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Soil legacies of a primary invader strongly drive secondary invasions for species that are phylogenetically distant

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ABSTRACT

Invasive plant species can alter soil abiotic and biotic properties, with some changes persisting long after the primary invader's eradication. However, how soil legacies will influence secondary invasions following control of primary invaders remains unclear, hindering development of targeted control and post-removal management strategies. We used *Solidago canadensis* as the primary invader and established five field soil conditioning treatments: control (bare plots), invasion treatment (unmanaged invaded plots), three management treatments (invaded plots managed by cutting, herbicide application or burning). Subsequently, we assessed responses of nine pairs of secondary invaders and native congeners in these conditioned soils within a greenhouse setting. We found that *Solidago* invasion decreased soil nutrients including available nitrogen, phosphorus and potassium and increased soil pathogen diversity. While these soil legacies reduced the growth of both secondary invaders and native congeners, they disproportionately enhanced the biomass advantage of secondary invaders, resulting in a predisposition to secondary invasions. Compared to unmanaged invaded plots, cutting did not further modify soil properties, and both herbicide application and burning had no effect on soil pathogen diversity but strongly increased soil available nutrients. Consequently, cutting had no impact on secondary invasions, while increased available nutrients in herbicide application and burning treatments weakened the intensity of secondary invasions. Notably, secondary invaders distantly related to *Solidago* benefited more from soil legacies, irrespective of management method. These results underscore the role of soil legacy effects in facilitating secondary invasions and highlight phylogenetic distance from the primary invader as a crucial factor in determining secondary invader success.

1. Introduction

Management of invasive plants has received considerable attention because of the growing recognition that invasive plants can pose substantial threats to biodiversity, infrastructure and public health (Early et al., 2016; Schaffner et al., 2020). Successful management actions not only aim to reduce the abundance and spread of the target invader but also to reestablish the diverse native community with its ecosystem functions and services (D'Antonio and Meyerson, 2002; Suding et al., 2004; Pearson and Ortega, 2009). In many cases, however, invaded ecosystems are unable to return to their original state even when the target invaders have been eliminated completely (Reid et al., 2009). This is partly due to the fact that other invaders rapidly occupy vacant space, as co-occurrence of multiple invasive plant species is common in most ecosystems (Kuebbing et al., 2013; D'Antonio et al., 2017; Shen et al., 2023). This process is termed "secondary invasion" and is considered as one of the major obstacles to ecological restoration (Pearson et al., 2016). So far, mechanisms underlying secondary invasions remain unclear, which limits the selection of both efficient management and post-removal management actions and thereby hinders ecological

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restoration.

Invasive plants can affect a wide range of soil chemical and biological properties through absorption and exploitation of resources, as well as by adding litter and chemicals to the soil (Dickie et al., 2014; Zhang et al., 2019). Many studies have documented that the eradication of a target invader does not directly lead to the recovery of target invader-mediated changes in soil properties, and some changes could even persist many years after eradication (Corbin and D'Antonio, 2012; Lankau et al., 2014; Nsikani et al., 2017). Therefore, secondary invaders experience soil legacies created by the target invader. As soil legacy

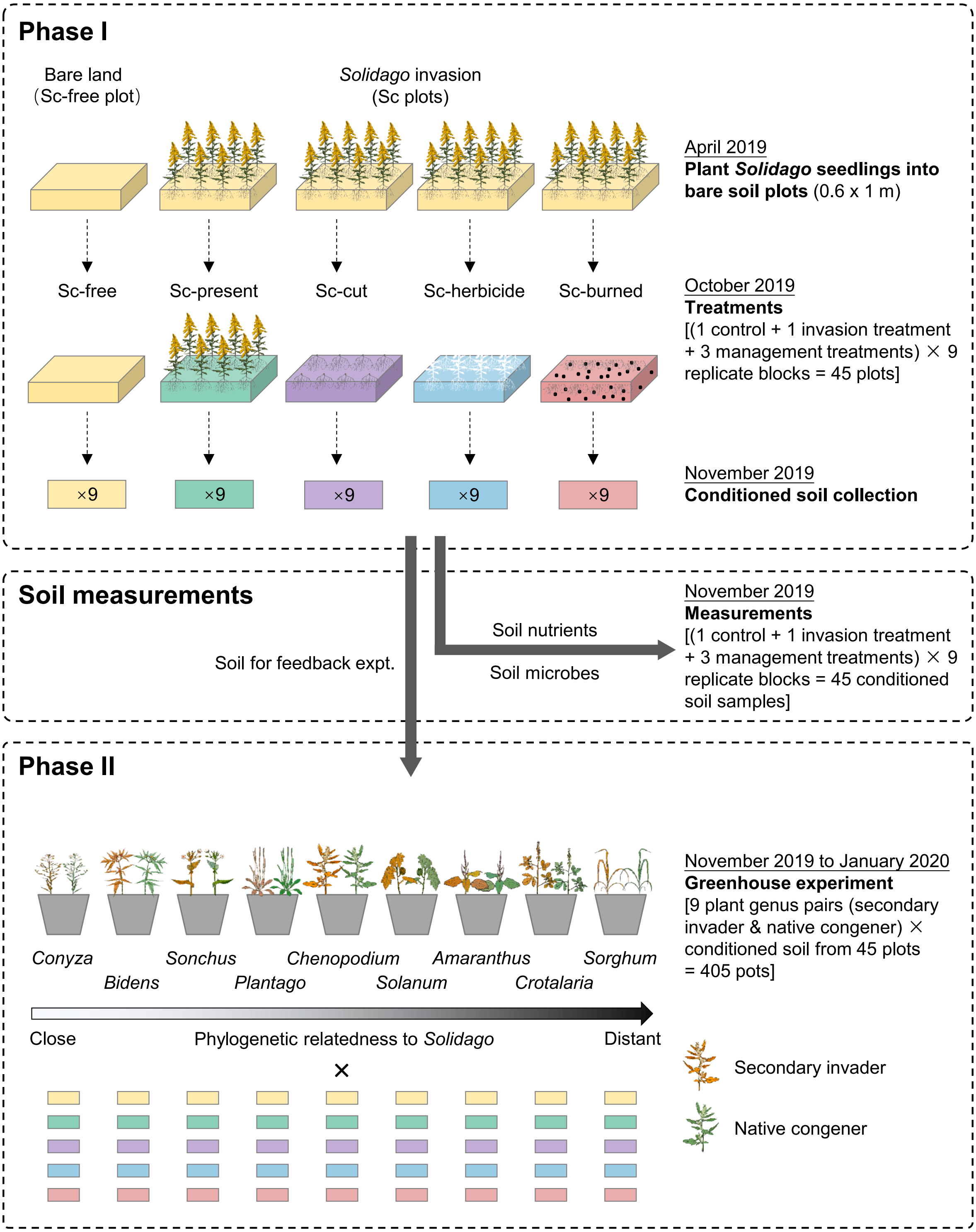

Fig. 1. Graphical illustration of the two-phase experiment. In phase I, we used *Solidago* as primary invader and established five types of plots in the field, including one control (bare land, Sc-free), one invasion treatment [*Solidago* invasion plots without management (Sc-present)] and three management treatments [*Solidago* invasion plots managed by cutting (Sc-cut), herbicide application (Sc-herbicide) or burning (Sc-burned)]. At the end of this phase, we collected soils which were divided into two subsamples, with one for soil property measurements and the other for phase II. In phase II, we examined the growth responses of nine pairs of secondary invaders and native congeners that varied in their phylogenetic relatedness to *Solidago* to the conditioned soil in greenhouse pots. Species information and phylogenetic relatedness among tested species are in Table S1 and Fig. S3, respectively. The illustration was made by Changchao Shen.

effects are documented to affect plant community assembly and successional trajectories (Wubs et al., 2019; Heinen et al., 2020), such effects caused by an initial target invader are thus also likely to affect secondary invaders. Yet to date, little is known about the causal relationship between soil legacies and secondary invasion mainly due to the lack of experimental evidence that links soil abiotic and biotic properties to the outcome of secondary invasions.

Little is also known about which secondary invaders will be specifically affected by soil legacies following target invader eradication. Darwin's naturalization hypothesis postulates that non-native species that are distantly related to native species in a community are more likely to invade successfully due to reduced competition (Daehler, 2001). In contrast, the pre-adaptation hypothesis posits that non-native species closely related to native species in a community are more likely to invade successfully because they share similar environmental adaptations (Ricciardi and Mottiar, 2006). Therefore, the phylogenetic relatedness of secondary invaders to the target invader that was removed could shape the success of secondary invaders. If resource competition is the major driver in secondary invasion, soil legacies could promote the colonization of secondary invaders that are distantly related to the target invader due to unexploited resources. This may also occur if distantly related secondary invaders are less likely to share pathogens with the target invader. Conversely, if secondary invasion is primarily driven by environmental adaptations, soil legacies would favor colonization of secondary invaders that are closely related to the target invader as they share similar adaptations to the changed soil conditions.

Solidago canadensis (Asteraceae, herafter "*Solidago*") is a herbaceous perennial native to North America that is invasive in large parts of Asia, Europe and Oceania (Dong et al., 2006). It often forms monospecific stands and modifies soil properties (Zhang et al., 2009; Pal et al., 2015). It is commonly managed by herbicides, manual cutting or prescribed burning (Zhang and Wan, 2017). These methods all cause soil disturbance that will inevitably influence soil abiotic and biotic properties. For instance, previous studies found increased soil nitrogen availability and microbial biomass nitrogen (Taylor and Midgley, 2018), and reduced bacterial and fungal abundance and altered bacterial and fungal composition (Glassman et al., 2023), after prescribed burning to control invasive plants in grasslands and forests. Thus, soil legacies following *Solidago* removal, and their impacts on secondary invasions, may further depend on management methods.

In this study, we used *Solidago* as the primary invader and established five soil conditioning treatments in a field: control (bare plot), invasion treatment (*Solidago* invasion plot without subsequent management), three management treatments (*Solidago* invasion plots managed by cutting, herbicide application or burning). Subsequently, we assessed the growth responses of nine pairs of secondary invaders and native congeners in these conditioned soils within a greenhouse setting (Fig. 1). To evaluate secondary invasion, we calculated the biomass ratio of the secondary invader in each pot by dividing the secondary invader's biomass by the total plant biomass of both the secondary invader and its native congener. A higher biomass ratio in invasion or management treatment pots compared to control pots suggests that soil legacies from *Solidago* invasion or its managements enhance the relative performance of secondary invaders over native congeners, thereby facilitating secondary invasion. This study aimed to address three key questions: (1) How do *Solidago* invasion and different management methods influence soil abiotic and biotic properties? (2) How do these soil properties affect the performance of secondary invaders and native congeners, thereby impacting secondary invasion? (3) How does secondary invasion depend on phylogenetic relatedness to *Solidago*?

2. Materials and methods

2.1. Study species and seed collections

In this study, we used *Solidago* as the primary invader. *Solidago* was introduced to China (Shanghai) in 1935 as an ornamental and has become a problematic invader, particularly in central and eastern China (Dong et al., 2006; Zhang and Wan, 2017). In the Wuhan area of central China, it typically invades bare land (Fig. S1). We collected a bulk sample from seeds of 15–30 individuals at each of five sites at least 2 km apart in suburban Wuhan (30.51°N, 114.54°E). As secondary invaders, we selected nine species that are invasive in China, comprising seven forbs, one legume, and one grass (Table S1). To create phylogenetically related pairs of secondary invaders and native plants, and to conduct a phylogenetically controlled comparison, we selected a native species within the same genus for each secondary invader (Table S1). All invasive and native species are common in Wuhan. We collected seeds of all invasive species and six native species using the same protocol described above for *Solidago*, and obtained seeds of three native species from the Germplasm Bank of Wild Species of China due to missed seed collection times (Table S1).

2.2. Phase I: conditioning soil in a field experiment

In order to facilitate the implementation of the various management treatments used to control *Solidago* (e.g. burning), we performed a field experiment. In February 2019, we selected an abandoned farmland that was occupied by typical native vegetation at Wuhan Botanical Garden (30.15°N, 114.30°E). We removed the standing vegetation and ploughed the topsoil to a depth of 15 cm to minimize potential confounding effects from any pre-existing vegetation. Then, we established nine blocks (0.6 × 9 m) and divided each into five plots (0.6 × 1 m). Blocks were separated by 2 m, and plots within each block were separated by 1 m. In early April, we randomly selected one plot within each block and maintained it as bare soil by weekly manual removal of all vegetation, ensuring no plant growth throughout the soil conditioning phase ("Sc-free" plot, Fig. 1). We used Sc-free plots as controls because *Solidago* commonly colonizes recently disturbed, open habitats (Fig. S1), and the presence of other vegetation in control plots might confound soil property measurements due to species-specific effects. Meanwhile, we established *Solidago* monoculture stands in the other four plots ("Sc" plots, Fig. 1). We germinated the *Solidago* seeds in seedling trays filled with soil substrate (Klasmann-Deilmann GmbH, Geeste, Germany) in a greenhouse (16/8 h light/dark cycle, 26 °C during the day and 18 °C at night, 50–70 % humidity). We transplanted eight similar-sized *Solidago* seedlings (5 cm in height) into each *Solidago* plot, spacing them 20 cm apart, which represents densities in heavily invaded sites from where we collected the seeds (8.2 ± 0.5 individuals/0.6 m^2 as measured in 30 plots). This procedure of newly established stands with constant density helps to avoid potential impacts of different durations and severities of *Solidago* invasions on soil properties. During the first two weeks after transplanting, we monitored the survival of *Solidago* seedlings and replaced dead seedlings. We removed all plants other than our planted *Solidago* from the plots every week over the whole conditioning phase. This frequent eradication of non-planted species minimizes their impacts on soil properties and thus on *Solidago*.

At the study site, *Solidago* typically starts to produce seeds by the end of October and management just before the reproductive stage is considered one of the most effective times to control this species (Dong et al., 2006). In early October 2019, we randomly assigned the four Sc plots within each block to an unmanaged *Solidago* invasion treatment ("Sc-present") or one of three management treatments: cutting ("Sc-cut"), herbicide application ("Sc-herbicide") or burning ("Sc-burned") (Fig. 1). For Sc-cut, we cut plants at the base of the stem using a sickle and removed the aboveground parts from the plots. For Sc-herbicide, we sprayed Roundup (41 % Glyphosate isopropyl ammonium salt AS, Monsanto Company, MO, USA) at the manufacturer's recommended rate of 9 L/ha. For Sc-burned, we first cut the aboveground parts of *Solidago* and placed them in the plot. We then applied 200 mL of gasoline as a combustion promoter and ignited the biomass using a lighter. Each plot experienced a surface fire lasting approximately 10 min. The fire consumed the *Solidago* biomass and litter, simulating the conditions of a typical prescribed burn used in *Solidago* management.

We collected topsoil from the center of each plot (80 × 40 × 15 cm, length × width × depth, approximately 48 L) one month after treatment applications (Fig. 1). Thus, total duration of conditioning phase was seven months (six months before management and one month after management). Soil of each plot (N = 45, 9 blocks × 5 treatments) was filtered through an 8 mm sieve to remove stones, roots and macroinvertebrates. Then, soil of each plot was divided into two subsamples, with one kept at −20 °C for soil property measurements, which were finished within a week, and the other at 4 °C for immediately testing soil legacy effects on nine pairs of secondary invaders and their native congeners (Fig. 1). During the conditioning phase (April to October), the total precipitation and average temperature were 783.1 mm and 24.1 °C, respectively, which were within the normal variation between 2009 and 2018 recorded for Wuhan (Hubei Provincial Statistics Bureau: https://tjj.hubei.gov.cn/).

2.3. Analyses of soil nutrients and microbes

To determine soil available nutrients, we measured available nitrogen (AN), available phosphorus (AP) and available potassium (AK). AN was determined using the alkaline hydrolysis diffusion method (Lu, 2000). Briefly, 5 g soil was incubated with an alkaline $KMnO_4$ solution. Ammonia released during hydrolysis was captured in a boric acid solution and quantified by titration with standard sulfuric acid. AP was measured using the Olsen method (Olsen et al., 1954). Soils were extracted with 0.5 M $NaHCO_3$ and the extract was then reacted with ammonium molybdate and ascorbic acid, and absorbance was measured at 880 nm using a spectrophotometer (UV-8500, Tianmei Co., Shanghai, China). AK was extracted with 1 M NH_4OAc (ammonium acetate) solution and quantified using a flame photometer (M410, Sherwood Scientific Ltd, Cambridge, UK) (Sparks et al., 1996). We also measured total carbon (TC), total nitrogen (TN), and total phosphorus (TP). However, these metrics are less indicative of plant-available nutrient pools and showed weaker associations with secondary invasion compared to AN, AP and AK. As a result, we focused our analysis and reporting on the more ecologically relevant available nutrients.

To characterize the soil fungal community, we extracted DNA using the PowerSoil DNA Isolation Kit (MoBio Laboratories, CA, USA) and measured the DNA quality and concentrations using a NanoDrop 2000 spectrophotometer (Thermo Scientific, Waltham, MA, USA). Then, we analyzed the DNA samples with concentrations higher than 10 ng/μL using a sequencing platform (NovaSeq 6000, Illumina, CA, USA). The primer pair ITS7F (5′-GTGARTCATCGAATCTTTG-3′) and ITS4R (5′-TCCTCCGCTTATTGATATGC-3′) was used to amplify the fungal ITS2 region (Ihrmark et al., 2012). The raw reads were merged using FLASH. The merged sequences were denoised and then used to generate an amplicon sequence variant (ASV) feature table with the DADA2 algorithm in QIIME2 (Callahan et al., 2016). Taxonomic assignment was conducted using the scikit-learn method (Pedregosa et al., 2011) based on the UNITE database (10.05.2021 release). The sequencing data were rarefied to 26,670 according to the minimum sequence number among all soil samples for diversity comparison. Rarefaction curves were assembled, and the rarefaction curves were almost saturated at the rarefaction depths used in this study (Fig. S2), suggesting that the current sequencing and rarefying depths were large enough to capture the community diversities for almost all samples. Finally, we categorized fungal ASVs into the pathogen functional group using the FUNGuild database (Nguyen et al., 2016). A total of 153 ASVs of putative pathogens were recorded. Glomeromycota (AMF) had extremely low abundances in most soil samples, so we did not further analyze the AMF data.

2.4. Phase II: interspecific competition in response to soil legacy

To examine the responses of secondary invaders and native congeners to soils conditioned by different treatments, we conducted a whole-soil experiment that allowed us to detect the effects of both abiotic and biotic soil properties (Fig. 1). Specifically, we divided the conditioned soil of each plot into nine 1.4 L portions and added them to each of nine 1.5 L plastic pots. To prevent cross contamination within and among treatments, we added a layer of sterilized sand (1 cm) on the top of each pot and placed pots on separate plastic dishes. We geminated seeds of each species as described above in the phase I. We transplanted similar-sized seedlings (2 cm in height) of each of the nine plant pairs (secondary invader and native congener) into the prepared pots, with one seedling per species (Fig. 1). The final design consisted of 405 pots (5 types of conditioned soils × 9 field blocks × 9 plant genus pairs; Fig. 1). As secondary invasion mainly depends on the relative performance of secondary invaders to co-occurring natives, we grew paired congener together under interspecific competition. Pots filled with soil from the same field block were arranged on a table (45 pots per table) and kept under the greenhouse conditions as described above. Throughout the experiment, we watered plants every 2–3 days, randomized pots on each table every week and changed table positions every two weeks. In most plant-soil feedback experiments, plant biomass is widely considered as a key metric to assess plant responses and competitive dynamics (Brinkman et al., 2010; Tao et al., 2024b; Yi et al., 2025). Therefore, after three months of growth, we separately harvested total (above- and belowground) biomass of the secondary invader and native congener in each pot, dried them at 80 °C for 72 h, and weighed them.

2.5. Analysis of phylogenetic relatedness

To calculate phylogenetic distances between *Solidago* and the nine pairs of congeneric plants at the genus level, we used four commonly sequenced genes (*mat*K, *rbc*L, ITS and *psb*A-*trn*H) of each secondary invader from GenBank (Table S1) and included *Amborella trichopoda* that diverged early in angiosperm evolution as an out-group (Cadotte et al., 2008). First, we independently aligned each separate DNA region using MUSCLE in the MEGA platform (v.10.1.7) (Tamura et al., 2011). We performed maximum likelihood searches on each separate region to check for outliers, which were diagnosed as long branches. No outliers were identified and no strongly supported conflict was found among DNA regions in separate analyses by DNA region. Then, we concatenated separate DNA regions into a single “supermatrix” using a total evidence approach (de Queiroz and Gatesy, 2007). After selecting the best-fit model (GTR + F + R3) of nucleotide substitution for the supermatrix by ModelFinder, we conducted maximum likelihood searches in IQ-TREE (v. 1.6.12) and 1000 bootstrap replicates to estimate confidence in each clade (Nguyen et al., 2015). The resulting phylogenetic tree is shown in Fig. S3. Finally, we calculated the phylogenetic distance in substitutions per site to *Solidago* for each genus from this phylogenetic distance matrix.

2.6. Data analyses

All analyses were conducted in R (version 4.0.5, R development Core Team) using “glmmTMB”, “emmeans”, “randomForest”, “vegan” and “piecewiseSEM” packages. Multiple comparisons were conducted using least squares means (LSM) post-hoc tests and *P* values were adjusted using false discovery rate (FDR).

To examine how soil conditioning treatments (Sc-free, Sc-present, Sc-cut, Sc-herbicide, or Sc-burned) affected soil properties in phase I, we performed generalized linear mixed models (GLMMs) separately for each available nutrient, ASV richness and Shannon diversity of putative fungal pathogens along with relative abundance of *Curvularia* (the pathogens with the most reads) with block as a random factor. We used a Poisson distribution for discrete response variables (e.g., ASV richness) and a Gaussian distribution for continuous response variables (e.g., AN, AP, AK). To explore the differences in community composition of putative pathogens among soil conditioning treatments, we performed principal coordinate analyses (PCoA, based on Bray-Curtis distance) followed by permutational multivariate analysis of variance (PerMANOVA, 999 permutations).

To examine how soil conditioning treatments affected plant growth and secondary invasion in phase II, we calculated total plant biomass (secondary invader + native congener) and biomass ratio of the secondary invader (secondary invader/total plant biomass) in a pot. Total plant biomass reflects overall response of plants in the pots, whereas the biomass ratio indicates whether the invader outperforms the native under given conditions (Niu et al., 2007; Yuan et al., 2013). A higher biomass ratio in invasion or management treatment pots compared to control pots suggests that soil legacies from *Solidago* invasion or management after its invasion enhance the relative performance of secondary invaders over native congeners, thereby facilitating secondary invasion. We performed GLMMs (Gaussian distribution) on total plant biomass and biomass ratio of secondary invader with soil conditioning treatment as the fixed factor, with plant genus and field plot nested within block (corresponding to greenhouse table in the phase II) as random factors accounting for the non-independence of the plants grown in the soil coming from the same plot. Total plant biomass was $\log_{10}$-transformed prior to analysis to meet the assumption of normal distribution of residuals.

To explore the relative importance of phylogenetic relatedness and soil properties in determining secondary invasion, we performed a random forest regression on the biomass ratio of secondary invader (excluding Sc-free to focus on management of *Solidago*). The random forest analysis evaluates the importance of each variable by looking at how much the mean square error (MSE) increased when the data for that variable is permuted randomly while others remain unchanged (Breiman, 2001).

To specifically explore the effect of phylogenetic relatedness, we performed GLMMs for total plant biomass and biomass ratio of secondary invader with the fixed factors of phylogenetic distance between the primary invader and secondary invaders, soil conditioning treatment and their interaction and the random factor of field plot nested within block. We carried out pairwise comparisons of the slopes of different treatments as a follow-up to a significant interaction term.

To specifically investigate how management methods mediated secondary invasions via modifying soil properties compared to Sc-present, we conducted piecewise structural equation models (SEM) for each management treatment (Sc-cut, Sc-herbicide or Sc-burned). This illustrates the different pathways through which management treatment influenced the biomass ratio of secondary invader. We conducted a SEM with paths from each soil property identified as important in the random forest model to the biomass ratio of secondary invader using data from Sc-cut, Sc-herbicide, Sc-burned and Sc-present treatments. These properties included AN, AP, AK, pathogen diversity, pathogen PCoA1 and relative abundance of *Curvularia*. A stepwise removal of the least significant paths from the models was conducted and Fisher's C statistic and Akaike information criteria (AIC) were used to evaluate the fit of the models. Then we conducted a separate SEM for each management treatment with a dummy variable (Sc-cut, Sc-herbicide or Sc-burned vs. Sc-present; 1 vs. 0) as a categorical exogenous variable, and each soil property retained in the initial SEM as an endogenous variable.

3. Results

3.1. *Solidago invasion and managements change soil properties*

Soil available nutrients were strongly affected by treatments (Fig. 2a–c). Compared to Sc-free, Sc-present significantly reduced soil AN, AP and AK (Fig. 2a–c). Furthermore, management treatments differentially impacted soil properties. Specifically, compared to Sc-present, Sc-cut did not further change these soil available nutrients (Fig. 2a–c), while Sc-herbicide increased AN but not to the level of Sc-free (Fig. 2a), and Sc-burned increased AP and AK to the level of Sc-free (Fig. 2b and c).

Putative soil fungal pathogens were also strongly affected by treatments (Fig. 2d–f). Compared to Sc-free, Sc-present did not affect pathogen richness (Fig. 2d) but increased pathogen Shannon diversity (Fig. 2e). Management treatments further modified soil fungal pathogen communities. Compared to Sc-present, Sc-cut and Sc-herbicide increased pathogen richness (Fig. 2d). Fungal pathogens were mainly composed of the genus *Curvularia* with their relative abundance up to 74.36 % of all fungal pathogens (Fig. S4). Compared to Sc-free, Sc-present strongly reduced the relative abundance of the dominant pathogen *Curvularia* (Fig. S5). Moreover, treatments also altered the community composition of pathogens, especially for Sc-burned that had dissimilar community structure to other treatments (Fig. 2f).

3.2. *Soil legacies inhibit plant growth, but promote secondary invasion*

Total plants biomass in a pot (secondary invader + native congener) and biomass ratio of secondary invader (secondary invader/total) depended significantly on the soil conditioning treatment (Fig. 3). Soils conditioned by *Solidago* invasion and management treatments significantly decreased total plant biomass, compared to soils conditioned by Sc-free (Fig. 3a). The negative impact on total plant biomass was stronger in soils conditioned by Sc-present, and weaker in soils conditioned by Sc-herbicide or Sc-burned (Fig. 3a). In contrast, soils conditioned by *Solidago* invasion and management treatments significantly increased the biomass ratios of secondary invaders, compared to soils conditioned by Sc-free (Fig. 3b). Positive impacts on secondary invaders were stronger in soils conditioned by Sc-present or Sc-cut, and weaker in soils conditioned by Sc-herbicide or Sc-burned (Fig. 3b).

3.3. *Secondary invasion depends on phylogenetic relatedness and soil properties*

The random forest regression showed that phylogenetic distance between secondary invaders and the primary invader was the most important determinant of the biomass ratio of secondary invader (Fig. 4). Furthermore, soil properties such as AN, AP, AK, pathogen PCoA1, and pathogen diversity significantly affected the biomass ratio of secondary invader (Fig. 4).

Total plant biomass in a pot only depended on soil conditioning treatment, but not phylogenetic distance or their interaction (Fig. 5a). But, the biomass ratio of secondary invader depended on phylogenetic distance, soil conditioning treatment and their interaction (Fig. 5b). Specifically, the biomass ratio of secondary invader increased significantly with increasing phylogenetic distance between secondary invaders and the primary invader in the treatments Sc-present, Sc-cut, Sc-herbicide and Sc-burned, but not in Sc-free (Fig. 5b). However, there were no significant differences in the slopes for phylogenetic distance among Sc-present, Sc-cut, Sc-herbicide and Sc-burned but they each differed from Sc-free (Table S2).

The SEM showed that the biomass ratio of secondary invader was negatively related to AN and AP contents (Fig. 6). Sc-cut, Sc-herbicide and Sc-burned all increased AN (Fig. 6). Sc-cut tended to decrease AP while Sc-herbicide and Sc-burned increased it (Fig. 6). The net effect of Sc-cut on biomass ratio was weak due to off-setting effects via increased

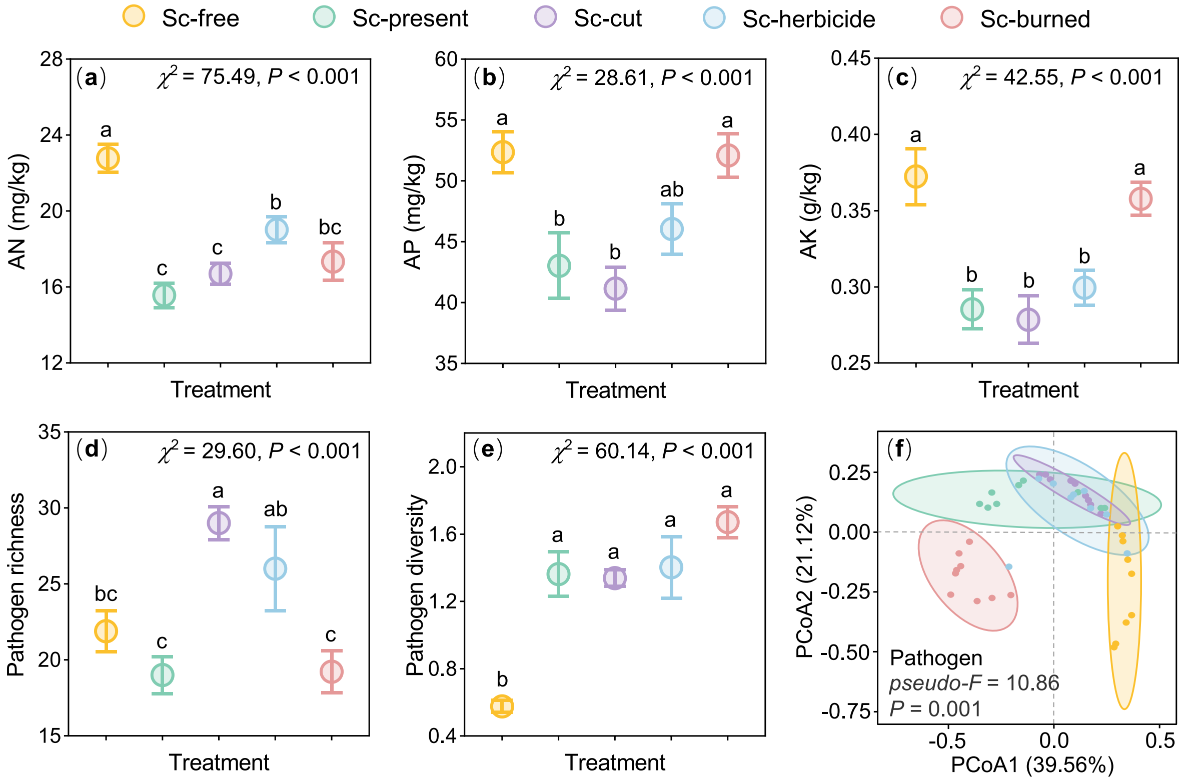

Fig. 2. Effects of treatments on soil properties in phase I. (a) Available nitrogen (AN), (b) available phosphorus (AP), (c) available potassium (AK), (d) ASV richness of pathogens, and (e) Shannon diversity of pathogens at the end of phase I. Points and error bars represent means ± SE (n = 9). χ^2-values and *P*-values indicate treatment significance and same letters indicate treatments that did not differ in post-hoc tests (based on GLMMs, followed by LSM post-hoc tests and FDR *P*-values correction). (f) Principal coordinate analyses (PCoA) based on Bray-Curtis distance of pathogen communities among treatments. The pseudo-*F* and *P* values are given (based on PerMANOVA). Ellipses represent 95 % confidence interval. Data points represent individual replicates (n = 9).

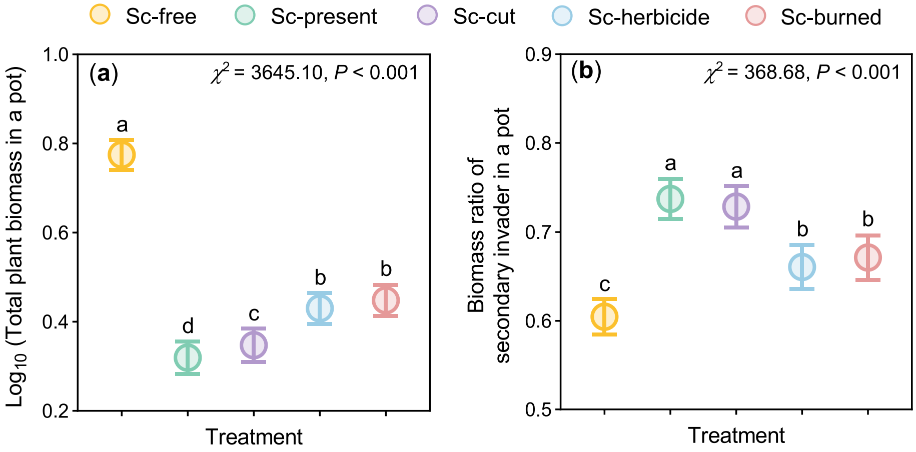

Fig. 3. Impacts of soil legacies created by *Solidago* invasion and management treatments on secondary invaders and native congeners. (a) Total plant biomass (secondary invader biomass + native congener biomass) and (b) biomass ratio of secondary invader (secondary invader biomass/total plant biomass) in a pot. Points and error bars represent means ± SE (n = 9). χ^2-values and *P*-values indicate treatment significance and same letters indicate treatments that did not differ in post-hoc tests (based on GLMMs, followed by LSM post-hoc tests and FDR *P*-values correction). The total plant biomass was $\log_{10}$-transformed prior to analysis to meet normal distribution of residuals.

AN and decreased AP. The negative effects of Sc-herbicide on biomass ratio via increased AN and Sc-burned on biomass ratio via increased AP were especially strong.

4. Discussion

Secondary invasion has been recognized as a major obstacle for sustainable management of invasive plants, but the underlying mechanisms are not well understood (Pearson et al., 2016). Through a two-phase experiment including different management methods of the invasive plant *Solidago*, we measured the resulting soil legacies and their effects on a set of secondary invaders and native congeners. Our results suggested that *Solidago* created soil legacies that could promote secondary invasion, but interventions to manage *Solidago*, such as herbicide application and burning, weakened these legacy effects. Furthermore, secondary invaders distantly related to *Solidago* benefited more from soil

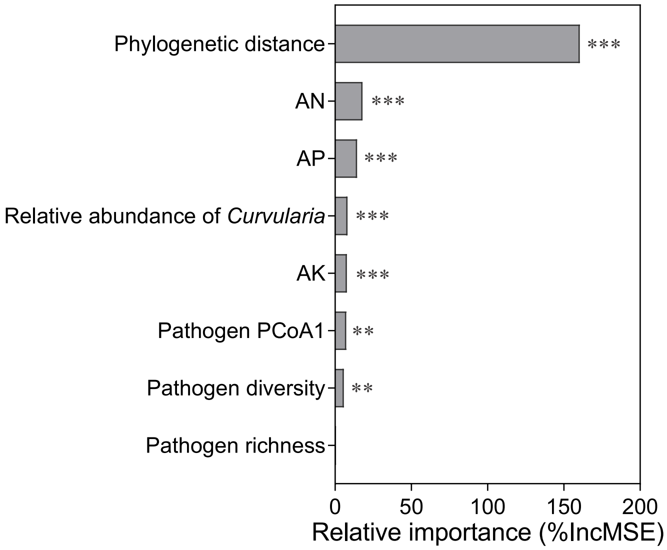

Fig. 4. Relative importance of phylogenetic relatedness and soil properties in determining the biomass ratio of secondary invader. The relative importance was analyzed by random forest regression based on the % of increased mean square error (%IncMSE). The asterisks indicate significant relationship between the biomass ratio of secondary invader and phylogenetic relatedness or each soil property (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$).

legacies, irrespective of the management method.

4.1. Soil legacies promote secondary invasion, but intensity depends on management methods

In our study, the biomass ratio of secondary invader with soils from Sc-free plots exceeded 0.5, indicating they are competitively superior over co-occurring natives, consistent with previous studies (Daehler, 2003; Golivets and Wallin, 2018). Notably, the biomass ratio was even higher in soils from managed *Solidago* plots, suggesting that soil legacies intensify secondary invasion by mediating interspecific competition between secondary invaders and native congeners. These results provide an explanation for the finding that invaded communities following management were less resistant against other invaders than uninvaded communities (Dickie et al., 2014; Sample et al., 2019). Furthermore, the biomass ratio of secondary invader in soils from Sc-cut plots was comparable to that of Sc-present plots, while it was lower in soils from Sc-herbicide and Sc-burned plots, indicating herbicide application and burning mitigated secondary invasion. These results indicate that soil legacy effects on secondary invasion depend on management methods which is consistent with previous studies showed that management methods influence secondary invasion (González et al., 2017; Peterson et al., 2020).

Soil legacy effects can strongly affect plant invasion (Callaway et al., 2004; Suding et al., 2013). Previous studies also explored how soil legacy effects created by a primary invader might favor the establishment of other invaders, potentially resulting in invasional meltdown. For example, invader conditioned soils had a positive effect on subsequent invaders (Kuebbing et al., 2015) or had less negative effects on subsequent invaders than on natives (Zhang et al., 2020a), promoting the coexistence of multiple non-native plant species. Together, we highlight that the role of soil legacy effects should be taken into account in plant invasions, particularly in ecosystems containing multiple invasive species, since it not only can promote invasional meltdown (Dickie et al., 2014; Zhang et al., 2020a), but also facilitate secondary invasion.

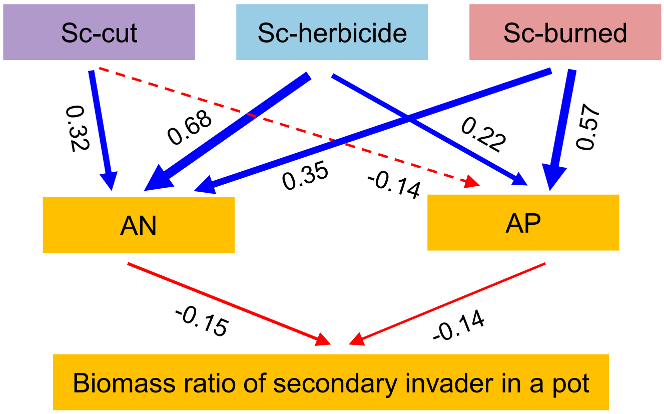

Fig. 6. Path diagrams showing the relationships between management treatments, soil properties, and biomass ratio of secondary invader. Blue arrows indicate positive relationships and red arrows indicate negative relationships. Solid arrows indicate a significant relationship ($P < 0.05$) while dashed arrows indicate a non-significant relationship ($P > 0.05$). Standardized path coefficients are shown next to the arrows and arrow size is scaled to the strength of the coefficients. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

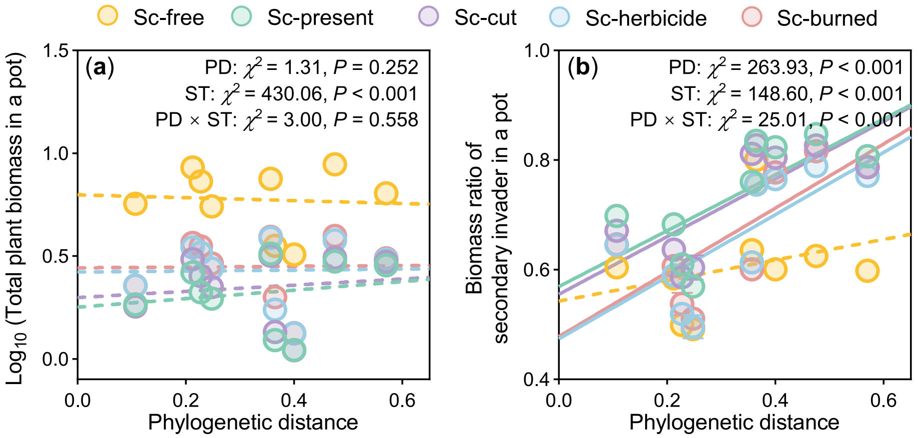

Fig. 5. Effects of phylogenetic distance (PD) and soil conditioning treatment (ST) on the growth of secondary invaders and native congeners. (a) Total plant biomass (secondary invader biomass + native congener biomass) and (b) biomass ratio of secondary invader (secondary invader biomass/total plant biomass) in a pot. The total plant biomass was $\log_{10}$-transformed prior to analysis to meet normal distribution of residuals. χ^2-values and P-values (based on GLMMs) are reported in each panel. Solid lines indicate significant linear relationships ($P < 0.05$) and dashed lines indicate non-significant linear relationship ($P > 0.05$).

4.2. *Solidago* invasion and managements alter soil properties and drive secondary invasion

Our findings align with previous studies showing that *Solidago* invasion reduces soil nutrient availability, particularly nitrogen and phosphorus (Zhang et al., 2009). We observed significantly lower levels of AN, AP, and AK in Sc-present soils compared to Sc-free plots, likely due to nutrient uptake by vegetation, as Sc-free plots were left bare. Interestingly, management methods further modified soil available nutrients. For example, compared to Sc-present, Sc-herbicide increased AN likely due to rapid dieback halting uptake (Allison and Vitousek, 2004; Mun and Lee, 2020), while Sc-burned increased AP and AK, likely due to ash inputs (Galang et al., 2010). Sc-cut, in contrast, had little effect, possibly because belowground uptake continued despite aboveground biomass removal. These results highlight the importance of management methods in shaping soil nutrient legacies. Importantly, we found that available nutrients, especially AN and AP, were negatively correlated with the biomass ratio of secondary invader, suggesting that lower nutrient availability may intensify secondary invasion. This may reflect invasive plants generally having higher nutrient resorption efficiencies than native plants in lower nutrient environments but comparable efficiencies in higher nutrient environments (Sardans et al., 2017). So, the lower available nutrients due to uptake by *Solidago* before management may lead to more intense secondary invasions while *Solidago* management may reduce the intensity of invasions as soil nutrient availabilities increase. While previous studies have demonstrated that available nutrients influence exotic plant success (Liu et al., 2018; Tao et al., 2024a), our findings provide empirical evidence that soil available nutrient legacies left by invasive plants and their management play critical roles in shaping secondary invasion outcomes.

Solidago invasion was also found to influence the soil fungal pathogen community (Zhang et al., 2011). We found that Sc-present tended to decrease pathogen richness, but strongly increased pathogen diversity when compared to Sc-free, indicating that *Solidago* may reduce the dominance of previously abundant taxa. By in-depth analysis of the dominant pathogens, we found that *Solidago* significantly reduced the relative abundance of *Curvularia* (the most dominant pathogens), which confirms our speculation. The increase in diversity can then be seen as an artifact of evenness, with overall pathogen reductions happening in a way that generated a more even distribution of the remaining pathogen species (*i.e.*, richness went down but evenness went up across the remaining species leading to higher diversity index). Sc-burned also remarkably altered the community composition of pathogens, which was likely due to the increased temperatures caused by burning which may kill microbiota in the topsoil (Wang et al., 2012). We had expected that increased diversity of pathogens would have less noxious effects on secondary invaders than native congeners and thus increase the intensity of secondary invasions according to the enemy release hypothesis that exotic plants escape from pathogens in the introduced range (Keane and Crawley, 2002; Mitchell and Power, 2003). But unexpectedly, these changes in soil fungal pathogen communities had little effect on secondary invasion. One possible explanation is that the soil pathogens are generalists, rather than specialists, which attacked both the secondary invaders and native congeners. Furthermore, *Solidago* invasion can also affect AMF community composition and thus facilitate its invasion as reported by Yang et al. (2014). We found AMF abundance to be extremely low in most soil samples, probably because of increased disturbance by the management treatments that decreased the richness and abundance of AMF (Druille et al., 2013; Xiang et al., 2015; Lekberg et al., 2017).

4.3. Success of secondary invaders depend on phylogenetic relatedness to the primary invader

In this study, we found that phylogenetic relatedness of the secondary invader to the primary invader was the most important determinant of secondary invasion. The biomass ratio of secondary invader increased significantly with increasing phylogenetic distance between secondary invaders and *Solidago* in soils conditioned by *Solidago* invasion, whether or not *Solidago* was managed, which is consistent with Darwin's naturalization hypothesis (Daehler, 2001). Closely related species often have similar nutrient requirements (Cadotte et al., 2018) and harbour similar pathogen communities (Gilbert and Webb, 2007; Gilbert et al., 2012). This may explain our observation that secondary invaders more distantly related to *Solidago* may benefit more than closely related ones through increased resource partitioning and pathogen dilution (Wang et al., 2023).

However, we found total plant biomass in a pot was independent of phylogenetic distance, which indicates that the native congeners may have a response to phylogenetic relatedness that is opposite to the secondary invaders. Many invasive plants including our primary invader *Solidago* have been shown to produce allelopathic compounds which are thought to be especially detrimental to native plants in their introduced ranges (Bais et al., 2003; Pal et al., 2015; Kato-Noguchi and Kato, 2022). These allelopathic compounds may accumulate in the soil and act as soil legacies even after the removal of the invaders (Kaur and Callaway, 2014; Zhang et al., 2020b) and allelopathic effects have been shown to less impact more closely than more distantly related neighbors (Zhang et al., 2021). Hence, we hypothesize that natives closely related to the primary invader are better adapted to its allelopathic legacies, resulting in better performance than distantly related ones, which is consistent with the pre-adaptation hypothesis (Ricciardi and Mottiar, 2006; Cadotte et al., 2018). Future studies should measure allelochemicals in primary invader conditioned soils, perhaps along with activated charcoal treatments, to explicitly evaluate this possibility. The lack of a relationship between phylogenetic distance and total plant biomass may also reflect nutrient-limited conditions in the pot experiment. Under such conditions, invasive species often exhibit superior nutrient uptake and utilization strategies, potentially outcompeting native congeners without increasing overall biomass (Funk and Vitousek, 2007). This supports a resource preemption mechanism, where the invader absorbs disproportionate amounts of available nutrients, limiting native plant growth. Future studies incorporating nutrient addition treatments could help clarify the roles of these mechanisms in mediating competition under legacy soil conditions.

5. Conclusions

A better understanding of how management methods affect secondary invasions and which species will be especially favored following successful management of a primary invader will be crucial in achieving urgently needed, more sustainable management methods to fight plant invasions. Our results indicate that commonly used management methods to control *Solidago*, such as herbicide application, hand-cutting, and burning are inadequate to restore the native community due to secondary invasions. More importantly, our findings reveal that soil legacy effects and phylogenetic relatedness play important roles in the success of secondary invaders after *Solidago* control.

A limitation of our study is that we did not experimentally separate biotic and abiotic soil legacy effects. While our results suggest that changes in soil nutrient availability played a dominant role in secondary invasion, the influence of microbial communities remains difficult to isolate. Future research should employ experimental approaches that can isolate abiotic from biotic effects, such as soil sterilization followed by selective microbial reinoculation or nutrient addition/removal experiments. Such methods would help disentangle the specific mechanisms, whether resource availability, microbial pathogens, mutualists, or allelopathic residues, driving the observed soil legacy effects on secondary invasion. We also acknowledge that other mechanisms have the potential to drive secondary invasions, such as propagule pressure, which tends to be high for invaders and low for natives in heavily invaded sites, human disturbance, and changes in environmental conditions that also tend to benefit invaders over natives (Pearson et al., 2016). Therefore, more comprehensive experiments incorporating these potential drivers are needed to better understand secondary invasions following the control of *Solidago* and other prominent plant invaders. Furthermore, while greenhouse experiments offer the advantage of controlling non-focal variables and are crucial for confirming specific mechanisms, further studies should also include manipulative common-garden experiments in the field to assess the long-term responses of secondary invaders to various invader management strategies.

CRediT authorship contribution statement

Changchao Shen: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Yan Sun:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Kaoping Zhang:** Writing – review & editing, Visualization, Supervision, Methodology, Data curation. **Jinlong Wan:** Visualization, Resources, Formal analysis, Data curation. **Zhibin Tao:** Visualization, Validation, Supervision, Methodology, Data curation. **Minyan He:** Validation, Supervision, Resources, Methodology. **Heinz Müller-Schärer:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Evan Siemann:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Wei Huang:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2025.109845.

Data availability

Data of soil nutrient and plant biomass associated with this study were deposited in the Figshare database (https://figshare.com/s/d766bea101b42d9c540b). Raw sequence data for soil fungi were deposited in the Genome Sequence Archive (CRA025143, https://ngdc.cncb.ac.cn/gsa/).

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