



Plant–soil biota interactions of an invasive species in its native and introduced ranges: Implications for invasion success



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ABSTRACT

Biotic interactions of exotic plant species in their introduced ranges may differ from those of co-occurring plant species and from interactions in their native range. Interactions less negative (Enemy Release Hypothesis) or more positive (Enhanced Mutualist Hypothesis) compared to native plants may enhance invasive success and change exotic plant traits. We investigated plant–soil interactions of Chinese tallow (*Triadica sebifera*) from China (native range) and US (invasive range) populations along with US and China species within four co-occurring genera (*Liquidambar*, *Ulmus*, *Celtis*, and *Platanus*) grown in both ranges. Treatments included sterilized, home, away, active mix, and fungicide treated soils. The net effect of soil biota on *Triadica* performance was generally negative or had no effect in its native range but was always positive in its invasive range. In China, *Triadica* had higher survival and biomass in “away” (hetero-specific) soils than in “home” (conspecific) soil, but in the US, only biomass was higher. The pattern of performance in home and away soils suggests a stronger negative effect of specific pathogens for *Triadica* in China (Enemy Release Hypothesis). No other species had a significant feedback in either range. *Triadica* mycorrhizal colonization was higher in the US than in China supporting the Enhanced Mutualist Hypothesis. On average, *Triadica* performance was similar for native and invasive populations. However, invasive populations had greater biomass in active mix than in sterilized or fungicide-treated soil and native populations had higher mycorrhizal colonization in home than in away soils or active mix. These population origin results suggest genetic differences in strength or specificity of mycorrhizal interactions. Overall, our results support both ecological and evolutionary variation in interactions with the soil community that may influence the invasion success of exotic plants.

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1. Introduction

The net effect of soil biota in the native ranges of an invasive plant can be more negative than the net effect of soil biota in introduced ranges of the same species (Reinhart et al., 2003; Reinhart and Callaway, 2006; Kulmatiski et al., 2008; Callaway et al., 2011). It is recognized that soil biota can play an important role in plant invasions (van der Putten et al., 2005; Wolfe and Klironomos, 2005; Inderjit and van der Putten, 2010). Depending on the relative strengths of mutualistic (positive) versus pathogenic (negative) effects of soil microbes in a plant species' native and introduced ranges, the net effects of soil microbial communities could facilitate or impede plant invasions.

Invasive species may escape soil-borne specialist enemies when they are introduced into new regions (“Enemy Release Hypothesis”, ERH) (Klironomos, 2002; Mitchell and Power, 2003; Reinhart and Callaway, 2006). Also, some invasive species can indirectly enhance their own performance in the non-native range by accumulating soil organisms that are adverse to native plant species, a hypothesis known as accumulation of local pathogens (ALP) (Eppinga et al., 2006). However, the effects of soil mutualists on invasive plants are less well understood than those of pathogens even though they are also likely to have an important role in plant invasions. For example, invaders may benefit from soil mutualists that they encounter in introduced ranges (“Enhanced Mutualist Hypothesis” or “EMH”) (Marler et al., 1999; Reinhart and Callaway, 2004; Parker et al., 2006). Invaders can also suppress soil mutualists of other plant species in introduced ranges more aggressively than mutualists in their native ranges (“Mutualism Disruption

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Hypothesis” or “MDH”) (Callaway et al., 2008). Most plant–soil mutualisms do not seem to have co-evolutionary relationships (Richardson et al., 2000), and some invasive plants can form mutualisms as effective as or more effective in the introduced ranges than in the native range (Parker et al., 2006).

Novel selection pressures imposed by an altered set of biotic interactions in the introduced range can also lead to rapid, evolutionary change for exotic plant traits (e.g. EICA) (Blossey and Nötzold, 1995; Bossdorf et al., 2005), which could influence the invasion potential of exotic plant species (Blossey and Nötzold, 1995; Leger and Rice, 2003; Blair and Wolfe, 2004). Most studies to date have focused on how changes in the aboveground herbivore or pathogen community affect invasive plant populations’ resistance or growth compared to native populations (Siemann and Rogers, 2003; Maron et al., 2004; Zou et al., 2008). However, studies of evolutionary changes involving soil biotic interactions of invasive species have been rare (Seifert et al., 2009). Understanding how plant–soil interactions influence evolutionary change in invasive plants is critical for understanding the roles of environmental differences, and differences in plant traits in determining invasion success (Mitchell et al., 2006).

One approach to studying plant invasions is to compare performance of an invasive plant in its native and introduced range, which can enhance our understanding of how variation in interactions between the introduced and native ranges influences an exotic plant’s invasion success (including genetic changes in plant traits in response to these variations), which is key to understanding mechanisms of plant invasion (Hierro et al., 2005). Several studies have examined plant performance in relation to soil communities in the native and introduced ranges within the same experimental set-up (Reinhart et al., 2003; Callaway et al., 2008; te Beest et al., 2009). For example, a study with spotted knapweed (*Centaurea maculosa*), native to Europe and invasive in northwestern USA, showed that negative plant–soil feedbacks occur in native range soil, whereas AM fungi play an important role in positive feedbacks in introduced range soil (Callaway et al., 2008). However, it did not include other species in the native and introduced ranges to understand how interactions impact the success of exotic versus co-occurring native plant species. Biogeographical experiments in the native and introduced ranges of black cherry (*Prunus serotina*), a tree species native to the USA but invasive in Europe, showed positive soil feedbacks in its introduced range and negative soil feedbacks in its native range (Reinhart et al., 2003; Callaway et al., 2008; te Beest et al., 2009). However, these did not compare native and invasive populations or include co-occurring native species in soils from both ranges to increase insight into competition level effects. To our knowledge, no studies have examined how interactions with the soil community influence plant performance in both native and non-native ranges using native and invasive populations and co-occurring native species, even though this is crucial to demonstrating evolutionary changes in soil biotic interactions and providing meaningful ecological context.

Here, we investigated plant–soil interactions with Chinese tallow (*Triadica sebifera*) from populations in the native (China) and introduced ranges (US – where it is invasive) and co-occurring species within four genera (*Liquidambar*, *Ulmus*, *Celtis*, *Platanus*) from US and China grown in common gardens in both ranges. Inclusion of other species increases the strength of inference for understanding soil feedbacks effects at the community level (Mitchell et al., 2006). Previous studies have shown that *Triadica* could have enhanced mycorrhizal associations in the introduced range relative to native trees (Nijjer et al., 2004, 2008) and that *Triadica* grew better in heterospecific (“away”) soils than in conspecific (“home”) soil (Nijjer et al., 2007). Moreover, soil

sterilization decreased *Triadica* performance in the introduced range (Nijjer et al., 2008). Taken together, these results suggest that a mix of positive and negative plant–soil feedbacks influence *Triadica* success in its introduced range from establishment through persistence. We addressed the following questions: 1) Does the net effect of the soil biota on plants vary between their native and introduced ranges? 2) Are there differences in the effects of specialist versus generalist soil organisms on plants in their native and introduced ranges? 3) Do positive effects of the soil biota (e.g. mycorrhizae) on *Triadica* vary between ranges? 4) Do native and invasive populations of *Triadica* vary in their interactions with soil biota in either range?

2. Materials and methods

2.1. Study system

We used the tree *T. sebifera* (synonym *Sapium sebiferum*; “*Triadica*” hereafter) as the focal invasive species in our experiment. It is native to China and Japan, and was first introduced to Georgia in the United States in the 18th century for agricultural and ornamental purposes, then to Texas, Florida and Louisiana in the early 20th century for the same uses (DeWalt et al., 2011). *Triadica* is currently invasive in the southeastern US (Bruce et al., 1997).

2.2. Seeds and soil

In November 2009, we collected *Triadica* seeds from eight populations across China (hereafter referred to as native populations) and eight populations throughout the southeastern United States (hereafter referred to as invasive populations, Table S1). For each population, seeds were collected from four to ten haphazardly selected trees. We removed the seeds’ waxy coats by soaking them water with laundry detergent (10 g/L) and surface sterilized them with 10% bleach [0.6% sodium hypochlorite]. We also collected co-occurring tree species seeds in *Triadica*’s native and introduced ranges (see below) and surface sterilized them.

We included congeneric pairs of US and China tree species on both continents to provide greater community level context for our results with *Triadica*. This paired structure with home and away soils collected in different ranges allows the *Triadica* responses to be compared to responses of other tree species that are native or introduced in those ranges. Species included hackberry (*Celtis sinensis* [C-C – “C” indicates native to China], *Celtis laevigata* [C-U – “U” indicates native to US]), sweetgum (*Liquidambar formosana* [L-C], *Liquidambar styraciflua* [L-U]), sycamore (*Platanus occidentalis* (P-U), *Platanus acerifolia* (P-hybrid of US and China species)) and elm (*Ulmus parvifolia* [U-C] and *U. americana* [U-U]). Each China species is sympatric in *Triadica*’s range in China and each was already introduced to the US. *C. sinensis* and *L. formosana* have not been reported to be invasive but *U. parvifolia* has been reported to be invasive in the northeastern US (USDA, 2012). *P. acerifolia* is a hybrid of *P. occidentalis* and *P. orientalis* and is extremely common throughout China. Seeds of the China species (and of *P. acerifolia*) were collected in a subset of areas in which *Triadica* seeds were collected and combined into a single bulk seed sample. Each US species is sympatric with *Triadica* in the US and was already introduced to China prior to this experiment. Non-*Triadica* seeds were collected in a subset of US *Triadica* collection areas and combined into bulk samples.

We collected soils associated with *Triadica* and co-occurring native species (C-U, L-U, P-U, U-U) from two US sites in March 2010 (Saratoga, TX, USA, 30°17′ 3″ N 94°31′44″ W; La Marque, TX, USA, 29°23′18″ N, 95°2′37″ W). We collected soils associated with *Triadica* and co-occurring native species (C-C, L-C, P-H, U-C) from

two China sites in April 2010 (Chongming Island, Shanghai, China, 31°37'06" N 121°33'12" E; Nanjing, Jiangsu, China, 32°02'19" N 118°50'50" E). At each site, we collected soil adjacent to each of five focal trees per species per site. We removed surface litter before collecting topsoil to a depth of 10–15 cm. We mixed together all the soil from the 10 trees (five from each site) for each species (e.g. soil from five C-C trees in Nanjing and five C-C trees from Chongming Island were combined to create *Celtis* soil for the China venue) and passed soil through a one cm mesh screen. Lastly, we split soil for each species into two parts, one to be sterilized and one to be left untreated to retain soil activity. Soil was sterilized by γ -irradiation (60Co- γ , 40 kGy) in China and by autoclaving in the US (122° C, 1 h with the center of the soil). The bulking of soils prevented us from examining spatial variation within ranges.

2.3. Experimental design

We compared plant–soil interactions of 16 populations of *Triadica* and co-occurring tree species in *Triadica*'s native and introduced ranges in open sided greenhouses located at Fudan University (Shanghai, China) and Rice University (Houston, TX, USA), respectively. In April 2010, we sowed 10 seeds of a single species into each pot filled with field soil (see details below). Soil collected in China was only used at Fudan University and soil collected in the US was only used at Rice University. Pots (diameter = 11.4 cm, height = 8.3 cm) were laid out randomly within the greenhouse ($N = 792$ pots per range). We established two sub-experiments (see Table S2 for details): one to compare plant performance in away (active component collected near heterogeneric plants) and home (congeneric plants) soils and one to compare plant performance in active mix (all five genera), sterilized, and fungicide-treated soils. We checked plant survival daily. After 12-weeks, we cut seedlings at ground level, and separated, dried and weighed stems and leaves. We extracted and washed root systems from the soil, collected a fine root fragment from each *Triadica* to measure mycorrhizae, and dried and weighed remaining roots. Clearing, staining, mounting, and measurements of mycorrhizal colonization (gridline intersect counts of hyphae of arbuscular mycorrhizal fungi) followed published protocols (Nijjer et al., 2008).

2.3.1. Home-away (feedback) experiment

To test whether plant–soil feedbacks differed between native and invasive *Triadica* and co-occurring tree species in the native and introduced ranges, we grew each plant species in active (non-sterilized) soil collected near congeneric plants (“home” soil) versus heterogeneric plants (“away” soil). Each pot received soil from all five genera (*Triadica*, *Celtis*, *Liquidambar*, *Platanus*, *Ulmus*) with 1/5 of the soil active (untreated) and 4/5 of the soil sterilized to keep soil properties such as texture, pH and nutrients constant. For each species, the “home” soil consisted of 1/5 active congeneric soil and 4/5 sterilized evenly divided mix of the four heterogeneric soils. For each species, the “away” soils consisted of 1/5 active soil from a single heterogeneric origin, 1/5 sterilized congeneric soil, and 3/5 sterilized soil which was an evenly divided mix of the other three heterogeneric soils (i.e. there were four different away soils for each species). For each species in each continent, home soil had six replicates and each away soil was represented three times for a total of 12 away soil replicates ($N = 432$ pots per range, Table S2).

2.3.2. Active mix vs. fungicide-treated experiment

We tested the effects of soil sterilization and fungicide treatment on *Triadica* and co-occurring species performance. We mixed together soils of each generic origin (5 equal parts) applied one of three treatments: active (ALL), sterilized (STER), or fungicide-treated (FUNG). Pots in the active mix treatment (ALL) had all of

the soil untreated. Pots in the sterilized treatments had all of the soil sterilized. Pots in the fungicide-treated treatment received a fungicide (iprodione, rate = 0.32 g/m²) drench prior to seedling planting and biweekly thereafter. All treatments were replicated five times ($N = 360$ pots per range, Table S2).

2.4. Data analyses

We performed ANOVA (PROC GLM in SAS) to examine whether different soil treatments affected seed germination or seedling survival of *Triadica* and co-occurring native species in common gardens in China and the US. The model included venue (continent where garden was located (China garden or US garden)), genus [*Triadica*, *Celtis*, *Liquidambar*, *Platanus*, *Ulmus*], species origin (the continent where the species is native [China or US]), soil treatment (away, home, ALL, STER, FUNG), and all the interactions as fixed effects. We square root transformed the seedling survival data to fit the assumptions of ANOVA.

The experimental design was limited in that each soil origin (i.e. mixed soil collected from replicate sites in the US vs. mixed soil collected from replicate sites in China) was only used in a single venue. This limits the inferences that can be drawn from this study compared to a study in which soil origins are crossed with greenhouse location. In order to focus on the effects of the soil biota, we normalized the data in each venue to performance in sterilized soil in that venue for presentation in the figures.

We then used ANOVA (PROC MIXED in SAS) to examine seedling survival and total biomass of *Triadica* in soil associated with away and home relative to performance in sterilized soil. The model included venue, inoculum treatment (away, home, and STER), population origin (origin of the populations of *Triadica* (China or US)) and all the interactions as fixed effects. Population nested in population origin was treated as a random effect. We performed a similar ANOVA for survival of non-*Triadica* species substituting species origin (fixed effect) for population origin. Data were sparse so the highest level interaction term could not be fit.

We performed another ANOVA (PROC MIXED in SAS) to examine seedling survival and total biomass of *Triadica* in ALL and FUNG soils relative to performance in sterilized soil in China (native range) and US (introduced range) gardens. We performed a similar ANOVA for survival of non-*Triadica* species substituting species origin (fixed effect) for population origin. The highest level interaction term could not be fit.

The inclusion of the hybrid *P. acerifolia* (P-H) in this experiment was not critical to the results. With the exception of one term in one analysis (non-*Triadica* survival for ALL vs. FUNG vs. STER, venue*genus*treat), the same factors were significant in every analysis when *Platanus* was excluded.

Finally we used ANOVA (PROC MIXED in SAS) to test arbuscular mycorrhizal colonization levels for *Triadica* in away, home, ALL, FUNG, and sterilized soils in China (native range) and US (introduced range) gardens. The model included venue, soil (away, home, ALL, FUNG, and STER), population origin and all the interactions as fixed effects. Population nested in population origin was treated as a random effect. We square root transformed the AM colonization data to fit the assumptions of ANOVA.

We performed all data analyses with the statistical analysis software SAS, ver. 9.1 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Seed germination and seedling survival for all species

Seed germination was higher in China than in the US (Table 1). Germination varied among genera and was higher for

Table 1

Effects of soil treatments on seed germination and seedling survival of *Triadica sebifera* and co-occurring species in common gardens in China and the US. Main ANOVA effects include: venue = continent where garden was located (China garden or US garden); genus = genus of plant in pot (*Celtis*, *Liquidambar*, *Platanus*, *Triadica* or *Ulmus*); species origin = the continent where the species is native (China or US); treatment = soil treatment (away [heterogeneous plants], home [congeneric plant], ALL [mix of active soil from each genus], FUNG [fungicide-treated], and STER [sterilized soil]). *F*-values (df error: germination = 1494, survival = 920) and *P*-values are shown. Significant results are in bold.

Source	Germination			Survival		
	df	<i>F</i>	<i>P</i> -value	df	<i>F</i>	<i>P</i> -value
Venue	1	56.93	<0.0001	1	37.24	<0.0001
Genus	4	149.27	<0.0001	4	40.42	<0.0001
Venue*genus	4	62.38	<0.0001	4	4.97	0.0006
Species origin	1	9.66	0.0019	1	0.26	0.6120
Venue*species origin	1	6.17	0.0131	1	2.32	0.1278
Genus*species origin	3	6.81	0.0001	3	1.22	0.3006
Venue*genus*species origin	3	5.00	0.0019	2	2.40	0.0913
Treatment	4	0.84	0.4970	4	2.84	0.0233
Venue*treatment	4	0.52	0.7201	4	2.90	0.0212
Genus*treatment	16	0.56	0.9174	16	1.95	0.0138
Venue*genus*treatment	16	0.88	0.5902	10	2.24	0.0140
Treatment*species origin	4	0.19	0.9446	4	0.55	0.7007
Venue*treatment*species origin	4	0.43	0.7869	3	0.18	0.9125
Genus*treatment*species origin	12	0.37	0.9728	6	5.99	<0.0001
Venue*genus*treatment*species origin	12	0.69	0.7638	2	0.96	0.3844

Triadica than for other genera in both ranges (Fig. 1A). Germination also depended on species origin, venue*genus, venue*species origin, genus*species origin and venue*genus*species origin (Table 1).

There were significant geographic effects on seedling survival of all species (i.e. seedling survival was higher in China than the US, Table 1). Survival also varied with genus (Fig. 1B) although it did not depend on species origin or species origin*genus. In a post-hoc Tukey test, survival was significantly higher for *Triadica* than for every other genus, particularly in the US where *Triadica* is introduced. Survival also depended on treatment and interactions with treatment (Table 1).

3.2. Home vs. away soils relative to sterilized soil for *Triadica*

Triadica seedling survival was higher in China in than the US range (venue) and depended on inoculum treatment (Table 2). In China, *Triadica* had higher seedling survival in away soils than in home soil but there was no difference between the two soils in the US (venue*inoculum, Fig. 2A). In China, seedling survival was higher in sterilized soil than home soil but there was no difference between away soils and sterilized soil. However, in the US, there was no difference in seedling survival among sterilized soil, away soils and home soil. Native and invasive *Triadica* populations did not differ in seedling survival (Table 2).

Triadica total biomass was higher in its native range than its introduced range and depended on inoculum treatment. Total biomass was higher in away soils than in home soil in both ranges. Biomass in sterilized soil was lower than in either home or away soils in US but biomass in sterilized soil was intermediate in China (venue*inoculum, Fig. 2B). There was no difference in biomass between native and invasive populations of *Triadica* (Table 2).

3.3. Home vs. away soils relative to sterilized soil for other genera

In ANOVAs with *Triadica* excluded, survival depended on venue ($F_{1,83} = 35.91$, $P < 0.0001$) and genus ($F_{3,83} = 3.50$, $P = 0.0191$) but

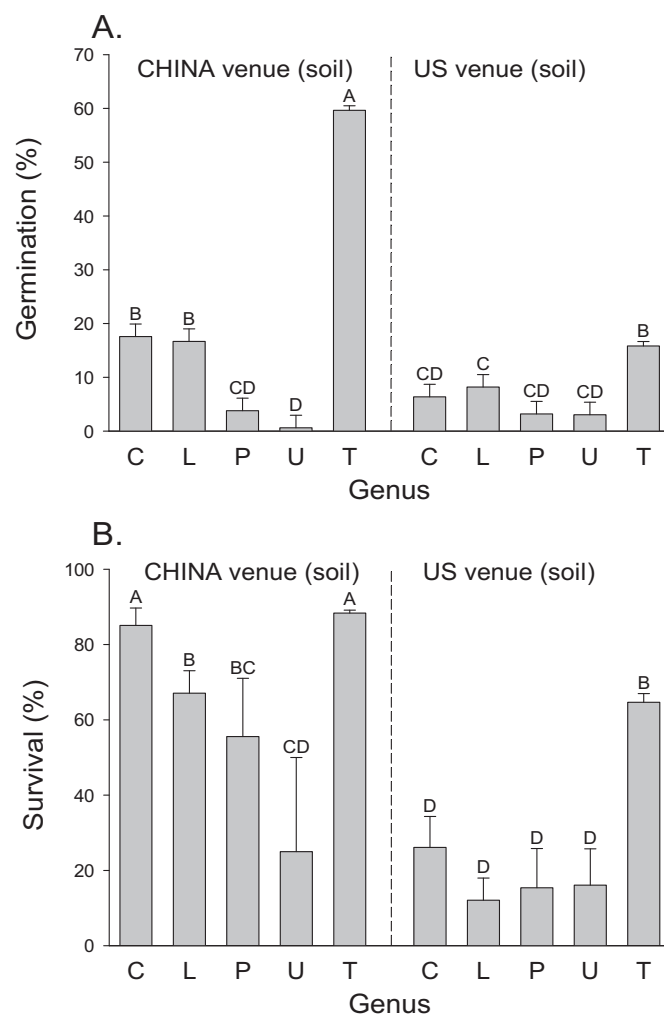


Fig. 1. (A) Seed germination and (B) seedling survival of tree genera (*Celtis* [C], *Liquidambar* [L], *Ulmus* [U], *Platanus* [P]) and invasive *Triadica sebifera* [T] grown in China and US gardens (venues). Means + 1 standard error. Letters indicate treatment means that were not statistically different in post-hoc tests ($P < 0.05$).

was independent of all other factors (Table S3). This included inoculum treatment ($P > 0.99$) and interaction terms with inoculum treatment (all $P > 0.39$). On average, survival was higher in China and for *Celtis* and *Liquidambar* (Fig. S1A).

Table 2

Variation in *Triadica sebifera* performance in away, home, and STER soils in China (native range) and US (introduced range) gardens. Main ANOVA effects were: venue = continent where garden was located (China garden or US garden); population origin = origin of the populations of *Triadica* (China or US); inoculum = soil treatment (away [heterospecific plants] soil, home [conspecific plant] soil, and STER [sterilized soil]). *F*-values and *P*-values are shown. Significant results are in bold.

Source	Survival			Biomass		
	df	<i>F</i>	<i>P</i> -value	df	<i>F</i>	<i>P</i> -value
Venue	1, 534	82.34	<0.0001	1, 501	260.50	<0.0001
Population origin	1, 14	1.34	0.2668	1, 14	4.18	0.0602
Inoculum	2, 534	6.01	0.0026	2, 501	55.16	<0.0001
Venue*population origin	1, 14	2.77	0.1181	1, 14	0.21	0.6556
Venue*inoculum	2, 534	11.61	<0.001	2, 501	19.18	<0.0001
Inoculum*population origin	2, 28	1.12	0.3410	2, 28	0.47	0.6277
Venue*inoculum*population origin	2, 28	2.28	0.1211	2, 28	1.20	0.3165

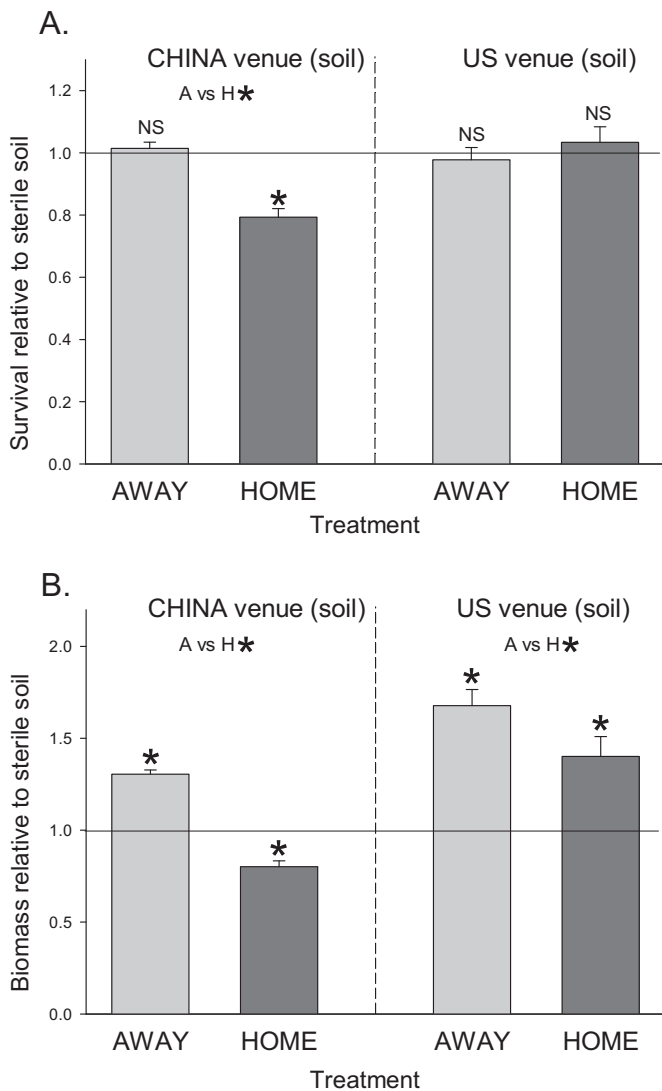


Fig. 2. (A) Seedling survival and (B) total biomass of native (China) and invasive (US) populations of *Triadica sebifera* grown in conspecific (HOME) and heterospecific (AWAY) soils relative to performance in sterilized soil in China (native range) or US (introduced range) gardens. Adjusted means + 1 standard error. Asterisks above bars indicate differences between that treatment and sterilized soils and "A vs. H ***" indicates significant differences between performance in home versus away soils ($P < 0.05$).

3.4. Active mix vs. fungicide-treated soil relative to sterilized soil for *Triadica*

Triadica seedling survival depended on venue (China > US) and soil treatment (ALL \approx FUNG < STER, Fig. 3A) but there was no interaction between venue and soil treatment (Fig. 3B). There was no difference in survival between native and invasive populations of *Triadica* (Table 3).

Total *Triadica* biomass was higher in China than in the US and depended on soil treatments (Table 3). Biomass was higher in sterilized soil (STER) than in a mix of active soils of all genera (ALL) but the opposite pattern occurred in the US (venue*treat, Fig. 3B). On average, performance was similar for native and invasive populations (population origin, Fig. 4A). However, invasive populations had greater biomass in a mix of active soils than in sterilized or fungicide-treated soil (treat*population origin, Fig. 4B, Table 3).

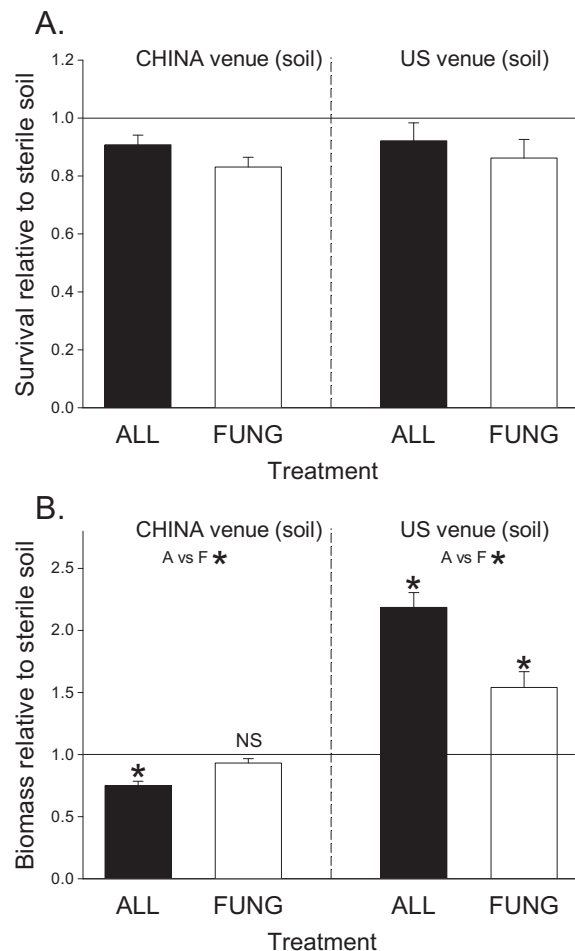


Fig. 3. (A) Seedling survival and (B) total biomass of *Triadica sebifera* grown in active mix (ALL) and fungicide-treated (FUNG) soils relative to performance in sterilized soil in China (native range) or US (introduced range) gardens. Adjusted means + 1 standard error. Asterisks above bars indicate differences between that treatment and sterilized soils and "A vs. F ***" indicates significant differences between performance in ALL versus FUNG soil ($P < 0.05$).

3.5. Active mix vs. fungicide-treated soil relative to sterilized soil for other genera

Non-*Triadica* seedling survival depended on venue ($F_{1,53} = 13.74$, $P = 0.0005$) with higher survival in China (Table S3, Fig. S1B). It was

Table 3

Variation in *Triadica sebifera* performance in ALL, FUNG, and STER soils in China (native range) and US (introduced range) gardens. Main ANOVA effects were: venue = continent where garden was located (China garden or US garden); population origin = origin of the populations of *Triadica* (China or US); treat = soil treatment (ALL [mix of active soil from each genus], FUNG [fungicide-treated], and STER [sterilized soil]). *F*-values and *P*-values are shown. Significant results are in bold.

Source	Survival			Biomass		
	df	<i>F</i>	<i>P</i> -value	df	<i>F</i>	<i>P</i> -value
Venue	1, 342	64.57	<0.0001	1, 313	74.65	<0.0001
Population origin	1, 14	0.97	0.3409	1, 14	0.17	0.6835
Treat	2, 342	5.51	0.0044	2, 313	4.10	0.0175
Venue*population origin	1, 14	2.52	0.1348	1, 14	1.47	0.2448
Venue*treat	2, 342	0.40	0.6678	2, 313	45.17	<0.0001
Treat*population origin	2, 28	1.84	0.1778	2, 28	4.46	0.0208
Venue*treat*population origin	2, 28	0.73	0.4910	2, 28	1.04	0.3661

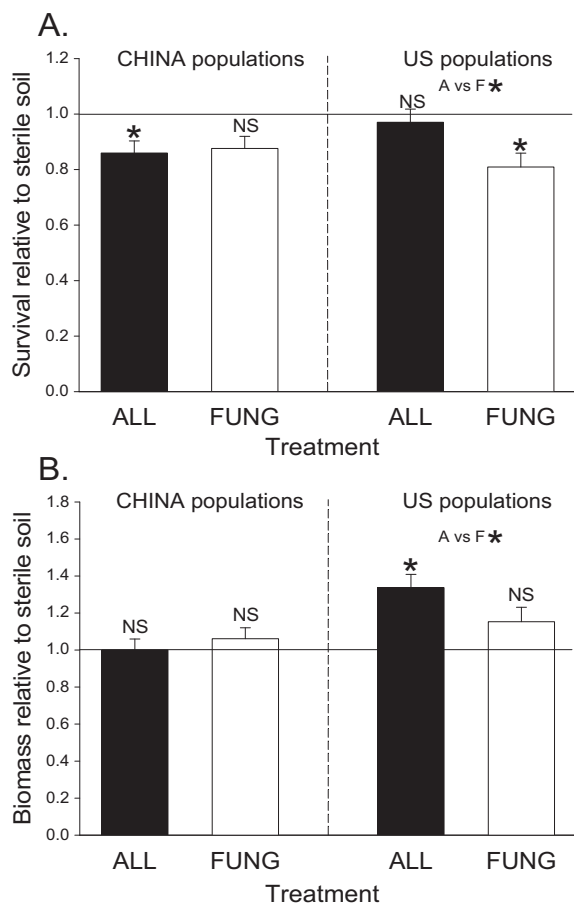


Fig. 4. (A) Seedling survival and (B) total biomass for native and invasive populations of *Triadica sebifera* grown in active mix (ALL) and fungicide-treated (FUNG) soils relative to sterilized soil. Adjusted means + 1 standard error. Asterisks above bars indicate differences between that treatment and sterilized soils and "A vs F*" indicates significant differences between performance in ALL versus FUNG soil ($P < 0.05$).

independent of all other factors except genus*species origin*treat ($F_{2,53} = 6.87$, $P = 0.0023$). This significant effect appeared to reflect negative effects of fungicide for all species except *C. laevigata* (C-U), *L. formosana* (L-C), and *L. styraciflua* (L-U) (Fig. S2).

3.6. Mycorrhizal colonization of *Triadica*

AM colonization of *Triadica* was significantly higher in the US than in China but did not vary among home, away, and the active mix soils (ALL) within each range (Table 4, Fig. 5A). Although AM colonization of native and invasive populations of *Triadica* was similar overall (population origin), native populations had higher AM colonization in home than in away soils or active mix while invasive populations had higher AM colonization in active mix soil than home soil (population origin*soil, Fig. 5B).

4. Discussion

The net effect of soil biota on *Triadica* performance was generally negative in its native range but was always positive in its introduced range (Fig. 3B). This was not only a difference in absolute performance because these results take into account the performances of pairs of US and China species. We found that soil biota generally decreased *Triadica* performance compared to sterilized soil in the native range with reduced performance in home soil

Table 4

Variation in mycorrhizal colonization of *Triadica sebifera* grown in away, home, ALL, FUNG, and STER soils in China (native range) and US (introduced range) gardens. Main ANOVA effects were: venue = continent where garden was located (China garden or US garden); population origin = origin of the populations of *Triadica* (China or US); soil = soil treatment (away [heterospecific plants], home [conspecific plant], ALL [mix of active soil from each genus], FUNG [fungicide-treated], and STER [sterilized soil]). F -values and P -values are shown. Significant results are in bold.

Source	Mycorrhizal colonization (%)		
	df	F	P -value
Venue	1, 150	6.55	0.0115
Population origin	1, 2	0.37	0.6065
Soil	4, 150	23.52	<0.0001
Venue*population origin	1, 2	1.10	0.4036
Venue*soil	4, 150	1.26	0.2886
Soil*population origin	4, 8	7.33	0.0088
Venue*soil*population origin	4, 8	0.93	0.4946

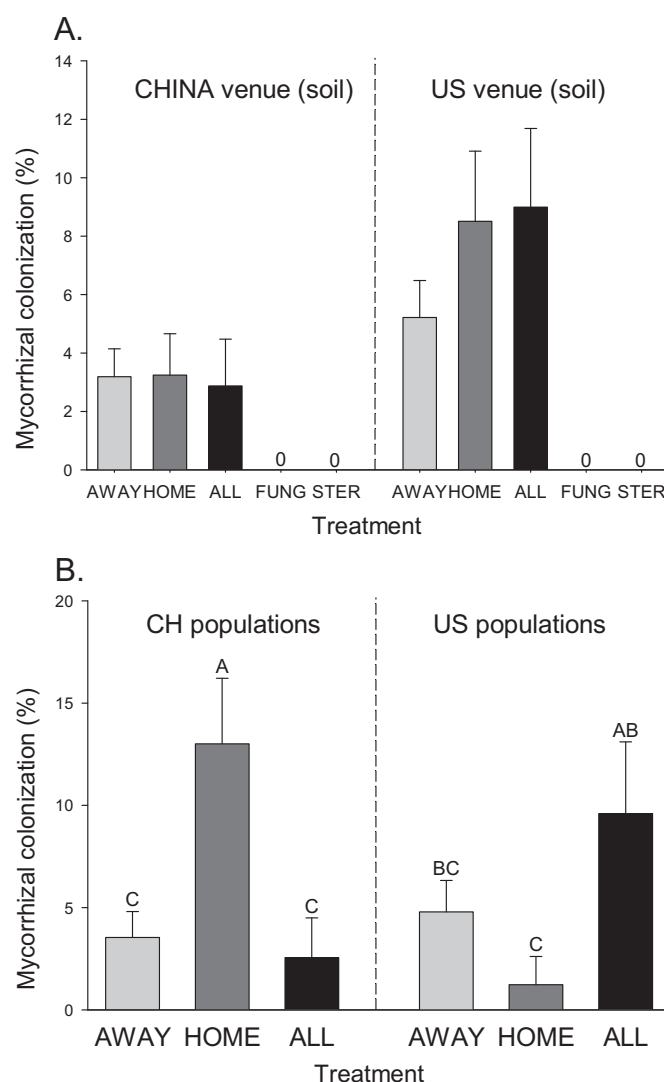


Fig. 5. (A) Arbuscular mycorrhizae colonization of *Triadica sebifera* in different soil treatments (AWAY = heterospecific soils; HOME = conspecific soil; ALL = active soil mix; FUNG = fungicide-treated soil; STER = sterilized soil) in China (native range) and US (introduced range) gardens. "0" indicates no mycorrhizal colonization in any samples of that treatment. (B) Arbuscular mycorrhizae colonization of native (China) and invasive (US) populations of *Triadica sebifera* in away, home, and ALL soils in China (native range) and US (introduced range) gardens. Adjusted means + 1 standard error. Letters indicate treatment means that were not statistically different in post-hoc tests ($P < 0.05$). Back-transformed means + 1 standard error.

(survival and biomass each 20% lower, Fig. 2) or active mix soil (biomass 25% lower, Fig. 3B), comparable in fungicide-treated soil (Fig. 3B), and higher only in away soils (biomass 25% higher, Fig. 2B). This suggests strong effects of soil pathogens in the native range. However, in the introduced range, the net effect of soil biota on biomass was always positive for *Triadica* (away: 68% higher; home: 40% higher; active mix: 119% higher; fungicide-treated: 54% higher, Figs. 2 and 3). Our results from this study that included a number of other US and China tree species suggest that soil communities in *Triadica*'s introduced range could have a net beneficial effect on its growth relative to other tree species which could contribute to high abundances in its introduced range (Klironomos, 2002; Reinhart et al., 2003; Callaway et al., 2011).

Plant–soil feedbacks for *Triadica* were negative in both native and introduced ranges which suggests that specialist soil biota with negative effects accumulate more quickly than specialist soil biota with positive effects. We found that *Triadica* had higher survival and total biomass in away soils than in home soil both in the native range (27% and 63%, respectively), however, in the introduced range, only biomass was higher in away soils than in home soil (27% higher) and there was no difference in seedling survival (Fig. 2). Although mycorrhizae could cause plant performance to be higher in home and away soils than sterilized soil, colonization rates were similar for home and away soils within both ranges (Fig. 5A). It is more likely that species-specific soil pathogens drove the difference in plant performance between away and home soils. This would occur if specialist pathogens had stronger effects in home soil compared to away soils in both native and introduced ranges but these more abundant specialists in home soils had relatively stronger effects in the native range. Negative plant–soil feedbacks have also been observed for some invasive plants in both native range (Reinhart et al., 2003) and introduced range soil (Nijjer et al., 2007; te Beest et al., 2009). The results of our feedback experiment are consistent with a general pattern of negative density dependence (Johnson et al., 2012) but in the introduced range the overall positive interactions with the soil biota meant that this negative feedback due to specialists only served to dampen an otherwise positive effect of belowground interactions.

Triadica appears to experience stronger positive effects from soil organisms in the US than in China. Our results showed that *Triadica* had higher mycorrhizal colonization in its introduced range than its native range (Fig. 5A, Table 4 – “venue” effect) and may benefit from mycorrhizal associations in the US (Fig. 3B). However, we also found that *Triadica* biomass was higher in fungicide-treated soil than in sterilized soil (Fig. 3B) in the introduced range despite complete suppression of mycorrhizal colonization in the fungicide-treated soil (Fig. 5A). This suggests that non-fungal soil organisms also have a positive effect on *Triadica* performance in its introduced range. Together these results reflected that both fungal (mycorrhizae) and non-fungal organisms (FUNG > STER in US, Fig. 3B) are involved in generating the positive effects for *Triadica* in the introduced range. Another study also found that *Triadica* could enhance mycorrhizal associations in its introduced range compared to its native range (Yang et al., unpublished). Such strong positive effects of soil interactions may facilitate *Triadica* establishment and invasion in the introduced range.

Once plants are introduced to new ranges, they may experience novel abiotic and biotic environments, which may in turn lead to genetic changes in plant traits (Blossey and Nötzold, 1995; Henery et al., 2010). In some cases, this may contribute to these species becoming established and invasive in the novel ranges (Müller-Schärer et al., 2004; Bossdorf et al., 2005; Henery et al., 2010). On average, *Triadica* performance and mycorrhizal colonization were similar for native and invasive populations (Tables 1 and 2). However, our results showed that invasive populations had greater biomass in

active mix soil than in sterilized or fungicide-treated soil, where higher mycorrhizal association may offer greater benefits for invasive populations of *Triadica* than native populations (Fig. 4B). Native populations of *Triadica* had higher mycorrhizal colonization in home soil than in away soils or active mix soil but invasive populations had low colonization on average in home soils (Fig. 5B). Together these suggest post-introduction changes in specificity of mycorrhizal interactions which may influence the net effects of plant–soil biota interactions as well as the strengths of soil feedbacks.

We found that genera varied in their seed germination and seedling survival (significant “genus” effect, Table 1). *Triadica* germination and survival were higher than other genera in both ranges, particularly for survival in the US where *Triadica* was introduced. Higher seed germination and seedling survival could increase the competitive ability and abundance for successful invasive species (such as *Triadica*) relative to co-occurring native species, which could be critical for their invasion success. However, soil treatment did not affect seed germination although it did influence seedling survival (“treatment” term, Table 1).

Understanding plant–soil community interactions associated with exotic plants in their native versus introduced ranges is critical for predicting invasion success (Hiero et al., 2005). Our results suggest that the soil communities with which *Triadica* interacts have different effects in its native and introduced ranges, and that these differences may contribute to success in its introduced range. In the introduced range, *Triadica* appears to have escaped from direct negative effects of host-specific soil pathogens and to be facilitated by AMF but it appears to be inhibited by the soil community in its native range. Net negative soil biota effects may contribute to *Triadica* coexistence with other species in its native range, while positive plant–soil interactions may contribute to the observed local dominance of *Triadica* in the introduced range. A general understanding the complex interactions between plants and soil communities at ecological and evolutionary time scales is needed for a comprehensive view on plant invasions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2013.05.004>.

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