Facilitation of invasive plants by soil biota becomes negative over time in short-term

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Abstract

Declining enemy release predicts that invasive plants accumulated more soil natural enemies, and the increase in enemies may inhibit growth of invasive plants themselves. But most studies focus on historical time rather than short-term. We designed a fully crossed factorial experiment, we grew individuals of four congeneric pairs of invasive and native plant species in 2.5 L pots that contained live or sterilized field soil under two harvest time (first vs second). Results shows that soil microbes tended to have a slight positive effect on total biomass of the native plant species over time in short-term, while the effect of soil microbes on invasive plants as their total biomass tended to change from promotion to inhibition over time in short-term. Overall, these results suggest that regardless of the direction and strength of plant-soil feedback on invasive plant species, invasive plant species consistently may grow larger than co-occurring native plant species over time in short-term.

Introduction

Alien plant invasions still accelerating (Seebens et al. 2020), and it has seriously threatened biodiversity and ecosystem function (Lewis et al. 2015, Pyšek et al. 2020, Schaffner et al. 2020, Vilà et al. 2011). Soil biota as a driver of successful alien plant invasions was supported by many studies (Callaway et al. 2004, Keane et al. 2002, Reinhart et al. 2006, Reinhart et al. 2003, Zhang et al. 2020). Mycorrhizal fungi contribute to increased water and nutrient utilization to promote plant growth (Batten et al. 2006, Keane et al. 2002), but pathogens decrease plant growth (Maron et al. 2011). The enemy release hypothesis (ERH) predicts that absence or reduced the numbers of enemies, such as microbial pathogens, in their introduced range drives invasion success of alien plants (Callaway et al. 2004, Keane et al. 2002). *Prunus serotina* as a native species in United States but invasive in Europe, a study showed that soil microbial from United States killed seedlings of*Prunus serotina* , while soil microbes in European (i.e., non-native range) produced positive feedback on seedling growth (Reinhart et al. 2003). On the other hand, invasive plants may benefit from beneficial microbes. The enhanced mutualist hypothesis (Callaway et al. 2004) predicts that invasive plants may recruit more arbuscular mycorrhizal fungi in their non-native ranges, which contributes to their successful invasion. For example, Tian et al. (2021) found that arbuscular mycorrhizal fungi colonization and biomass of invasive plants were higher than that in their native range. Compared to native plants, invasive plants tend to enhance their mutualistic relationship with arbuscular mycorrhizal fungi (Davis 2018). However, this advantage may weak over time, as either alien invasive species benefit from the presence of beneficial bacteria or the escape of soil natural enemies in short-term, while enemies accumulate in large numbers with the abundance of invasive species (Dostál et al. 2013, Lau et al. 2016, Mitchell et al. 2010).

Several studies have shown that soil microbes are influenced by temporal variation in alien plant invasions. In introduced range, pathogen richness increased with the invasive plant residence time, while the proportional release from pathogens decreased, and the increase in pathogenic microbes may suppress the growth of invasive plants themselves, thereby inhibited their invasion (Callaway et al. 2013, McGinn et al. 2018, Mitchell et al. 2010, Stricker et al. 2016). But a study showed that promotion of soil microbes on invasive plants independent of invasion period (Day et al. 2015). There are also studies have found that microbes richness tended to decrease with increasing invasion history, but arbuscular mycorrhizal fungal communities showed increasing recovery (Lankau 2011). The mixed results suggest that whether invasive plants benefit from beneficial microbes, escape from soil pathogens, or are more strongly suppressed by soil pathogens are related to temporal variation, but how soil microbes affect invasive plants over time remains uncertain.

Although it has been confirmed soil microbes affect invasive plants was relative to temporal variation. But we usually focus on the effect of soil microbes on a certain growth stage of invasive plants and native plants (e.g., seedlings; Reinhart et al. 2003), rather than changes in continuous growth processes. A meta-analysis found that soil microbes had a greater effect on invasive plants than native plants, and this effect by soil microbes tended to weak over time since introduction (Liu et al. 2023). However, the above research results are all based on comparing the historical time of invasion, and no research has focused on that in the short term. Therefore, understanding the differences how soil microbes affect invasive plants and native plants in short term may help us better understand the mechanisms of invasive plant invasion.

To test the effects of soil biota and temporal variation in short-term, as well as their interactions on invasive plant species and native plants species, we grew four congeneric perennials pairs of invasive plant species and native plant species under soil treatments (living vs sterilized) and harvest time treatments (first vs second). We predicted that soil microbes have different effects on invasive plant species and native plant species over time in short-time, and for invasive plants, will show a result of promoting first and then inhibiting.

Material and Methods

Study location and species

We conducted the experiment in a greenhouse at the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences (125°24'3"E, 43°59'49"N). An invasive and a native plant species from the same genus form a pair, all plants coexist commonly in the field in China, and four plant species pairs were used in this experiment (Table S1). We classified the species as invasive or native to China based on the book "The Checklist of the Alien Invasive Plants in China" (Ma, et al. 2018) and the Flora of China database (*www.efloras.org*). The seedings material came from the seeds and vegetatively (Table S1).

Experimental set-up

From a pre-experiment, we known that species germination rates were different. Therefore, we sowed them on different date (Table S1) to ensure that all species had a similar developmental stage at the start of the experiment. From 26 June to 14 August 2020 (Table S1), we used plastic trays (19.5 cm × 14.6 cm × 6.5 cm) which filled with peat moss as subtrate (Pindstrup Plus, Pindstrup Mosebrug A/S, Denmark) to sow seeds and transplanted stolons of each plant, and placed all trays in a greenhouse under natural light conditions, with a temperature between 20 °C and 28 °C.

On 21 September 2020, we collected the field soil from different sites, a natural grassland site (Changling: 123°30'32.26"E, 44°33'21.74"N) and two abandoned farmland sites (Anhui: 117°12'45.58"E, 31°55'7.68"N; Taizhou: 121°40'43.60"E, 19°1'0.12"N), where the test plants occur commonly. We collected soil at a depth of 0-25 cm in each site, and then used a 0.5 cm mesh to sieved and homogenized the three sites at a ratio of 1:1:1. Then we stored half of the soil at 4 °C until pot-filling. The other half of the soil we sterilized four days with a dose of 25 kGy of$^{60}CO_{\gamma}$ irradiation at the Harbin Guangya Radiation New Technology Co., Ltd (Harbin, China). To ensure that plants can fully grow, we homogenized 5 g slow-release fertilizer (Osmocote® Exact Standard, Everris International B.V., Geldermalsen, The Netherlands) with the substrate in each pot.

We used 2.5 L circular pots (top diameter × bottom diameter × height: 18.5 cm × 12.5 cm × 15 cm) and filled with a mixture of 37.5% (v/v) sand, 37.5% (v/v) vermiculite and 25% live or sterilized field soil. On

29 August 2020, we selected the similar seedlings for each species, and transplanted at total of 20 seedlings into 20 pots (i.e., one seedling per pot, see Figure 1). The pot size was selected for that the size was large enough to avoid that growth restriction until the end of the experiment. To test the effects of soil microbes on invasive and native plant species at different time periods, we assigned the 20 pots of each species to two levels of soil (live *vs* sterilized) treatments fully crossed with two times of harvest (first *vs* second). In other words, per species, we had five pots (i.e., replicates) in each of the four treatment combinations, 160 pots in total (2 levels of plant invasion status [invasive *vs* native] × 4 plant species pairs × 2 soil [live *vs* sterilized] × 2 harvest time (first *vs* second) × 5 replicates). The resulting 160 pots were randomly assigned to the four shelves in the greenhouse under natural light conditions, with a temperature between 20 °C and 28 °C, and rerandomized again after six weeks (i.e., on 8 October 2020). We gave each pot a separate tray in order to avoided the loss of nutrients and water, and also avoided soil biota cross contamination. We checked the pots every day and watered fully. It was noted that 80 pots of the first harvest were shared for data with another experiment (reported in Zhang et al. 2022).

We had twice harvest on 10 November and 2 December 2020, respectively. For each harvest, we separately harvested the above-ground biomass and below-ground biomass of all plants, as one plant transplanted error and four plants experienced drought, the total number of harvested plants was 155. All above-ground biomass and below-ground biomass were dried for at least 72 h at 65 °C, and then weighed. We calculated total biomass (i.e., above-ground biomass + below-ground biomass) and root mass fraction (RMF; below-ground biomass/total biomass).

Statistical analysis

To test the effects of soil biota, harvest time and their interactions on performance of invasive and co-occurring native plant species, we fitted Bayesian multilevel models using the function brm of the R package brms (Bürkner 2017) in R 4.0.3 (R Core Team 2020). To meet the assumption of normality, total biomass was sqrt-root-transformed, while the root mass fraction was natural-log transformed. We included plant species invasion status (invasive vs native), presence of soil biota (live vs sterilized), harvest time (i.e., first *vs* second) and their interactions as fixed effects in all models.

To account for non-independence of individuals of the plant species and for phylogenetic non-independence of the same species, we included species nested within genus as random factors in all models. In addition, to control for the potential effects of reproductive strategy of the different plant species (i.e., sexual vs vegetative), we included reproductive strategy as a random factor in the models.

We used the default priors set by the brms package, ran four independent chains. The total number of iterations per chain was 4000, and the number of warm-up samples was 2000. To effectively 'centers' the effects to the grand mean (i.e., the mean value across all data observations), we used the sum coding to directly test hypotheses about the main effects and interactive effects based on each coefficient's posterior distribution (Schad et al. 2020). And we used the functions contrasts and contr.sum of the stats package to implement this in brms. We considered the fixed effects of soil biota, harvest time and invasive status, and their interactions as significant when their 95% credible interval of the posterior distribution did not overlap zero, and when the 90% credible interval did not overlap zero as marginally significant. In addition, we analyzed the effects of soil biota, harvest time and their interactions on performance each congeneric pairs of invasive and native plant species using the same statistical analysis.

Results

Averaged across the harvest time and soil treatments, invasive plant species tended to produce higher total biomass (+102.5%) than native plants species (marginally significant effect of invasion status; Table 1; Figure 2A). Total biomass production was significantly increased over time (+88.0%) (significant effect of harvest time; Table 1 & Fig. 2A), and the increase in total biomass was significantly stronger for invasive plant species (+112.1%) than for native plant species (+49.0%) (significant effect of invasion status × harvest time; Table 1 & Figs. 2A & S1) over time. But root mass fraction was significantly decreased over time (-3.3%) of the plants (significant effect of harvest time; Table 1 & Fig. 2B), and this effect were stronger on native plant species than on invasive plant species, the decrease in root mass fraction of native plant species (-17.0%) over time, but increased of invasive plant species (+11.8%) (significant effect of invasion status × harvest time; Table 1 & Figs. 2B & S1) over time. The presence of soil microbes significantly decreased the root mass fraction (-13.6%) of the plants (significant effect of soil; Table 1 & Figs. 2B & S2).

For total biomass of the plants, we found a marginally significant three-way interaction of the invasion status, harvest time and soil microbes treatments (marginally significant effect of plant invasion status × harvest time × soil; Table 1 & Fig. 2A). Specifically, the presence of soil microbes decreased the total biomass of invasive plant species when at second harvest (-14.5%), however, under the other three combinations of harvest time and invasion status treatments, it tended to increase total biomass (first & invasive: +4.1 %; first & native: +7.3%; second & native: +2.7%).

Separate analyses of the main and interactive effects of plant invasion status, soil, harvest time treatments on total biomass found that significant differences in invasion status on *Sphagneticola* ,*Paspalum* , and *Solidago* (Table S3; Figs. 2a-1 to a-3), and significant differences in harvest time on *Sphagneticola* and*Paspalum* (Table S3; Figs. 2a-1 & a-2). Significant interactions between invasion status and soil treatments, and significant interactions between invasion status and harvest time treatments were found in *Paspalum* (Table S3; Fig. 2a-2). Significant interactions between invasion status and harvest time treatments were found in*Solidago* and *Alternanthera* , respectively (Table S3; Figs. 2a-3 & a-4). In addition, significant three-way interaction was found in *Paspalum* (Table S3; Fig. 2a-2).

Separate analyses of the main and interactive effects of plant invasion status, soil, harvest time treatments on root mass fraction found that significant differences in invasion status on *Sphagneticola* ,*Paspalum* , and *Alternanthera* (Figs. 2b-1, b-2 & b-4), and marginally significant differences in invasion status on *Solidago*(Table S4; Fig. 2b-3). Significant differences in harvest time on*Paspalum* (Fig. 2b-2), and marginally significant differences in harvest time on *Sphagneticola* , *Solidago* and*Alternanthera* , respectively (Table S4; Figs. 2b-1, b-3 & b-4). Soil treatment had a significant effect on three congeneric pairs of invasive and native plant species (Table S4; Figs. 2b-1 to b-3). Significant interactions between invasion status and harvest time were found in *Paspalum* and *Alternanthera* (Table S4; Fig. 2b-3 & b-4). Significant interactions and marginally significant interactions between invasion status and soil treatments was found in*Paspalum* and *Solidago* , respectively (Table S4; Fig. 2b-2 & b-3). But only significant interactions between soil and harvest time treatments was found in *Solidago* (Table S4; Fig. 2b-3). In addition, two significant three-way interaction were found in*Paspalum* , and *Solidago* (Table S4; Fig. 2b-2 & b-3).

Discussion

Total biomass of invasive plant species tended to higher than that of co-occurring native plant species, and the growth rate over time was also significantly higher than that of co-occurring native plant species regardless of the presence of soil microbes (Fig. 2A & Fig. S1). It is likely that invasive plants generally have a higher growth rate than native plants (van Kleunen et al. 2010), the current test invasive plant species also exhibited the trait as invasive plants grow larger than native plant species over time.

Soil microbes tended to had a slight positive effect on total biomass of the native plant species over time, while the effect of soil microbes on invasive plant species as their total biomass tended to change from promotion to inhibition over time (Fig. 2A). Consistent with our predictions, these results suggest that soil microbes affected the growth of invasive plant species and native plant species over time, and presence of soil microbes inhibited the growth of invasive plant species over time. This founding supports a prediction of declining enemy release over time that invasive plants accumulated more microbial natural enemies, and the increase in enemies (e.g., pathogen) may inhibit the growth of invasive plants themselves (Callaway et al. 2013, Diez et al. 2010, Mitchell et al. 2010, Stricker et al. 2016). Another possible explanation is that invasive plant responses to mutualisms weaken over time (Seifert et al. 2009), thus intensifies the inhibitory effect on the growth of invasive plants. In addition, the reduction of soil nutrients over time can also alter plant-soil feedback (Bennett et al. 2019), especially the rapid resource acquisition of invasive plants (Dukes et al. 1999), it may further amplify the negative feedback effects caused by pathogen accumulation or reduced mutualists dependence.

Local adaptations may be responsible for positive feedback in native plant species. Native plant species may be able to quickly adapt to the local soil microbial community (Kawecki et al. 2004). In generally, native plants tend to be conservative, have stronger tolerance to antagonists, and enhance adaptability to the local environment. Our research results showed that soil microbes always promote native plant species, which may be due to local adaptation in short-term, because it is found that this promotion effect weakens over time (first to second: 7.3% to 2.7%; Fig. 2A). We speculate that the promotion effect may also become inhibition in the future for a longer period, but the current results cannot prove it. Although the growth performance of invasive plant species was found to be different in individual analysis of species in each genus, and only the three-factor interaction was found in *Paspalum* (Fig. 2a-2), we speculated that temporal variations exist in the direction and strength of interactions between different plant species and soil microbes. Therefore, future studies may text the growth of different species over continuous time, to determine whether the strength and direction of invasive plant-to-soil feedback emerges with a general pattern.

Harvest time significantly decreased proportional allocation of biomass on roots (Fig. 2B), this result may be dominated by native plant species. We found that native plant species allocated proportionally biomass to their roots decreased over time, while an opposite pattern was observed for invasive plant species that tended to increase over time (Fig. 2B). It is consistent with plants growth responses, with invasive plant species allocated more root biomass to resource acquisition on growth. This is not surprising as more roots can help plants obtain more nutrients, and plants will preferentially allocate biomass to roots that can improve resource acquisition (Casper et al. 1997, Poorter et al. 2000). Although we found no significant three-way interaction between the invasion status, harvest time and soil treatments on root mass fraction (Fig. 2B), but the three-way interaction was observed in *Paspalum* (Fig. b-2) and*Solidago* (Fig. b-3). While the two genera did not show a same pattern, As guessed above, it is due to that the interaction between plant species and soil microbes is strongly related to temporal variations. In addition, we found that the presence of soil microbes significantly reduced the proportion of root biomass allocation, which indicates that soil microbes contain many pathogens, because soil-borne pathogens damage roots (Packer et al. 2003, Reinhart et al. 2010).

Caveats

We acknowledge that the study is too short-term and not a continue time, it was determined by another experiment (reported in Zhang et al. 2022), include the time interval between two harvests. But we still emphasize the phenomenon of soil microbes on invasive plants tended to change from promotion to inhibition over time in short-time.

Conclusion

In summary, we found that invasive plant species were larger and grew faster than co-occurring native plant species over time in short-term. Our results support a prediction of declining enemy release over time that the effect of soil microbes on the growth of invasive plant species changes from promotion to inhibition over time in short-term. Overall, these results suggest that regardless of the direction and strength of soil microbial feedback on invasive plant species, invasive plant species consistently may grow larger than co-occurring native plant species.

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Tables

Table 1 Output of the Bayesian multilevel models testing effects of plant invasion status (invasive *vs* native), soil (live*vs* sterilized), harvest time (first *vs* second) treatments, and their interactions on total biomass and root mass fraction of four pairs of invasive and native plants. Shown are the model estimates and standard errors (SE), as well as the lower (L) and upper (U) values of the 95% and 90% credible intervals (CI).

	Estimate	**SE**	**L95% CL**	**U95% CL**	**L90% CL**	**U90% CL**

Total biomass (sqrt-root-transformed)	**Total biomass (sqrt-root-transformed)**	**Total biomass (sqrt-root-transformed)**	**Total biomass (sqrt-root-transformed)**	**Total biomass (sqrt-root-transformed)**	**Total biomass (sqrt-root-transformed)**	**Total biomass (sqrt-root-transformed)**
Intercept	3.346*	0.971	1.446	5.372	1.847	4.903
Invasion status (I)	-0.693^{+}	0.427	-1.547	0.195	-1.346	-0.021
Harvest time (H)	-0.472*	0.049	-0.570	-0.376	-0.553	-0.392
Soil (S)	-0.015	0.045	-0.103	0.071	-0.089	0.058
I × H	0.253*	0.050	0.153	0.349	0.169	0.333
I × S	0.07	0.045	-0.018	0.159	-0.003	0.145
S × H	0.035	0.042	-0.047	0.118	-0.034	0.105
I × H × S	-0.078^{+}	0.041	-0.159	0.004	-0.146	-0.011
Root mass fraction (natural-log-transformed)	**Root mass fraction (natural-log-transformed)**	**Root mass fraction (natural-log-transformed)**	**Root mass fraction (natural-log-transformed)**	**Root mass fraction (natural-log-transformed)**	**Root mass fraction (natural-log-transformed)**	**Root mass fraction (natural-log-transformed)**
Intercept	-2.097*	0.788	-3.768	-0.474	-3.333	-0.900
Invasion status (I)	-0.027	0.302	-0.647	0.533	-0.496	0.416
Harvest time (H)	0.060*	0.020	0.020	0.100	0.026	0.094
Soil (S)	-0.072*	0.021	-0.114	-0.032	-0.106	-0.039
I × H	0.085*	0.021	0.045	0.125	0.051	0.119
I × S	-0.011	0.021	-0.051	0.029	-0.045	0.023
S × H	-0.005	0.021	-0.046	0.037	-0.04	0.029
I × H × S	0.016	0.021	-0.025	0.055	-0.018	0.049

Model estimates whose 95% credible intervals do not overlap with zero are indicated with asterisks (*), and those whose 90% credible intervals do not overlap with zero are indicated with daggers (+). Residual standard deviations *sigma* for individual non-native species are given in Table S2.

Figure1

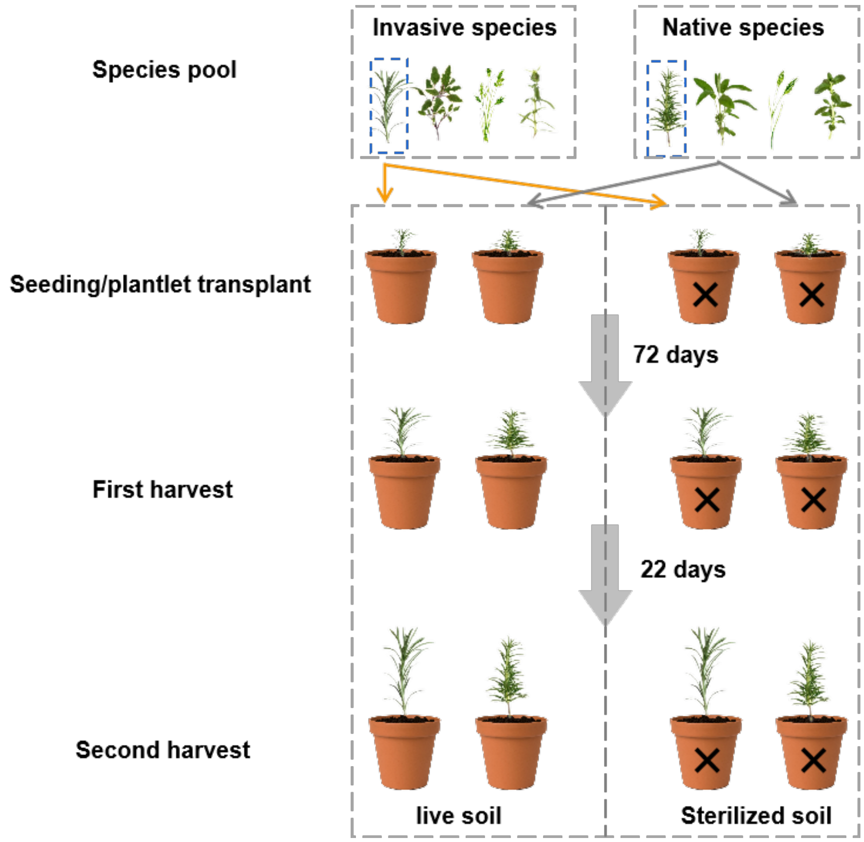

Figure 1 A schematic illustration of the experimental design.

Figure 2

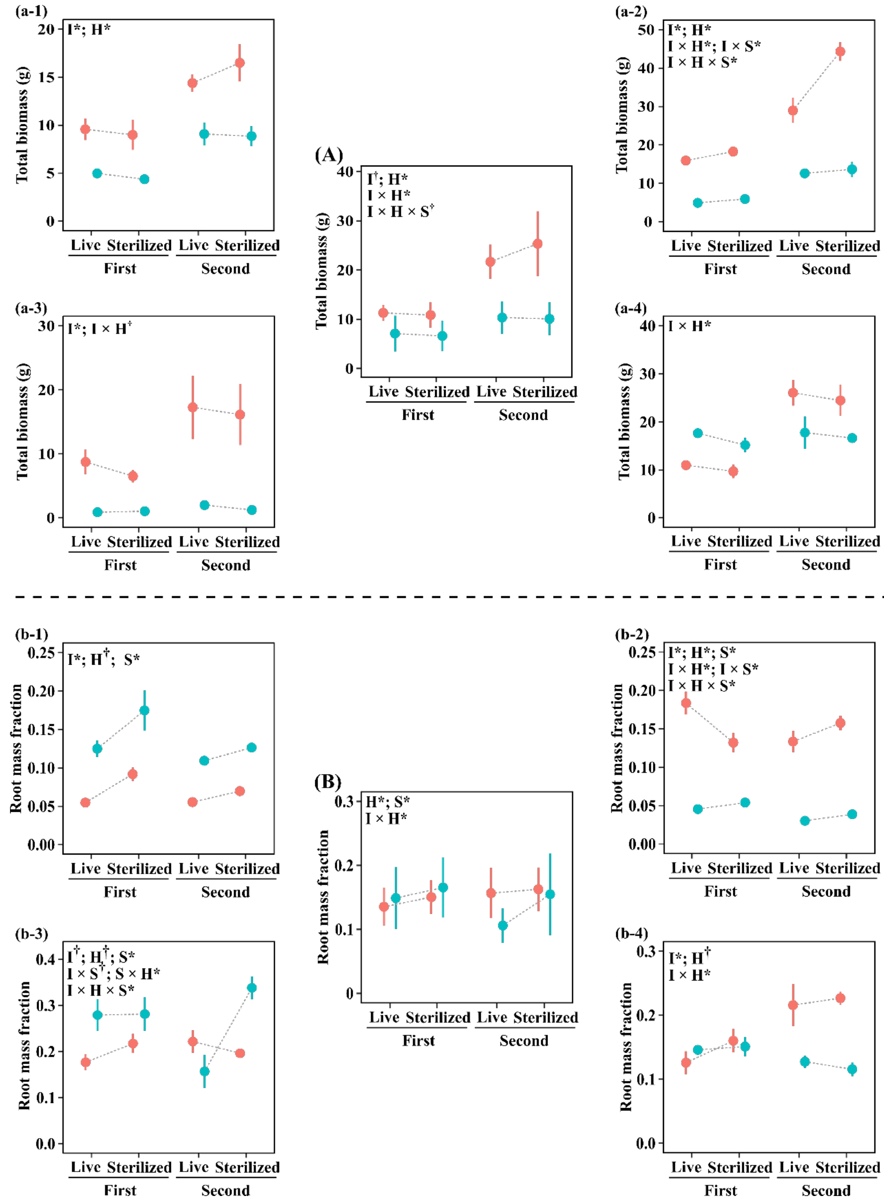

Figure 2 Mean (±1SE) values of total biomass (A) and root mass fraction (B) for four congeneric pairs of invasive and native plant species under a factorial combination of two levels of soil treatments (live *vs* sterilized) and two levels of harvest time treatments (first *vs* second). The 4 subgraphs above represent the mean values of total biomass of *Sphagneticola* (a-1), *Paspalum*(a-2), *Solidago* (a-3), *Alternanthera* (a-4) respectively, under a factorial combination of two levels of soil treatments (live*vs* sterilized) and two levels of harvest time treatments (first*vs* second). And the 4 subgraphs below represent the mean values of root mass fraction of *Sphagneticola* (b-1),*Paspalum* (b-2),*Solidago* (b-3), *Alternanthera* (b-4) respectively, under a factorial combination of two levels of soil treatments (live *vs*sterilized) and two levels of harvest time treatments (first *vs*second). Model terms (I: invasion status; S: soil treatment; H: harvest treatment) whose 95% credible intervals do not overlap with zero are indicated with asterisks (*), and those whose 90% credible intervals do not overlap with zero are indicated with daggers (+).

Appendix

Table S1 Details of the test plant species that were used in the current experiment.

Species	**Family**	**Invasion status**	**Seed source**
Solidago canadensis L.	Compositae	Invasive	Zhejiang, China
Solidago decurrens Lour.	Compositae	Native	Zhejiang, China
Alternanthera philoxeroides (Mart.) Griseb.	Amaranthaceae	Invasive	Zhejiang, China
Alternanthera sessilis (L.) R.Br. ex DC.	Amaranthaceae	Native	Zhejiang, China
Paspalum notatum Flüggé	Poaceae	Invasive	Green alliance ecological enterprise sho
Paspalum scrobiculatum L.	Poaceae	Native	Hubei, China
Sphagneticola trilobata (L.) Pruski	Compositae	Invasive	Hubei, China
Sphagneticola calendulacea (L.) Pruski	Compositae	Native	Hubei, China

Table S2 Output of the Bayesian multilevel models' estimates of the residual standard-deviation *sigmas* for individual species. Shown are the model estimates and standard errors as well as the lower (L) and upper (U) values of the 95% and 90% credible intervals (CI).

		Estimate	**SE**	**L95% CL**	**L95% CL**	**U95% CL**	**L90%C**
Total biomass	*Alternanthera_philoxeroides*	-0.504*	0.178	-0.834	-0.137	-0.137	-0.782
	Alternanthera_sessilis	-0.851*	0.19	-1.195	-0.442	-0.442	-1.145
	Paspalum_notatum	-0.509*	0.202	-0.888	-0.096	-0.096	-0.829
	Paspalum_scrobiculatum	-0.388*	0.177	-0.707	-0.017	-0.017	-0.665
	Solidago_canadensis	0.004	0.17	-0.297	0.37	0.37	-0.256
	Solidago_decurrens	-1.506*	0.205	-1.871	-1.072	-1.072	-1.82
	Sphagneticola_calendulacea	-0.930*	0.185	-1.272	-0.54	-0.54	-1.222
	Sphagneticola_trilobata	-0.634*	0.192	-0.991	-0.236	-0.236	-0.934
Root mass fraction	*Alternanthera_philoxeroides*	-1.098*	0.18	-1.43	-0.716	-0.716	-1.38
	Alternanthera_sessilis	-1.622*	0.197	-1.979	-1.212	-1.212	-1.93
	Paspalum_notatum	-1.275*	0.19	-1.634	-0.886	-0.886	-1.576
	Paspalum_scrobiculatum	-1.959*	0.182	-2.284	-1.573	-1.573	-2.236
	Solidago_canadensis	-1.547*	0.181	-1.876	-1.168	-1.168	-1.83
	Solidago_decurrens	-0.710*	0.178	-1.029	-0.336	-0.336	-0.984
	Sphagneticola_calendulacea	-1.521*	0.171	-1.835	-1.165	-1.165	-1.792
	Sphagneticola_trilobata	-1.302*	0.193	-1.655	-0.901	-0.901	-1.604

Model estimates whose 95% credible intervals do not overlap with zero are indicated with asterisks (*).

Table S3 Output of the Bayesian multilevel models testing effects of soil (live *vs* sterilized), harvest time (first*vs* second) treatments, and their interactions on total biomass of each congeneric pairs of invasive and native plant species. Shown are the model estimates and standard errors (SE), as well as the lower (L) and upper (U) values of the 95% and 90% credible intervals (CI).

	Estimate	**SE**	**L95% CL**	**U95% CL**	**L90% CL**	**U90% CL**
Total biomass of *Sphagneticola* (sqrt-root-transformed)	**Total biomass of *Sphagneticola* (sqrt-root-transformed)**	**Total biomass of *Sphagneticola* (sqrt-root-transformed)**	**Total biomass of *Sphagneticola* (sqrt-root-transformed)**	**Total biomass of *Sphagneticola* (sqrt-root-transformed)**	**Total biomass of *Sphagneticola* (sqrt-root-transformed)**	**Total biomass of *Sphagneticola* (sqrt-root-transformed)**

Intercept	2.562*	0.094	2.373	2.746	2.406	2.717
Invasion status (I)	0.902*	0.131	0.644	1.164	0.689	1.118
Harvest time (H)	-0.409*	0.093	-0.592	-0.221	-0.56	-0.256
Soil (S)	0.043	0.094	-0.146	0.23	-0.112	0.196
I × H	-0.04	0.132	-0.303	0.218	-0.256	0.174
I × S	-0.077	0.133	-0.338	0.183	-0.295	0.14
S × H	0.029	0.093	-0.153	0.214	-0.124	0.18
I × H × S	0.062	0.132	-0.193	0.316	-0.152	0.277
Total biomass of *Paspalum*	**Total biomass of *Paspalum***	**Total biomass of *Paspalum***	**Total biomass of *Paspalum***	**Total biomass of *Paspalum***	**Total biomass of *Paspalum***	**Total biomass of *Paspalum***
Intercept	9.239*	0.897	7.507	11.004	7.802	10.717
Invasion status (I)	17.611*	1.301	15.05	20.137	15.511	19.747
Harvest time (H)	-3.854*	0.929	-5.722	-2.055	-5.385	-2.35
Soil (S)	-0.522	0.928	-2.371	1.297	-2.036	0.997
I × H	-5.915*	1.308	-8.505	-3.328	-8.045	-3.796
I × S	-3.900*	1.293	-6.441	-1.383	-6.034	-1.806
S × H	0.014	0.939	-1.845	1.874	-1.527	1.561
I × H × S	3.240*	1.324	0.594	5.856	1.044	5.41
Total biomass of *Solidago* (sqrt-root-transformed)	**Total biomass of *Solidago* (sqrt-root-transformed)**	**Total biomass of *Solidago* (sqrt-root-transformed)**	**Total biomass of *Solidago* (sqrt-root-transformed)**	**Total biomass of *Solidago* (sqrt-root-transformed)**	**Total biomass of *Solidago* (sqrt-root-transformed)**	**Total biomass of *Solidago* (sqrt-root-transformed)**
Intercept	1.104*	0.177	0.753	1.45	0.816	1.395
Invasion status (I)	2.203*	0.254	1.698	2.697	1.787	2.621
Harvest time (H)	-0.141	0.176	-0.488	0.206	-0.427	0.151
Soil (S)	0.057	0.18	-0.302	0.413	-0.235	0.353
I × H	-0.466^{+}	0.25	-0.962	0.02	-0.879	-0.061
I × S	0.054	0.255	-0.45	0.556	-0.362	0.475
S × H	-0.096	0.178	-0.452	0.253	-0.391	0.198
I × H × S	0.158	0.252	-0.343	0.642	-0.256	0.566
Total biomass of *Alternanthera* (natural-log-transformed)	**Total biomass of *Alternanthera* (natural-log-transformed)**	**Total biomass of *Alternanthera* (natural-log-transformed)**	**Total biomass of *Alternanthera* (natural-log-transformed)**	**Total biomass of *Alternanthera* (natural-log-transformed)**	**Total biomass of *Alternanthera* (natural-log-transformed)**	**Total biomass of *Alternanthera* (natural-log-transformed)**
Intercept	2.804*	0.061	2.685	2.925	2.706	2.905
Invasion status (I)	-0.051	0.082	-0.209	0.11	-0.184	0.083
Harvest time (H)	-0.023	0.062	-0.145	0.098	-0.124	0.078
Soil (S)	0.051	0.062	-0.072	0.173	-0.051	0.153

I × H	-0.427*	0.083	-0.589	-0.262	-0.562	-0.29
I × S	0.007	0.084	-0.158	0.172	-0.131	0.142
S × H	0.033	0.062	-0.088	0.157	-0.068	0.134
I × H × S	-0.011	0.084	-0.175	0.152	-0.146	0.126

Model estimates whose 95% credible intervals do not overlap with zero are indicated with asterisks (*), and those whose 90% credible intervals do not overlap with zero are indicated with daggers (+).

Table S4 Output of the Bayesian multilevel models testing effects of soil (live vs sterilized), harvest time (first vs second) treatments, and their interactions on root mass fraction of each congeneric pairs of invasive and native plant species. Shown are the model estimates and standard errors (SE), as well as the lower (L) and upper (U) values of the 95% and 90% credible intervals (CI).

	Estimate	**SE**	**L95% CL**	**U95% CL**	**L90% CL**	**U90% CL**
Root mass fraction of *Sphagneticola* (natural-log-transformed)	**Root mass fraction of *Sphagneticola* (natural-log-transformed)**	**Root mass fraction of *Sphagneticola* (natural-log-transformed)**	**Root mass fraction of *Sphagneticola* (natural-log-transformed)**	**Root mass fraction of *Sphagneticola* (natural-log-transformed)**	**Root mass fraction of *Sphagneticola* (natural-log-transformed)**	**Root mass fraction of *Sphagneticola* (natural-log-transformed)**
Intercept	-2.044*	0.051	-2.144	-1.942	-2.127	-1.959
Invasion status (I)	-0.687*	0.072	-0.826	-0.544	-0.804	-0.57
Harvest time (H)	0.102+	0.051	-0.002	0.202	0.018	0.185
Soil (S)	-0.113*	0.051	-0.213	-0.015	-0.198	-0.03
I × H	-0.035	0.073	-0.178	0.108	-0.156	0.082
I × S	-0.07	0.072	-0.212	0.07	-0.187	0.045
S × H	-0.039	0.05	-0.139	0.06	-0.124	0.043
I × H × S	-0.03	0.073	-0.171	0.111	-0.148	0.089
Root mass fraction of *Paspalum* (logit-transformed)	**Root mass fraction of *Paspalum* (logit-transformed)**	**Root mass fraction of *Paspalum* (logit-transformed)**	**Root mass fraction of *Paspalum* (logit-transformed)**	**Root mass fraction of *Paspalum* (logit-transformed)**	**Root mass fraction of *Paspalum* (logit-transformed)**	**Root mass fraction of *Paspalum* (logit-transformed)**
Intercept	-3.154*	0.046	-3.244	-3.062	-3.229	-3.079
Invasion status (I)	1.408*	0.064	1.281	1.533	1.302	1.513
Harvest time (H)	0.187*	0.045	0.097	0.275	0.113	0.261
Soil (S)	-0.104*	0.045	-0.193	-0.018	-0.179	-0.032
I × H	-0.143*	0.064	-0.269	-0.017	-0.248	-0.038
I × S	0.150*	0.063	0.026	0.278	0.048	0.258
S × H	0.022	0.046	-0.07	0.113	-0.054	0.098
I × H × S	0.129*	0.064	0.004	0.255	0.022	0.237
Root mass fraction of *Solidago* (natural-log-transformed)	**Root mass fraction of *Solidago* (natural-log-transformed)**	**Root mass fraction of *Solidago* (natural-log-transformed)**	**Root mass fraction of *Solidago* (natural-log-transformed)**	**Root mass fraction of *Solidago* (natural-log-transformed)**	**Root mass fraction of *Solidago* (natural-log-transformed)**	**Root mass fraction of *Solidago* (natural-log-transformed)**

Intercept	-1.426*	0.08	-1.586	-1.266	-1.556	-1.296
Invasion status (I)	-0.189+	0.113	-0.419	0.033	-0.38	-0.001
Harvest time (H)	0.129+	0.08	-0.028	0.288	0.001	0.262
Soil (S)	-0.232*	0.081	-0.39	-0.072	-0.365	-0.1
I × H	-0.162	0.112	-0.387	0.061	-0.348	0.021
I × S	0.205+	0.115	-0.022	0.434	0.019	0.39
S × H	0.231*	0.081	0.071	0.389	0.099	0.362
I × H × S	-0.307*	0.114	-0.532	-0.076	-0.494	-0.11
Root mass fraction of *Alternanthera* (natural-log-transformed)	**Root mass fraction of *Alternanthera* (natural-log-transformed)**	**Root mass fraction of *Alternanthera* (natural-log-transformed)**	**Root mass fraction of *Alternanthera* (natural-log-transformed)**	**Root mass fraction of *Alternanthera* (natural-log-transformed)**	**Root mass fraction of *Alternanthera* (natural-log-transformed)**	**Root mass fraction of *Alternanthera* (natural-log-transformed)**
Intercept	-2.018*	0.058	-2.134	-1.902	-2.114	-1.922
Invasion status (I)	0.260*	0.08	0.103	0.42	0.128	0.392
Harvest time (H)	0.101+	0.06	-0.017	0.218	0.003	0.198
Soil (S)	0.02	0.06	-0.099	0.137	-0.079	0.117
I × H	-0.327*	0.081	-0.493	-0.166	-0.462	-0.194
I × S	-0.106	0.081	-0.262	0.053	-0.236	0.027
S × H	-0.031	0.059	-0.145	0.086	-0.127	0.065
I × H × S	-0.01	0.08	-0.168	0.147	-0.14	0.122

Model estimates whose 95% credible intervals do not overlap with zero are indicated with asterisks (*), and those whose 90% credible intervals do not overlap with zero are indicated with daggers (+).

Figure S1

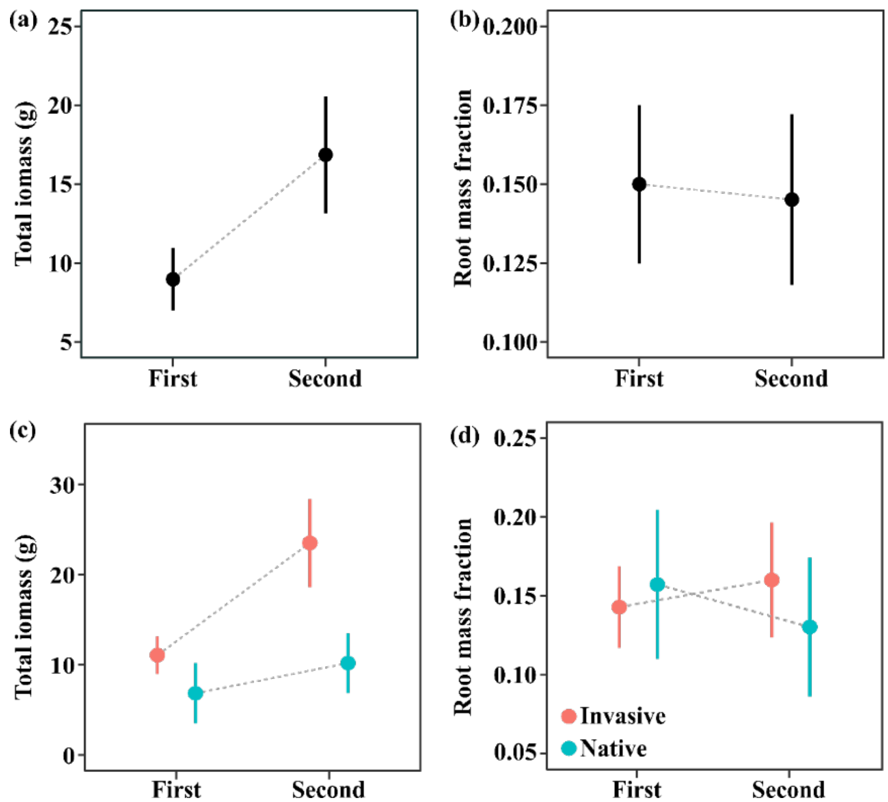

Figure S1 Mean values (±1SE) of total biomass (a) and root mass fraction (b) of plants under harvest time treatments (first vs. second), and mean values (±1SE) of total biomass (c) and root mass fraction (d) of four congeneric pairs of invasive and native plant species under two harvest time treatments (first vs. second).

Figure S2

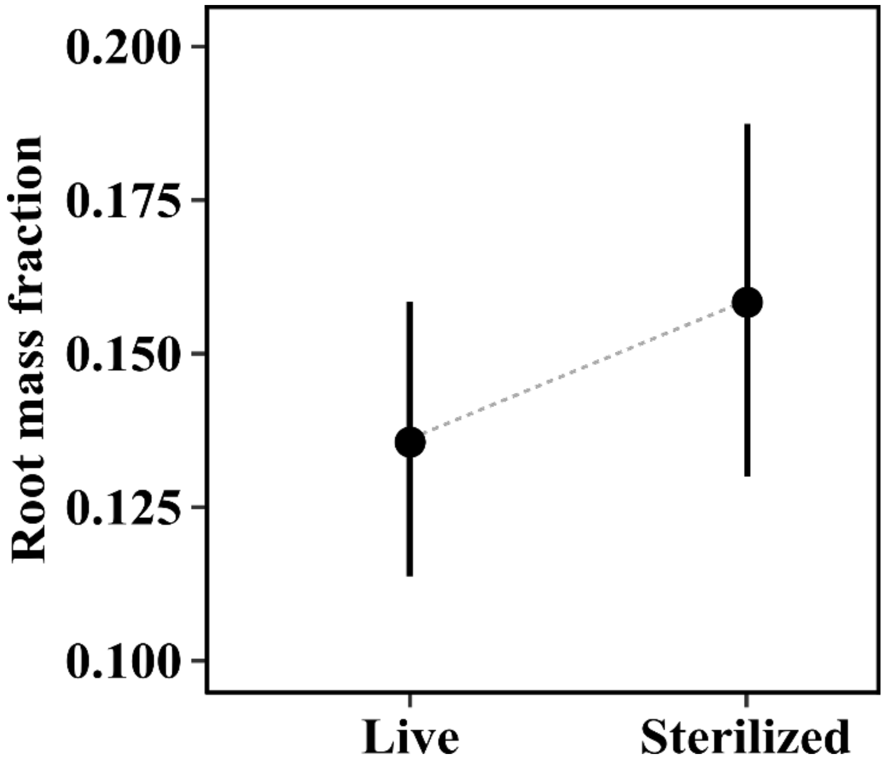

Figure S2 Mean (±1SE) values of root mass fraction (a) under of plants under two levels of soil treatments (live vs sterilized).