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# Arbuscular mycorrhizal fungi help explain invasion success of *Solidago canadensis*

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ABSTRACT

The importance of soil microbes as a whole has long been recognized in plant invasions, yet relatively few studies address the relative importance of different soil microbial guilds. To this end, we collected soils that were conditioned by plants in 18 pairs of invaded and uninvaded communities and conducted an assemblage experiment (invasive *Solidago canadensis* and five native plants) via four inoculations. Arbuscular mycorrhizal fungi (AMF) increased the growth of *S. canadensis* and its competitive suppression (the potential of *S. canadensis* to suppress its neighboring native plants). The positive feedback effect of AMF on *S. canadensis* was stronger than their negative feedback effect on five native plants. *Solidago canadensis* grew larger and had lower competitive suppression in conspecific soils than heterospecific soils. These findings suggest that AMF play a crucial role in driving *S. canadensis* invasions and also highlight that conspecific and heterospecific soils contribute to the success of *S. canadensis* through different pathways.

## 1. Introduction

Plant invasions are a primary threat to natural ecosystems and their functioning (Lockwood et al., 2013). This consequence has stimulated a surge of interest over the past decades. Of all factors influencing plant invasions, soil microbes are thought to be a key driver (Reinhart and Callaway, 2006; Dawson and Schrama, 2016; Wróbel et al., 2019; Chen et al., 2020). For example, arbuscular mycorrhizal fungi (AMF) could help some invaders to gain growth and/or competitive advantages (Marler et al., 1999; Jin et al., 2004; Sun and He, 2010; Zhang et al., 2010; Callaway et al., 2011; Aschehoug et al., 2012; Menzel et al., 2017). Intriguingly, a recent study suggests that AMF may be a double-edged sword in plant invasions (Chen et al., 2020). More specifically, AMF may be beneficial for invasions under low phosphorus (P) conditions and the opposite is the case under high P conditions (Chen et al., 2020). Soil bacteria are indeed detrimental for invasion when acting as pathogens (Reinhart and Callaway, 2006); however, they could be beneficial for it when favoring root colonization (Baldrich and Meyers, 2019). Consequently, the amazing role of soil microbes in plant invasions has gained considerable traction.

Plant-soil feedbacks (PSFs), which can be defined as an iterative process in which plant-induced changes in the soil subsequently alter plants and soil-induced changes in plants in turn alter the soil (Brinkman et al., 2010), profoundly influence soil microbes (Klironomos, 2002; Callaway et al., 2004; Reinhart and Callaway, 2006; Suding et al., 2013; Dawson and Schrama, 2016; van der Putten et al., 2016; Wang et al., 2019). As a result, studying PSFs has become a rapidly expanding research area (Gundale et al., 2019). PSFs can benefit some invasive plants more than natives (also called as the enhanced mutualism hypothesis) (Reinhart and Callaway, 2006; Suding et al., 2013; van der Putten et al., 2016) or inhibit some invasive plants less than natives (Mangla et al., 2008). PSFs could not always favor plant invasions, in particular the presence of negative PSFs (Reinhart and Callaway, 2006; van der Putten et al., 2016). Diverse PSFs (i.e., positive, neutral or negative), to a larger extent, determine the changes in microbes in conspecific and heterospecific soils (Klironomos, 2002; Diez et al., 2010; Liang et al., 2015; Gundale et al., 2019).

There are some limitations in previous studies on the role of PSFs in plant invasions. For example, current understanding of PSF effects comes mainly from artificial soil conditioning but not natural soil conditioning (Heinze et al., 2016), and PSF-mediated soil microbes are studied as a whole and the individual role of their different components

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remains poorly understood (Callaway et al., 2011; Dong et al., 2017). Successful plant invaders commonly exclude the former native dominants where they are introduced (Callaway and Maron, 2006; Lockwood et al., 2013), and this success could seem to be associated with their superior growth and competitive ability (van Kleunen et al., 2010). Given plant invasions are always relevant to communities (Lockwood et al., 2013), PSF effects should be considered in the context of plant communities. To date, the studies examining community-level PSF effects on growth and competitive ability are relatively limited.

Our central hypothesis was that AMF may play a key role in shaping the growth and competitive ability of invasive and native plants. Our secondary hypothesis was that invasive plants may benefit more from conspecific soils than heterospecific soils in terms of growth and competitive ability. We tested these hypotheses by performing a community-level inoculation experiment with invasive *Solidago canadensis* and five native plant species (i.e., *Cichorium intybus*, *Kummerowia striata*, *Poa pratensis*, *Solidago decurrens*, and *Setaria plicata*). To completely quantify competitive ability, we simultaneously assessed competitive tolerance (the ability of a plant to avoid being suppressed by its neighboring plants) and competitive suppression (the potential of a plant to suppress its neighboring plants) (Fletcher et al., 2016).

## 2. Materials and methods

### 2.1. Study species

*Solidago canadensis* is native to North America and an invader in Europe, Asia, Australia, and New Zealand (Weber, 2003; Abhilasha et al., 2008). *Solidago canadensis* was introduced into China in 1935 and is now one of the most noxious invasive forbs in southern China (Dong et al., 2006). This invader can strongly interact with its surrounding soil (i.e., strong PSFs) (Yuan et al., 2013; Dong et al., 2015a; Dong et al., 2017) so that it is an ideal model species for understanding the role of PSF-mediated soil microbes in plant invasions.

We found that there were 4–10 plant species per 1 m × 1 m quadrat (Dong et al., 2015b). To create synthetic plant assemblages, we selected five native plant species as target species in this study. They were *Cichorium intybus* (Asteraceae, perennial forb), *Kummerowia striata* (Leguminosae, annual forb), *Poa pratensis* (Poaceae, perennial grass), *Solidago decurrens* (Asteraceae, perennial forb), and *Setaria plicata* (Poaceae, annual grass). These five species commonly occur in the range invaded by *S. canadensis* in China (Dong et al., 2015b). On the other hand, their seeds were available in 2015.

### 2.2. Sampling soils conditioned by plants in the field

Fig. 1A shows how we sampled soils that were conditioned by plants in nature. First, we selected six locations from Hangzhou, Zhoushan, Shangrao, Ningguo, Hefei, and Huainan. It is noteworthy that we sampled soils either from *S. canadensis* communities or from native communities including the above-mentioned native species (i.e., the same species from the experiment conditioned the soil in the field). These locations had the same habitat (abandoned fields) and soil type (sandy soil), and similar invasion regimes (i.e., the cover of *S. canadensis* was over 80%). The information about sampling locations is presented in Tables S1 and S2. Second, we selected three sampling sites per location (Fig. 1A), which were spaced ca. 50 m apart. Thus, these sites shared similar climatic conditions and topography. Third, we located one pair of invaded and uninvaded 1 m × 1 m communities at each site (Fig. 1A). Pairwise invaded and uninvaded communities were chosen according to the following criteria: they were spatially proximate and occurred on similar soil and topographic conditions, and they had the same dominant/subdominant native species (Powell et al., 2013). In our study, the dominant plant native species were *C. intybus*, *K. striata* or *S. plicata*. This approach has widely been used in the related studies (Gaertner et al., 2009). The invaded and uninvaded communities were 2–5 m apart, and we were sure that the *S. canadensis* roots had not entered the uninvaded communities (see below).

*Solidago canadensis* is a typical clonal plant and has numerous rhizomes (Dong et al., 2006). We attempted to locate uninvaded plant communities without *S. canadensis* rhizomes for the following criteria: no ramets (aboveground observation) and no rhizomes (digging at 0–30 cm depths). Five soil subsamples were collected from the rhizospheres of *S. canadensis* per invaded community, and five soil subsamples were taken through removing soil from the individual rhizospheres of the above-mentioned native plants per uninvaded community. All the soil subsamples from each community were composited as a soil sample (ca. 800 g). Thus, we collected 18 invaded soil samples and 18 uninvaded soil samples (Fig. 1A), which were completely independent, regardless of sources. All soil samples were shipped to the laboratory and stored at 4 °C.

Prior to our bioassay experiment, each soil sample was divided unequally into two portions: one (ca. 50 g) was used for live inoculation via the wet-sieving method (Klironomos, 2002) and the other (ca. 750 g) was mixed with vermiculite (1:1 volume) as growth substrate for the following bioassay experiment in the laboratory. This mixture (ensuring good drainage) was sterilized with a dose of 40 kGy of gamma radiation to kill soil biota and to standardize growth conditions, and then filled into pots (8 cm in diameter and 10 cm in height).

### 2.3. Assemblage-level bioassay experiment in the laboratory

We used the sterilized mixture of soil and vermiculite as growth substrate (i.e., the sterilized portion of two portions was used in the bioassay experiment). It is noteworthy that we used field soils to achieve live inoculation because they are less artificial and more feasible than experimentally conditioned soils (Brinkman et al., 2010; Heinze et al., 2015; Rutten et al., 2016). To quantify the feedback effect of soil microbes, we conducted an assemblage-level bioassay experiment (Fig. 1B). We created three plant assemblages: a monoculture of *S. canadensis* (Sc monoculture), an assemblage of both *S. canadensis* and five native plants (invaded assemblage), and an assemblage of five native plants (native assemblage) (Fig. 1B). A few seeds of each species were sown in pots; once seeds germinated, seedlings were randomly thinned to only one per species. For the Sc monoculture, one *S. canadensis* seedling was grown in a pot; for the invaded assemblage, one *S. canadensis* seedling and five native seedlings were grown in a pot (i.e., six seedlings per pot); for the native assemblage, five seedlings from five native species were grown in a pot (i.e., five seedlings per pot).

The three synthetic plant assemblages were inoculated with four different soil filtrates (i.e., inoculation treatments) from pairwise invaded and uninvaded soils (i.e., soil source) (Fig. 1B). Specifically, we divided each unsterilized soil portion (ca. 50 g) into three 10 g subsamples, and then each of the three subsamples was passed through a 250-μm sieve into a 20 mL suspension to remove larger organisms, in total three soil suspensions. The first suspension was sterilized with a dose of 40 kGy of gamma radiation as the control treatment. The second suspension was not sterilized and thus roughly represented the microbes in natural soils (hereafter referred to as all microbes). The third suspension was used to extract AMF (AMF spores on a 45-μm sieve were collected and sterilized with 10% sodium hypochlorite to remove bacteria) and the other microbial guild (filtrate passing through a 20-μm sieve was collected, hereafter referred to as AMF-free microbe). We inoculated each pot with a 20 mL suspension, because this inoculation might not alter soil nutrients and other abiotic properties substantially (Liang et al., 2015; Heinze et al., 2015). We repeated the four filtrate inoculations using 18 pairs of invaded and uninvaded soils (Fig. 1B). Accordingly, there were 432 pots in total (3 plant assemblages × 4 inoculation treatments × 18 invaded soils + 3 plant assemblages × 4 inoculation treatments × 18 uninvaded soils).

All the pots were put on a bench in a greenhouse at the Institute of Botany, Chinese Academy of Sciences, where the temperatures and

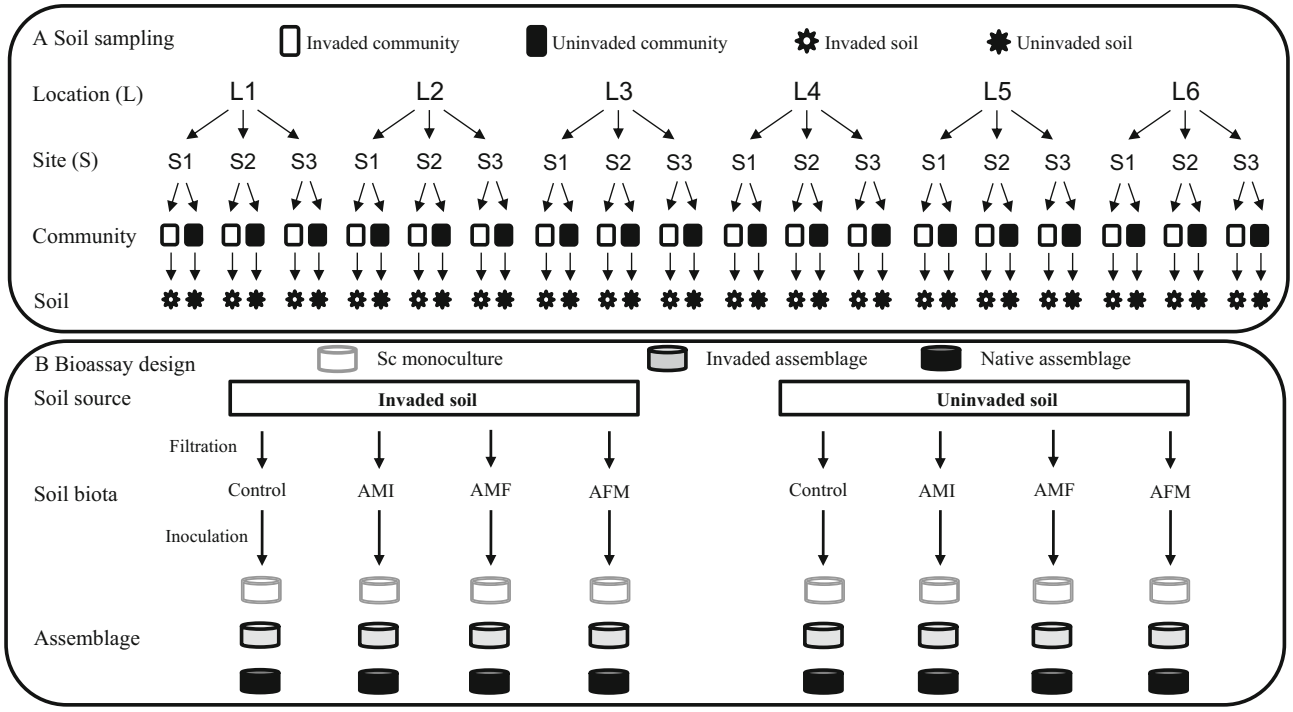


**Fig. 1.** An illustration of (A) soil sampling in the field and (B) bioassay design in the laboratory. At panel A, six sampling locations, each with three sampling sites, were selected; at each sampling site, a pair of invaded and uninvaded plant communities were chosen, and then soil was sampled from each community. At panel B, two sources of soils were filtrated to obtain four different soil microbes, and then these microbes were inoculated in the monoculture of *Solidago canadensis* (Sc monoculture), assemblage of both *S. canadensis* and native plants (invaded assemblage), and assemblage of native plants (native assemblage). AMI: all microbe; AMF: arbuscular mycorrhizal fungi; AFM: AMF-free microbe.

humidity were maintained between 20 and 30 °C and 50–60%, and the photosynthetically active radiation during the day remained above 1200 μmol $m^{-2}$ $s^{-1}$. The positions of pots were randomized during the experiment to minimize possible position effects. Water was supplied to all plants every 2–4 days, no additional fertilizer was supplied, and the other growing conditions were identical for all plants. This experiment lasted for four months, roughly corresponding to the rapid growth period in the field. All natives survived and 23 *S. canadensis* individuals died over the course of the experiment.

At the end of the experiment, all individuals in a pot were harvested, rinsed, and separated into roots and a shoot. We first collected 10 1-cm root fragments of *S. canadensis* from each experimental manipulation to determine mycorrhizal colonization. Then, the rest of the harvested plant material was oven-dried at 85 °C for 48 h and weighed. Finally, for measurements of mycorrhizal colonization, we washed root fragments with potassium hydroxide distilled water and stained them with trypan blue. Each stained root fragment was examined with a fluorescence stereomicroscope (SteREO, Carl Zeiss, Germany) at 150× magnification to determine the percentage of colonization by AMF (Liang et al., 2015). We found that the average root colonization of *S. canadensis* was 2 ± 1.0%, 65 ± 2.0%, 66 ± 2.0%, and 1 ± 0.5% for the control soil, soil inoculated with all microbes, soil inoculated AMF, and soil inoculated with AMF-free microbe.

### 2.4. Data analysis

While three different plant assemblages (i.e., Sc monoculture, invaded assemblage, and native assemblage) were involved in our competitive experiment, we focused largely on the invaded assemblage because it was a proxy of real invasions in the field and provided a stage for understanding the performance of invasive plants themselves and their effects on native plant species. Note that the Sc monoculture and native assemblage both were considered as a control only when the competitive ability of *S. canadensis* in invaded assemblages was quantified. Additionally, we concentrated on the whole-plant performance of *S. canadensis* and five native species growing in invaded assemblages. Accordingly, the whole-plant biomass, which was defined as the sum of shoot dry mass and root dry mass, was used in the following analysis. However, shoot biomass and root biomass both cannot completely reflect the whole-plant performance. We used a two-way analysis of variance (ANOVA) with Tukey *post-hoc* tests to test the effects of soil source and inoculation treatment on the whole-plant biomass of *S. canadensis* and five native plants.

We quantified PSF effects as follows (Brinkman et al., 2010):

$$\text{PSF effect} = (Bc - Bh)/Bh$$

where *Bc* is the whole-plant biomass of *S. canadensis*/native plants grown in conspecific soils and *Bh* is the whole-plant biomass of *S. canadensis*/native plants grown in heterospecific soils. When calculating the PSF effect on *S. canadensis*, the invaded soil in the field was its conspecific soil and the uninvaded soil was its heterospecific soil; when calculating the PSF effect on native plants, the uninvaded soil in the field was their conspecific soil and invaded soil was their heterospecific soil. This approach eliminated soil source so that there was only one factor (i.e., inoculation). Thus, we used a one-way ANOVA with Tukey *post-hoc* tests to test the effects of inoculation on PSF effects. A one-way ANOVA was also used to test whether PSF effects differed between *S. canadensis* and native plants.

We considered the competitive tolerance and suppression of *S. canadensis* at the same time. Recently, Fletcher et al. (2016) proposed two indices to quantify competitive tolerance (CT) and competitive suppression (CS). Here, we followed their method to quantify the competitive tolerance and suppression of *S. canadensis*.

$$CT = \frac{(Biomasss_{\_S.canadensis}\ in\ competition - Biomass_{\_S.canadensis}\ alone)}{(Biomasss_{\_S.canadensis}\ in\ competition + Biomasss_{\_S.canadensis}\ alone)}$$

$$CS = \frac{(Biomass_{\_five\ natives}\ in\ competition - Biomass_{\_five\ natives}\ alone)}{(Biomass_{\_five\ natives}\ in\ competition + Biomass_{\_five\ natives}\ alone)}$$

Biomass$_{_S.\ canadensis}$ in competition and Biomass$_{_S.\ canadensis}$ alone are the whole-plant biomass of *S. canadensis* grown in the invaded assemblage and Sc monoculture; Biomass$_{_five\ natives}$ in competition and Biomass$_{_five\ natives}$ alone are the whole-plant biomass of five native plants grown in the invaded assemblage and native assemblage. Note that a less negative CT value indicates that a *S. canadensis* individual is more tolerant to competition with five native plant species, and a more negative CS value indicates the increased ability of *S. canadensis* to suppress five neighboring species. We did not consider assemblage types as a fixed factor. This was due to the fact that the Sc monoculture and native assemblage acted as controls when calculating the competitive tolerance and suppression of *S. canadensis* in the invaded assemblages. Accordingly, we determined the effects of soil sources (i.e., conspecific versus heterospecific soil) and soil microbes (i.e., four inoculations) on the competitive tolerance and suppression of *S. canadensis* using a two-way ANOVA with Tukey *post-hoc* tests. All statistical analyses were carried out using SPSS 19.0.

## 3. Results

Two-way ANOVA showed that soil source (i.e., conspecific versus heterospecific soils) and inoculation treatment (i.e., four different inoculations) independently influenced the whole-plant biomass of *S. canadensis* in the invaded assemblages (Table 1). *Solidago canadensis* grew much larger in conspecific soils (0.459 ± 0.045 [1 SE] g) than heterospecific soils (0.332 ± 0.039 g) (Table 1: effect of soil source; Fig. 2A). Its biomass varied with inoculation treatments (Table 1: effect of inoculation; Fig. 2A): the biomass was greater when inoculating all microbes (0.595 ± 0.063 g) or AMF (0.570 ± 0.069 g) than the control (0.200 ± 0.025 g) or when inoculating AMF-free microbes (0.219 ± 0.044 g), and there were no differences between the control and AMF-free microbes or between all microbes and AMF. Soil source, inoculation treatment, and their interaction had no effects on the whole-plant biomass of five native species as a whole in the invaded assemblages (Table 1: non-significant effects of treatments; Fig. 2B).

One-way ANOVA showed that the PSF effects were unaffected by inoculation treatments, regardless of *S. canadensis* or five native plant species in the invaded assemblages (Table 1: effect of inoculation; Fig. 2C). However, the positive feedbacks on *S. canadensis* (2.23 ± 0.39) were much stronger than the negative feedbacks on native plants (−0.19 ± 0.05) in the presence of soil microbes ($F = 23.34$ [$df_{1,106}$], $P < 0.001$; Fig. 2C).

The ability of *S. canadensis* to tolerate native plants was not impacted by soil source, inoculation treatment, and their interaction (Table 1, Fig. 3A). However, its ability to suppress native plants was impacted by soil source or inoculation treatment, but not by their interaction (Table 1, Fig. 3B). Specifically, its suppression was weaker in conspecific soils (−0.129 ± 0.017) than heterospecific soils (−0.189 ± 0.021); this suppression was greater when inoculating AMF (−0.267 ± 0.031) than inoculating AMF-free microbes (−0.081 ± 0.039), and there were no differences among the control, all microbes, and AMF-free microbes (Fig. 3B).

## 4. Discussion

While the importance of AMF alone in soil has long been acknowledged in plant invasions (Marler et al., 1999; Callaway et al., 2011; Dawson and Schrama, 2016), yet relatively few studies examine the role of PSF-mediated AMF in the context of communities and natural soil conditioning. Here, we show that PSF-mediated AMF might help *S. canadensis* to perform better, supporting our central hypothesis. Our results also support the enhanced mutualism hypothesis (Reinhart and Callaway, 2006) and the paradigm that AMF must be considered as a crucial driver of plant invasions (Dawson and Schrama, 2016).

*Solidago canadensis* grew similarly in the presence of AMF and complete microbes, but grew larger in the AMF-inoculated soil than the control. Similar AMF effects have been detected at the individual level of *S. canadensis* (Jin et al., 2004; Sun and He, 2010). Such superior growth, which was induced by AMF, could be attributable to several mechanisms. For example, plant invasions can increase the richness of AMF (Gomes et al., 2018), AMF can help individuals to access soil nutrients and water (Selosse et al., 2006; van der Heijden et al., 2008; Pringle et al., 2009), and AMF can extend over several meters and be shared among different plant species (Selosse et al., 2006).

Interestingly, the positive feedback effect of AMF on *S. canadensis* was stronger than their negative feedback effect on native plants. Zhang et al. (2010) reported that soil fungi were positive for *S. canadensis* and negative for its neighbors, in line with our finding. Pendergast et al. (2013) found that soil microbes facilitated *S. canadensis* through complex belowground interactions. These diverse feedback effects of soil microbes might be linked to different types of interactions occurring among various microbial identities (Bonfante and Anca, 2009).

AMF greatly increased the competitive suppression of *S. canadensis* but not its competitive tolerance, in support of the hypothesis that successful invaders have stronger competitive suppression (Fletcher et al., 2016). Here, we propose two possibilities for this AMF-enhanced competitive suppression. First, AMF non-proportionally enhanced the growth of *S. canadensis* and native plants and thus endowed a growth advantage to *S. canadensis*. In other words, the competitive suppression of *S. canadensis* was linked to its growth advantage. Second, the root production of *S. canadensis* was enhanced due to the presence of AMF (data not shown); its competitive suppression could be partly attributed to its harmful root allelopathic effects on neighboring plants (Abhilasha et al., 2008; Zhang et al., 2010).

Interspecific competition plays a crucial role in shaping plant communities (Grace and Tilman, 1990; Levine and Rees, 2002). For

**Table 1**
The effects of soil sources (i.e., conspecific versus heterospecific soils) and/or inoculation (i.e., control, all microbe, AMF, and AMF-free microbe) on the total biomass of *Solidago canadensis* (*Solidago*) and native plants (natives), the plant-soil feedback of *S. canadensis* (PSF_*Solidago*) and native plants (PSF_natives), and the competitive tolerance (tolerance) and competitive suppression (suppression) of *S. canadensis*. Values of $P < 0.05$ are in bold. NA: not available. For plant-soil feedback effects, a one-way analysis of variance was used to test the effects of inoculation. Therefore, there are many NAs for soil source and the interaction between soil source and inoculation in the table.

| | Soil source (S) | | | Inoculation (I) | | | S × I | | |
|---|---|---|---|---|---|---|---|---|---|
| | *df* | *F* | *P* | *df* | *F* | *P* | *df* | *F* | *P* |
| Biomass of *Solidago* | 1136 | **5.952** | **0.016** | 3136 | **17.20** | **0.000** | 3136 | 0.577 | 0.644 |
| Biomass of natives | 1136 | 1.048 | 0.308 | 3136 | 0.632 | 0.595 | 3136 | 0.723 | 0.540 |
| PSF_*Solidago* | NA | NA | NA | 3,68 | 1.198 | 0.317 | NA | NA | NA |
| PSF_natives | NA | NA | NA | 3,68 | 2.155 | 0.101 | NA | NA | NA |
| Tolerance | 1136 | 2.720 | 0.101 | 3136 | 1.905 | 0.132 | 3136 | 2.075 | 0.106 |
| Suppression | 1136 | **5.199** | **0.024** | 3136 | **5.004** | **0.003** | 3136 | 0.630 | 0.597 |

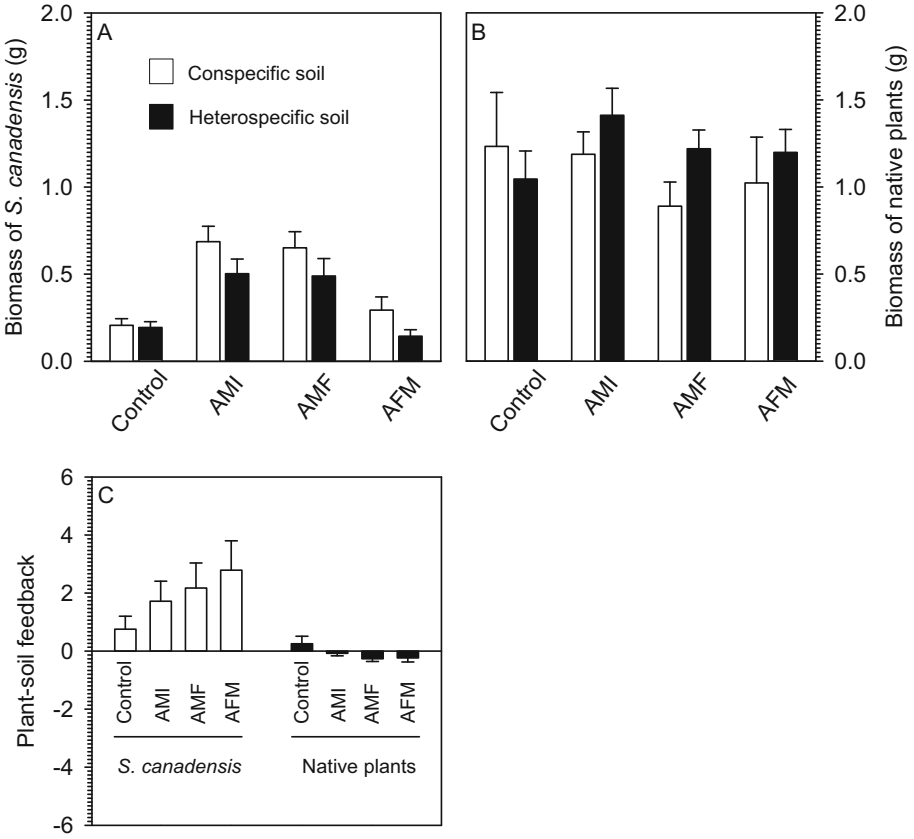


**Fig. 2.** The whole-plant biomass of (A) *Solidago canadensis* and (B) native plants as affected by different microbial filtrates from conspecific and heterospecific soils, and (C) the plant-soil feedback of *S. canadensis* and native plants grown under different soil microbial filtrates. Data are means +1 SE. AMI: all microbe; AMF: arbuscular mycorrhizal fungi; AFM: AMF-free microbe.

example, competitive exclusion could shift dominance in herbaceous vegetation (Grime, 1973). The AMF-enhanced competitive ability of *S. canadensis* might have a few benefits for its invasion. First, AMF could help *S. canadensis* to become a good competitor in invaded ranges (Marler et al., 1999; Jin et al., 2004; Sun and He, 2010; Zhang et al., 2010; Callaway et al., 2011; Aschehoug et al., 2012; Menzel et al., 2017). Second, this enhanced competitive ability could increase the dominance of *S. canadensis* in invaded plant communities and thus decrease the dominance of the other species, because AMF are ubiquitous in the field (Brundrett, 2009; Pringle et al., 2009). Additionally, our findings could, to some extent, explain why *S. canadensis* invasion decreased the richness of native plant species (i.e., competitive exclusion) (Dong et al., 2015b).

*Solidago canadensis* grew larger in conspecific soils than heterospecific soils, supporting our secondary hypothesis. This differential growth response of *S. canadensis* could be ascribed to the differences in soil microbial composition and abundance between conspecific and heterospecific soils (Perkins and Nowak, 2013; DeBellis et al., 2019). Additionally, plant invaders can modify soils in a way that benefits their growth more than the growth of native plants (Crawford and Knight, 2017). However, we did not identify microbes from conspecific and heterospecific soils so that we failed to know the exact difference in this aspect. Zhang et al. (2010) found that *S. canadensis* altered AMF spore composition by increasing *Glomus geosporum* while reducing *G. mosseae*. In contrast, the growth of five native plants was unchanged with soil source. These opposing responses to soil sources between invasive and native plants highlight that *S. canadensis* is more likely to obtain a growth advantage over native plants once it invades

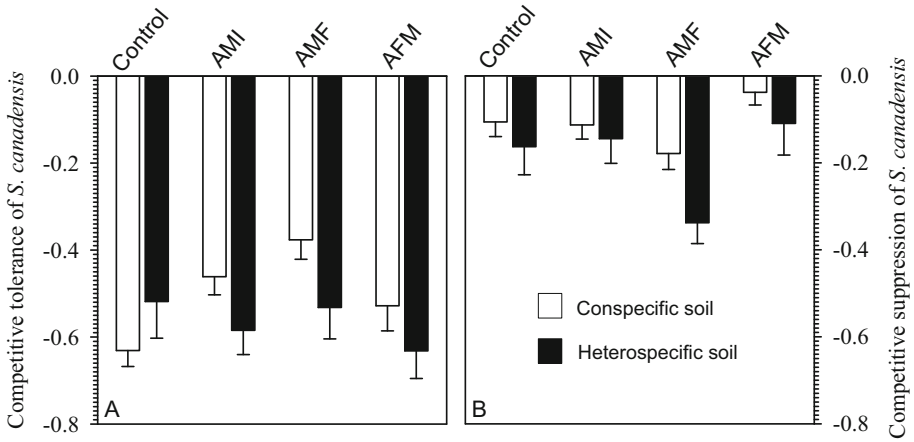


**Fig. 3.** (A) The competitive tolerance and (B) competitive suppression of *Solidago canadensis* as affected by different microbial filtrates from conspecific and heterospecific soils. Data are means +1 SE. AMI: all microbe; AMF: arbuscular mycorrhizal fungi; AFM: AMF-free microbe.

recipient communities.

As opposed to our secondary hypothesis, *S. canadensis* did not exhibit stronger competitive ability in conspecific soils than heterospecific soils. However, *S. canadensis* had similar tolerance between two soil sources and its suppression was weaker in conspecific soils than heterospecific soils. This finding suggests that the competitive tolerance and suppression of *S. canadensis* might not be congruent. Overall, these patterns could be related to the microbial regimes of conspecific and heterospecific soils (Perkins and Nowak, 2013). For example, rhizospheric microbes depend strongly on the identity of plant species (e.g., $C_3$ and $C_4$ plants) (DeBellis et al., 2019). Our finding that *S. canadensis* exhibited greater competitive suppression in uninvaded soils might help us to partly understand why some novel plant communities are susceptible to *S. canadensis* in the field.

We found that soil fungi and bacteria had different effects on the growth and competitive ability of *S. canadensis* (Sun and He, 2018). AMF effects on plant invasion may vary with soil P availability (Chen et al., 2020). Soil bacteria may be a double-edge sword in plant invasions depending on their specific functions (Reinhart and Callaway, 2006; Baldrich and Meyers, 2019). In this study, the < 20 μm filtrate contained bacteria and fungi, and the < 250 μm filtrate included bacteria, fungi, and some mesofauna (Wagg et al., 2014). While these filtrates had overlapped microbial components (Wagg et al., 2014), they indeed had disparate influences on the growth and competitive ability of *S. canadensis* (Figs. 2, 3). As a result, our findings, combined with other findings, suggest that different soil microbial components might play differential roles in regulating the performance of invasive plants.

## 5. Conclusions

This study provides community-level evidence that AMF may play a key role in *S. canadensis* invasion and that conspecific and heterospecific soils both could facilitate its invasion. Specifically, AMF simultaneously increased its growth and competitive ability, which are two key drivers of plant invasion success (van Kleunen et al., 2010; Lockwood et al., 2013); conspecific soils could favor *S. canadensis* to persist in invaded plant communities due to its superior growth, and heterospecific soils might help *S. canadensis* to spread into new communities due to its increased competitive suppression. Consequently, PSF microbial effects could favor *S. canadensis* communities to develop towards monocultures. Future PSF experiments that include competition and different soil microbial guilds, which are important factors shaping plant communities (Casper and Castelli, 2007; Wagg et al., 2014; Lekberg et al., 2018), will be useful for understanding invasion success.

## Submission declaration

The authors declare that all the presented data have neither been already published nor are they being considered for publication elsewhere.

## CRediT authorship contribution statement

WMH and LJD conceived and designed the experiments. LJD and LNM performed the experiments. WMH, LJD and LNM analyzed the data and wrote the manuscript.

## Declaration of competing interest

The authors declare that they have no conflict of interest.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2020.103763.

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