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Plant–Soil Feedback Does Not Contribute to the Competitive Outcome Between Invasive and Resident Native Species in a Species-Rich Grassland

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ABSTRACT

Question: Native and invasive species interact simultaneously with each other and with their species-specific soil biota, yet the relative importance of native plant–soil feedback (PSF) on the outcome of competition between these species with different origins is poorly understood. Therefore, we studied the influence of native PSF on the performance of two invasive and two native target species in two situations: (1) when the species were grown alone, and (2) when the target species were grown in pairwise competitive setup with the native conditioning species. We also tested the importance of phylogenetic relatedness between target and conditioning species on the simultaneous effect of PSF and competition.

Location: Cluj-Napoca, Romania.

Methods: We used native species from a semi-dry grassland dominated by *Brachypodium pinnatum* and *Festuca rupicola* to study how their species-specific PSFs affect the performance of invasive (*Solidago canadensis, Erigeron canadensis*) and native (*Centaurea jacea, Crepis foetida*) Asteraceae species. In the first year, soil was conditioned by six native grassland species (three Asteraceae and three species from other families); while in the second year, we performed a pairwise competition experiment in pots between the four target and six native species in conditioned and control soils.

Results: We found that although the native species exerted a strong negative PSF on the performance of the target species, this effect mostly disappeared in the real presence of the native competitors. We also showed that the identity of native resident species is more important in determining PSF and competitive outcome than whether it is dominant or subordinate, or whether it is phylogenetically related to the target species.

Conclusions: We showed that PSF of native species may not influence the competitive outcome between invasive and resident native species, thus PSF does not significantly contribute to the invasion resistance of the studied grassland community.

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1 | Introduction

Plant invasions are cited as one of the major threats to native plant and animal diversity, and scientists strive to comprehend the mechanisms by which some non-native plant species become the dominant element in the invaded communities (Vilà et al. 2011; Crystal-Ornelas and Lockwood 2020). Invasive plants can alter ecosystem processes, such as nutrient cycling (Xu et al. 2022; Gioria et al. 2023), soil biota (Torres et al. 2021; Liu et al. 2023) or pollination services (Kovács-Hostyánszki et al. 2022), and these alterations may cause a self-reinforcing feedback, which may enhance their dominance and the exclusion of native plants (Yelenik and D'Antonio 2013). Therefore, to anticipate the effects of invasive species on native communities, we should focus on understanding the mechanisms that may strengthen the invasion resistance of native communities (Funk et al. 2008; Tortorelli et al. 2022).

Plants may have species-specific impacts on soil biota and soil properties with which they interact, thus potentially affecting their own and successive plants' performance through feedback loops (Klironomos 2002; Kulmatiski et al. 2008). The plant–soil feedback (PSF) may impact the plants from the same species that conditioned the soil (intraspecific PSF) or may affect other species of the community (interspecific PSF), and may lead to various community dynamics from coexistence to exclusion (Bukowski et al. 2018). PSF can range from negative to positive: enhanced access to nutrients or accumulation of mutualists contribute to the positive PSF, while pathogens' accumulation or resource depletion contribute to negative PSF (Bennett and Klironomos 2019). Soil biota may facilitate biological invasions when non-native species encounter a soil microbial community that enhances their own performance and/or competitive ability compared to native resident species, or by “escaping” from soil pathogens (Crawford and Knight 2017). However, native species may condition soils that suppress non-native species, and thus contribute to invasion resistance (Ning et al. 2016; Chen et al. 2021). While early studies clearly showed less negative or even positive PSFs for invasive plant species compared to their native competitors within their non-native range (Klironomos 2002; Van der Putten et al. 2013), recent studies emphasize a more nuanced and context-dependent situation (Chen et al. 2021; Li et al. 2024).

Although the majority of experiments have focused on native and invasive plant individuals' responses to different soil histories (conditioned by native or invasive species), field studies emphasize the importance of community context when evaluating plant–soil interactions (Casper and Castelli 2007; Callaway et al. 2011; Yelenik and D'Antonio 2013). Individual-level studies showed the importance of PSFs to plant invasions, but this effect might disappear or might become even more apparent in a competitive environment. For example, Crawford and Knight (2017) showed that the invasive *Lespedeza cuneata* showed a highly positive intraspecific PSF compared to soils conditioned by co-occurring native species. However, this positive effect of soil biota disappeared in the presence of competition by native species, highlighting that PSFs may not influence the competitive outcome between an invasive and native species. Larios and Suding (2015) found that the native *Stipa pulchra*'s positive intraspecific PSF was neutralized under competition with the invasive *Avena fatua*, while competition had no impact on the growth of the invasive species with intraspecific or interspecific PSF or without PSF interaction. Contrary, Buerdsell et al. (2021) proved that PSF can provide an advantage to the invasive *Eragrostis lehmanniana* in competition with the native *Bouteloua gracilis*, but only at the highest competition ratio, suggesting a density-dependent effect. Due to the controversial results, further studies are required to decipher how PSFs affect the outcome of the competition between invasive and native plant species and whether PSFs may or may not contribute to the invasion resistance of native plants in the face of invasive species.

Darwin's naturalization hypothesis predicts that successful invasive species are likely to differ taxonomically from native species because highly related species exhibit higher niche overlap and experience increased biotic resistance (Darwin 1859; Thuiller et al. 2010). However, the establishment of invasive species can be greater next to closely related species due to similar abiotic conditions required for germination and growth (Duncan and Williams 2002). Although the phylogenetic relatedness should be a critical factor governing also the PSFs in invaded communities, it is rarely considered in soil feedback studies. Soils conditioned by closely related species may share the same pathogens, thus may lead to more negative PSF for close relatives compared to distantly related species (Liu et al. 2012; Sweet and Burns 2017). In addition, as competition between closely related species is also expected to be more pronounced (Valiente-Banuet and Verdú 2008), due to these two mechanisms, the invasion resistance may increase with the increasing phylogenetic relatedness between invasive and native species.

The present study aims to integrate PSFs into competition experiments between invasive and native species to scale the effect of species-specific soil biota observed at the individual plant level up to the community level. Our model system was a species-rich semi-dry grassland from Transylvania, Romania, invaded by *Solidago canadensis* and *Erigeron canadensis*. In a two-phase greenhouse experiment, we could separate the relative role of PSF and competition in the case of two invasive target species and two native target species. The soil conditioning species and competitor species were other native resident species from the same grassland. To test Darwin's naturalization hypothesis, three of these conditioning and competitor native grassland species were chosen to belong to the same family as the target species (Asteraceae), while the other three belonged to different families. With our experiment, we intended to answer the following questions:

1. Does resident native species influence the performance of two invasive and two native target species through species-specific PSFs?
2. Does the effect, if any, of the resident native's PSF on the performance of target species alter the competitive outcome between the target and the resident native plant individuals?
3. Does phylogenetic relatedness between target species and the resident native species influence the outcome of competition between them when also influenced by native resident species' PSF?

2 | Materials and Methods

2.1 | Species Selection

Our study ecosystem was a species-rich semi-dry grassland dominated by *Brachypodium pinnatum* and *Festuca rupicola* near Cluj-Napoca, Romania (46°46′48″ N, 23°33′34″ E). To study the joint effect of PSF and competition of resident native grassland species on the performance of invasive species, we have chosen two highly invasive and widespread herbaceous species from this grassland, both belonging to the Asteraceae family: *Solidago canadensis* (hence: *Solidago*) and *Erigeron canadensis* (syn. *Conyza canadensis*) (hence: *Erigeron*). Both species are native to North America and thrive in disturbed, open habitats, mostly grasslands. While *S. canadensis* is perennial, *E. canadensis* is a short-lived (annual, rarely biennial) species. We also selected two native species from the same grassland to compare the effect of PSF and competition of resident native species on the performance of invasive species to those of native ones: *Centaurea jacea* (hence: *Centaurea*) and *Crepis foetida* (hence: *Crepis*). These species were also selected to belong to the Asteraceae family, having similar abundances in the chosen grassland stand as the two invasive species (among the most abundant subordinate species), and similarly to the invasive species, one is annual (*Crepis*), while the other is perennial (*Centaurea*). We refer to these four species as 'target species' throughout this study.

Further 10 common, native perennial grassland species from the same grassland community were selected as soil conditioning and competitor species: these species were let to accumulate their own species-specific soil biota in the conditioning phase, and which also took part in the competitive setup as competitor species. Two species are dominant grass species, while eight are subordinate native species (Table 1). For the sake of simplicity, we refer to these species by their genus names throughout the paper.

2.2 | Soil Conditioning Phase

In the conditioning phase, our purpose was to obtain soils with species-specific soil biota of each of the 10 conditioning species. Therefore, monocultures of the 10 species were established for c. 20 months (September 2017–April 2019). Forty liter containers with 40 cm diameter were filled with commercial potting soil (FloraSol, 70% topsoil, 30% peat), and six individuals of one target species were planted in them, with six replicates for each species (10 conditioning species × 6 replicates = 60 containers). The plants were transplanted from the indicated semi-dry grassland by carefully extracting their roots with a spade that was washed with water and sterilized with 96% ethanol prior to each digging. The containers were placed in a roofed and fenced outdoor facility in the University Botanical Garden in Cluj-Napoca, Romania, and watered and weeded regularly.

2.3 | Plant–Soil Feedback Phase and Competition Experiments

Seeds of both conditioning and target species were collected from the same grassland stand from July to September 2018. Fruits or seeds were collected from at least 50 individuals per species, mixed per species, and kept in paper bags in darkness at room temperature. In December 2018, seeds were placed in Petri dishes and subjected to cold-wet stratification at 4°C for

TABLE 1 | Overview of species included in our study, their role in our experiment (target, conditioning and competitor species), status in the grassland community they were collected from (invasive, native dominant or native subordinate), and taxonomic family.

Species	Species' role	Status	Family
Solidago canadensis	Target	Invasive	Asteraceae
Erigeron canadensis	Target	Invasive	Asteraceae
Centaurea jacea	Target	Subordinate, native	Asteraceae
Crepis foetida	Target	Subordinate, native	Asteraceae
Brachypodium pinnatum	Conditioning & competitor	Dominant, native	Poaceae
Festuca rupicola	Conditioning & competitor	Dominant, native	Poaceae
Achillea collina	Conditioning & competitor	Subordinate, native	Asteraceae
Inula ensifolia	Conditioning & competitor	Subordinate, native	Asteraceae
Hieracium bauchinii	Conditioning & competitor	Subordinate, native	Asteraceae
Plantago lanceolata	Conditioning & competitor	Subordinate, native	Plantagiaceae
*Euphorbia cyparissias**	Conditioning	Subordinate, native	Euphorbiaceae
*Hypericum perfoliatum**	Conditioning	Subordinate, native	Hypericaceae
*Pimpinella saxifraga**	Conditioning	Subordinate, native	Apiaceae
*Dactylis glomerata**	Conditioning	Subordinate, native	Poaceae

*These species could not be involved in the second phase of the experiment because their seeds germinated very poorly. Therefore, their species-specific conditioned soils were used only to create the control soil in the second phase of the experiment (see Materials and Methods).

3 months to break seed dormancy. In March 2019, seeds of both conditioning and target species were separately put on the surface of soil in 42 pots (14 × 40 × 12 cm, 3 pots/species). Pots were filled with a 2:1 mixture of commercial potting soil and sand. After germination, seedlings were kept for two more weeks and then transplanted individually to the 1 L pots filled with conditioned or control soils. Only six out of ten native species produced enough seedlings, so we continued the experiments with these six conditioning species (Table 1).

To fill the pots, we mixed the conditioned soil from the six conditioning containers per species with sterilized commercial potting soil (1:1 ratio) to have ample volume of soil for this second phase of the experiment, and to boost the available nutrients of conditioned soils potentially depleted during the long conditioning phase. Soil was sterilized in sealed autoclave bags by steam pasteurization at 100°C for 3 h in a Witeg WAC-47 autoclave. We chose to use a relatively low temperature for a longer time to avoid the side effects of higher temperature on soil chemical and physical properties (Endlweber and Scheu 2006). One part of the conditioned soil was used to test species-specific PSF effects, while the rest of the soil was used to create control soil. The control soil consisted of a mixture of soils conditioned by each of the 10 conditioning species (5% of each conditioned soils of the 10 conditioning species and 50% sterilized soil).

Conditioned and control soils were put in 1 L pots, and 3 experimental plant treatments were set up, with 10 replicates per treatment (Figure 1):

1. One seedling of the target species was planted in each one of the conditioned soils and control soil, respectively, totaling 4 target species × (6 conditioned soils + 1 control soil) × 10 replicates = 280 pots
2. One seedling of the conditioning species was planted in its own conditioned soil and in control soil, totalizing 6 conditioning species × 2 soil types × 10 replicates = 120 pots
3. One target seedling was planted together with one seedling of the six conditioning species in the soil conditioned by the conditioning species and in control soil as well, totaling 4 target species × 6 conditioning species × 2 soil types × 10 replicates = 480 pots.

The transplantations took place on 10–15 April 2019. Pots were arranged using a randomized block design in five blocks in the same outdoor facility and watered twice a week with the same amount of water. Pots were re-randomized within blocks monthly. After 3 months of growth, at the peak of the vegetative growth, the aboveground parts of all plants were collected separately. Roots were carefully separated and washed free of soil. Aboveground and belowground biomass was dried at 60°C for 72 h, then weighed. Total biomass was calculated as the sum of the two fractions.

2.4 | Statistical Analyses

All statistical analyses were performed using the R statistical environment, version 4.1.1 (R Core Team 2021). Intraspecific PSF of conditioning species was calculated according to Brinkman et al. (2010): feedback = ln ($\text{biomass}_{\text{conditioned}}/\text{biomass}_{\text{control}}$), where $\text{biomass}_{\text{conditioned}}$ represents the biomass of an individual plant when grown alone in conditioned soil, and $\text{biomass}_{\text{control}}$ represents the average biomass of plants grown alone in control soil. A feedback value < 0 indicates negative feedback: the plant performs worse in the conditioned soil compared to the control soil. A feedback value > 0 indicates a positive feedback: the plant performs better in conditioned soil compared to the control soil, while a feedback = 0 indicates a lack of differences in a plant's biomass between the control and conditioned soil. We used this index because it provides symmetrical feedback scores around the no-effect point (feedback = 0) (Brinkan et al. 2010). Plant–soil feedback of conditioning species on the target species (interspecific PSF) was calculated for each competitor species grown in each conditioning species' soil separately using the same equation. To test whether the intra- and interspecific PSF effect on plant performance was significant in the case of plants that were grown alone, we used one-sample *t*-tests to analyze whether the PSF effect differed from zero.

To examine the effect of interspecific PSF and competition of native resident species on the performance of each target species, we calculated the relative performance of the target species under competition as a log-response ratio (Hedges et al. 1999; Jing et al. 2015) both for conditioned and control soils: relative performance of target species = ln ($\text{biomass}_{\text{competition}}/\text{biomass}_{\text{alone}}$). $\text{Biomass}_{\text{competition}}$ data were derived from pots with interspecific competition, either on conditioned or control soil, while $\text{biomass}_{\text{alone}}$ was calculated as the average biomass of an individual plant when grown without competition in control soil. A relative performance value < 0 indicates that the plant performs worse with competition than without competition. By comparison, a relative performance value > 0 indicates that the plant performs better with competition than without competition, while a relative feedback = 0 indicates a lack of differences in a plant's biomass when grown with or without competition.

To statistically test the effects of soil conditioning on the relative performance of the target species when grown in the real presence of conditioning species, linear mixed effect models (LMEM) with block as a random term were used separately for each target species. Conditioning species (six species) and soil types (control or conditioned) nested into the conditioning species were included as factors in the models. We needed to nest soil type into the conditioning species due to the nested design of the experiment: conditioning species were planted in their own and control soil but not in other native resident species' conditioned soil. Tukey post hoc tests were performed to compare the relative performance of target species between conditioning species or soil types using the *glht* function in the "multcomp" package. LMEM was also run to determine whether there were differences among the native and invasive target species regarding their average relative performance (without considering the identity of the conditioning native species) in conditioned and control soils with target species and soil type as fixed factors and with block as a random term. The possible differences between phylogenetically related and not related target and conditioning species were tested also with an LMEM, relative performance of target species being the response variable, while 'relatedness' (with two levels; related: conditioning species belonging to the Asteraceae; and not-related: conditioning species belonging to

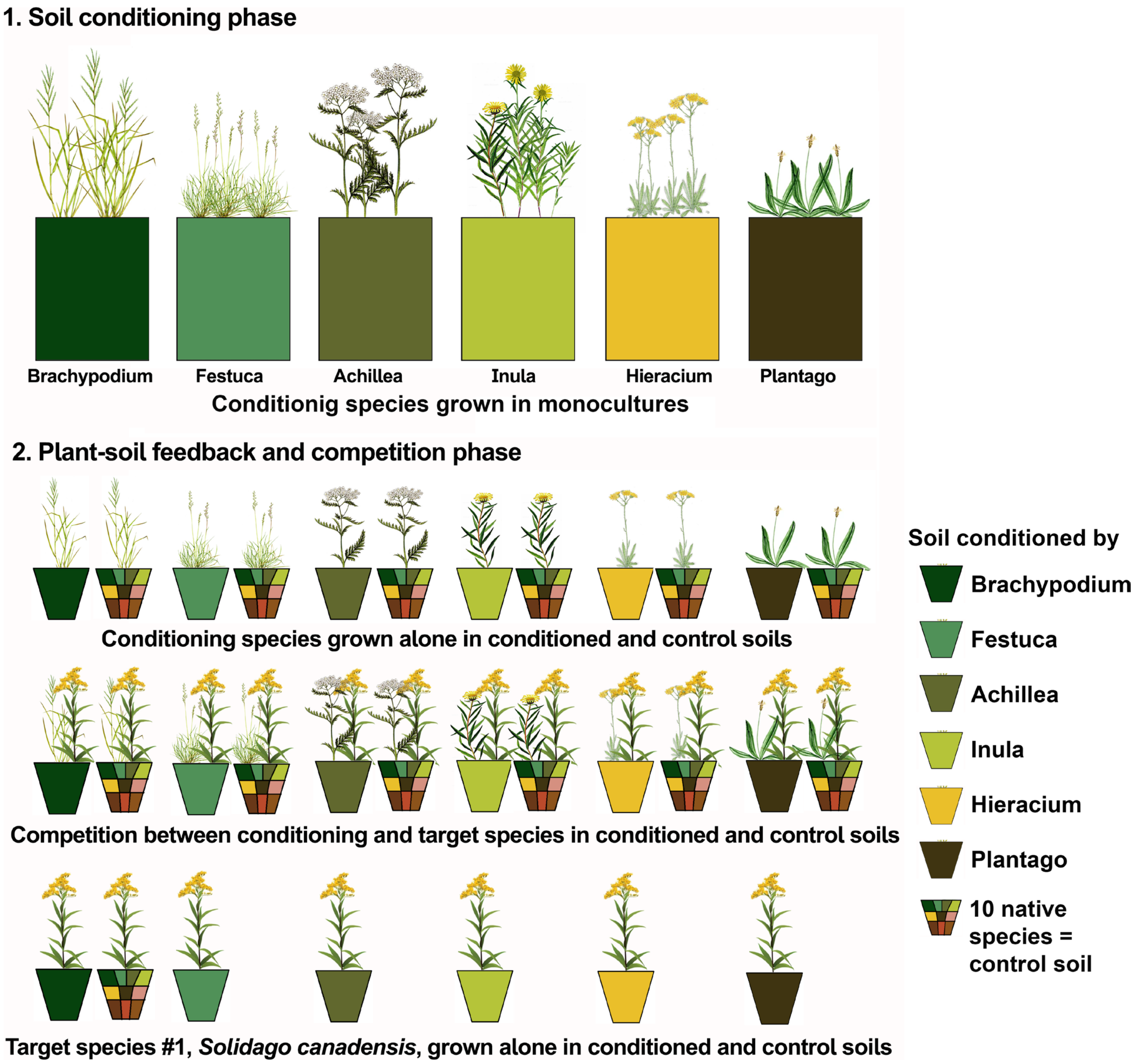

FIGURE 1 | Experimental design. In the soil conditioning phase, six native perennial species (conditioning species), each replicated by six times, were grown for 20 months in 40 L containers. In the plant–soil feedback and competition phase, conditioning species were grown alone or with one of the four target species in conditioned or control soils, each replicated by 10 times. Target species were also grown alone in conditioned and control soils with 10 replicates. Here we show the design with only one of the target species (*Solidago canadensis*), but a total of four target species were used in our experiment. For full species names see Table 1.

other families than the Asteraceae) and soil type, and their interactions, were included as fixed factors, while block as random term.

3 | Results

3.1 | The Effect of Intraspecific and Interspecific PSF

Out of the six conditioning native species, only *Brachypodium* showed positive feedback in its own conditioned soil (positive intraspecific PSF effect). By comparison, *Festuca* and *Plantago* showed negative intraspecific PSF effects, and none of the three native Asteraceae species were significantly influenced by their own conditioned soils (no intraspecific PSF effect) (Figure 2).

The conditioning native species exerted mostly negative interspecific PSF effects on the target species (Figure 2). *Solidago* showed moderate but significantly decreased performance (negative PSF) when grown in the soils conditioned by *Brachypodium*, *Festuca*, and *Plantago*. The soils conditioned by the three native Asteraceae species did not significantly alter the performance of *Solidago* individuals compared to control soils (Figure 2). The two annual target species, *Erigeron* and *Crepis*, showed similar results: they showed negative interspecific PSF

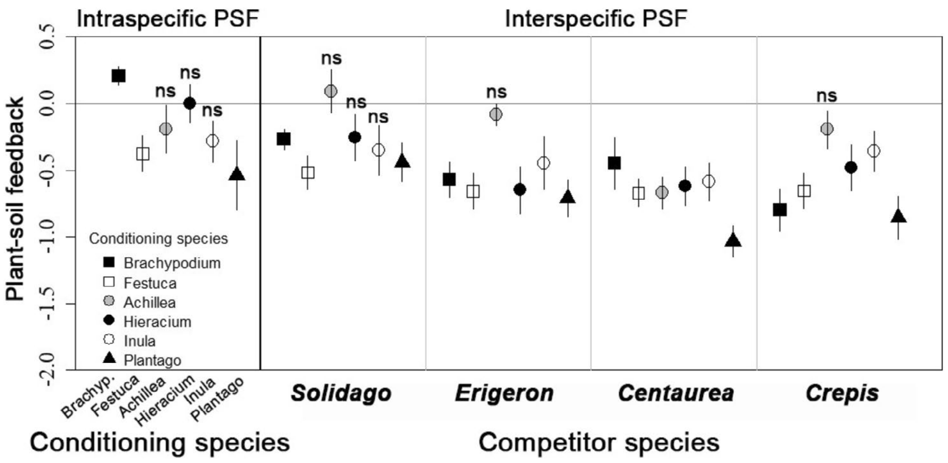

FIGURE 2 | Species-specific soil feedback of six resident native species (conditioning species) on their own performance (intraspecific PSF) and on the performance of the target species, two invasive (*Solidago*, *Erigeron*) and two native species (*Centaurea*, *Crepis*) (interspecific PSF). In these cases, all plants were grown alone in pots filled with conditioned or control soils. For species names see Table 1. 'ns' indicates non-significant difference from zero at $p > 0.05$ according to one-sample *t*-tests. Data are mean ± SE.

in all cases, except the soil conditioned by *Achillea* (Figure 2). The native perennial target species, *Centaurea*, showed negative interspecific PSF in all cases (Figure 2).

3.2 | The Joint Effect of PSF and Competition on the Performance of Target Species

The relative performance of *Solidago* did not differ with the conditioning species ($F_{(5,98)} = 1.24$, $p = 0.296$), but it changed with the soil type (control Vs. conditioned soil; $F_{(6,98)} = 2.27$, $p = 0.042$): the conditioned soil of *Brachypodium* increased, while that of *Achillea* decreased the performance of *Solidago* compared to control soil, when also in competition with these native species (Figure 3a). Contrary, the identity of conditioning species as a competitor altered the relative performance of *Erigeron* ($F_{(5,99)} = 3.58$, $p = 0.005$), while the soil type did not ($F_{(6,99)} = 0.50$. $p = 0.803$). The post hoc test revealed that the competition with *Hieracium* decreased the relative performance of *Erigeron* the most, significantly in comparison with *Festuca* ($z = 3.44$, $p = 0.007$) or *Inula* ($z = 3.37$, $p = 0.009$, Figure 3b). The competitive ability of native *Centaurea* and *Crepis* was not altered either by the soil type or by the identity of competitor species (*Centaurea*: conditioning species $F_{(5,96)} = 1.48$, $p = 0.203$, conditioning species/soil $F_{(6,96)} = 1.80$, $p = 0.105$, Figure 3c; *Crepis*: conditioning species $F_{(5,99)} = 0.68$, $p = 0.638$, conditioning species/soil $F_{(6,99)} = 0.55$, $p = 0.761$, Figure 3d).

The average relative performance of the four target species (e.g., when we did not take into account the identity of the conditioning/competitor species) significantly differed among the target species ($F_{(3)} = 22.75$, $p < 0.001$); while the soil type ($F_{(1)} = 0.09$, $p = 0.762$) and the interaction between soil type and target species identity had no significant effect on their relative performance ($F_{(3)} = 1.32$, $p = 0.263$). Tukey post hoc test indicated that *Crepis* had the greatest relative performance, while *Centaurea* had the lowest one among the four target species (Figure 4a).

When analyzing the relative performance of target species when grown with phylogenetically related or not related species, we found that neither the relatedness ($F_{(1)} = 0.81$, $p = 0.366$), nor the soil type ($F_{(1)} = 0.02$, $p = 0.881$), nor the soil type × relatedness interaction ($F_{(1)} = 0.004$, $p = 0.946$) had significant effects on their relative performance (Figure 4b).

4 | Discussion

In this research, we tested the hypothesis that soil conditioned by resident native species influences the performance of invasive and native target species. In addition, we asked whether the resident native species' plant–soil feedback significantly influences the competitive outcome between resident native species and the target species. We found that although the native species exerted a strong negative influence on the performance of the target species (with clear species-specific variation) solely through the plant–soil feedback, this effect mostly disappeared in the real presence of the native competitors. Therefore, our results indicate that the PSF of native species may not influence the competitive outcome between invasive and resident native species, and that the PSF does not significantly contribute to the invasion resistance of native plant communities.

4.1 | Interspecific and Intraspecific PSFs of Native Resident Species

It was repeatedly proven that PSF may contribute to the invasiveness of non-native plant species and to the invasibility of recipient communities (Callaway et al. 2004; Buerdsell et al. 2021; Liu et al. 2023). Therefore, our first question was whether the performance of invasive and native target species was influenced by the species-specific PSF of the resident native species in the selected, semi-dry grassland. We found that native conditioning species exerted various intraspecific PSFs and mostly negative interspecific PSFs. These results are in contrast to previous studies, which found that native species often generate negative intraspecific plant–soil feedbacks (Bever et al. 1997; Klironomos 2002; Kulmatiski et al. 2008). In our study, the dominant grass species, *Brachypodium pinnatum*, tended to generate

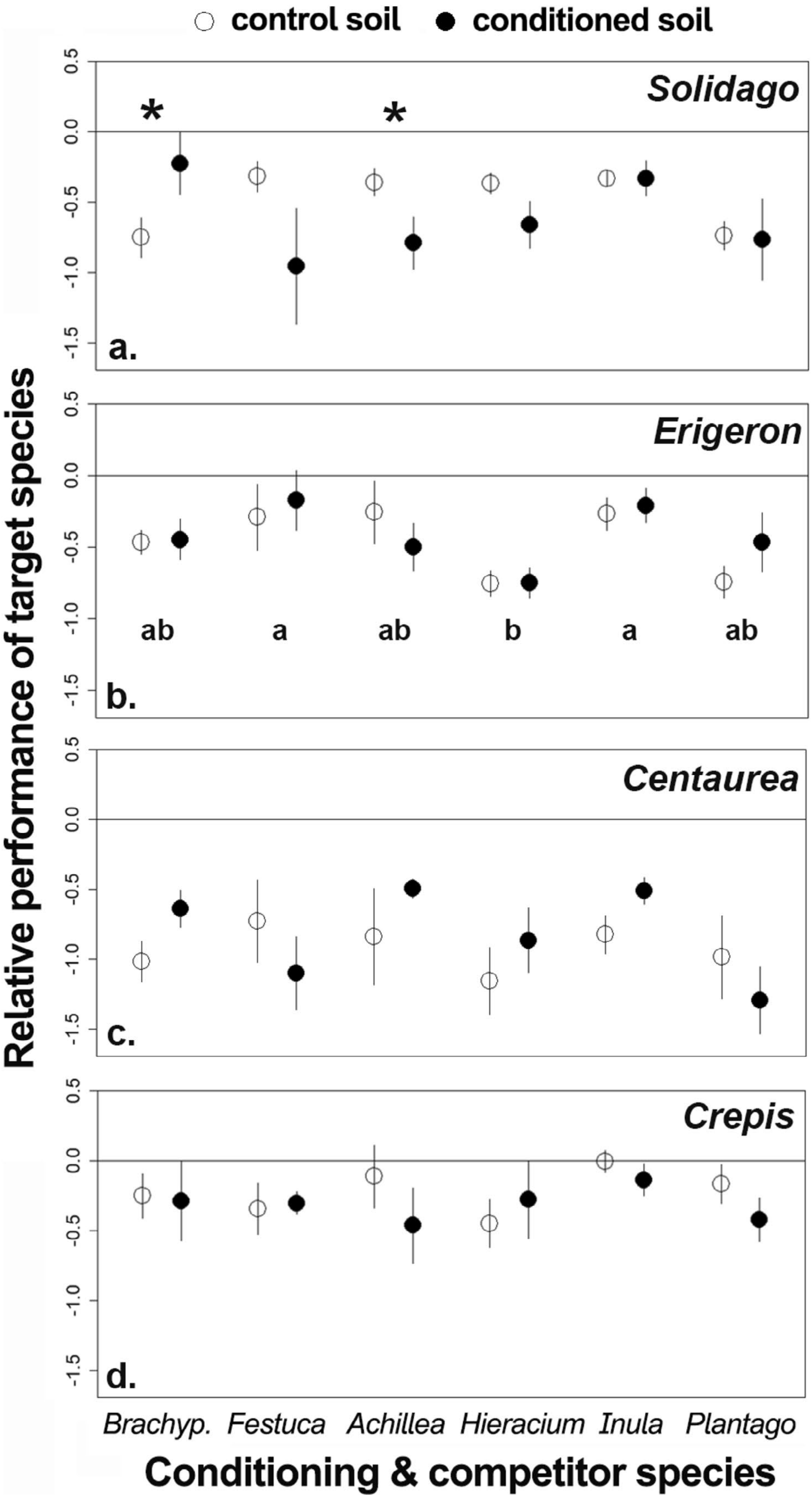

FIGURE 3 | Legend on next page.

FIGURE 3 | Relative performance of target species *Solidago canadensis* (a), *Erigeron canadensis* (b), *Centaurea jacea* (c), *Crepis foetida* (d), when grown with one of the six conditioning species in a competition set-up (*Brachypodium pinnatum*, *Festuca rupicola*, *Achillea collina*, *Hieracium bauchinii*, *Inula ensifolia*, *Plantago lanceolata*) in control soil or in soils conditioned by these conditioning species. Asterisks indicate significant differences in target species' performance between conditioned and control soil at $p < 0.05$, while different letters denote significant differences among conditioning species according to linear mixed effect models followed by Tukey post hoc tests. Data are mean ± SE.

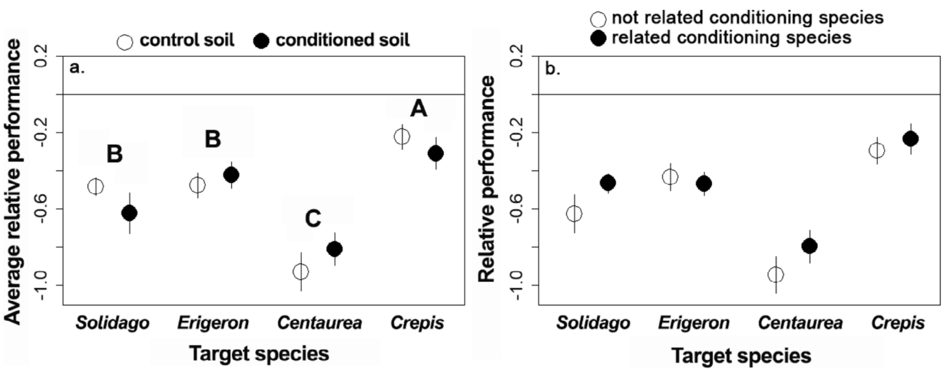

FIGURE 4 | Average relative performance of the two invasive target species (*Solidago canadensis*, *Erigeron canadensis*) and the two native target species (*Centaurea jaceae*, *Crepis foetida*) in conditioned and control soils, without considering the identity of conditioning and competitor species (a). Relative performance of target species when grown with phylogenetically not related conditioning species (*Brachypodium, Festuca, Plantago*) or with phylogenetically related Asteraceae species (*Achillea, Hieracium, Inula*) (b). Different letters denote significant differences between species at $p < 0.05$ according to linear mixed effect models followed by Tuckey post hoc tests. Data are mean ± SE.

positive intraspecific PSF, which may contribute to its high abundances and persistence in semi-dry grasslands (Willner et al. 2019). Interestingly, all the three conditioning Asteraceae species showed neutral intraspecific effect, which may partly explain their coexistence in the selected grassland stand, but also their low abundances within the community. Only two species had negative intraspecific PSFs, *Festuca rupicola* and *Plantago lanceolata*, which means that they can suppress individuals of the same species in their surroundings by accumulation of specialist pathogens or by the depletion of some nutrients that are limiting for that species (Hemrová et al. 2016).

Native resident species exerted mostly negative soil feedbacks on the target species in three out of four species, which suggest that the conditioning phase of our experiment (20 months) was long enough for pathogens to accumulate (Wang et al. 2020). Our results are partly in line with the assumption that fast-growing, annual and early successional plant species, such as the native *Crepis foetida* and the invasive *Erigeron canadensis* are more likely to be impacted by negative PSFs (Lemmermeyer et al. 2015). However, slow-growing and late successional species are suggested to show more neutral or even positive interactions with soil biota (Lemmermeyer et al. 2015), which was partly true for invasive perennial *Solidago canadensis*, but false for the native perennial *Centaurea jacea*. Besides, these results also indicate that the native or non-native origin was not especially important in the outcome of interspecific PSFs in these Asteraceae species. Wang et al. (2020) also found in an experiment with three native and three invasive Asteraceae, that the status of species could not explain the different PSF responses.

As an exception to other target species, the invasive *Solidago canadensis* showed neutral PSFs to soils conditioned by the three native Asteraceae species, and negative PSFs when grown in soils conditioned by native species from other families. As *Solidago canadensis* is known to have strong mutual interactions with arbuscular mycorrhizal fungi in their introduced range (Yang et al. 2014), these mutualists could have been acquired more easily in soils conditioned by phylogenetically related species (Anacker et al. 2014). As a result, the accumulation of mutualists could counterbalance the effect of pathogens, which was the leading effect of soil conditioning of native resident species, given the overall negative effects of interspecific PSFs. Former studies also proved that some invasive species are less responsive to soil pathogens and can profit more from mutualists (Klironomos 2002; Reinhart and Callaway 2006; Engelkes et al. 2008).

4.2 | Plant–Soil Feedback and Competition

The second question of this study was to evaluate the role of native plant–soil feedback on the competitive outcome between the resident native species and the target species, either invasive or native. In particular, we were interested whether the dominant native species or the subordinate, but confamilial species can exert a better defense in face of invasion by *Solidago canadensis* and *Erigeron canadensis* through the joint effect of PSF and competition. When studying the simultaneous effect of PSF and competition, most of the studies focus on the effect of invasive species on the resident native species (Crawford and Knight 2017; Lekberg et al. 2018; Wang et al. 2020; Buerdsell et al. 2021), but less attention has been paid in understanding the role of PSFs in invasion resistance of recipient communities (but see Chen et al. 2021; Cheng et al. 2024). Our results showed that the PSFs had minor effect on the performance of target species, either invasive or native, when in competition setup, as the mostly negative effect of resident native plant–soil feedback on target species disappeared in the real presence of competition by native species. Similarly, a meta-analysis by Lekberg et al. (2018) did not find significant effect either, but only when the effect of competition was much stronger than that of PSF. These facts clearly indicate that the effect of PSFs may be dampened by the diversity of abiotic and biotic above- and belowground interactions which takes place in a competitive situation (Larios and Suding 2015; Crawford and Knight 2017; Lekberg et al. 2018). This was true both for dominant and subordinate resident native species when facing competition with either invasive or native target species.

Solidago canadensis, an invasives species with a high competitive ability (Fenesi, Geréd et al. 2015) and measurable impact on the invaded communities (Fenesi, Vágási et al. 2015; Fenesi et al. 2023) was the only species to be significantly affected by the conditioned soils of some of the native species in competition situation. Interestingly, the establishment and early growth of *Solidago* was facilitated when grown together with *Brachypodium pinnatum* in soils conditioned by this dominant grass species. This was surprising because *Brachypodium* showed a positive intraspecific PSF, thus an enhanced performance when grown in its own soil; and because of the negative interspecific *Brachypodium*-soil feedback effect when *Solidago* grown alone (Figure 2). Therefore, the effect of PSFs may be not just dampened, but even turned to opposite by the complex abiotic and biotic interactions of a competition situation. *Solidago canadensis* might alter the composition of soil bacterial and fungal communities or change the nutrient composition when grown together with *Brachypodium* in the conditioned soil, and these new circumstances favored the growth of *Solidago*. Indeed, *Solidago canadensis* was proved to be a superior competitor when grown in pairwise manner with *Brachypodium pinnatum* (Fenesi, Geréd et al. 2015). As an alternative explanation, this outcome of the experiment might be also attributed to the short time period of the second phase of the experiment (cc. 90 days). Perhaps this was suitable for annuals with a short life cycle, but perennials (e.g., *Brachypodium*) had a slower growth rate and could not exert their real competitive ability in such a short period of time. Indeed, the biomass of the two annual species was considerably higher than that of the perennial target and resident native species (Appendix S1). Therefore, future studies should allocate longer time, at least two vegetative growth period, to study similar questions (Lekberg et al. 2018), however, the effect of soil legacy fades with time as the plants start to develop their own soil biota.

The lack of soil-mediated effects of resident native species on the performance of invasive species when grown in the same pots does not necessarily mean that plant–soil interactions do not play a role in the invasion resistance of the studied native grassland community. Instead, it suggests that (1) the importance of plant–soil interactions are context dependent: it may shift over time, it may depend on the intensity of disturbance, or soil nutrient content (Crawford and Knight 2017; in't Zandt et al. 2019); and (2) pairwise experiments can elicit unrealistically strong competitive effects (Aschehoug and Callaway 2015) and mask the overall effect of PSF by native species. It is likely that a diverse native plant community may suppress invasive species through different biotic and abiotic pathways, even by conditioning soils that suppress invasion (Perkins and Nowak 2013; Ning et al. 2016; Wei et al. 2020). However, it is unlikely that plant–soil interactions alone enable native species to provide competitive resistance in face of the invasion of *Solidago canadensis* or *Erigeron canadensis*.

4.3 | PSF and Competition in Phylogenetic Related and Not Related Species

As the effect of PSF and competition are usually additive (Lekberg and Waller 2016), we expected that the negative PSF of native species on the target species will generate a more negative competitive outcome between two Asteraceae species compared to phylogenetically distant species pairs. Despite these assumptions, we found no general evidence that native Asteraceae species had a more negative effect on the performance of the target Asteraceae species compared to phylogenetically not related native species, neither through PSFs or competition, nor by their joint effect. However, there were species-specific exceptions in this sense. For example, the performance of *Solidago canadensis* was reduced when competing with *Achillea collina* in soils conditioned by *Achillea*. Another exception was the competitive relationship between the invasive *Erigeron* and the native *Hieracium*, as this resident native species was the worst competitor of *Erigeron*, irrespective of the soil type. Therefore, species-specific responses, rather than phylogenetical relatedness drove our results. Further studies should consider including more species with diverse phylogenetic relationships to reliably study this question. Darwin's naturalization hypothesis predicts that non-native species closely related to the species of the native community have a lower chance of becoming successful invaders compared to more distantly related non-native species as a result of competitive exclusion between close relatives (Darwin 1859). Indeed, phylogenetic relatedness may influence the strength of species' interactions, but the outcome of species interactions depends on many circumstances (Burns and Strauss 2011). For example, more closely related species can show intense competition under field conditions compared to distantly related species, but this pattern can be reversed in potting soils due to accentuated accumulation of soil mutualists (Burns and Strauss 2011). Although our target species and three conditioning species were confamilial species, only one competing pair belonged to the same tribe: *Crepis* (target species) and *Hieracium* (conditioning species) belonging to the Cichorieae tribe (Mandel et al. 2019); the other pairs were more distantly related. Therefore, it might be that our species were not closely related enough to show the benefits (more mutualistic soil biota) or drawbacks (intense interspecific competition) of phylogenetically closely related species. A more targeted study that adequately address the phylogenetic relationships between native and invasive species (e.g., using confamilial, congener and even conspecific levels) might shed light on our third question more properly.

5 | Conclusions

Evaluating the influence of native species' plant–soil feedback on the outcome of competition between invasive species and resident native species enhances our understanding on invasion resistance of native species and thus provides information that may be useful for grassland conservation. Although the native resident species of the selected grassland exerted strong negative plant–soil feedback on the performance of the invasive species, this effect mostly disappeared in the real presence of the native competitors. We also showed that the identity of native resident species is more important in determining PSF and competitive outcome than whether it is dominant or subordinate, or whether it is phylogenetically related to the target species.

Author Contributions

A.F. designed the study. A.F. and L.S. performed the experiment. A.F., E.R., and P.T. wrote the manuscript. All authors contributed critically to the draft and approved the final version for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The original data are accessible as Supporting Information (Appendix S2).

References

Anacker, B. L., J. N. Klironomos, H. Maherali, K. O. Reinhart, and S. Y. Strauss. 2014. "Phylogenetic Conservatism in Plant-Soil Feedback and Its Implications for Plant Abundance." *Ecology Letters* 17: 1613–1621.

Aschehoug, E. T., and R. M. Callaway. 2015. "Diversity Increases Indirect Interactions, Attenuates the Intensity of Competition, and Promotes Coexistence." *American Naturalist* 186: 452–459.

Bennett, J. A., and J. Klironomos. 2019. "Mechanisms of Plant–Soil Feedback: Interactions Among Biotic and Abiotic Drivers." *New Phytologist* 222: 91–96.

Bever, J. D., K. M. Westover, and J. Antonovics. 1997. "Incorporating the Soil Community Into Plant Population Dynamics: The Utility of the Feedback Approach." *Journal of Ecology* 85: 561–573.

Brinkman, P. E., W. H. van der Putten, E. J. Bakker, and K. J. F. Verhoeven. 2010. "Plant-Soil Feedback: Experimental Approaches, Statistical Analyses and Ecological Interpretations." *Journal of Ecology* 98: 1063–1073.

Buerdsell, S. L., B. G. Milligan, and E. A. Lehnhoff. 2021. "Invasive Plant Benefits a Native Plant Through Plant-Soil Feedback but Remains the Superior Competitor." *NeoBiota* 64: 119–136.

Bukowski, A. R., C. Schittko, and J. S. Petermann. 2018. "The Strength of Negative Plant–Soil Feedback Increases From the Intraspecific to the Interspecific and the Functional Group Level." *Ecology and Evolution* 8: 2280–2289.

Burns, J. H., and S. Y. Strauss. 2011. "More Closely Related Species Are More Ecologically Similar in an Experimental Test." *Proceedings of the National Academy of Sciences of the United States of America* 108: 5302–5307.

Callaway, R. M., E. J. Bedmar, K. O. Reinhart, C. G. Silvan, and J. Klironomos. 2011. "Effects of Soil Biota From Different Ranges on *Robinia* Invasion: Acquiring Mutualists and Escaping Pathogens." *Ecology* 92: 1027–1035.

Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben. 2004. "Soil Biota and Exotic Plant Invasion." *Nature* 427: 731–733.

Casper, B. B., and J. P. Castelli. 2007. "Evaluating Plant-Soil Feedback Together With Competition in a Serpentine Grassland." *Ecology Letters* 10: 394–400.

Chen, P., Q. Huang, Y. Zhuge, C. Li, P. Zhu, and Y. Hou. 2021. "The Effects of Plant–Soil Feedback on Invasion Resistance Are Soil Context Dependent." *Oecologia* 197: 213–222.

Cheng, C., Z. Liu, Q. Zhang, et al. 2024. "Genotype Diversity Enhances Invasion Resistance of Native Plants via Soil Biotic Feedbacks." *Ecology Letters* 27: 1–12.

Crawford, K. M., and T. M. Knight. 2017. "Competition Overwhelms the Positive Plant–Soil Feedback Generated by an Invasive Plant." *Oecologia* 183: 211–220.

Crystal-Ornelas, R., and J. L. Lockwood. 2020. "Cumulative Meta-Analysis Identifies Declining but Negative Impacts of Invasive Species on Richness After 20 Years." *Ecology* 101: e03082.

Darwin, C. R. 1859. *The Origin of Species*, edited by J. Murray.

Duncan, R. P., and P. A. Williams. 2002. "Ecology: Darwin's Naturalization Hypothesis Challenged." *Nature* 417: 608–609.

Endlweber, K., and S. Scheu. 2006. "Establishing Arbuscular Mycorrhiza-Free Soil: A Comparison of Six Methods and Their Effects on Nutrient Mobilization." *Applied Soil Ecology* 34: 276–279.

Engelkes, T., E. Morriën, K. J. F. Verhoeven, et al. 2008. "Successful Range-Expanding Plants Experience Less Above-Ground and Below-Ground Enemy Impact." *Nature* 456: 946–948.

Fenesi, A., Z. Botta-Dukát, Z. Miholcsa, et al. 2023. "No Consistencies in Abundance–Impact Relationships Across Herbaceous Invasive Species and Ecological Impact Metrics." *Journal of Ecology* 111: 1120–1138.

Fenesi, A., J. Geréd, S. J. Meiners, B. Tóthmérész, P. Török, and E. Ruprecht. 2015. "Does Disturbance Enhance the Competitive Effect of the Invasive *Solidago canadensis* on the Performance of Two Native Grasses?" *Biological Invasions* 17: 3303–3315.

Fenesi, A., C. I. Vágási, M. Beldean, et al. 2015. "*Solidago canadensis* Impacts on Native Plant and Pollinator Communities in Different-Aged Old Fields." *Basic and Applied Ecology* 16: 335–346.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. "Restoration Through Reassembly: Plant Traits and Invasion Resistance." *Trends in Ecology & Evolution* 23: 695–703.

Gioria, M., P. E. Hulme, D. M. Richardson, and P. Pyšek. 2023. "Why Are Invasive Plants Successful?" *Annual Review of Plant Biology* 74: 635–670.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. "The Meta-Analysis of Response Ratios in Experimental Ecology." *Ecology* 80: 1150–1156.

Hemrová, L., J. Knappová, and Z. Münzbergová. 2016. "Assessment of Habitat Suitability Is Affected by Plant-Soil Feedback: Comparison of Field and Garden Experiment." *PLoS One* 11: 1–26.

in't Zandt, D., A. van den Brink, H. de Kroon, and E. J. W. Visser. 2019. "Plant-Soil Feedback Is Shut Down When Nutrients Come to Town." *Plant and Soil* 439: 541–551.

Jing, J., T. M. Bezemer, and W. H. van der Putten. 2015. "Interspecific Competition of Early Successional Plant Species in ex-Arable Fields as Influenced by Plant-Soil Feedback." *Basic and Applied Ecology* 16: 112–119.

Klironomos, J. N. 2002. "Feedback With Soil Biota Contributes to Plant Rarity and Invasiveness in Communities." *Nature* 417: 67–70.

Kovács-Hostyánszki, A., V. Szigeti, Z. Miholcsa, et al. 2022. "Threats and Benefits of Invasive Alien Plant Species on Pollinators." *Basic and Applied Ecology* 64: 89–102.

Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. "Plant-Soil Feedbacks: A Meta-Analytical Review." *Ecology Letters* 11: 980–992.

Larios, L., and K. N. Suding. 2015. "Competition and Soil Resource Environment Alter Plant-Soil Feedbacks for Native and Exotic Grasses." *AoB Plants* 7: 1–9.

Lekberg, Y., J. D. Bever, R. A. Bunn, et al. 2018. "Relative Importance of Competition and Plant–Soil Feedback, Their Synergy, Context Dependency and Implications for Coexistence." *Ecology Letters* 21, no. 8: 1268–1281. https://doi.org/10.1111/ele.13093.

Lekberg, Y., and L. P. Waller. 2016. "What Drives Differences in Arbuscular Mycorrhizal Fungal Communities Among Plant Species?" *Fungal Ecology* 24: 135–138.

Lemmermeyer, S., L. Lörcher, M. van Kleunen, and W. Dawson. 2015. "Testing the Plant Growth-Defense Hypothesis Belowground: Do Faster-Growing Herbaceous Plant Species Suffer More Negative Effects From Soil Biota Than Slower-Growing Ones?" *American Naturalist* 186: 264–271.

Li, Y. P., W. T. Li, J. Li, and Y. L. Feng. 2024. "Temporal Dynamics of Plant–Soil Feedback and Related Mechanisms Depend on Environmental Context During Invasion Processes of a Subtropical Invader." *Plant and Soil* 496: 539–554.

Liu, Y., S. Yu, Z. P. Xie, and C. Staehelin. 2012. "Analysis of a Negative Plant-Soil Feedback in a Subtropical Monsoon Forest." *Journal of Ecology* 100: 1019–1028.

Liu, Y., Y.-L. Zheng, L. V. Jahn, and J. H. Burns. 2023. "Invaders Responded More Positively to Soil Biota Than Native or Noninvasive Introduced Species, Consistent With Enemy Escape." *Biological Invasions* 25: 351–364.

Mandel, J. R., R. B. Dikow, C. M. Siniscalchi, R. Thapa, L. E. Watson, and V. A. Funk. 2019. "A Fully Resolved Backbone Phylogeny Reveals Numerous Dispersals and Explosive Diversifications Throughout the History of Asteraceae." *Proceedings of the National Academy of Sciences of the United States of America* 116: 14083–14088.

Ning, L., F. H. Yu, and M. van Kleunen. 2016. "Allelopathy of a Native Grassland Community as a Potential Mechanism of Resistance Against Invasion by Introduced Plants." *Biological Invasions* 18: 3481–3493.

Perkins, L. B., and R. S. Nowak. 2013. "Native and Non-Native Grasses Generate Common Types of Plant-Soil Feedbacks by Altering Soil Nutrients and Microbial Communities." *Oikos* 122: 199–208.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Reinhart, K. O., and R. M. Callaway. 2006. "Soil Biota and Invasive Plants." *New Phytologist* 170: 445–457.

Sweet, D. D., and J. H. Burns. 2017. "Plant Performance Was Greater in the Soils of More Distantly Related Plants for an Herbaceous Understory Species." *AoB Plants* 9: 1–8.

Thuiller, W., L. Gallien, I. Boulangeat, et al. 2010. "Resolving Darwin's Naturalization Conundrum: A Quest for Evidence." *Diversity and Distributions* 16: 461–475.

Torres, N., I. Herrera, L. Fajardo, and R. O. Bustamante. 2021. "Meta-Analysis of the Impact of Plant Invasions on Soil Microbial Communities." *BMC Ecology and Evolution* 21: 4–11.

Tortorelli, C. M., B. K. Kerns, and M. A. Krawchuk. 2022. "Community Invasion Resistance Is Influenced by Interactions Between Plant Traits and Site Productivity." *Ecology* 103: 1–9.

Valiente-Banuet, A., and M. Verdú. 2008. "Temporal Shifts From Facilitation to Competition Occur Between Closely Related Taxa." *Journal of Ecology* 96: 489–494.

Van der Putten, W. H., R. D. Bardgett, J. D. Bever, et al. 2013. "Plant-Soil Feedbacks: The Past, the Present and Future Challenges." *Journal of Ecology* 101: 265–276.

Vilà, M., J. L. Espinar, M. Hejda, et al. 2011. "Ecological Impacts of Invasive Alien Plants: A Meta-Analysis of Their Effects on Species, Communities and Ecosystems." *Ecology Letters* 14: 702–708.

Wang, Y., G. Ni, Y. Hou, Q. Wang, and Q. Huang. 2020. "Plant–Soil Feedbacks Under Resource Limitation May Not Contribute to the Invasion by Annual Asteraceae Plants." *Oecologia* 194: 165–176.

Wei, W., P. Zhu, P. Chen, et al. 2020. "Mixed Evidence for Plant–Soil Feedbacks in Forest Invasions." *Oecologia* 193: 665–676.

Willner, W., J. Rolecek, A. Korolyuk, et al. 2019. "Formalized Classification of Semi-Dry Grasslands in Central and Eastern Europe." *Preslia* 91: 25–49.

Xu, H., Q. Liu, S. Wang, G. Yang, and S. Xue. 2022. "A Global Meta-Analysis of the Impacts of Exotic Plant Species Invasion on Plant Diversity and Soil Properties." *Science of the Total Environment* 810: 152286.

Yang, R., G. Zhou, S. Zan, F. Guo, N. Su, and J. Li. 2014. "Arbuscular Mycorrhizal Fungi Facilitate the Invasion of *Solidago canadensis* L. in Southeastern China." *Acta Oecologica* 61: 71–77.

Yelenik, S. G., and C. M. D'Antonio. 2013. "Self-Reinforcing Impacts of Plant Invasions Change Over Time." *Nature* 503: 517–520.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.