 17:0, cyl7:0, 18:1ω5c, 18:1ω7c, 11Me 18:1ω7c and cyl9:0; and the fatty acids chosen to represent fungi were 16:1ω5c, 18:1ω9c, 18:2ω6,9c, and 18:3ω6,9,12c [26,27].

We conducted a growth experiment with *S. canadensis*, which was subjected to one of the above soils. All plants from seed were grown in 250-mL pots, and there were 10 replicates for each soil. All the pots were put in a greenhouse at the Institute of Botany, Chinese Academy of Sciences, where temperatures and humidity were maintained between 20–30°C and 50%–60%, and photosynthetically active radiation during the day remained above 1200 µmol m^{-2} s^{-1}. During the experiment, water was supplied to all plants as required, and other growing conditions were identical for all plants. All the pots were rotated every week to avoid the possible effects of greenhouse microsite variability.

Prior to harvest, we randomly collected five leaves per *S. canadensis* plant and measured their chlorophyll contents with SPAD (SPAD 502, Japan) to obtain the average chlorophyll content of each plant; we also determined the root hydraulic conductivity (Lpr) of *S. canadensis* plants with PMS (PMS Instrument Company, USA. See the guidelines of PMS for more details about measuring Lpr.). At the end of the experiment, all *S. canadensis* plants were harvested, separated into shoots and roots, and rinsed; total leaf area per plant and total root surface area per plant were determined with the WinRhizo system (Regent Instruments, Inc., Canada). All experimental materials were oven-dried at 85C for 48 h and weighed.

Correlation analysis was used to determine the relationships between soil properties with SPSS 13.0. We analyzed all soil abiotic and biotic data using principal component analyses (PCA), allowing us to locate the most important soil drivers. Accordingly, we selected one abiotic trait and one microbial trait according to the explained variance. PCA analysis was performed using the vegan package of R 3.5.3 [28].

One-way analysis of variance (ANOVA) with Post Hoc Tests was used to test the effects of soil sources on plant traits (i.e., plant height, whole-plant biomass, leaf area, root surface area, leaf chlorophyll contents, and root hydraulic conductivity) and soil characteristics (i.e., soil pH, SOM, N, P, soil bacteria, soil fungi, and fungi/bacteria ratio). Correlation analysis also was used to determine the relationships either between plant growth and key soil properties or between plant traits. Statistical analyses were carried out using SPSS 16.0.

Experiment 2: the growth of plants subject to microbial removal

We conducted a second growth experiment in the greenhouse. Our goal was to quantify the direct effects of soil bacteria, fungi or both. We sampled soils from the same three sites involved in experiment 1. On each dike we collected soils from the upper 10 cm of the profile at 10 locations, which were at least 5 m apart from each other. Soils from all sampling locations was sifted free from rocks and roots, and used for the experiment.

All experimental plants from seed were grown in 250-mL pots. We set up a factorial experiment consisting of sterilization and sites. Sterilization included four treatments: control, bactericide addition, fungicide addition, and bactericide and fungicide addition. Experimental plants from *S. canadensis* were randomly assigned to each of the 12 treatments (four sterilizations × three sites). We supplemented bactericide, fungicide, and a mixture of streptomycin sulphate and

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chlortetracycline (2:1) and benomyl, in aqueous solution in five applications totaling 0.3 g bactericide m^{-2} and 0.2 g fungicide m^{-2}, respectively. These doses of bactericide and fungicide have been widely used in previous studies [29-31]. In addition, we also found that this dose of the mixed bactericide had no significant side effects on the growth of *S. canadensis*. There were 20 replicates for each treatment.

All the pots were placed in the same greenhouse used in experiment 1 and rotated every week to avoid the possible effects of greenhouse microsite variability. During the experiment, all plants were watered as required to be sure that larger plants did not become relatively more water-limited than smaller plants, and other growing conditions were identical for all plants.

At the end of the experiment, leaf chlorophyll concentrations were measured in situ. We selected five fully developed leaves from each individual for measuring their chlorophyll contents with SPAD-502 (Konica Minolta, Japan), three readings per leaf (i.e. three measurements at different leaf positions) were recorded, and all readings per individual were averaged. All experimental plants were harvested, separated into shoot and roots, and rinsed. All the samples were oven-dried at 85°C for 48 h and weighed.

We ran general linear models to test the effects of experimental manipulations on biomass and leaf chlorophyll contents. Two-way ANOVA with Post Hoc Tests was used, where sterilization and sites were treated as fixed factors. All statistical analyses were carried out with SPSS (16.0).

Results

Soil pH, SOM, and N were significantly varied with sites, and P was marginally varied with sites (Table 1). Soil bacteria were marginally varied with sites, soil fungi were unvaried with sites, and soil fungi/bacteria ratios significantly differed among sites (Table 1). There were significant correlations between soil microbial properties (Table 2). Soil bacteria and fungi/bacteria ratio exhibited completely opposite correlations with soil pH, SOM, N, and P, and soil fungi were positively correlated to SOM but negatively correlated with soil P (Table 2). Soil pH was negatively correlated with both SOM and soil N, and SOM was positively correlated with soil N but negatively correlated with soil P (Table 2).

Principal component (PC) analysis clearly distinguished the relative importance of soil abiotic properties and biotic properties (Figure. 1). In this analysis, PC1 alone accounted for over 96.6% of the total variation among sites and thus could be indicator for soil properties; soil N and soil bacteria overwhelmingly explained the variances of soil abiotic properties and biotic properties, respectively (Figure. 1). Accordingly, soil N and bacteria were selected as key soil drivers when the relationships of plant growth with soil properties were analyzed below.

For *S. canadensis* plants, their height and total biomass were greatly affected by sites (Figure 2A,B: all $P<0.001$). Although plant height and total biomass were positively correlated ($r=0.998$, $P=0.038$), their patterns differed in response to sites (Figure 2A,B). Whole-plant biomass of *S. canadensis* was significantly positively correlated with soil N ($r=0.965$, $P<0.001$) and soil bacteria ($r=0.798$, $P=0.002$) (Figure 3).

Sterilization ($F=10.25$, $P<0.001$), site ($F=26.45$, $P<0.001$), and their interaction ($F=7.45$, $P<0.001$) affected the leaf chlorophyll content of *S. canadensis* (Figure 4A). Specifically, bactericide and fungicide increased the leaf chlorophyll content compared to the controls, but the addition of bactericide and fungicide had no influence on the leaf chlorophyll content (Figure 4A).

Table 1: Soil variables (means ± 1 SE) describing abiotic and biotic differences among the three sites.

Variable	Site			*F*	*P*
	1998 dike	1990 dike	1968 dike		
pH	6.85±0.04 ^{a}	6.73±0.05 ^{ab}	6.63±0.06 ^{b}	4.77	0.02
SOM	6.46±0.44 ^{b}	6.43±0.73 ^{b}	9.90±1.31 ^{a}	4.895	0.028
N	12.1±0.43 ^{c}	24.8±2.1 ^{b}	38.4±4.6 ^{a}	20.763	<0.001
P	2.42±0.21 ^{a}	2.88±0.23 ^{a}	2.07±0.19 ^{a}	3.589	0.061
Bacteria (B)	8.49±1.17 ^{ab}	6.61±0.80 ^{b}	13.1±2.76 ^{a}	3.502	0.063
Fungi (F)	2.29±0.36 ^{a}	1.68±0.23 ^{a}	2.75±0.59 ^{a}	1.611	0.24
F/B	0.27±0.01 ^{a}	0.25±0.01 ^{a}	0.21±0.01 ^{b}	7.352	0.008

Notes: SOM, soil organic matter. Different letters in the same row represent significant differences among the sites. Boldface type indicates *P* values < 0.05, and boldface and italic type indicates *P* values < 0.1.

Table 2: Bivariate relationships between the seven soil traits.

	Bacteria	Fungi	Fungi/ bacteria	pH	SOM	N	P
Bacteria		0.951***	-0.860***	-0.696*	0.967***	0.722**	-0.928***
Fungi			-0.659*	-0.438^{ns}	0.839**	0.472^{ns}	-0.998***
Fungi/ bacteria				0.965***	-0.962***	-0.974***	0.607*
pH					-0.857***	-0.999***	0.377^{ns}
SOM						0.876***	-0.801**
N							-0.412^{ns}
P							

Notes: SOM, soil organic matter. Boldface type indicates P values < 0.05; ns: not significant.

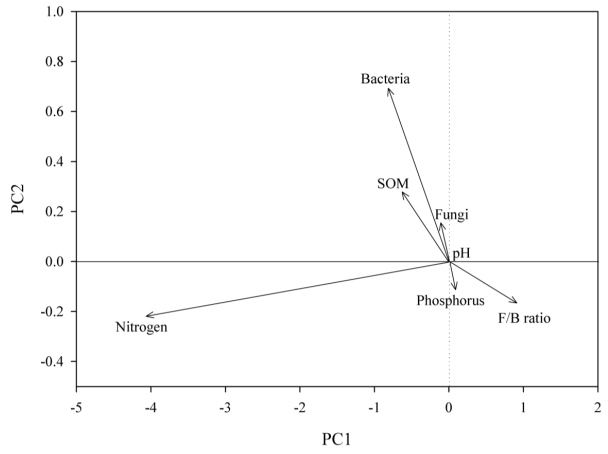

Figure 1: Principal component analysis (PCA) of the seven soil properties. The first axis explains 96.6% of the variation; the second axis, 3.4%. SOM: soil organic matter.

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Sterilization (F=6.95, P<0.001), site (F=7.76, P=0.001), and their interaction (F=4.67, P<0.001) influenced the whole-plant biomass of *S. canadensis* (Figure 4B). Bactericide alone did not suppress *S. canadensis* growth relative to the controls, but fungicide alone or bactericide and fungicide together greatly decreased its growth (Figure 4B). Importantly, *S. canadensis* grew much larger in the presence of bactericide than in the presence of fungicide or bactericide and fungicide together (Figure 4B).

The total leaf area and total root surface area of *S. canadensis* exhibited similar responses, increasing from site 1 to site 3 (Figure 5A: F=71.91, P<0.001; Figure 5B: F=54.09, P<0.001). The leaf chlorophyll content and root hydraulic conductivity also showed similar responses, and were greater when *S. canadensis* plants were grown at site 3 than when grown at sites 1 and 2 (Figure 5C: F=17.30, P<0.001; Figure 5D: F=5.96, P=0.018). The whole-plant biomass of *S. canadensis* was positively linked to leaf area and root surface area (all P<0.05), instead of the leaf chlorophyll content and root hydraulic conductivity (all P>0.05).

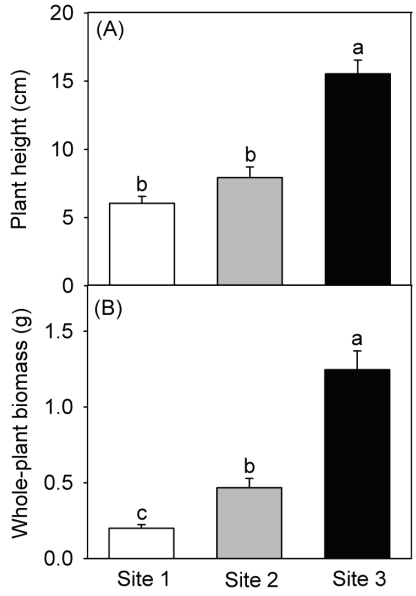

Figure 2: Plant height (A) and whole-plant biomass (B) of *Solidago canadensis* with respect to different sites. Data are means + 1 SE. The bars with shared letters represent no significant difference (P > 0.05). See text for statistical analyses.

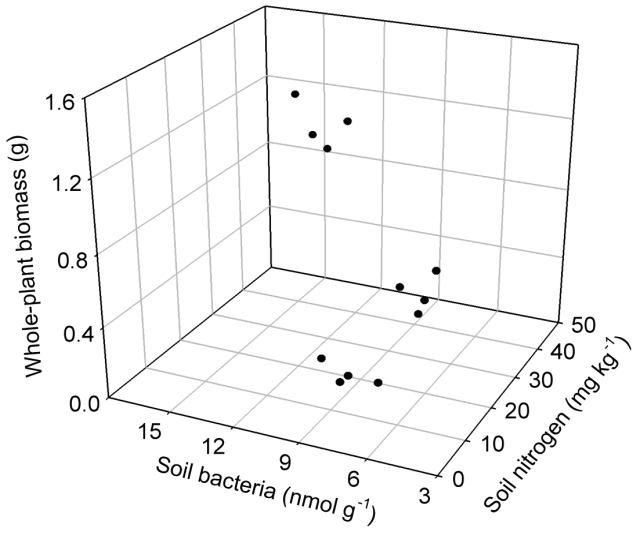

Figure 3: Three-way trait relationships among soil N, soil bacteria, and whole-plant biomass. Each filled circle represents the related values of a given site. See text for statistical analyses.

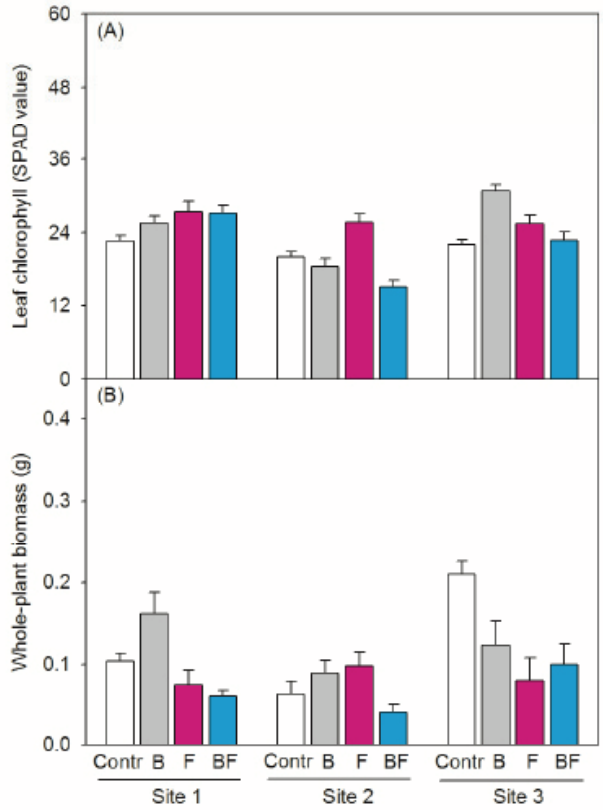

Figure 4: Leaf chlorophyll (A) and whole-plant biomass (B) of *Solidago canadensis* with respect to different sterilizations on three different sites. Contr: control; B: bactericide; F: fungicide; BF, bactericide and fungicide. Data are means + 1 SE. See text for statistical analyses.

Discussion

Soil legacies are among the most important determinants for the invasibility of a new range, and thus have become a hot issue [3,5,14,6,24]. We here focused on the soils invaded by *S. canadensis* for a few decades to address the consequences of soil abiotic and biotic legacies for its subsequent growth and the associated mechanisms. This study might add to our understanding of the importance of soil legacies as a whole in plant invasions.

The most key finding of this study was that soil abiotic and microbial legacies jointly influenced *S. canadensis* growth. Compared to the individual role of soil microbes or abiotic legacies [6,15,32], their joint role in plant invasions remains poorly understood [9,24]. We found that there were significant correlations among soil abiotic properties and/or biotic properties. More importantly, the effects of soil microbes on the growth of *S. canadensis* heavily depended on soil abiotic properties, and vice versa. These findings suggest that soil abiotic legacy pathways and biotic legacy pathways are

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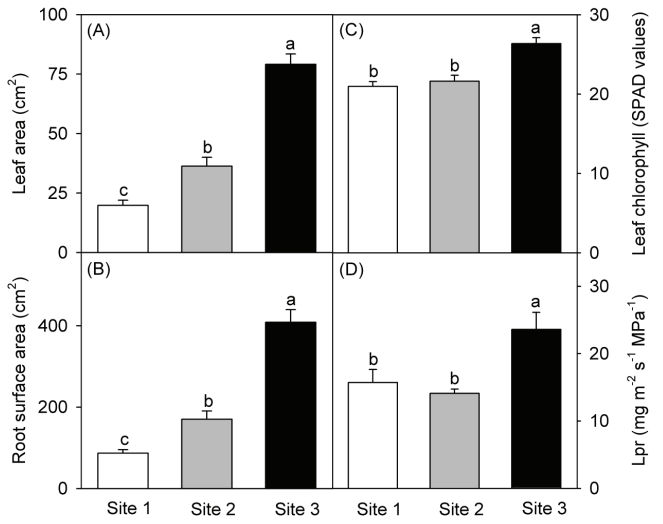

Figure 5: Total leaf area per plant (A), total root surface area per plant (B), leaf chlorophyll contents, as indicated by SPAD values (C), and root hydraulic conductivity (Lpr) (D) of *Solidago canadensis* with respect to different sites. Data are means + 1 SE. The bars with shared letters represent no significant difference ($P > 0.05$). See text for statistical analyses.

dependent on each other, but not independent. Our recent work also suggests that soil N and soil microbes jointly influence *S. canadensis* growth [24]. These findings highlight that soil abiotic and biotic legacies should be considered at the same time when addressing the role of soil as a whole in plant invasions.

Some studies suggest that soil biotic factors are more important for plant invasions than soil abiotic factors [32-34]. However, this perception is not supported by our results. When soil N and bacteria were selected as explanatory variables, soil N contributed to *S. canadensis* growth more than soil bacteria. Similar phenomenon has been found in a recent study by Dong et al., [24], who found that the interaction between *S. canadensis* and soil decreased soil available N, thereby suppressing *S. canadensis* growth greatly. Accordingly, soil N appears to play a key role in controlling *S. canadensis* invasion, and the relative importance of soil abiotic and biotic properties may depend on the soil regimes of given sites.

Plant-soil interactions commonly vary over time [32,33,35]. For the regular soils from the Chongming Island, there were substantial variations in soil abiotic and biotic properties among sites. The causes for these variations are diverse, but these variations can be partially ascribed to long-term interactions between *S. canadensis* and soil. The three sites used in our study roughly represent a gradient of invasion history [19]. Based on our results, we propose a hypothesis that the positive interactions between *S. canadensis* and its surrounding soil may accumulate over time. This hypothesis is contrary to previous findings by Diez et al. [35], who reported that negative plant-soil interactions accumulated over time. If this positive interaction is widespread, it has important implications. For example, positive plant-soil interactions enhance the dominance of a given species [6,32,36]. *Solidago canadensis* grew larger and larger along the gradient of invasion history. Thus, positive *S. canadensis*-soil interactions may be crucial to increase its dominance in the long term [11].

The second key finding of this study was that soil bacteria and fungi exhibited additive effects. When three sites were considered together, soil bacteria had neutral effects on *S. canadensis* growth. In contrast, soil fungi had positive effects on *S. canadensis* growth across three sites, suggesting that its growth strongly depends on soil fungi [19,23]. More importantly, *S. canadensis* grew much bigger in the absence of soil fungi per se than in the absence of both soil bacteria and fungi. Thus, soil bacteria and fungi might act in concert to promote the growth of *S. canadensis*, and differentially contribute to the net effects of soil microbes as a whole. In natural ecosystems, the relative dominance between soil bacteria and fungi is spatially variable [37]. This phenomenon also was detected in our study.

Microbial removal had contrasting effects on the leaf chlorophyll content and plant growth of *S. canadensis*. Specifically, bacterial removal had no effects on plant growth but enhanced leaf chlorophyll contents, fungal removal decreased plant growth but increased leaf chlorophyll contents, and the removal of soil bacteria and fungi decreased plant growth but had on effects on leaf chlorophyll contents. Thus, the decrease in biomass accumulation can enhance leaf chlorophyll contents. This group-dependent effect may allow *S. canadensis* to effectively cope with different soil microbial conditions through compensatory mechanisms.

Additionally, the effects of soil bacteria and fungi strongly depended on sites [38]. In other words, invasion history may play an important role in determining the contribution of soil microbes to *S. canadensis*, suggesting the importance of historical contingency in microbial effects [7,18]. Our findings also imply that there are complex interactions between soil microbes and soil abiotic properties. Here we proposed two possibilities for this complexity. First, due to competition for nutrients between plants and soil microbes [39,40], changes in soil nutrients can affect the functioning of soil microbes. Second, changing soil pH can influence the effects of soil microbes, because soil pH plays a dominant role in determining soil microbial communities [12,41]. Accordingly, we should address soil microbial effects in the context of multiple sites or historical contingency.

A third key finding of this study was that changes in soil legacies simultaneously altered the root and leaf performance of *S. canadensis*, thereby influencing its growth [42]. It is well-documented that roots and leaves are two fundamental interfaces between plants and their environments [43]. Accordingly, we focused on the performance of roots and leaves. In our study, root area and leaf area were coordinated. Increases in both root surface area and leaf area allowed *S. canadensis* to grow higher and larger through enhancing the uptake of soil resources and the potential of photosynthesis. These findings provide a clear framework why *S. canadensis* exhibited growth superiority along a gradient of invasion history.

However, we found that growth traits of *S. canadensis* were more sensitive to changing soil properties and had greater

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effects on its growth than its physiological traits. Theoretically, root and leaf physiological traits should be more sensitive to changing conditions than growth responses, because the former is fast variable while the latter is slow variable. In terms of final consequences, the whole-plant biomass of *S. canadensis* was linked with total leaf area and total root surface area of a plant, but unlinked with leaf chlorophyll contents and root hydraulic conductivity. Unfortunately, we do not know the exact causes for these differences.

In summary, this study suggests that soil abiotic and biotic legacies may act in concert to benefit invasive plants and highlights that soil properties play a key role in determining the invasibility of recipient communities. Soil microbial groups may differentially contribute to invasion success and this contribution varies with invasion stages. Additionally, changing soil microbial communities can affect food webs because different decomposers feed on different soil microbes [44-47].

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