


Differing interactions between an introduced beetle and a resident root nematode mediated by an invasive plant and its native congener

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Abstract Interactions between above- and below-ground herbivores play an important role in shaping plant competition and invasion, while the effects of non-native species invasions on above- and below-ground interactions remain unexplored. In this study, we report the interactions between an above-ground introduced beetle and a resident root nematode hosted by an invasive plant or its native congener with a laboratory bioassay and a greenhouse experiment in Wuhan, China. Nematode infections decreased beetle food conversion rates and larval biomass on the native plant, and increased beetle food conversion rates with no detectable impact on the larval biomass on the invasive plant. Beetle defoliation decreased nematode egg production on both the native and invasive plants. The interactions of the introduced beetle and the

nematode were different by the invasive and native plants, which suggests that invasive plants and their introduced herbivores have the potential to alter above- and below-ground interactions and affect associated community members, which may in turn affect invasion processes and the safety of classical biocontrol practices.

Keywords Biological invasion · Above- and below-ground interactions · *Alternanthera philoxeroides* · *Agasicles hygrophila* · *Meloidogyne incognita*

Introduction

Non-native plant invasions are important drivers of species loss at the global scale (Vila et al. 2011). Understanding the mechanisms that underlie the ecological impacts of invasive plants is of critical importance for addressing their negative impacts on invaded ecosystems (Harvey et al. 2010). Increasing

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number of studies have found that invasive plants can alter co-evolved interactions among native species, and this is acknowledged as one important mechanism underlying invasive plants' detrimental impacts (Murphy and Feeny 2006; Bertheau et al. 2010). However, the focus of most current studies is on the interactions between above-ground species or below-ground species (van der Putten et al. 2001; van Hengstum et al. 2014). As a result, our understanding of how plant invasions affect interactions between above- and below-ground herbivores is still limited. In addition, there is increasing evidence indicating that above- and below-ground herbivores could interact with each other via shared host plants (Wardle et al. 2004; Johnson et al. 2012). Furthermore, the interactions between above- and below-ground herbivores also play an important role in structuring above-ground communities (van der Putten et al. 2009; Harvey et al. 2010; van Dam and Heil 2011). Thus, understanding the impacts of plant invasions on the interactions between above- and below-ground herbivores is critical for fully exploring their ecological effects.

Host plants play an important role in facilitating above- and below-ground biotic interactions. Empirical evidence shows that the occurrence, direction, and magnitude of above- and below-ground biotic interactions are largely determined by a host plant's systematic defense responses, resource allocation patterns, and nutrition (Haase et al. 2008; Kutyniok and Müller 2012). In comparison with co-occurring native species, invasive plants frequently host fewer herbivores in their invasive ranges (enemy release hypothesis, Keane and Crawley 2002) and thus allocate less resources to defense than when they are in their native ranges (evolutionary increased competitive ability hypothesis, Blossey and Notzold 1995). However, some invasive plants may possess novel chemical or physiological defenses that deter susceptible resident herbivores (novel weapon hypothesis, Callaway and Ridenour 2004). Therefore, the interactions of above- and below-ground herbivores may be facilitated differently by native and invasive plant species, which has not been substantially explored to date.

In this study, we compared the interactions between the introduced above-ground biocontrol beetle *Agasicles hygrophila* (Coleoptera: Chrysomelidae) and the native root nematode *Meloidogyne incognita* (Kofoid & White) Chitwood via the invasive plant

Alternanthera philoxeroides (Mart.) Griseb. (Amaranthaceae) and the native plant *Alternanthera sessilis* (L.) R. Br. ex DC (Amaranthaceae) with a greenhouse experiment and a laboratory bioassay. *Alternanthera philoxeroides*, native to South America, is now a noxious weed in the USA, China, Australia, and New Zealand (Julien et al. 1995). In China, *A. philoxeroides* co-occurs with the native congener *A. sessilis* across its invaded ranges (Lu et al. 2015a). Both species have been infested not only by the introduced *A. hygrophila*, but also by a native generalist root nematode, *M. incognita*, as far north in China as 31°N. The native and invasive plants have also been attacked to a lesser degree by some native defoliators, including *Cassida piperata* Hope (Coleoptera: Cassididae) (Lu et al. 2015a). Although interactions between the introduced beetle or the root nematode and the native or invasive plants have been well studied independently (Lu and Ding 2010; Lu et al. 2015a, b, 2016), the potential interaction between the biocontrol beetle and the resident root nematode facilitated by the native or invasive hosts has not yet been examined.

Previously, we found that the invasive plant *A. philoxeroides* was more tolerant to above-ground herbivory and more resistant to root nematode infection than the native plant *A. sessilis* (Lu et al. 2015b). As a consequence, the damage caused by either the above-ground herbivore or the root nematode had a greater effect on *A. sessilis* (Lu et al. 2015b). Thus, we expected that (1) the root nematode infection may have a greater impact on above-ground herbivore via the susceptible native plant than via the resistant invasive plant, and (2) defoliation by introduced beetle may also have a greater impact on the root nematodes via the native plant than via the invasive plant. In this study, we conducted a greenhouse experiment and a laboratory bioassay to test the impacts of *A. hygrophila* on *M. incognita*, and vice versa, when the two species are hosted by the invasive and native hosts.

Materials and methods

Study species

Alternanthera philoxeroides, native to South America, is a noxious weed throughout the world (Julien et al. 1995). First introduced into China in Shanghai in the 1930s, it is now found as far north as 36.8°N (Lu et al.

2015a). *Alternanthera sessilis* is a native annual or perennial herb in China, Australia, and some Pacific islands (Global Invasive Species Databases, <http://www.iucngisd.org/gisd/>). These two plant species often co-occur in natural habitats up to 36.8°N in China, where both species have been mainly infested by the introduced specialist beetle *A. hygrophila* and the native generalist root-knot nematode *M. incognita* (Mao et al. 2011; Lu et al. 2015a). Compared to the native congener, the invasive *A. philoxeroides* has been reported to have a higher root-to-shoot mass ratio, its roots are coarse with a thick cuticle, and it is more tolerant to above-ground herbivory and more resistant to root nematode infection than the native *A. sessilis* (Sun et al. 2010; Lu et al. 2015b). There is no difference in the foliar N content or C/N ratio between the two plant species across a latitudinal cline (Lu et al. 2015a).

Agasicles hygrophila, native to South America, has been used to control *A. philoxeroides* in the USA, Australia, New Zealand, and Asia since the 1970s (Julien et al. 1995). The beetle was introduced into China in 1986 and now occurs as far north as 31.8°N (Lu et al. 2015a). To date, the beetle has suppressed *A. philoxeroides* in aquatic habitats in southern China but has had only a limited impact on this weed in terrestrial habitats due to the high tolerance of the plant and low beetle population size (Lu and Ding 2010; Lu et al. 2013). In China, the beetle also attacks the native plant *A. sessilis*, and its influence on the native congener may increase in a warmer climate (Lu et al. 2015a).

The generalist root-knot nematode *M. incognita* is the most widespread and common nematode pest in agricultural and semi-natural systems in tropical and subtropical regions (Castagnone-Sereno et al. 2013). The life cycle of this nematode is composed of the egg, juvenile, and adult stages, and is approximately 30 days depending on the host plant species and soil temperature. The nematode can overwinter in the soil as eggs, juveniles, and adults and can survive up to 3 years without a host plant (Liu 2000). Infective second-stage juveniles penetrate root tips, initiate the development of giant cells, and cause the formation of root galls (i.e., root knot) (Ibrahim et al. 1973). *Meloidogyne incognita* infection can reduce plant growth and lead to low yields in agricultural systems (Sasser 1980). Although it is mitotically parthenogenetic, empirical evidence indicates that *M. incognita*

populations differ in their ability to infect different plant species with unknown mechanism (Ehwaeti et al. 1999).

Experiment 1: effect of root nematode infection on beetle performance on the native and invasive plants

To test the effect of the *M. incognita* infection on *A. hygrophila*, we conducted a laboratory bioassay using plants that received different treatments in a greenhouse in the Wuhan Botanical Garden of the Chinese Academy of Sciences from May to August 2013.

The invasive plant can propagate only clonally in China, while the native plant can propagate both sexually and clonally. To minimize potential differences resulting from sexual or clonal propagation, we used similar-sized cut stems (4–5 cm in length, with one node for each) of *A. philoxeroides* and *A. sessilis* collected in the Wuhan Botanical Garden for this experiment. Cut stems of the same species were planted on May 24, 2013 in pots filled with 5 L of autoclave-sterilized soil (2 cut stems per pot) which were then placed in nylon cages (60 mesh sieve, 20 cm in diameter, and 70 cm high) to exclude herbivores. The topsoil (0–15 cm) was collected from an *A. philoxeroides* and *A. sessilis*-infested field near the Wuhan Botanical Garden. After removing coarse roots and debris, the soil was mixed intensively with sand and sphagnum peat moss at the ratio of 3:1:1 (v/v), and then the mixed soil was sterilized at 0.15 m pa, 121 °C for 90 min to kill root-knot nematodes with an autoclave sterilizer (YXQ.WY21.600, Zhengzhou Nanbeiyi Instrument and Equipment Co. Ltd, China). Then, all the pots were placed randomly in a greenhouse. To minimize the negative impact of the high temperature on the plants and insects, air temperature in the greenhouse was controlled with an air conditioner and ranged from 25 °C at night to 35 °C in the noon. All the greenhouse vents were opened to increase the air flow, and the greenhouse roof was covered with a shade cloth from 11:00 am to 16:00 pm.

After one month, each pot was thinned to one individual and randomly assigned to one of the following treatments: inoculation with c. 2000, 5000, 10,000, or 20,000 eggs of *M. incognita*, which represented the gradient of nematode density that occurs in the field (He et al. unpublished data), and

sterilized water as the corresponding control. Eggs of *M. incognita* were extracted from infected tomato roots using the NaOCl method (Bybd et al. 1983). Eggs were counted under a microscope, and nematode egg solutions of 500 eggs/ml, 1250 eggs/ml, 2500 eggs/ml, and 5000 eggs/ml were prepared with sterilized water. For nematode egg inoculation, two holes (0.5 cm in diameter and 5 cm deep) were made close to the plant roots (approximately 1 cm apart) and filled with 4 ml of egg solution (2 ml for each hole per pot) of the selected density, while the control received the same volume of sterilized water. Each treatment (species \times nematode egg density) was replicated ten times, and 50 seedlings were used for each plant species. All the pots were distributed randomly, and their positions were randomly moved every 2 weeks in the greenhouse. Throughout the trial, all plants received approximately 300 ml of sterilized water every other day.

Three weeks after nematode inoculation, a laboratory bioassay was conducted to test the impact of root nematode infection on beetle larvae performance. Wei et al. (2016) found that this duration is sufficiently long for nematodes to trigger host plant responses and indirectly affect above-ground herbivores. Offspring of the second-generation *A. hygrophila* that originated from a field near the garden and that had been reared on *A. philoxeroides* in a laboratory were used for this experiment. To examine the fresh to dry weight conversion rate, calculated as leaf dry mass/leaf weight mass, fifteen newly fully opened leaves from additional plants were collected and their fresh and dry (dried at 60 °C for 48 h) masses were weighed for each plant species. The conversion rates of plant leaf fresh mass to dry mass for *A. philoxeroides* and *A. sessilis* were 0.1163 and 0.1614, respectively.

Leaves of treated plants were collected for the bioassay and their fresh mass was weighed before the experiment. Then plant leaves were placed individually into Petri dishes (9 cm in diameter) lined with moist filter paper, which were held at 28 °C with a natural light/dark photoperiod (approximately 14:10 h) throughout the trial. One newly hatched larva was transferred into each Petri dish. Leaf disks in each Petri dish were replaced with newly fully opened leaves collected from the same individual plant every other day, and five larvae in total were raised from leaves of each individual plant for repeat. Leftover leaf disks in each Petri dish were collected and placed in a

plastic bag for later weighing. The bioassay lasted for 1 week, after which all the plant materials from the same Petri dish were collected and dried at 60 °C for 48 h. The beetles were also weighed after 48 h of starvation before the bioassay.

Thirty beetle larvae were randomly selected and weighed fresh and then dried (60 °C for 48 h) to calculate fresh to dry weight conversion rate (coefficient of dry weight to fresh mass: 0.1533; for details, see Fig. S1). We calculated insect food consumption as fresh leaf biomass \times leaf fresh to dry weight conversion factor-dry leaf uneaten leaf mass, and the insect food conversion rate as (fresh insect biomass \times 0.1533)/(fresh leaf biomass \times leaf fresh to dry weight conversion factor-dry leaf uneaten leaf mass). At the same time, plant roots were collected and washed in the laboratory. We used the NaOCl-acid fuchsin-glycerin technique (Bybd et al. 1983) to stain nematodes within the root tissues and counted the number of adult nematodes from each plant under a microscope.

Experiment 2: effect of beetle defoliation on root nematodes

A greenhouse experiment was conducted with the same source populations of plants, beetles, and root nematodes as in Experiment 1 from August to November 2013 to test the impact of beetle defoliation on the root nematodes. Instead of releasing herbivores before nematode inoculation, plants received root nematode infections and above-ground herbivory at the same time in this experiment to mimic the natural condition where nematodes were always present in the soils. In August, cut stems of both plant species were planted horizontally in pots (2 cuttings per pot) that were then filled with 5 L of autoclave-sterilized soil and immediately placed in nylon cages (60 mesh sieve, 20 cm in diameter, and 70 cm in height). All the pots were then placed randomly in the same greenhouse as in the above experiment. After 1 month, each pot was thinned to one individual plant. The plants of *A. philoxeroides* and *A. sessilis* were 20 and 15 cm in length, respectively, and inoculated with *c.* 3500 *M. incognita* eggs using the same method as in Experiment 1. This egg density represents the most frequently observed nematode density in the field (He et al. unpublished data). At the same time, plants were randomly assigned to one of the following herbivory

treatments: defoliation by 1, 2, 3, or 5 freshly hatched larvae of *A. hygrophila*, representing the beetle density gradient observed in the field, for 7 days, and an undamaged control for each plant species. Evidence indicates that above-ground herbivory could stimulate *A. philoxeroides* responses (e.g., changes in nutrition contents) and thus indirectly affect root nematodes even in 1 week (Wilson et al. 2007). Each treatment (species \times larvae defoliation) was replicated 10 times, and 50 plants were used for each plant species. After the experimental period, the percentage of defoliation for each plant was visually estimated to the nearest 5%. We then removed the beetles and allowed the plants to grow for additional 40 days when they were at peak biomass. All pots were distributed randomly, and their positions were switched every 2 weeks in the greenhouse. At the end of the experiment, we collected plant roots and washed them in a laboratory. The numbers of nematode eggs and knots formed in the roots of each individual plant were measured with the NaOCl method (Bybd et al. 1983). Throughout the trial, all plants received approximately 300 ml of sterilized water every other day.

Data analysis

For the data of experiment 1, we first carried out ANOVA to test the dependence of nematode number at the end of the experiment on the host plant species (native vs. invasive plant, fixed factor) and the number of eggs released (fixed factor). We then ran ANCOVA to test the dependence of beetle larval performance (i.e., biomass, food conservation rate) on host species identity (native vs. invasive, fixed factor) and nematode population size (covariate). In addition, we regressed the number of nematode with the number of eggs released, and beetle performance with nematode population size for the native and invasive plants with linear regression model, respectively. Their slopes were compared with ANCOVA.

For the data of the experiment 2, we carried out ANOVA to test the dependence of defoliation level (percentage of leaf area been removed) on host plant species identity (native vs. invasive plant, fixed factor) and the number of beetles that had been released (fixed factor). We then carried out ANOVAs to test the dependence of number of nematode eggs and root knots on plant species identity (native vs. invasive,

fixed factor) and the number of beetle larvae that had been released (fixed factor).

All the analyses were conducted with SAS 9.4 (the two plant species separately) (SAS Institute, Cary, North Carolina, USA). When significant effects occurred, we examined the differences among the treatment combinations using adjusted means partial difference tests ($P < 0.05$). Data were \log_{10} -transformed when necessary to meet the assumptions of normality and homogeneity of variances.

Results

Effect of root nematode infection on beetle performance

Plant species ($F_{1, 89} = 28.33$, $P < 0.0001$), the number of nematode eggs released ($F_{4, 89} = 47.64$, $P < 0.0001$), and their interaction ($F_{4, 89} = 2.57$, $P = 0.0434$) affected nematode population size at the end of the trial. In general, nematode population size increased linearly with the number of nematode eggs released for both plant species (invasive plant: $R^2 = 0.5701$, $P < 0.0001$; native plant: $R^2 = 0.4863$, $P < 0.0001$), and there was no differences in slopes between the two plant species ($t_{1, 95} = 1.34$, $P = 0.1836$). The nematode population was highest when initially incubated with 10,000 and 20,000 eggs for both the native and invasive plants and was lowest when initially incubated with 2000 eggs for the native plant, and no differences were detected when initially incubated with 2000 and 5000 eggs for the invasive plant (Fig. 1). The nematode population size was higher on the native plant than on the invasive plant when incubated with 5000, 10,000, and 20,000 eggs initially, and no differences were detected between the two species when initially incubated with 2000 eggs (Fig. 1).

The interaction of the plant species and total number of nematodes affected beetle biomass ($F_{1, 75} = 4.24$, $P = 0.0431$) and the food conversion rate ($F_{1, 74} = 7.80$, $P = 0.0066$), suggesting that beetles respond to nematode infection differently via the two host plant species. For the native plant species, we found that nematode population size had a negative linear relationship with beetle food conversion rate ($R^2 = 0.0880$, $P = 0.0406$, Fig. 2a) and larval mass ($R^2 = 0.1026$, $P = 0.0142$, Fig. 2b). In contrast, we

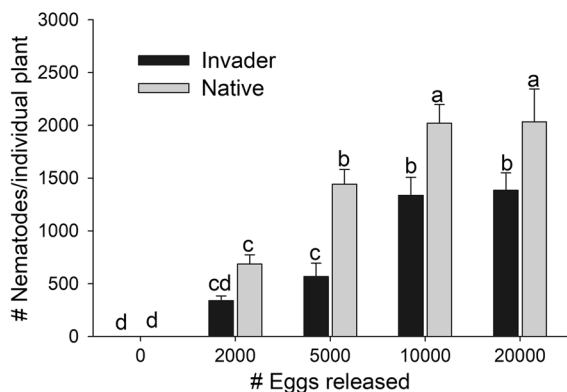


Fig. 1 The number of nematodes per individual of the native and invasive plants at the end of the trial when initially incubated with varying numbers of nematode eggs in the first experiment. Means with the same letters were significantly different in post hoc tests, $P < 0.05$

detected a positive linear relationship between beetle food conversion rates with nematode population size ($R^2 = 0.1155$, $P = 0.0097$, Fig. 2a) for the invasive species. However, we detected no relationship between beetle biomass and nematode population size ($P = 0.6073$, Fig. 2b) for the invasive plant. The slopes for beetle food conversion rate against nematode abundance were significantly different between the native and invasive plants ($t_{1, 93} = 3.41$, $P = 0.001$), but there was no difference in the slopes for beetle mass against nematode population size between the two plant species ($t_{1, 93} = 1.70$, $P = 0.092$).

Effect of beetle defoliation on nematode performance

The plant defoliation level was only affected by the number of larvae that had been released ($F_{1, 76} = 126.81$, $P < 0.0001$), while it was not affected by plant species identity ($F_{4, 76} = 1.48$, $P = 0.2273$) or its interaction with larvae number ($F_{4, 76} = 0.51$, $P = 0.7268$). For both plant species, beetles caused the highest level of defoliation when 3 and 5 larvae had been released, and they caused the lowest level of defoliation when 1 larva had been released (Fig. 3).

There were more nematode eggs ($F_{1, 76} = 49.74$, $P < 0.0001$, Fig. 4a) and root knots ($F_{1, 76} = 63.22$, $P < 0.001$, Fig. 4b) on the native plant than on the invasive plant regardless of the number of beetle

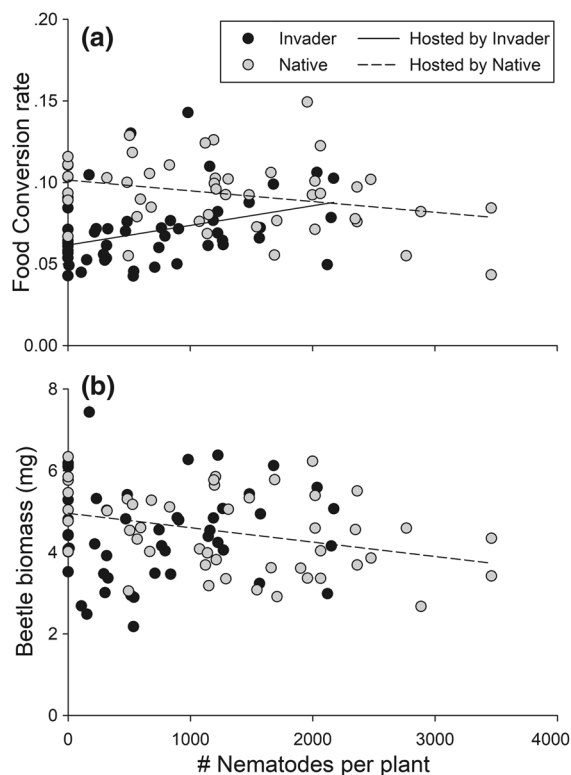


Fig. 2 Relationship between beetle food conversion rate (a) or biomass (b) with the number of nematodes per plant in the laboratory bioassay. Only significant relationships were shown

larvae released. The numbers of eggs ($F_{1, 76} = 49.74$, $P < 0.0001$, Fig. 4a) and root knots ($F_{4, 76} = 4.63$, $P = 0.0021$, Fig. 4b) were also affected by the number of beetle larvae regardless of species identity (interaction between species identity and number of beetle larvae, for both species $P > 0.05$). Beetles negatively affected the number of nematode eggs and root knots for both species when 1, 3, and 5 individuals were released (Fig. 4a, b), but had neutral impact on the number of nematode eggs when 2 individuals were released (Fig. 4a), and there was no difference in the number of nematode eggs among differing beetle densities.

Discussion

With a laboratory bioassay and a greenhouse experiment, we showed that the beetle *A. hygrophila* can interact differently with the resident generalist root nematode *M. incognita* on the native and invasive host

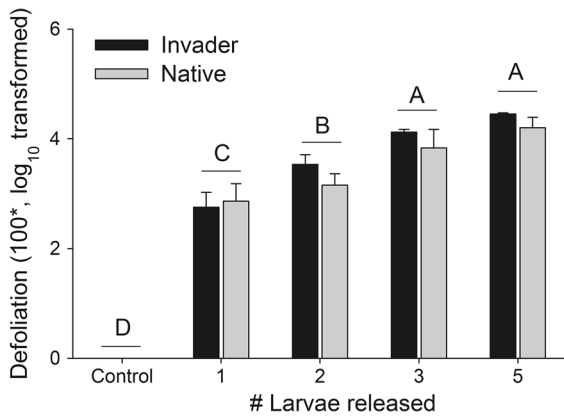


Fig. 3 The defoliation level (percentage of leaf area that has been removed) that the beetle caused for the native and invasive plants when differing numbers of beetle larvae were released in the second experiment. Means with different letters were significantly different in post hoc tests, $P < 0.05$

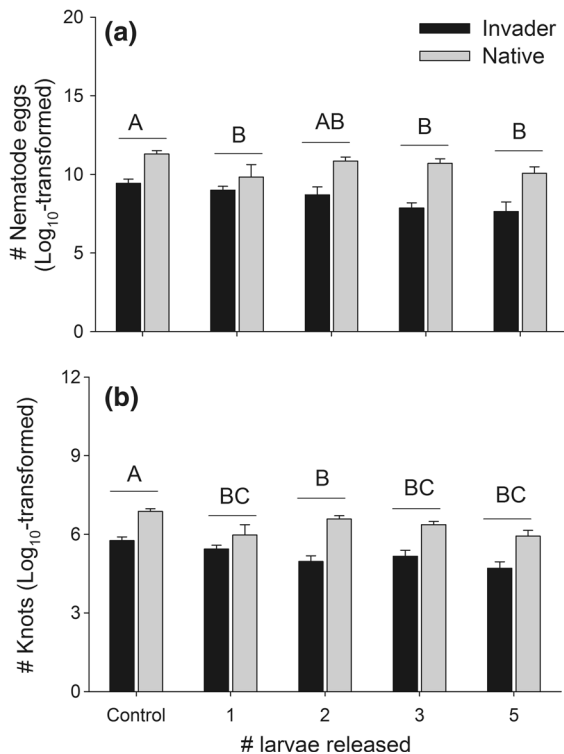


Fig. 4 The number of nematode eggs (a) and root knots (b) the nematode caused on the native and invasive species when plants were exposed to differing densities of beetle larvae in the second experiment. Means with different letters were significantly different in post hoc tests, $P < 0.05$

plants. *Meloidogyne incognita* infection decreased *A. hygrophila* performance (e.g., food conversion rate)

on the native plant but had no impact on its performance on the invasive plant, as we expected. Inconsistent with our prediction, beetle defoliation suppressed nematode population growth on both plant species. In a previous study, we detected negative interactions between the root nematode *M. incognita* and the native beetle *C. piperata* on the invasive plant *A. philoxeroides*, but no interaction between the above- and below-ground herbivores via the native host *A. sessilis* (Wei et al. 2016). These results suggest that non-native plant invasions and their introduced herbivores could indirectly affect recipient communities by altering existing above- and below-ground interactions. Given the importance of above- and below-ground linkages in structuring communities and maintaining ecosystem functions, invasive species and introduced herbivores may have cascading effects on a community or ecosystem that should be carefully considered in future studies and biological control practices.

Root nematode infections decreased beetle performance (e.g., food conversion rate) via the native plant but had no impact on beetle biomass on the invasive plant (though they increased its food conservation rate). An increasing number of studies have found that infection of soil-borne herbivores, including root nematodes and soil-borne pathogens, can alter plant nutrition contents or trigger plant defensive responses, and as a result, they indirectly affect above-ground herbivores (Wardle et al. 2004; Mundim et al. 2017). Previously, we found that the *M. incognita* infection slightly decreased *A. philoxeroides* nitrogen content but had no impacts on *A. sessilis* (Wei et al. 2016). Thus, the observed differing impacts of the root nematode on beetles may be attributed to variations in the defenses between the two plant species. The native plant roots were mainly composed of fine roots, which were susceptible to soil-borne herbivores, while the invasive plant roots were mainly composed of coarse roots with thick cuticles (Lu et al. 2015b). As a result, the invasive plant was infected less by the root nematode than the native plant in this study, which was consistent with our previous findings (Lu et al. 2015b). With such a low infection rate, it may be hard to detect the impact of the root nematode on the beetle. In addition, the *M. incognita* infection may have triggered defensive responses of the native and invasive plants. For instance, the *M. incognita* infection increased the contents of defensive terpenoids in

leaves of the tropical shrub *Solanum lycocarpum* (Mundim et al. 2017). Without co-evolution history, the defensive chemicals of the native plant may be novel to the introduced beetle and thus deter its performance, while with co-evolutionary history, the beetle may have adapted to the defenses of the invasive plant. This may explain the differing impacts of the root nematode on the beetle, but it needs further clarification.

We found that above-ground defoliation suppressed root nematode population growth (i.e., egg number) on both the native and invasive plants in our study. Water-soluble carbohydrates are crucial for individual growth and population growth of root nematodes (Hofmann et al. 2009). In a previous study, we found that defoliation increased root water-soluble carbohydrates of the invasive plant in the presence of root nematodes (Mao et al. 2011), which suggests that above-ground beetle defoliation may increase nematode population growth. In contrast, beetle defoliation decreased root nematode performance, and we detected no difference between the two species in this study. The negative impacts of above-ground herbivory on below-ground root infection have also been found in other systems (Soler et al. 2007; Kaplan et al. 2009). Mundim et al. (2017) found that above-ground herbivory could increase the below-ground defenses of plants, e.g., increase the concentration of defensive chemicals. This may underlie the observed negative impacts of above-ground herbivory on the nematode in our study. As the nematode in this study occurs across the world (Castagnone-Sereno et al. 2013), it may have experienced and adapted to defense responses of both the native and invasive plants, thus showing similar responses to beetle defoliation via the native and invasive plants. Future work is needed to test such an adaptation.

Based on the enemy release hypothesis (Keane and Crawley 2002), a large number of above- and below-ground herbivores were introduced to re-establish plant–insect interactions in invaded ranges to decrease the negative impacts of the invasive species and to restore native ecosystems (classical biological control) (McFadyen 1998). However, some introduced agents can directly or indirectly interact with resident species and thus can pose a new threat to the target ecosystem (Louda et al. 1997; Henneman and Memmott 2001). To date, most studies are limited to above-ground species (see reference in Louda et al. 2003). In

this study, we found that an above-ground biocontrol herbivore can also indirectly affect below-ground herbivores, as facilitated by shared native or invasive hosts. Especially, the biocontrol beetle decreased root nematode infection for both the native and invasive plants. These effects may further change soil communities and indirectly impose selection on the interacting resident herbivore or plant species.

In summary, our results suggest that invasive plants and their introduced herbivores have the potential to alter above- and below-ground interactions in their introduced ranges. In addition, the same types of above- and below-ground herbivores could interact differently on native and invasive hosts. The altered above- and below-ground interactions could in turn bring about changes in an herbivore population and in pest accumulation and change competition between non-native and native plant species.

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