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# Biogeographic variation of distance-dependent effects in an invasive tree species

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## Abstract

1. Plant pathogens and herbivores can maintain forest diversity by reducing survival of tree seedlings close to conspecifics. However, how biogeographic variation in these natural enemies affects such distance-dependent processes is unknown. Because invasive plants escape ecologically important enemies when introduced to a new range, distance-dependent mortality may differ between their native and introduced ranges.
2. Here, we test whether the invasive tree *Triadica sebifera* escaped distance-dependent mortality when introduced to the United States from China, and examine the roles of natural enemies in native and introduced ranges. In both the United States and China, we performed field surveys along with field and greenhouse experiments with field-collected soils and soil sterilization treatments.
3. In field surveys and the field experiment, insect damage on *T. sebifera* seedlings decreased with distance to conspecific trees in the native range (China), but damage was low at all distances in the introduced range (United States). In the greenhouse experiment testing the effects of soil pathogens, *T. sebifera* seedling mortality decreased with soil distance from conspecific trees in both ranges but distance-independent mortality was higher in native range soils.
4. Our findings indicate that both insect herbivores and the soil biota contribute to distance-dependent effects on *T. sebifera* in its native range. They suggest, however, that plants may more readily escape herbivore than soil biota distance-dependent effects when introduced to a new range and so herbivores, rather than soil pathogens, contribute more strongly to biogeographic variation in distance-dependent effects. These results highlight the importance of considering species biogeographic variation in distance-dependent effects and teasing apart the roles that different natural enemies play when studying species coexistence, community diversity and biological invasions.

KEYWORDS
biological invasions, herbivores, Janzen–Connell effect, natural enemies, pathogens, *Triadica sebifera*

## 1 | INTRODUCTION

Herbivore and pathogen natural enemies may maintain forest diversity by reducing survival in a density- or distance-dependent manner, namely as a density- or distance-dependent effect with higher seedling mortality at higher densities near conspecific adult trees (Janzen–Connell effect) (Connell, 1971; Janzen, 1970). Specialist fungal pathogens and insect herbivores are the enemy types most commonly hypothesized to cause this phenomenon (Bell, Freckleton, & Lewis, 2006; DeWalt, Denslow, & Ickes, 2004; Halbritter, Carroll, Güsewell, & Roy, 2012; Liang et al., 2016; Mangan et al., 2010; Reinhart, Tytgat, Putten, & Clay, 2010; Visser, Muller-Landau, Wright, Rutten, & Jansen, 2011). However, debate over this theory is ongoing because many abiotic and biotic factors (e.g., species genotypes) can affect both natural enemies and plants (Mitchell et al., 2006; Yang, Li, & Siemann, 2015). Moreover, such abiotic and biotic factors vary biogeographically which may cause natural enemies and plants to differ and drive changes in their interactions. For example, introduced populations of invasive woody plants could escape from specialist enemies (herbivores, fungal and viral pathogens) when they are introduced to new ranges so plant–natural enemy interactions differ from those of populations in the native range (Blossey & Nötzold, 1995; Bossdorf et al., 2005; Hierro, Maron, & Callaway, 2005; Reinhart et al., 2010). However, it is unclear whether invasive tree species escape distance-dependent enemy effects when introduced to new ranges, and if so, which types of enemies (e.g., soil pathogens or above-ground insect herbivores) exhibit species-specific effects that generate distance-dependent effects on plant performance.

Soil pathogens (e.g., fungus, virus) are generally considered to be the most important agents in determining distance-dependent mortality. Studies show that seedling survival decreases near conspecific adults, at high conspecific density, or when grown in soil from closer to conspecifics (e.g., Bennett et al., 2017; Johnson, Beaulieu, Bever, & Clay, 2012; Liu et al., 2012; Liang et al., 2016; Mangan et al., 2010). Other studies showed that treating soil with fungicide removes distance-/density-dependent effects (e.g., Bagchi et al., 2010; Bell et al., 2006; Hood, Swaine, & Mason, 2004). These findings indicate that fungal pathogens are a critical driver of distance-dependent mortality possibly because they are highly specialized and passive dispersers (Augspurger & Wilkinson, 2007; Bell et al., 2006; Benítez, Hersh, Vilgalys, & Clark, 2013; Bever et al., 2010). In addition, insect herbivores are another important type of enemy contributing to a distance-/density-dependent effect on survival (Sullivan, 2003; Visser et al., 2011). However, studies testing the relative roles of soil pathogens and insect herbivores in distance-dependent effects are rare (but see Bagchi et al., 2014; Fricke, Tewksbury, & Rogers, 2014), particularly for a globally invasive tree species and no such tests have been performed in both the introduced and native ranges.

Invasive plant species often escape from enemies of their home ranges ("enemy release hypothesis" or "ERH") (Keane & Crawley, 2002), including fungal and viral pathogens and herbivores both above- and below-ground (Knevel, Lans, Menting, Hertling, & Putten, 2004; Maron & Vila, 2001; Mitchell & Power, 2003; Reinhart et al., 2010; van der Putten, Yeates, Duyts, Reis, & Karssen, 2005). Moreover, invasive species may gain greater benefits in their introduced ranges by forming new associations with mutualists ("enhanced mutualist hypothesis" or "EMH"), potentially facilitating plant invasions (Reinhart & Callaway, 2006). Such weaker negative and/or stronger positive interactions could allow introduced plants to escape or resist distance-dependent effects. Although studies found arbuscular mycorrhizal fungi colonization and soil enemies together cause distance-dependent survival and promote species coexistence in natural ecosystems (Bachelot, Uriarte, McGuire, Thompson, & Zimmerman, 2017; Liang et al., 2015), no one has studied these processes in a plant's native and introduced ranges.

*Triadica sebifera* (synonym *Sapium sebiferum*; "*Triadica*" hereafter) is an ideal model tree to investigate distance-dependent effect biogeography. *Triadica* is a rapidly growing, polycarpic tree. It is native to China and Japan, and now invasive in the south-eastern United States (Pile et al., 2017). *Triadica* could escape above-ground herbivores, as only a few herbivores were recorded in the introduced range, but nearly 200 herbivores were found in its native range (Zhang, Wang, & Ding, 2015). Previous work shows that introduced *Triadica* populations have lower resistance to specialists but higher tolerance of herbivore damage than native populations (Carrillo & Siemann, 2016; Wang et al., 2011). *Triadica* may also escape below-ground soil pathogens (Yang et al., 2013). Moreover, introduced *Triadica* populations have higher frequencies of mycorrhizal associations than native populations (Yang, Wei, et al., 2015). Hence, *Triadica* has experienced different above-ground and below-ground natural enemies and biotic interactions in its native and introduced ranges.

In this study, we performed field surveys along with field experiments and greenhouse experiments with field-collected soils in both the United States and China to examine biogeographic variation in the effects of distance between seedlings to adult tree and natural enemy impacts on seedlings. We included native and introduced populations of *Triadica* to examine the importance of variation in plant origin for distance-dependent effects. Specifically, we asked following questions: (a) Do distance-dependent natural enemy effects differ between *Triadica*'s native and introduced ranges? (b) Do above-ground herbivores and/or the soil biota play key roles in mediating distance-dependent effects? (c) Do their roles differ between ranges?

## 2 | MATERIALS AND METHODS

### 2.1 | Field surveys

We conducted field surveys of the distance from seedlings to naturally occurring adult *Triadica* trees and the number of *Triadica* seedlings in six sites in the native range (China) and three sites in the introduced range (United States) (Supporting Information Table S1). At each site, we counted the number of *Triadica* seedlings in 1-$m^2$ plots that were located 1, 2, and 4 m from the trunk in a random direction from at least six isolated (at least 10 ms from another *Triadica* tree) mature (dbh > 10 cm) *Triadica* trees per site. We also recorded the average percent of leaf area damaged by chewing insects for each leaf on each seedling by visual estimate (to the nearest 5%) in both the native range and introduced ranges. We then averaged the visual estimates for all damaged leaves on each seedling. We conducted surveys in China and the United States in June 2015, but there were zero *Triadica* seedlings in the US survey plots due to a severe drought, so we repeated the survey in the United States in June 2016.

## 2.2 | Field common garden experiment

In October 2014, we collected *Triadica* seeds from six populations across China ("native populations") and six populations throughout the south-eastern United States ("invasive populations," Supporting Information Table S2) that included both introduction events (DeWalt, Siemann, & Rogers, 2011).

For each *Triadica* population, we hand-collected seeds from 4 to 10 randomly selected trees. To evaluate the potential impacts of seed provisioning on seedling performance, 20 seeds from each population were weighed. There was no significant difference in seed mass of invasive and native populations [nested analysis of variance (ANOVA), $F_{1,10} = 1.60$, $p = 0.2277$]. We removed the seeds' waxy coats by soaking them in water with laundry detergent (10 g/L) for 2 days, and then surface sterilized them with 10% bleach [0.6% sodium hypochlorite] for 2 min then rinsing with water. We germinated seeds in greenhouses in China and the United States.

We transplanted *Triadica* seedlings of the 12 populations (six China, six United States) to field sites in the United States and China (one site in each, Supporting Information Tables S1 and S2) at different distances from five isolated adult *Triadica* trees. The experiment was a factorial design with three factors: experimental venue (native range [China], introduced range [United States]), origin (six native and six invasive populations), and distance treatment (1, 2 or 4 m) and focal tree as a block (12 randomly selected seedlings at each distance for each tree). There were 360 plants total in the experiment ($N = 180$ plants per venue [12 population origins × 3 distance treatment × 5 focal trees]). After 1 week, we recorded seedling survival and average percent leaf damage from herbivores for surviving seedlings.

## 2.3 | Greenhouse experiment

To investigate the distance-dependent effects of soil pathogens, we conducted a greenhouse experiment with blocks in both China and the United States. We collected soils associated with *Triadica* from three sites used for the field surveys in each range (for details see Supporting Information Table S1). We removed surface litter before collecting topsoil to a depth of 10 to 15 cm. In each site, we collected soil at different distances from isolated adult *Triadica* trees (1, 2 and 4 m) in three or four transects away from each of five focal trees per site. We mixed soils of five trees to make a single soil for each distance at each site (three sites in the United States, three sites in China) and then removed larger sticks, rocks and root fragments by passing soil through a 1-cm mesh screen. Lastly, we split soil for each site and distance combination ($N = 9$ in the United States, $N = 9$ in China) into two parts, one to be sterilized and one to be left untreated to retain soil activity. Soil was sterilized by autoclaving in both China and the United States.

We compared the distance dependence of plant–soil interactions of 12 populations of *Triadica* in the native range in an open-sided greenhouse located at Wuhan Botanical Garden (WBG) (Wuhan, China) and in its introduced range in an open-sided greenhouse located at Rice University (Houston, TX, USA). In April 2015, we sowed 5 seeds of a single type into each pot filled with field soil (see details below). Soil collected in China was only used in the WBG greenhouse, and soil collected in the United States was only used in the Rice University greenhouse.

The experiment was a full-factorial design with five factors: experimental venue (native range [China], introduced range [United States]), soil collection site (three sites in China, three sites in the United States), seed origin (six native and six invasive populations), soil activity treatment (active or soil sterilization), and soil distance treatment (1, 2, or 4 m). There were three replicates with a total of 1,296 pots ($N = 648$ pots per venue [3 soil sites × 2 soil activity treatments × 3 soil distance treatments × 12 populations [6 US + 6 China] × 3 replicates]). Pots (diameter = 11.4 cm, height = 8.3 cm) were arranged randomly within each greenhouse. We checked seed germination and seedling survival weekly. After 12 weeks of growth, we cut seedlings at ground level, and separated, dried and weighed stems and leaves.

## 2.4 | Data analysis

For the field surveys, we used ANOVA (Proc mixed; SAS 9.4 for all analyses) to test the dependence of seedling number and leaf damage percent on venue, distance to focal tree, and their interaction as fixed effects and site nested in venue as a random effect. We used adjusted means partial difference tests to examine differences among means for significant factors with more than two levels.

For the field experiment, we used ANOVA (Proc mixed) to test the dependence of leaf damage percent on venue, distance, origin, and their interactions as fixed effects. We included population nested in origin and focal tree as random effects. We used adjusted means partial difference tests to examine differences among means for significant factors with more than two levels.

For the greenhouse experiment, we used binomial GLMM (Proc glimmix—binomial distribution, logit link) to examine the dependence of seed germination and seedling survival odds on venue, soil sterilization treatment, population origin, distance to focal tree, and their interactions as fixed effects and soil site nested in venue and population nested in origin as random effects. We used contrasts to test whether the effect of soil sterilization on mortality varied between China and US soils.

# 3 | RESULTS

## 3.1 | Field surveys

*Triadica* seedling density increased with distance from adult *Triadica* tree (Table 1; Figure 1a). Seedling density was independent of venue, venue × distance, and site nested in venue (Table 1). The amount of damage was higher at 1 m in China than at larger distances in China or any distance to focal tree in the United States (Table 1; venue × distance; Figure 1b) but was independent of site nested in venue (Table 1).

**TABLE 1** ANOVA results for *Triadica sebifera* seedling numbers and leaf damage percent in field surveys in the native and introduced range

| | Seedling number | | | Leaf damage | | |
|---|---|---|---|---|---|---|
| **Fixed effects** | *df* | *F* | *p* | *df* | *F* | *p* |
| Venue | 1, 7 | 0.16 | 0.7048 | 1, 5 | 3.11 | 0.1382 |
| Distance | 2, 242 | **3.70** | **0.0262** | 2, 98 | **3.64** | **0.0298** |
| Venue × distance | 2, 242 | 3.02 | 0.0508 | 2, 98 | **3.37** | **0.0385** |
| **Random effect** | | *Z* | *p* | | *Z* | *p* |
| Site (venue) | | 1.31 | 0.0943 | | 1.04 | 0.1482 |

*Note*. Fixed effects were as follows: venue: continent where site was located (China or United States); distance—seedling distance to focal adult *T. sebifera* tree (1, 2 and 4 m). Site nested in venue was included as a random effect. *F*-values, *Z*-scores and *p*-values are shown. Significant results are in bold.

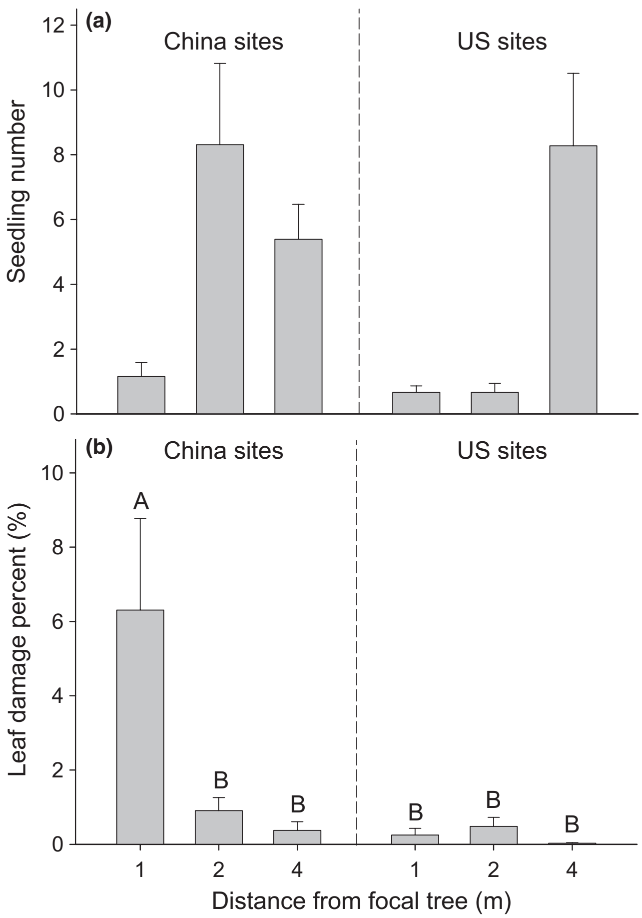


**FIGURE 1** The dependence of *Triadica sebifera* (a) seeding number and (b) percent chewing damage on seedling distance to a focal adult *T. sebifera* tree in the field sites in the native and introduced range. Letters denote means that did not differ in post hoc tests. Means + 1 *SE*

## 3.2 | Field common garden experiment

Damage to *Triadica* seedlings was higher in China than in the United States ("venue"), and it decreased with distance to adult *Triadica* tree in China but was similarly low at all distances in the United States ("venue × distance"; Table 2; Figure 2). Seedling population origin did not affect the amount of damage seedlings received but damage varied with focal tree (Table 2).

**TABLE 2** ANOVA results for *Triadica sebifera* leaf damage percent for greenhouse grown plants placed in the field in the native and introduced ranges

| **Fixed effects** | *df* | *F* | *p* |
|---|---|---|---|
| Venue | 1, 286 | **12.46** | **0.0005** |
| Distance | 2, 286 | **15.86** | **<0.0001** |
| Origin | 1, 15 | 0.39 | 0.5440 |
| Venue × distance | 2, 286 | **19.40** | **<0.0001** |
| Venue × origin | 1, 286 | 0.55 | 0.4699 |
| Distance × origin | 2, 286 | 0.15 | 0.6988 |
| Venue × distance × origin | 2, 286 | 0.37 | 0.5435 |
| **Random effects** | | *Z* | *p* |
| Population (origin) | | 1.28 | 0.0997 |
| Focal tree | | **1.72** | **0.0430** |

*Note*. Fixed effects were as follows: venue: continent where field sites were located (China or United States); origin—population from China or United States; distance—seedling distance to focal adult *T. sebifera* tree (1, 2, 4 m). Population nested in origin and focal tree were included as random terms. *F*-values, *Z*-scores and *p*-values are shown. Significant results are in bold.

## 3.3 | Greenhouse experiment

Germination depended on all experimental factors ("Venue × origin × distance × treatment") with the pattern influenced in part by lower germination in US (odds = 0.15) than China (odds = 0.21) soils (Supporting Information Table S3; Figure S1). Germination varied with population (nested in origin) but not site (nested in venue).

Seedling mortality was higher in soils collected closer to focal trees ("distance"; Table 3), which was strongly influenced by decreasing mortality with distance in active soils (Figure 3a). Mortality varied with venue and soil treatment with similarly low mortality in sterilized China and US soils with higher mortality in active soils, especially in China soils (Figure 3b). The decreases in mortality with soil

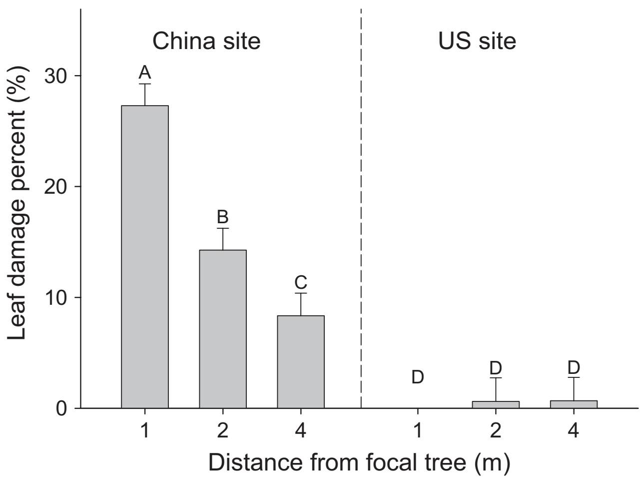


**FIGURE 2** The dependence of *Triadica sebifera* seedling leaf damage percent on seedling distance from a focal adult *T. sebifera* tree in the China or US site in the field common garden experiment. Adjusted means + 1 *SE*. Means with the same letter were not significantly different in post hoc tests

**TABLE 3** ANOVA results for seedling survival (binomial distribution) of *Triadica sebifera* populations grown in different ranges

| Fixed effects | *df* | *F* | *p* |
|---|---|---|---|
| Venue | 1, 4 | 0.02 | 0.8850 |
| Origin | 1, 15 | 0.06 | 0.8081 |
| Distance | 2, 922 | **4.04** | **0.0179** |
| Treatment | 1, 922 | **56.28** | **<0.0001** |
| Venue × origin | 1, 922 | 0.80 | 0.3708 |
| Venue × distance | 2, 922 | 0.77 | 0.4644 |
| Venue × treatment | 1, 922 | **12.06** | **0.0005** |
| Origin × distance | 2, 922 | 2.54 | 0.0795 |
| Origin × treatment | 1, 922 | 3.27 | 0.0710 |
| Distance × treatment | 2, 922 | 1.06 | 0.3454 |
| Venue × origin × dist | 2, 922 | 0.07 | 0.9337 |
| Venue × origin × treatment | 1, 922 | 0.54 | 0.4645 |
| Origin × distance × treatment | 2, 922 | 0.50 | 0.6061 |
| Venue × origin × distance × treatment | 4, 922 | 1.67 | 0.1545 |
| **Random effects** | | *Z* | *p* |
| Population (origin) | | 0.95 | 0.1704 |
| Site (venue) | | 1.38 | 0.0833 |

*Note*. Fixed effects were as follows: venue: continent where soils were collected and garden was located (China garden or US garden); origin—where populations were collected (United States or China); distance—soil collection distance to focal adult *Triadica* tree (1, 2 or 4 m); soil treatment (active or sterilized) and their interactions as fixed effects and site nested in venue (where soils were collected—China: Luotian, DaWu, Wuhan; USA: Baytown, Houston, La Marque) and population (where seeds were collected) nested in origin as random effects. *F*-values, *Z*-scores and *p*-values are shown. Significant results are in bold.

sterilization were larger in China soils than in US soils ($F_{1,922}$ = 12.06, $p$ = 0.0005). Mortality was independent of origin, site, and population (Table 3).

## 4 | DISCUSSION

Testing variation in distance-dependent effects among plant populations at biogeographic scales provides insights into how tree survival depends on biotic factors such as herbivores and pathogens in general. Our study is the first to report that an invasive tree species could escape distance-dependent effects when introduced to a new range. According to our field and greenhouse experiments, we found significant distance-dependent effects of herbivory on *Triadica* in the native range but no such effects in the introduced range. Thus, biogeographic variation in above-ground herbivore enemies may be the largest contributor to the differing distance-dependent effects on *Triadica* in its introduced and native ranges.

We found significant distance-dependent effects of herbivory for *Triadica* in the native range but not in the introduced range where herbivore damage was always extremely low. Herbivorous insects have been found to cause distance- or density-dependent mortality (Cardenas, Valencia, Kraft, Argoti, & Dangles, 2014; Katz & Ibanez, 2016; Norghauer et al., 2016), as several studies show distance- and density-dependent effect by recording boreholes, mines and chewing from herbivores (Cardenas et al., 2014; Katz & Ibanez, 2016; Mangan et al., 2010; Norghauer et al., 2016; Visser et al., 2011), and herbivore manipulations demonstrated distance-dependent impacts of insects (Sullivan, 2003). In this study, our field common garden and field survey results showed that *Triadica* leaf damage percent was much higher in the native range than the introduced range. Moreover, leaf damage decreased as distances to adult tree increased in the native range; however, there were no differences among the distance treatments in the introduced range, suggesting that, in the introduced range, *Triadica* escaped insect enemies from the native range. In the field survey, we found that *Triadica* leaf damage percent was much higher within 1m of an adult *Triadica* tree. Together, these results suggest that herbivores, which varied with ranges, play a different role in regulating distance-dependent effects between native and introduced ranges, and escaping insect enemies, likely specialists, could allow *Triadica* to escape density-dependent effects in the introduced range.

A number of studies have reported that soil pathogens cause distance- and density-dependent mortality (Bagchi et al., 2010; Bell et al., 2006; Liang et al., 2016; Liu et al., 2012; Packer & Clay, 2000). According to our greenhouse experiment results, *Triadica* seedling mortality decreased with increasing distance in active soils, which suggests that soil pathogens play a role in this negative distance-dependent effect. This was also supported by no distance-dependent effects in sterilized soils. In addition, we found that there were distance-dependent effects on *Triadica* germination, suggesting that germination may be influenced by both soil properties and soil microbes.

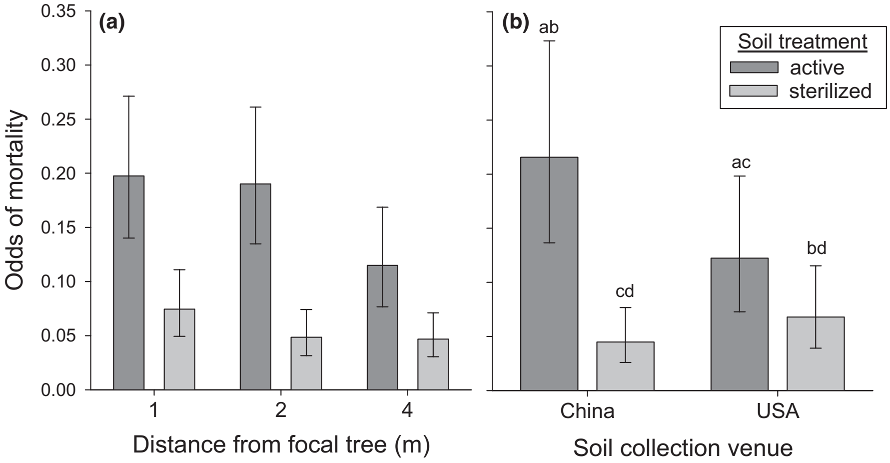


**FIGURE 3** The dependence of odds of mortality in the greenhouse experiment for *Triadica sebifera* seedlings on soil treatment (active or sterilized) and (a) distance soil was collected from a focal adult *T. sebifera* tree and (b) soil collection venue (China or United States). Means ± 1 *SE*. Letters indicate means that were not significantly different in post hoc tests

There is a debate about the use of different experimental approaches in plant-soil feedback experiments. Here, we kept soils separate by sites ("independent soil sampling" or "ISS") and used site nested in venue as a random term to test for venue effects, which has been suggested to better control type I error rates but to have a higher type II error rate compared to mixing soils among sites within venues ("mixed soil sampling" or "MSS") (Cahill et al., 2017; Gundale, Wardle, Kardol, Putten, & Lucas, 2017; Reinhart & Rinella, 2016; Rinella & Reinhart, 2017; Smith-Ramesh & Reynolds, 2017). Our ability to detect a main effect of venue was likely reduced by keeping soils separated by site, but the *p*-value was quite high (0.89), which argues against a strong overall venue effect that was not detected. The mixing of soils among focal trees within a site and distance combination in our experimental design prevented us from testing for differences among focal trees and may have caused our *p*-value for the effect of site nested in venue to be artificially low. However, there was no significant effect of site nested in venue so this is not a concern. Because we were interested in how seedling mortality differed in active versus sterilized soils between ranges at a variety of sites, our choice of experimental approach is appropriate.

When tree species are introduced to new ranges, they may escape specialist soil pathogens and encounter new generalist pathogens and have enhanced mutualism associations, which could shift negative plant–soil interactions to positive or neutral, and then allow these species to successfully invade in these areas (Gundale et al., 2014; Reinhart, Packer, Putten, & Clay, 2003; Yang et al., 2013). In this study, we found a significant distance-dependent effect of *Triadica* in the introduced range, which is consistent with the negative effect of the soil biota in dense monocultures that was shown in another study in the introduced range (Nijjer, Rogers, & Siemann, 2007), although the net effect of the soil biota on *Triadica* performance was positive in its introduced range (Yang et al., 2013). Given that escaping soil pathogens and establishing mutualistic associations could initially lead to a positive plant-soil feedback with increasing time after introduction, invasive species might accumulate pathogens, which could turn positive plant-soil feedback into negative ones, potentially causing negative density-dependent effects (Eppinga, Rietkerk, Dekker, Ruiter, & Putten, 2006). Here, we found that the negative effect of the soil biota varied on the scale of metres from a mature *Triadica* tree in both ranges, but the effect of the soil biota was more negative in the native range than the introduced range. Thus, although *Triadica* experiences a distance-dependent effect in both ranges, some more generalized types of interaction, perhaps more overall positive effects of mycorrhizae or weaker effects of generalist pathogens, may cause the overall effect of the soil biota to be more negative in China than in the United States.

Distance-/density-dependent effects are important in explaining species coexistence and community diversity. An increasing number of studies have focused on different types of enemies and their roles in these effects (Bagchi et al., 2014; Fricke et al., 2014; Gripenberg et al., 2014). Our work including both soil organisms and above-ground enemies is the first study examining distance-dependent effects at a biogeographical scale using an invasive tree species. Contrary to a previous meta-analysis showing density-dependent effects are unrelated to latitude and study region (Comita et al., 2014), we found that the distance-dependent effect was different in a plant species' native and introduced ranges. A density-/distance-dependent effect may exist throughout a tree species' native range, promoting species coexistence and species diversity. However, invasive trees might escape this effect, because they escape specialist natural enemies when introduced to other ranges.

Understanding the roles of different types of enemies in distance-/density-dependent effects, particularly for an invasive tree species, is critical for predicting species community composition and invasion success. In this study, we found that both insect herbivory and the soil biota are important for determining distance-dependent effects on *Triadica* in its native range. However, plants may more readily escape herbivore distance-dependent but not soil biota distance-dependent effects when introduced from their native ranges, indicating herbivory, rather than soil pathogens, is the major factor influencing the biogeographic variation of distance-dependent effects for this and perhaps other species. In the context of the globalization, plant communities are increasingly influenced by alien tree species which often escape specialist natural enemies. Therefore, we should consider species introduction history and biogeographic factors in studying species coexistence and community diversity. Teasing apart the roles different organisms play in distance-dependent effects may help to better understand these mechanisms from a biogeographic perspective.

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## AUTHOR CONTRIBUTIONS

Q.Y., J.D. and E.S. conceived the experiments. Q.Y. and E.S. carried out the experiments and data analysis. Q.Y., J.D. and E.S. wrote the manuscript.

## DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.t952j0k (Yang, Ding, & Siemann, 2019).

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## SUPPORTING INFORMATION

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