

Co-occurring nonnative woody shrubs have additive and non-additive soil legacies

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Abstract. To maximize limited conservation funds and prioritize management projects that are likely to succeed, accurate assessment of invasive nonnative species impacts is essential. A common challenge to prioritization is a limited knowledge of the difference between the impacts of a single nonnative species compared to the impacts of nonnative species when they co-occur, and in particular predicting when impacts of co-occurring nonnative species will be non-additive. Understanding non-additivity is important for management decisions because the management of only one co-occurring invader will not necessarily lead to a predictable reduction in the impact or growth of the other nonnative plant. Nonnative plants are frequently associated with changes in soil biotic and abiotic characteristics, which lead to plant–soil interactions that influence the performance of other species grown in those soils. Whether co-occurring nonnative plants alter soil properties additively or non-additively relative to their effects on soils when they grow in monoculture is rarely addressed. We use a greenhouse plant–soil feedback experiment to test for non-additive soil impacts of two common invasive nonnative woody shrubs, *Lonicera maackii* and *Ligustrum sinense*, in deciduous forests of the southeastern United States. We measured the performance of each nonnative shrub, a native herbaceous community, and a nonnative woody vine in soils conditioned by each shrub singly or together in polyculture. Soils conditioned by both nonnative shrubs had non-additive impacts on native and nonnative performance. Root mass of the native herbaceous community was 1.5 times lower and the root mass of the nonnative *L. sinense* was 1.8 times higher in soils conditioned by both *L. maackii* and *L. sinense* than expected based upon growth in soils conditioned by either shrub singly. This result indicates that when these two nonnative shrubs co-occur, their influence on soils disproportionately favors persistence of the nonnative *L. sinense* relative to this native herbaceous community, and could provide an explanation of why native species abundance is frequently depressed in these communities. Additionally, the difference between native and nonnative performance demonstrates that invasive impact studies focusing on the impact only of single species can be insufficient for determining the impact of co-occurring invasive plant species.

Key words: *Celastrus orbiculatus*; co-occurring or codominant invaders; exotic; invasive; *Ligustrum sinense*; *Lonicera maackii*; plant–soil interactions; soil legacies.

INTRODUCTION

Nonnative, invasive species can have long-lasting, pervasive negative impacts on native communities and ecosystems (Pyšek and Richardson 2010, Simberloff et al. 2013). Accurate assessment of nonnative species impacts is essential for ensuring that limited conservation resources are prioritized for management projects with a high likelihood of success (Parker et al. 1999, Pyšek and Richardson 2010). A common challenge to prioritization is a limited knowledge of how invader impacts

may vary depending on the environmental context of the invasion (Hulme et al. 2013), and in particular little is known regarding the difference between the impacts of a single nonnative species compared to the impacts of nonnative species when they co-occur (Kuebbing et al. 2013, Jackson 2015). Although it is common to find conservation habitats that contain multiple nonnative species, most invader impact research has primarily focused on the impacts of invaders singly (Kuebbing et al. 2013, Jackson 2015, Kuebbing and Nuñez 2015). This mismatch between research and conservation reality means that conservation practitioners must prioritize in co-invaded landscapes based on single-species impact studies. This may be appropriate if impacts of nonnative species are additive (i.e., the sum of the individual impacts of both nonnative species) or if the nonnative species do

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not interact with one another. In these cases, managers can extrapolate how the management of either species will influence the overall impact of both species (Kuebbing et al. 2013, Pearson et al. 2015).

The use of single-species impact studies could be misguided if co-occurring invaders have non-additive impacts or interactions that are not captured by single-species impact research (Kuebbing et al. 2013). The terms “invasional meltdown” (Simberloff and Von Holle 1999) and “invasional interference” (Yang et al. 2011) describe extreme forms of non-additivity where interactions between co-occurring invaders either increase or decrease the per capita effect or population growth of both invasive species. However, nonnatives can have non-additive impacts that do not lead to full “invasional meltdown” scenarios, and understanding the effects of non-additive impacts is useful for management. Non-additivity occurs when the sum of the per capita impact or population growth of each nonnative species singly does not equal the per capita impact of each species when it is found with the other species (Kuebbing et al. 2013, Jackson 2015). Non-additivity can have net positive effects; for example, nonnatives can promote the occurrence of other nonnatives through changes in soil properties (Vitousek 1986, Kuebbing et al. 2015) or reduction in herbivory or competition (Cushman et al. 2011, Flory and Bauer 2014). Non-additivity can also be negative when a nonnative species suppresses the population growth or reduces the per capita impact of another nonnative, as is the case for two invasive thistles (*Carduus* spp.) that have lowered reproductive success in areas where they co-occur (Yang et al. 2011). Understanding positive and negative non-additivity is important for management decisions because in both cases the management of only one co-occurring invader will not necessarily lead to a predictable reduction in the impact or growth of the other nonnative plant.

In co-invaded ecosystems, a potential source of non-additivity could be belowground interactions of co-occurring nonnatives. Co-existing nonnatives will influence soils concurrently and could cause non-additive impacts if the growth of a neighboring invasive plant affects belowground competition, soil resources, or microbial communities of focal nonnatives (Hawkes et al. 2013). On average, plant growth rates are faster in soils conditioned by multiple species compared to soils conditioned by single species monocultures (Kulmatiski and Kardol 2008), which indicates that plant performance may be greater in soils conditioned by multiple invasive species relative to soils conditioned by only a single invader. Previous single-invader studies demonstrate that nonnative plants affect soil biotic and abiotic properties, which leads to plant–soil interactions that influence the performance of other species grown in those soils. Singleton nonnative plant–soil impacts can decrease the performance of native species (Stinson et al. 2006, Mangla et al. 2008, Schradin and Cipollini 2012), enhance their own species performance (Klironomos 2002, Callaway et al.

2004, Felker-Quinn et al. 2011), or promote the performance or invasion of other nonnative species (D’Antonio et al. 2011, Kuebbing et al. 2015). Neighboring nonnative plants could mitigate or amplify these species-specific feedbacks by altering soil abiotic properties or biotic communities. For example, in the presence of potential competitors some plants release phytotoxic root exudates that directly depress the growth of neighbors (Bais et al. 2004, Bais et al. 2006). If a nonnative plant exudes these compounds in the presence of another nonnative species, the result may be decreased performance or suppression of the other nonnative or neighboring native species. Plants can indirectly depress neighbor growth by reducing populations of beneficial soil organisms (Stinson et al. 2006, Vogelsang and Bever 2009) or increasing populations of pathogenic soil organisms (Mangla et al. 2008). In contrast, negative soil feedbacks of a species grown singly could be alleviated if the addition of a second nonnative species promotes a microbial community that is more beneficial to the neighboring nonnative (Nuñez and Dickie 2014, Bogar et al. 2015). The magnitude and direction of non-additive impacts will revolve around the species-specific plant–soil interactions as well as the interactions of the co-occurring nonnative plants.

We test for non-additive soil impacts of two nonnative woody shrubs, *Lonicera maackii* (Rupr.) Herder (bush honeysuckle) and *Ligustrum sinense* Lour. (Chinese privet), that are commonly found co-occurring in southeastern United States deciduous forests. Although most research on the impacts of these species has focused on impacts when the species are found in monoculture, when they co-occur the species have additive effects on nonnative plant species richness and non-additive effects on soil properties (Kuebbing et al. 2014). Both nonnative shrubs alter soil abiotic and biotic properties when found in monoculture (Greipsson and DiTommaso 2006, Mitchell et al. 2011, Arthur et al. 2012, Kuebbing et al. 2014, 2015), and plant–soil interactions of these shrubs singly can promote other nonnative species (Kuebbing et al. 2015) or suppress native species (Gorchov and Trisel 2003, Schradin and Cipollini 2012). However, the relative impact of each invasive shrub individually may differ depending on species-specific plant–soil interactions (Shannon et al. 2014), and the performance of other nonnative shrubs is slightly higher in soils conditioned by *L. maackii* relative to *L. sinense* (Kuebbing et al. 2015). Because these two nonnative shrubs are commonly found growing side-by-side in invaded forests (Kuebbing et al. 2014, 2015) and both species are associated with altered soil properties, it is possible that the species may be interacting to create unique and non-additive impacts in soils invaded by both species.

We designed a plant–soil feedback experiment to determine whether plant–soil interactions in soils influenced by both nonnative shrubs are additive or non-additive, relative to soils influenced by each nonnative shrub individually. Because the presence of both species is associated with lowered native understory herbaceous

community richness and abundance (Hutchinson and Vankat 1997, Collier et al. 2002, Hanula et al. 2009, Greene and Blossey 2011) and higher nonnative plant species richness (Kuebbing et al. 2014), we test how different soil treatments influence the growth of *L. maackii* and *L. sinense*, a common understory nonnative woody vine, *Celastrus orbiculatus* Thunb. (Asiatic bittersweet), and a five-species native herbaceous plant community. We include a sterile soil treatment to test whether the presence or absence of microbial communities are responsible for differences in plant performance across soil treatments (Bever et al. 2010) and to elucidate whether the presence or absence of soil microbes differs in its effects between native and invasive species. Nonnative woody plants may require associations with beneficial soil microbes to invade (Nuñez and Dickie 2014), and may explain previous findings that *L. maackii* and *L. sinense* performance is significantly depressed in sterilized soils relative to soils with live soil microbial communities (Kuebbing et al. 2015). Conversely, because nonnative plants can reduce beneficial soil organisms (Stinson et al. 2006, Vogelsang and Bever 2009) or increase harmful soil organisms (Mangla et al. 2008) associated with native species, native plants may experience a benefit from sterilized soils relative to soils conditioned by an invasive plant. We test the following hypotheses in this experiment: (1) Nonnative plant performance will be higher and native plant performance will be lower in soils conditioned by nonnative shrubs relative to uninvaded soils that have not been conditioned by a nonnative shrub. (2) Nonnative plant performance will be higher in *L. maackii*-conditioned soils relative to *L. sinense*-conditioned soils; native plant performance will not differ between *L. maackii*-conditioned soils and *L. sinense*-conditioned soils. (3) Nonnative and native plant performance will be higher in soils conditioned by both nonnative shrubs (polyculture) relative to soils conditioned by each shrub singly (monoculture). (4) There will be a non-additive effect on plant performance in soils conditioned by both nonnative shrubs relative to performance in soils conditioned by each nonnative singly. (5) Nonnative plant performance will be lower and native plant performance will be higher in sterilized soils relative to unsterilized soils.

METHODS

To determine whether the influence of plant–soil interactions between co-occurring nonnative shrubs is additive or non-additive, we conducted a two-phase plant–soil feedback experiment (Bever et al. 2010, Brinkman et al. 2010) in greenhouses at the University of Tennessee, Knoxville, Tennessee, USA. Our design allowed us to assess additivity by comparing plant performance in soils conditioned by nonnative shrub monocultures (*Ligustrum sinense* or *Lonicera maackii*), soils conditioned by nonnative polycultures (*L. sinense* and *L. maackii*), sterilized soils, and uninvaded control soils. In order to determine whether potential non-additivity

was driven by rhizosphere interactions between the non-native shrubs, we compared feedbacks in nonnative polyculture soils to a monoculture composite soil treatment that was a mixture of *L. sinense*- and *L. maackii*-conditioned soils.

Seed and soil sources

We collected nonnative plant fruit from a minimum of 10 maternal plants in natural areas in Knoxville, Tennessee in the fall of 2012. *Ligustrum sinense* and *L. maackii* seeds were collected at IC King Natural Area (35°53'58.88" N, 83°56'41.65" W) and *Celastrus orbiculatus* seeds were collected from Maloney Road Park (35°54'10.49" N, 83°57'37.73" W) and Sharp's Ridge Memorial Park (36°0'14.89" N, 83°56'24.19" W). We removed the pulpy fruit exterior, air-dried seeds for 2 weeks, and stored dry seeds in brown paper bags at 4°C. We purchased native plant seeds (*Allium canadense* L., *Anemone virginiana* L., *Bromus pubescens* Muhl. Ex Willd., *Elymus hystrix* L., *Elymus villosus* Muhl. Ex Willd.) from Prairie Moon Nursery (Winona, Minnesota, USA). We conducted germination tests for all seeds prior to the experiment to ensure seed sources had germination rates >50% for all species. We used uninvaded forest soils as a soil microbial inoculum source, and we collected these soils from the upper 10 cm of mineral soil from three uninvaded areas more than 150 m apart in IC King Natural Area. Our uninvaded sites did not contain nonnative plant species and were a minimum of 20 m from any nonnative plant. The uninvaded forest was dominated by *Acer* L. (maple), *Fagus grandifolia* Ehrh. (American beech), *Fraxinus* L. (ash), and *Quercus* L. (oak), and the native plants *A. canadense* and *A. virginiana* are present in the forest understory. Collected soil was homogenized and sieved to 4 cm to remove any branches, large roots, and debris and stored until use at 4°C.

Soil conditioning phase

The initial conditioning phase of the experiment consisted of four soil treatments: nonnative monoculture pots (*L. sinense* or *L. maackii* seedlings), nonnative polyculture pots (*L. sinense* and *L. maackii* seedlings), and control pots (no seedlings). We created 60 replicates of each soil treatment for a total of 240 pots. Each 800-mL square pot (30 × 30 × 40 mm) was filled with a 9:1 ratio of twice-autoclaved potting soil (Fafard 2 Mix, Fafard, Anderson, South Carolina) and uninvaded forest soil. In the monoculture and polyculture pots, we planted 2–6-week old nonnative plant seedlings ~4 cm apart. Prior to planting, *L. sinense* and *L. maackii* seeds were surface-sterilized (3% hydrogen peroxide) and germinated in autoclaved sand (Quikrete Hardscapes Play Sand, item #212779; Quikrete, Marcellus, New York, USA) in a growth chamber (22°C, 55% humidity, and a 14:10 h day/night light cycle). We randomized pots on greenhouse benches and watered pots as necessary.

After 90 d of growth, we removed the above- and belowground biomass from each pot, rinsed roots to remove excess soil, and dried biomass at 60°C for 72 h before weighing. For the three soil treatments that included seedlings, we removed the conditioned soil and refilled each pot with nine parts twice-autoclaved potting soil (Fafard 2 Mix) and one part soil inocula from soil collected from the conditioned pot. We kept individual pots separate to maintain independent replicates and to assess possible nutrient depletion in pots owing to differences in the final size of the conditioning plant (Kulmatiski and Kardol 2008, Brinkman et al. 2010). We did not replace sterilized soils in control pots, which did not receive any seedlings during the initial phase, but we did mix soils in each pot by hand to replicate the soil disturbance in the planted pots.

In addition to these four soil treatments, we created two more soil treatments: sterilized soil and a “monoculture composite” soil. Sterilized soils were twice-autoclaved sterilized potting soil (Fafard 2 Mix) with no soil inocula added. The monoculture composite soil treatment received the same 9:1 sterilized-to-live soil inoculum, but the live soil inoculum was a 1:1 combination of *L. sinense*- and *L. maackii*-conditioned soils. In total, we had six soil treatments: sterilized soils, uninvaded control soils, nonnative monoculture soil treatments (*L. sinense*- or *L. maackii*-conditioned soil), a nonnative polyculture soil treatment (*L. sinense*- and *L. maackii*-conditioned soils), and a monoculture composite soil treatment (mixture of *L. sinense* and *L. maackii* monoculture soils).

Plant–soil response phase

We tested how *L. sinense*, *L. maackii*, the nonnative woody vine *C. orbiculatus*, and a native herbaceous understory plant community (*A. canadense*, *A. virginiana*, *B. pubescens*, *E. hystrix*, *E. villosus*) performed in each of the six soil treatments. The nonnative, invasive vine and the native herbaceous plants are widely distributed and common understory species in eastern Tennessee woodlands and overlap in range with areas invaded by *L. maackii* and *L. sinense*. We replicated each soil-by-plant treatment 15 times for a total of 360 pots. We added ten seeds of each of the three nonnative plant species to each pot. For the native plant community pots we planted four seeds each of *A. canadense*, *B. pubescens*, *E. hystrix*, *E. villosus*, and one-quarter tsp (~1.2 mL) of *A. virginiana*, whose seeds were too small to count reliably. These ratios were determined based on previous germination trails to increase the likelihood that all native species germinated in each pot. After seedling germination and establishment, we weeded the invader treatment pots to one seedling per pot. The native herbaceous community pots were not weeded, and all established seedlings were allowed to remain. We randomized pots on greenhouse benches and watered pots as necessary. After 6 months, we harvested all pots and measured number of leaves and above- and

belowground biomass. For the native community pot, we did not partition biomass by species or count number of leaves. Biomass was assessed as in the first phase of the experiment.

Statistical analysis

We used one-way ANOVAs to test for the effects of soil treatment on seedling height, number of leaves, and above- and belowground biomass (Brinkman et al. 2010). When we found a significant influence of soil treatment on plant performance, we tested our five hypotheses with non-orthogonal a priori contrasts (Appendix S1: Table S1), and we corrected for multiple tests using Bonferroni corrections (Brinkman et al. 2010). Response variables were transformed as necessary to meet model assumptions (Appendix S1: Table S2). Because the final plant size in the feedback stage could be influenced by the size of the seedling used to condition the soils, we used Pearson’s correlation test to test for a relationship between conditioning plant biomass and feedback plant final growth. We found no significant correlation ($P = 0.1$) between plant biomass in the soil conditioning phase and the feedback phase.

When we found significant effects of soil treatment, we calculated the relative growth response of plants between soil types. We used the formula $(S1_i - S2_i) / \max(S1_i, S2_i)$ where $S1_i$ is the plant performance (e.g., plant biomass, height, or number of leaves) in pots with soil type 1 and $S2_i$ is the plant performance in pots with soil type 2. This method centers values around 0 (i.e., values range from –1 to 1), which allows for easier comparison of negative and positive values (Brinkman et al. 2010). Because we did not have natural pot pairings, we adapted this method to accommodate the random pairings of pots in our tests by calculating the relative response for all possible combinations of pot pairs (Kuebbing et al. 2015). In the figures, we present the mean response values and 95% confidence intervals, but we derive statistical significance of soil treatments from the a priori contrasts.

We tested for non-additivity by calculating the proportional deviation (D_i) of observed and expected growth of plants in soils conditioned by a single nonnative shrub (i.e., *L. sinense*- or *L. maackii*-conditioned soils) vs. soils conditioned by both nonnative shrubs (i.e., nonnative polyculture soils). We used the formula $D_i = (O_i - E_i) / E_i$, where O_i is the observed plant performance in nonnative shrub polyculture soils and E_i is the expected additive plant performance based upon the plant’s growth in each nonnative monoculture soil (i.e., the mean plant performance in *L. sinense*- and *L. maackii*-conditioned soils). We tested whether D_i values differed from 0 with t tests and interpreted D_i values that differed from 0 as indications of non-additivity (Hawkes et al. 2013). A significantly positive D_i value represents positive non-additivity (e.g., the observed yield was greater than the expected yield) and a significantly negative D_i value represents negative non-additivity (e.g., the observed yield was less than the expected yield).

TABLE 1. Native and nonnative (*Celastrus orbiculatus*, *Lonicera maackii*, *Ligustrum sinense*) plant performance varied among six soil treatments (sterilized soils, uninvaded control soils, *L. sinense*-conditioned soils, *L. maackii*-conditioned soil, a nonnative polyculture soil treatment [*L. sinense*- and *L. maackii*-conditioned soils], and a monoculture composite soil treatment [mixture of *L. sinense* and *L. maackii* monoculture soils] in a plant–soil feedback experiment. ANOVA table reports the degrees of freedom (df), mean square value (MS), F statistic (*F*) and *P*-value (*P*).

Treatment	Shoot biomass		Root biomass		Number of leaves		Height (cm)	
	Soil	Error	Soil	Error	Soil	Error	Soil	Error
<i>L. sinense</i>								
df	5	80	5	80	5	80	5	80
MS	3.55	0.21	3.08	0.30	4.47	0.30	1.54	0.09
<i>F</i>	16.9		10.34		14.99		16.96	
<i>P</i>	<0.001		<0.001		<0.001		<0.001	
<i>L. maackii</i>								
df	5	84	5	84	5	84	5	84
MS	0.14	0.01	4.52	0.28	2.21	0.14	1.60	0.15
<i>F</i>	21.3		16.0		16.0		10.6	
<i>P</i>	<0.001		<0.001		<0.001		<0.001	
<i>C. orbiculatus</i>								
df	5	78	5	78	5	78	5	78
MS	0.02	0.21	0.48	0.04	0.20	0.09	0.19	0.10
<i>F</i>	8.76		10.9		2.08		2.00	
<i>P</i>	<0.001		<0.001		0.08		0.09	
Native community								
df	5	84	5	84	–	–	–	–
MS	0.76	0.12	1.10	0.19	–	–	–	–
<i>F</i>	6.54		5.9		–	–	–	–
<i>P</i>	<0.001		<0.001		–	–	–	–

Note: The native plant community consisted of the following herbaceous plants: *Allium canadense*, *Anemone virginiana*, *Bromus pubescens*, *Elymus hystrix*, and *Elymus villosus*.

Because plants release different root exudates in the presence of neighboring species (Walker et al. 2003, Bais et al. 2004, Bais et al. 2006), we used a priori contrasts to test whether the source of non-additivity was related to root interactions between the two nonnative shrubs. This contrast compared plant performance in soils conditioned by both invasive shrubs (e.g., nonnative polyculture soils) to soils that comprised a composite of monoculture-conditioned soils (i.e., monoculture composite soils). If the contrast was significant, we assumed that root interactions between the two nonnative shrubs created a unique soil condition that could not be duplicated by mixing soils conditioned by each species singly.

RESULTS

Native and nonnative plant performance varied by species and soil treatment (Tables 1 and 2).

H1: Nonnative plant performance will be higher and native plant performance will be lower in soils conditioned by nonnative shrubs relative to uninvaded soils that have not been conditioned by a nonnative shrub.—Nonnative and native plants performed better in uninvaded control soils compared to soils conditioned by a nonnative shrub in monoculture or polyculture (Fig. 1, Appendix S1; Table S2). The native herbaceous plant community had,

on average, 1.5 times higher shoot biomass and two times higher root biomass in uninvaded soils than in soils conditioned by nonnative shrubs singly or in polyculture (Table 2). The nonnative vine, *Celastrus orbiculatus*, had approximately two times higher shoot biomass and approximately three times higher root biomass in uninvaded soils than in soils conditioned by nonnative shrubs singly or in polyculture (Table 2). The two nonnative shrubs performed better in uninvaded soils, but the relative performance between uninvaded and invaded soils differed between the soil conditioning treatments. *Lonicera maackii* shoot biomass was approximately nine times higher in uninvaded soils than in *L. maackii*-conditioned soils but only three times higher than in *L. sinense*-conditioned soils. Shoot biomass of *L. sinense* was three times higher in uninvaded soils than in soils conditioned by both *L. maackii* and *L. sinense* and approximately four times higher than that in either *L. maackii*- or *L. sinense*-conditioned soils (Table 2).

H2: Nonnative plant performance will be higher in L. maackii- than in L. sinense-conditioned soils; native plant performance will not differ between L. maackii- soils and L. sinense-conditioned soils.—The nonnative shrub *L. maackii* was the only species whose performance varied between soils conditioned by each nonnative shrub singly (Fig. 2, Table 2). *Lonicera maackii* plants

TABLE 2. Native and nonnative plant performance varied across soils conditioned by different nonnative shrub monocultures or mixtures.

Treatment, by plant	Shoot mass (g)	Root mass (g)	Leaves (number)	Height (cm)
<i>L. sinense</i>				
Uninvaded	0.12 ± 0.019	0.13 ± 0.022	26.2 ± 2.7	10.31 ± 0.69
<i>L. maackii</i> -conditioned	0.03 ± 0.007	0.05 ± 0.014	8.1 ± 1.5	4.68 ± 0.48
<i>L. sinense</i> -conditioned	0.03 ± 0.004	0.03 ± 0.006	6.6 ± 0.8	4.54 ± 0.46
<i>L. maackii</i> - and <i>L. sinense</i> -conditioned	0.04 ± 0.004	0.07 ± 0.009	8.4 ± 1.2	6.03 ± 0.31
Monoculture composite	0.03 ± 0.004	0.03 ± 0.006	5.3 ± 0.6	4.63 ± 0.37
Sterile	0.03 ± 0.005	0.04 ± 0.006	11.3 ± 3.4	4.61 ± 0.47
<i>L. maackii</i>				
Uninvaded	0.17 ± 0.028	0.15 ± 0.025	17.7 ± 1.2	10.44 ± 1.01
<i>L. maackii</i> -conditioned	0.02 ± 0.003	0.02 ± 0.002	7.2 ± 0.6	4.01 ± 0.21
<i>L. sinense</i> -conditioned	0.05 ± 0.012	0.05 ± 0.009	10.9 ± 1.4	6.15 ± 0.89
<i>L. maackii</i> - and <i>L. sinense</i> -conditioned	0.03 ± 0.006	0.02 ± 0.005	7.6 ± 0.9	4.79 ± 0.39
Monoculture composite	0.03 ± 0.007	0.03 ± 0.007	6.3 ± 0.7	4.37 ± 0.53
Sterile	0.03 ± 0.006	0.03 ± 0.006	7.8 ± 0.6	4.79 ± 0.48
<i>C. orbiculatus</i>				
Uninvaded	0.85 ± 0.009	0.14 ± 0.02	6.7 ± 0.7	7.49 ± 0.44
<i>L. maackii</i> -conditioned	0.04 ± 0.006	0.05 ± 0.005	5.7 ± 0.7	5.71 ± 0.59
<i>L. sinense</i> -conditioned	0.04 ± 0.006	0.05 ± 0.009	4.7 ± 0.6	6.53 ± 0.87
<i>L. maackii</i> - and <i>L. sinense</i> -conditioned	0.03 ± 0.003	0.05 ± 0.005	5.2 ± 0.5	5.58 ± 0.53
Monoculture composite	0.04 ± 0.005	0.05 ± 0.005	4.4 ± 0.2	6.21 ± 0.41
Sterile	0.05 ± 0.007	0.09 ± 0.01	5.7 ± 0.6	6.48 ± 0.46
Native community				
Uninvaded	0.66 ± 0.08	1.10 ± 0.17	—	—
<i>L. maackii</i> -conditioned	0.47 ± 0.03	0.69 ± 0.06	—	—
<i>L. sinense</i> -conditioned	0.42 ± 0.02	0.47 ± 0.04	—	—
<i>L. maackii</i> - and <i>L. sinense</i> -conditioned	0.41 ± 0.02	0.38 ± 0.03	—	—
Monoculture composite	0.37 ± 0.03	0.55 ± 0.07	—	—
Sterile	0.33 ± 0.04	0.65 ± 0.11	—	—

Notes: Soil conditioning treatments were sterilized potting soil (sterile) or mixtures of sterilized potting soils plus the following soil inocula: soils collected from uninvaded forested areas (uninvaded), soils conditioned by the nonnative shrub *L. maackii*, soils conditioned by the nonnative shrub *L. sinense*, soils conditioned by both nonnative shrubs *L. maackii* and *L. sinense*, or monoculture composite soils that were a 1:1 combination of monoculture nonnative-conditioned soils (*L. sinense*- and *L. maackii*-conditioned soils). Data here are means and standard errors.

had ~2.5 times higher shoot and root biomass and plants were ~1.5 times taller with 1.5 times more leaves in soils conditioned by *L. sinense* than in soils conditioned by *L. maackii* (Table 2). The performance of the nonnative shrub *L. sinense* and the nonnative vine *C. orbiculatus* did not differ between *L. maackii*- and *L. sinense*-conditioned soils (Fig. 2, Table 2). The root biomass of the native herbaceous community was nearly 1.5 times greater in soils conditioned by *L. maackii* compared to that in soils conditioned by *L. sinense*, but this was only marginally significant at the Bonferroni-corrected $\alpha = 0.02$ ($P = 0.05$, Appendix S1: Table S2).

H3: Nonnative and native plant performance will be higher in soils conditioned by both nonnative shrubs (polyculture) relative to soils conditioned by each shrub singly (monoculture).—The performance of the native plant community and the nonnative shrub *L. sinense* varied between

soils conditioned by one nonnative shrub (monoculture) and soils conditioned by both nonnative shrubs (polyculture; Table 2, Fig. 3). Native plant root biomass was 1.3 times higher in *L. maackii*-conditioned soils and 1.8 times higher in *L. sinense*-conditioned soils than in soils conditioned by both *L. maackii* and *L. sinense*. In contrast, the shoot and root mass of *L. sinense* in soils conditioned by both nonnative shrubs was ~1.5 times higher than in *L. maackii*-conditioned soils. Comparatively, *L. sinense* shoot mass was 1.5 times higher and the root mass was two times higher in soils conditioned by both nonnatives compared to plants grown in soils conditioned by a conspecific. The performance of the nonnative shrub *L. maackii* and the nonnative vine *C. orbiculatus* did not differ between soils conditioned by one or two nonnative shrubs.

H4: There will be a non-additive effect on plant performance in soils conditioned by both nonnative shrubs (polyculture)

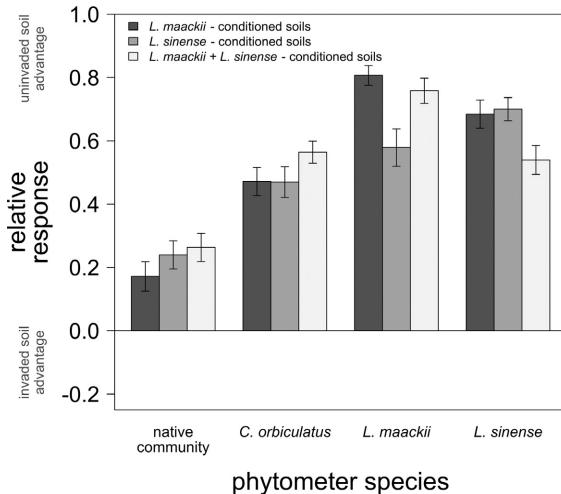


FIG. 1. Shoot biomass of a five-species native herbaceous plant community and nonnative plants (*Celastrus orbiculatus*, *Ligustrum sinense*, and *Lonicera maackii*) was significantly higher in uninvaded control soils than in soils conditioned by an invasive shrub in monoculture or mixture. Significance was determined from a priori contrast tests and error bars are 95% confidence intervals from relative response calculations.

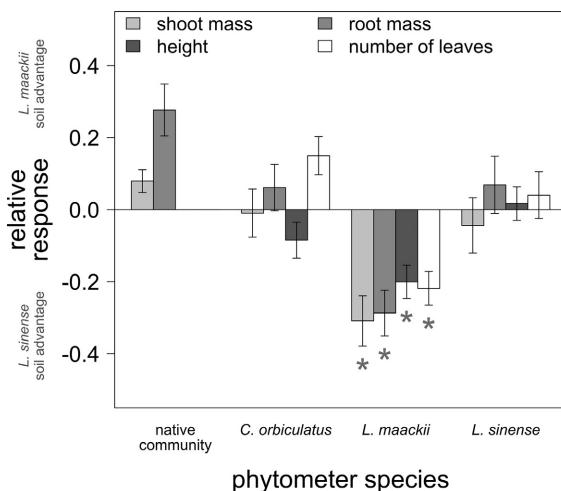


FIG. 2. Performance of the nonnative shrub *Lonicera maackii* was greater in soils conditioned by the nonnative shrub *Ligustrum sinense* than in soils conditioned by a conspecific. The performance of other nonnatives (*Celastrus orbiculatus* and *L. sinense*) or a native plant community comprised of five forbs and grasses did not differ between *L. sinense*- and *L. maackii*-conditioned soils. Error bars are 95% confidence intervals from relative response calculations and asterisks represent significance ($P < 0.05$) from a priori contrast tests.

relative to performance in soils conditioned by each nonnative singly.—The native herbaceous community had negative non-additive performance and the nonnative shrub *L. sinense* had positive non-additive performance in soil conditioned by both nonnative shrubs compared to their expected performance in soils conditioned by either nonnative singly (Fig. 4). Root mass of the native herbaceous

community grown in soils conditioned by both *L. maackii* and *L. sinense* was 1.5 times lower than expected based upon growth in soils conditioned by either *L. maackii* or *L. sinense* singly (expected yield, $E_i = 0.58$ g; observed yield, $O_i = 0.37 \pm 0.03$ g [mean \pm standard error]; Fig. 4). In contrast, the shoot biomass of the nonnative shrub *L. sinense* was 1.5 times higher ($E_i = 0.028$ g; $O_i = 0.043 \pm 0.004$ g; Fig. 4) and the root biomass was 1.8 times higher ($E_i = 0.04$ g; $O_i = 0.072 \pm 0.009$ g; Fig. 4) in soils conditioned by both *L. maackii* and *L. sinense* relative to expectations based upon growth in soils conditioned by *L. maackii* and *L. sinense* singly. The nonnative vine *C. orbiculatus* and the nonnative shrub *L. maackii* showed no signs of non-additivity in soils conditioned by both species. We found no evidence that non-additivity was a function of root interactions between the two shrubs. Contrasts between nonnative polyculture soils and the monoculture combination soils were not significant, indicating that soil conditions could be duplicated by mixing soils conditioned separately by *L. maackii* and *L. sinense* (Appendix S1: Table S2).

H5: Nonnative plant performance will be lower and native plant performance will be higher in sterilized soils relative to unsterilized soils.—Native and nonnative plant performance was lower in sterilized soils. The shoot biomass of the native herbaceous plant community was two times lower in sterilized soils than in soils of the uninvaded control (Table 2), and shoot biomass was 1.2, 1.3, and 1.5 times lower in soils conditioned by a *L. sinense* and *L. maackii* polyculture, *L. sinense*-conditioned monoculture soils, and *L. maackii*-conditioned monoculture soils, respectively. Root biomass of the native herbaceous community did not differ significantly between sterilized and live soils, no matter the conditioning plant of the live soil. Nonnative plant performance varied in sterilized soils compared to live soils conditioned by nonnative species (Table 2), but these differences were only marginally significant ($P < 0.1$; Appendix S1: Table S2). Root mass of the nonnative vine *C. orbiculatus* was ~ 1.7 times higher in sterilized soils than in soil conditioned by the nonnative shrubs, but was 1.6 times lower in sterilized soils compared to uninvaded control soils (Table 2). Shoot mass of the nonnative shrub *L. maackii* was six times lower in sterilized soils than in uninvaded control soils and 1.8 times lower in sterilized soils than in *L. sinense*-conditioned soils but did not differ between sterilized soils and *L. maackii*-conditioned soils or polyculture soils. Shoot mass and root mass of *L. sinense* were four and 3.5 times lower, respectively, in sterilized soils than in uninvaded controls soils. Shoot and root mass of *L. sinense* were also 1.5 times lower in sterilized soils than in soils conditioned by both *L. sinense* and *L. maackii*.

DISCUSSION

Two nonnative, invasive shrubs had non-additive impacts on native and nonnative plant growth, which

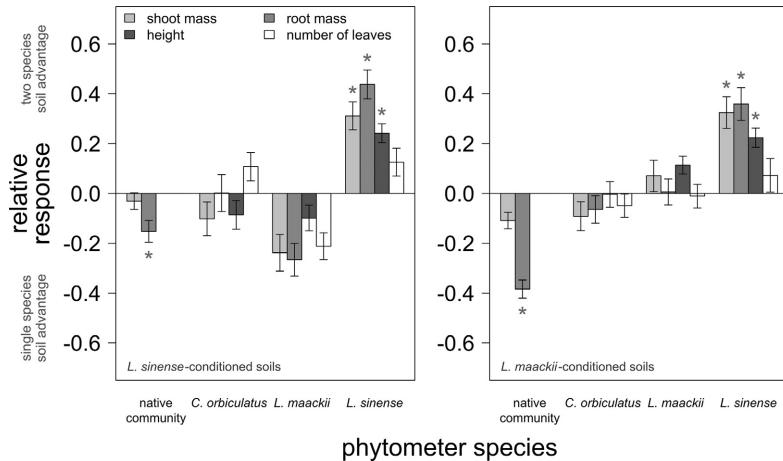


FIG. 3. Root biomass of a five-species native herbaceous community was on average 67% lower and overall performance of the nonnative shrub *Ligustrum sinense* was on average 60% higher in soils conditioned by a singleton nonnative shrub than in soils conditioned by both nonnative shrubs. The performance of other nonnatives (*Celastrus orbiculatus* and *Lonicera maackii*) did not differ between soils conditioned by a single nonnative and soils conditioned by two nonnatives. Error bars are 95% confidence intervals from relative response calculations and asterisks represent significance ($P < 0.05$) from a priori contrast tests.

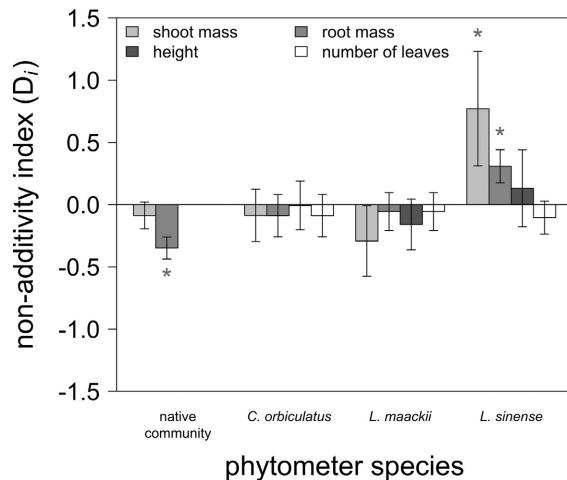


FIG. 4. Soils conditioned by the two nonnative shrubs *Ligustrum sinense* and *Lonicera maackii* had a negative non-additive impact on the root biomass of a five-species native plant community but a positive non-additive impact on the shoot and root biomass of the nonnative shrub *L. sinense*. Non-additivity was calculated by comparing the observed performance of a species in soils conditioned by two nonnative shrubs to the expected performance of that species based upon its growth in soils conditioned by a nonnative shrub singly. A significantly positive D_i value represents positive non-additivity (e.g., the observed yield was greater than the expected yield) and a significantly negative D_i value represents negative non-additivity (e.g., the observed yield was less than the expected yield). Error bars are 95% confidence intervals from non-additivity index calculations and asterisks represent significance ($P < 0.05$) from t tests.

indicates that invasive impact studies focusing only on the impact of single species can be insufficient for determining the impact of co-occurring invasive plant species. Furthermore, the direction of the non-additive impacts differed between native and nonnative plants. The

combined impact of the two nonnative shrubs depressed growth of the native herbaceous community but increased growth of the nonnative shrub *Ligustrum sinense* more than expected based upon the performance of the plants in soils conditioned by single nonnative shrubs. This indicates that when these two nonnative shrubs co-occur their impacts disproportionately favor the persistence of the nonnative *L. sinense* relative to these native herbaceous plants. This discrepancy between native and nonnative performance in soils conditioned by two nonnative shrubs further demonstrates that non-additive invader impacts should be considered when one prioritizes management decisions for co-invaded landscapes.

Observed decreases in native species richness and abundance in areas invaded by these nonnative shrubs (Hutchinson and Vankat 1997, Collier et al. 2002, Hanula et al. 2009, Greene and Blossey 2011) could be attributed to nonnative shrubs altering soil biotic communities or abiotic properties (Schradin and Cipollini 2012, Kuebbing et al. 2015) in ways that reduce native herbaceous plant performance. Frequently, competition for resources such as light or pollination services (McKinney and Goodell 2010, Greene and Blossey 2011) are implicated as the cause of native plant decline in invaded areas, but soil alteration by these invasive shrubs could be an additional mechanism leading to the reduction of native plant abundance in invaded areas. Although we did not test native plant response in soils conditioned by the native community itself, we did find that the performance of the native herbaceous community was significantly reduced in soils conditioned by nonnative shrubs and plant biomass was higher in uninvaded control soils compared to invaded soils. Native herbaceous species can have lower arbuscular mycorrhizal fungi root colonization in soils conditioned by *Lonicera maackii* and a congener of *L. sinense*, *L. vulgare* (Shannon et al. 2014), suggesting

that these invasive shrubs may have weaker associations with mycorrhizal fungi species that are important for native plant growth (Vogelsang and Bever 2009). Furthermore, the alteration of soil properties by these shrubs could lead to soil legacy effects (Corbin and D'Antonio 2012), which could explain why removal of these nonnative shrubs does not necessarily lead to re-establishment of a native herbaceous community similar to those in nearby uninvaded areas (Vidra et al. 2007, Hanula et al. 2009).

In addition to lowered performance in invaded soils than in uninvaded soils, native plant root biomass was significantly and non-additively lower in soils conditioned by both *L. sinense* and *L. maackii* than in soils conditioned by either shrub individually. Non-additive impacts of nonnative plants could alter management priorities across invaded landscapes and suggests that management outcomes of co-invaded areas will not necessarily be predictable from areas managed for the species singly (Kuebbing et al. 2013). In the case of negative non-additivity for these native herbs, managers may choose to prioritize management of areas that contain both nonnative shrubs over areas with only one shrub species, predicting that management benefits of treating co-invaded areas will be nonlinear and positive relative to treating areas with only *L. sinense* or *L. maackii*.

Non-additive impacts of co-occurring nonnative shrubs on soils properties could provide an explanation for apparent recalcitrance of nonnative communities through time (Kulmatiski 2006, Kuebbing et al. 2015). While soils conditioned by both nonnative shrubs non-additively reduced performance of the native herbaceous species, they promoted non-additive growth of the nonnative shrub *L. sinense*. In addition, the performance of the nonnative shrub *L. maackii* did not differ between soils conditioned by a single nonnative shrub and soils conditioned by both shrubs, but *L. maackii* did grow more in *L. sinense*-conditioned soils. The negative synergy between reduced growth of the native herbaceous plants and increased growth of these two nonnative shrubs in invaded soils decreases the likelihood that, without management interventions, invaded communities will revert to forests with a diverse native community. Instead, invaded forest understories may remain dominated by these two nonnative shrubs (Kuebbing et al. 2015).

Although we found non-additive effects on plants grown in soils conditioned by both nonnative shrubs (i.e., D_i values significantly different from 0), we did not find evidence that these effects were related to root interactions between the two nonnative shrub species (i.e., significant differences between plant growth in monoculture composite soils versus polyculture soils conditioned by both nonnative shrubs). The study of how root–root interactions influence root exudation is still in the early stages (Bais et al. 2006, Depuydt 2014), and we suggest a few possible reasons we did not see differences in plant growth between monoculture composite soils and polyculture soils. First, if the root–root interactions

between the two nonnative shrub species were minimal and did not lead to release of root exudate, then it is likely that our monoculture composite soil treatment was biotically and abiotically similar to the nonnative polyculture soil treatment. However, when we harvested the plants used in the initial conditioning phase of the experiment we saw that the plants had intertwined root systems, which indicates that the individual plants in the pots had overlapping rhizospheres and thus the possibility for root–root interactions (Weir et al. 2006). Second, if root–root interactions stimulated root exudates but those exudates had minimal effect on the soil biota or its abiotic properties, then we may not expect to find differences in growth of plants in each soil treatment. Although leaves and roots of the nonnative shrub *L. maackii* contain phenolic compounds that reduce germination of target plants (Stevenson et al. 2008), it is unknown whether root–root interactions stimulate the exudation of these allelopathic compounds or if they are always present in *L. maackii* tissue. As the study of root–microbe–soil interactions progresses and incorporates more sophisticated technologies and tools to understand root interactions (Weir et al. 2006, Depuydt 2014), we may be able to further understand the potential causes of non-additive responses in plant–soil interaction studies.

While the two nonnative shrubs had varied performance in invaded soils, the growth of the nonnative woody vine, *Celastrus orbiculatus*, did not differ between soils conditioned by the nonnative shrubs grown singly or together. Other woody shrubs have shown increased growth in soils conditioned by *L. sinense* and *L. maackii* relative to uninvaded control soils (Kuebbing et al. 2015), which could be linked to changes in soil mycorrhizal communities that promote other nonnatives relative to natives (Vogelsang and Bever 2009, Kuebbing et al. 2015). Although *C. orbiculatus* is known to form mycorrhizal associations under certain soil conditions in its invaded range (Lett et al. 2011), the fact that we found no difference between the vine's growth in sterilized soils and in live soils suggests that non-biotic soil properties may be more important for promoting its growth (Leicht-Young et al. 2007).

Interestingly, the performance of all three nonnative woody species was higher in uninvaded soils than in invaded soils, a result that differs from that in a previous greenhouse experiment where *L. maackii* performance was higher in invaded soils relative to uninvaded soils and *L. sinense* did not differ between invaded and uninvaded soils (Kuebbing et al. 2015). Differences in the experimental designs may be responsible for the dissimilarity. The length of the plant–soil feedback phase was half as long than in the previous experiment (6 months vs. 12 months), and in this experiment plants were introduced as seeds, whereas the other experiment used 8-week-old seedlings. The combined effect of these two differences was that the final seedlings harvested were younger and smaller than individuals in the previous experiment. Plant–soil feedbacks can vary temporally for a single species (Hawkes et al. 2013), which may be linked

to differences in mycorrhizal colonization as seedlings age (Husband et al. 2002) or general differences in seedling growth (Casper et al. 2008). This discrepancy highlights the temporal nature of some plant–soil interactions and the fact that greenhouse experiments representing a single time point provide only a snapshot of plant–soil interactive dynamics, dynamics that may change with plant ontogeny (Casper et al. 2008, Hawkes et al. 2013).

Co-occurring nonnative plants affect soil properties, and these changes can feed back to affect the performance of both native and nonnative plant species. The combined impact of these two shrub species were additive and non-additive, which indicates that how co-occurring invaders affect other species will be contingent upon the species involved in the interactions and the environmental context of the invasion. Our results suggest that non-additive interactions between these two nonnative shrubs are simultaneously promoting the continued coexistence of the dominant nonnative while depressing native herbaceous plants, but whether this is a common occurrence for co-occurring nonnative plants is unknown. If we are to provide better management recommendations for co-invaded landscapes, then we need to further explore how nonnative species interactions shape soil properties over time, and whether changes to soil properties will be responsive to restoration back to native-dominated communities in light of altered conditions by previous nonnative residents.

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