



# Antagonistic interactions between above- and belowground biota reduce their negative effects on a tree species

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## Abstract

**Aims** Plants in nature are confronted by a variety of beneficial and antagonistic above- and belowground organisms, including leaf herbivores, soil fungi, and soil nematodes. While their individual effects are usually well studied, their joint effects on plant performance are less well known. Synergistic or antagonistic interactions between these organisms would mean that their joint effects on plant performance are more or less detrimental or beneficial than expected from their individual effects.

**Methods** We conducted a factorial greenhouse experiment in which we manipulated the presence of aboveground herbivores (weevils), soil nematodes, and soil

fungi using addition (weevil) or removal (fungicide, nematicide) treatments to test how these groups of organisms alone and in combination affect *Triadica sebifera* biomass production, when grown individually or under intraspecific competition.

**Results** Soil fungi and aboveground weevils alone each strongly decreased plant root and total biomass. Interestingly, soil nematodes alone slightly reduced plant biomass but they mitigated the negative impacts of aboveground weevils, indicating antagonism in their effects on plant biomass. However, in the presence of soil fungi this antagonism was less pronounced, illustrating the complexity of interactive effects of aboveground and belowground biota on plant biomass.

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Aboveground herbivory increased nematode infections, but only in the absence of soil fungi. Intraspecific competition strongly enhanced nematode infection loads and slightly decreased *T. sebifera* root biomass but did not modulate the direction or the strength of interactions among these aboveground and belowground biota.

**Conclusions** Our findings indicate that joint effects of antagonistic above- and belowground biota on plant performance can be less detrimental than expected from their individual effects. These results highlight the importance of considering the roles of plant aboveground and belowground interactions from a systems perspective.

**Keywords** Aboveground-belowground interactions · Antagonistic effects · Fungicide · *Heterapoderopsis bicallosicollis* · *Meloidogyne incognita* · Soil biota · *Triadica sebifera*

## Introduction

Plants interact with multiple above- and belowground organisms, forming a complex biotic network. Organisms involved in such plant-associated interaction webs include both plant antagonists such as herbivores and pathogens and potential mutualists such as arbuscular mycorrhizal (AM) fungi. For instance, plants face an array of aboveground and belowground enemies, and an increasing number of studies show that these enemies influence the performance of plants and the dynamics of plant communities in natural ecosystems (Bardgett and Wardle 2003; Bardgett and Wardle 2010). Many studies investigating the effects of biotic interactions on plants have focused separately on interactions of plants with a single group of organisms, for instance either aboveground insect herbivores or soil fungi (e.g., Bardgett and Wardle 2003; Bennett and Bever 2007). However, under natural conditions, plants are often simultaneously attacked by a wide diversity of aboveground and belowground organisms (Erwin et al. 2014; Huang et al. 2014; Masters et al. 1993; Pangesti et al. 2013; Scherber et al. 2010; Stam et al. 2014). Yet, much is still unknown about the consequences of such simultaneous attacks on plant growth and fitness, which could have a significant impact on plant community dynamics, succession, or biological invasions (but see Huang et al. 2014; Meier and Hunter 2018; Scherber et al. 2010).

Many types of plant-mediated interactions between organisms sharing the same host plant have been documented and such interactions can affect the net effect of these organisms on plant performance. For instance, herbivores can affect soil community composition and function via changes in the quality and quantity of resources that enter the soil (Barto and Rillig 2010; Bezemer et al. 2013; Broeckling et al. 2008; Hamilton and Frank 2001; Kong et al. 2016; Schittko and Wurst 2014; Yang et al. 2011), which in turn can change the effects of the soil biota on plant performance (Bardgett and Wardle 2003; Bezemer et al. 2013). These herbivore-induced changes in the effects of soil microbes can include both pathogenic (Biere and Goverse 2016) and beneficial microbes such as AM fungi (Barto and Rillig 2010). Conversely, interactions with the soil biotic community can alter interactions between plants and herbivores. For instance, interactions with AM fungi can increase the growth, nutritional quality and water status of leaf tissues with subsequent effects on the performance of herbivores feeding on these plants (Jung et al. 2012; Real-Santillan et al. 2019). In addition, many beneficial soil microbes such as AM fungi can increase plant resistance and tolerance to herbivory (Bennett and Bever 2007; Heinen et al. 2018a; Koricheva et al. 2009). Notably, there is growing evidence that symbiotic microbes associated with plants can prime plants for enhanced defenses signaled through the phytohormone jasmonic acid (JA) (e.g., Jung et al. 2012; Pieterse et al. 2014; Pozo and Azcon-Aguilar 2007). Similarly, pathogenic soil fungi can modulate plant resistance to herbivores (Biere and Goverse 2016). Moreover, variation in plant-soil association history may impact interactions of plants with aboveground organisms, such as herbivores. Exploration of the effects of soil legacies on aboveground herbivores has only recently been initiated (Heinen et al. 2018a, b; Kos et al. 2015; Kostenko et al. 2013).

Plants not only mediate interactions between herbivores and pathogenic or beneficial soil microbes, but also between aboveground herbivorous insects and belowground soil nematodes (Biere and Goverse 2016; Machado et al. 2018; Wondafrash et al. 2013). Herbivorous insects and plant-parasitic nematodes are the most diverse and abundant groups of multicellular animals feeding on plants on either side of the soil-air interface. Root-feeding nematodes can positively or negatively affect aboveground-feeding herbivorous insects (and vice versa) and the outcomes of interactions between

these spatially separated groups of organisms appear to be influenced by the feeding strategy of the nematodes and the insects, as well as by host plant susceptibility to both types of organisms (e.g. Hoysted et al. 2017; Kos et al. 2015; Soler et al. 2012; Wondafrash et al. 2013).

The outcome of the interactions between plant-associated organisms on their shared host plant and their net effect on plant performance further depend on abiotic and biotic environmental factors such as the presence of inter- or intraspecific competitors. Plant competition can strongly alter the interactions of plants with herbivores, pathogens and beneficial microbes. First of all, competition can strongly alter plant phenotypes with concomitant effects on their biotic interactions. For instance, intra- and interspecific competition leads to strong transcriptional changes in genes involved in both symbiotic and antagonistic interactions (Bowsher et al. 2017; Geisler et al. 2012) and intraspecific competition has been shown to increase levels of specific defense metabolites (Skoneczny et al. 2019). Second, plant densities can strongly affect the rates of colonization by spatially foraging herbivores as well as by soil- and airborne microbes (Folgarait et al. 1995), for example by affecting the leaf microclimate which is important for spore germination and infection (Copes and Scherm 2005) or root exudation patterns important in the attraction of belowground organisms (Weidenhamer et al. 2019). However, studies on how density and intraspecific plant competition affect plant-mediated interactions between different organisms on a plant and their net impact are scarce.

Simultaneous interactions of plants with aboveground herbivores, soil fungi, and plant-parasitic nematodes are important determinants of plant performance (Biere and Govers 2016; Wondafrash et al. 2013). Effects of organisms on plant performance may simply add up, or they can be non-additive, strengthening (synergism) or mitigating (antagonism) each other's effects on plant performance. From the plant's perspective, the consequences of such non-additive effects may be either beneficial or detrimental. For instance, synergism between pathogens or pests will cause extra damage, whereas synergism between plant-beneficial organisms will enhance the benefits from their simultaneous presence. A meta-analysis of interactive effects of aboveground herbivores and pathogens on plant performance (Hauser et al. 2013) found that their effects are predominantly additive. However, interactive effects of above- and belowground biota such as soil fungi and

plant-parasitic nematodes on plant performance have been less well documented. Previous studies suggest that aboveground herbivores and soil biota could have additive effects on native and range-expanding exotic plants (Engelkes et al. 2008; Mörrien et al. 2011). It is therefore important to examine the combined effects of above- and belowground biota on plant performance, which will help to better understand how plant-associated organisms influence plant diversity, community structure and potential biological invasions because plants might encounter diverse above- and belowground beneficials and antagonists under natural conditions.

In this study, we used tallow tree (*Triadica sebifera*) and some of its above- and belowground biota as a model system to investigate the individual and combined effects of aboveground insect herbivores (weevils), soil fungi, and soil nematodes on plant performance with or without intraspecific plant competition. Under natural conditions these plants are often simultaneously attacked by an array of enemies in both the above- and belowground domains (Huang et al. 2014; Yang et al. 2015b, c). We used a factorial design of one addition (weevils) and two removal treatments (nematicide and fungicide use) to manipulate the densities of each of these three groups of organisms. We addressed the following questions: 1) Do aboveground herbivores, soil fungi, and soil nematodes have additive effects on plant height and biomass? 2) Does intraspecific competition modulate the individual and combined effects of aboveground herbivores, soil fungi, and soil nematodes on plant height and biomass? In addition, we assessed how the treatments affected the densities of two of the most abundant subgroups of nematodes and soil fungi that we could detect, i.e. root knot nematodes (RKN) and arbuscular mycorrhizal (AM) fungi to test the effectiveness of the removal treatments as well as the additive and non-additive impact of the treatments on their densities.

## Methods

### Study system

Native to Asia, *Triadica sebifera* (Euphorbiaceae) is a fast growing, deciduous tree naturally distributed in central and southern China (Zhang and Lin 1994). In November 2014, we hand-collected *T. sebifera* seeds from 10 randomly selected trees in Dawu, Hubei, China

(31°32'N, 114°24' E). The surrounding vegetation includes subtropical evergreen broad-leaved forest, shrubs and grasses. In April 2015, we removed the seeds' waxy coats by soaking them in water with laundry detergent (10 g / L), surface sterilized them with 10% bleach [0.6% sodium hypochlorite], and germinated them in sterilized, field-collected soil. We used first-year *T. sebifera* seedlings as previous studies suggested that young plants may be especially susceptible to the effects of herbivory (Reader 1992).

In April 2015, we collected soils from underneath 8 different *T. sebifera* trees at Dawu. We removed surface litter before collecting topsoil to a depth of 10 to 15 cm and removed sticks, rocks and root fragments by passing soil through a 1 cm mesh screen. We kept the soils associated with each tree separate throughout the experiment ("soil source" hereafter).

*Heterapoderopsis bicallosicollis* (Coleoptera: Attelabidae) is a specialist leaf-rolling weevil, with four to five generations per year in the Hubei Province in China (Wang et al. 2009). Adults feed on leaves by nibbling holes but avoid veins and lay eggs inside rolled leaves (nidi). One nidus usually contains 1 or 2 eggs. Larvae and pupae live inside the nidus until they emerge as adults (Wang et al. 2009, 2011). In July 2015, we collected nidi of *H. bicallosicollis* at Luotian, Hubei, China (30°47' N, 115°24' E), reared them to adulthood in cages at Wuhan Botanical Garden, Hubei, China (31°32' N, 114°24' E), and used their offspring for this experiment.

In the field, tallow seedlings are often damaged by the root-knot nematode *Meloidogyne incognita* (Ding et al. unpublished data) and other soil nematodes (Liu et al. 2019). Common garden experiments have shown that the rate of colonization of tallow seedlings collected from Chinese populations by AM fungi is around 8–20% (Yang et al. 2015a). Previous studies also reported that either soil fungal pathogens or the weevil *H. bicallosicollis* could negatively affect *T. sebifera* performance in its native range (Yang et al. 2013; Wang et al. 2011).

## Experimental design

To test how aboveground herbivory, soil fungi, and soil nematodes individually and jointly affect plant root and shoot biomass accumulation, we performed a common garden pot experiment at Wuhan Botanical Garden. The experiment consisted of a factorial combination of four

treatments: aboveground herbivores (weevils), soil fungicide, soil nematicide, and intraspecific competition, each with two levels (explained below), replicated in each of the 8 soil sources (128 pots in total). In May 2015, we filled each pot (diameter = 15 cm, height = 9 cm) with soil from a single soil source (16 pots per soil source). We treated 32 pots with soil fungicide (iprodione, rate 0.32 g/m<sup>2</sup>), 32 pots with a nematicide drench (aldicarb [Temik], rate 0.17 g/m<sup>2</sup>), 32 pots with both fungicide and nematicide, and 32 pots with only water. Iprodione is a general, systemic, dicarboximide contact fungicide that inhibits germination of fungal spores and blocks the growth of fungal mycelium and is used to control a wide variety of fungal diseases (Whitehead 1998). Aldicarb is a carbamate that is primarily used to control a wide variety of nematodes (Ebene et al. 2019). It is a cholinesterase inhibitor that prevents breakdown of acetylcholine in the synapsis and has neurotoxic activity. After initiating the treatments, we transplanted either one (no competition) or two (competition) first-year seedlings into each pot, enclosed each pot in a mesh cage, and arranged them randomly in a greenhouse. In July 2015, we added 5 adult *H. bicallosicollis* into half of the cages and left the others without weevils. We left weevils on the plants until they had damaged ~30% of leaf area (12–15 days), then measured plant height at 15 days and let plants regrow for an additional 60 days to allow sufficient time for differences in tolerance (regrowth) and effects of soil biota on regrowth ability to be expressed. Plants were watered every day and did not receive any additional fertilizer. After that, plants were cut at ground level, separated into leaves and stems, dried at 50 °C for 6 days, and weighed.

Since our main interest in this study was to quantify the interactive effects of aboveground herbivores, root nematodes, soil fungi and competition on plant biomass, the most important variables that we measured were shoot and root biomass of the plants. However, in addition we measured densities of two groups of organisms, root-knot nematodes (RKN) and arbuscular mycorrhizal (AM) fungi. These measurements were performed not only to check whether fungicide and nematicide treatments were effective, at least for these two subgroups, but also to quantify how RKN and AM fungi were affected by aboveground herbivores and by soil fungi or nematodes, respectively.

We carefully washed the roots to remove all soil and collected fine root fragments. These fragments were

cleared, stained, mounted, and assayed for colonization by arbuscular mycorrhizal fungi (100 gridline intersect counts of intra- plus extra-radical hyphae) following published protocols (McGonigle et al. 1990; Nijjer et al. 2008). Even though based on the morphology of the irregularly septate hyphae we were fairly confident that these hyphae indeed belonged to AM fungi, no vesicles or arbuscules were detected in plants used in the experiment, hence we lack any indication of a functionally significant transfer of C or P through these hyphae that might have had a net effect on plant biomass. We also counted the number of nematode root-knots of the whole root system. We dried and weighed roots and divided the number of root knots by root biomass to estimate infection loads (McBride et al. 1999). For all variables, we either summed (plant biomass, nematodes) or averaged (AM fungi) the values for the two plants in competition pots. There were no significant differences in the abundances of root knot nematodes or AM fungi among soils used in the experiment (no significant “soil source” effect in the data analyses, see Table 1, 2 and 3). Furthermore, for these focal groups we can be confident that our removal treatment truly resulted in complete removal (=zero numbers) (see Fig. 4 for nematodes and Fig. 5 for AM fungi).

#### Data analysis

We used Generalized Linear Models (proc GLM, SAS 9.4, 2013) to examine the dependence of plant total, shoot and root biomass and height at day 15 on aboveground herbivory, soil fungi, soil nematodes, competition, their interactions and soil source as fixed effects. For pots that had not been treated with nematicide, we used a GLM to test the dependence of root-knot nematode loads on aboveground herbivory, soil fungi, competition, their interactions and soil source as fixed effects. Likewise, for pots that had not been treated with fungicide, we used a GLM to test the dependence of AMF colonization (square root transformed) on aboveground herbivory, soil nematodes, competition, their interactions and soil source as fixed effects. Assumptions of normality and homoscedasticity were tested with Shapiro-Wilk and Levene tests, respectively, and post-hoc comparisons were performed with Tukey-HSD. We inferred additivity of the effects of multiple treatments from the absence of significant interaction terms among treatments when testing their effects on plant performance. In case of significant interactions, we

inspected the direction of the interaction to infer whether it was indicative of an interaction that was beneficial or detrimental for plant performance.

Note that, for illustrative purposes, we have represented the treatments involving suppression of soil biota (i.e., nematicide and fungicide application) in such a way that they refer to the presence (natural abundance) of soil biota, which makes it easier to compare addition and removal treatments. Thus, H = herbivores (weevil addition treatment); F = soil fungi (no fungicide application treatment); N = nematodes (no nematicide application treatment); C = competition (two plants in a pot). We acknowledge that “presence” in the case of F and N refers to their natural abundance, rather than to a fixed addition; however, natural abundances of our focal species did not significantly differ among the eight soils used in the experiment (see Tables 2 and 3). To visualize whether observed interactive effects of H, F and N on plant performance lead to a higher or lower plant performance than expected based on their additive contributions, we also plotted estimated values for plant biomass that would have been expected if their effects had been additive in the figures. For the two-way interactions, these estimated biomasses were simply calculated as  $F + N - C$ ,  $F + H - C$  or  $N + H - C$ , where F, N, and H are the plant biomass in the presence of only Fungi, Nematodes, or Herbivores, respectively, and C is the plant biomasses of the control treatment where neither of these organisms was present. Likewise, for the three-way interaction the estimated biomass was calculated as  $F + N + H - 2 * C$ . Calculations were done for plants grown on each of the eight soil sources separately to obtain standard errors for the expected biomasses.

#### Results

Overall, soil fungi had a strongly negative impact on total plant biomass (Fig. 1, S1a), reducing both root (Fig. 2, S1b) and shoot (Fig. 3, S1c) biomass (Table 1). Effects of aboveground herbivores (weevils, measured two months after a two-week feeding period) on plant biomass strongly depended on the presence of soil nematodes (“Nematode x herbivore” interactions, Table 1). Specifically, total plant biomass and shoot biomass were strongly reduced (by 32% and 24%, respectively) by aboveground herbivores when nematodes were absent, but were not significantly reduced by aboveground herbivores in the presence of

**Table 1** Results of GLMs analyzing the effects of aboveground herbivory, soil fungi, soil nematodes, competition, their interactions and soil source on *Triadica sebifera* total, root and shoot biomass

Effect	df	Total biomass		Root biomass		Shoot biomass	
		F	P	F	P	F	P
Nematode	1105	0.2	0.6242	0.1	0.7397	0.3	0.6034
Fungi	1105	<b>50.6</b>	<b>&lt;0.0001</b>	<b>17.0</b>	<b>&lt;0.0001</b>	<b>63.9</b>	<b>&lt;0.0001</b>
Herbivore	1105	<b>11.6</b>	<b>0.0009</b>	<b>28.9</b>	<b>&lt;0.0001</b>	2.8	0.1002
Competition	1105	2.1	0.1472	<b>9.3</b>	<b>0.0029</b>	0.1	0.8126
Nematode × fungi	1105	0.1	0.7047	<0.1	0.9169	0.3	0.6177
Nematode × herbivore	1105	<b>9.5</b>	<b>0.0026</b>	<b>9.4</b>	<b>0.0028</b>	<b>7.1</b>	<b>0.0092</b>
Nematode × competition	1105	0.1	0.7237	<0.1	0.9202	0.4	0.5543
Fungi × herbivore	1105	0.9	0.3437	2.1	0.1542	0.3	0.6148
Fungi × competition	1105	0.9	0.3530	0.5	0.4655	0.9	0.3567
Herbivore × competition	1105	0.5	0.4701	0.2	0.6951	1.8	0.1854
Nematode × fungi × herbivore	1105	<b>4.1</b>	<b>0.0449</b>	<b>4.2</b>	<b>0.0422</b>	3.0	0.0886
Nematode × fungi × competition	1105	<0.1	0.8896	0.3	0.6093	0.3	0.5940
Nematode × herbivore × competition	1105	0.1	0.7442	<0.1	0.9101	0.2	0.6781
Fungi × herbivore × competition	1105	0.1	0.8204	0.1	0.8230	<0.1	0.8443
Nematode × fungi × herbivore × competition	1105	<0.1	0.8752	0.3	0.5886	<0.1	0.9118
Soil source	7105	1.3	0.2754	0.8	0.5842	1.4	0.2253

Significant results are in bold

nematodes (Figs. 1 and 3, compare “H” and “NH” with “CTRL”), even though nematodes by themselves did not affect shoot biomass (Fig. 3) and even slightly reduced total plant biomass by 10% (Fig. 1). Similarly, for root biomass we observed that the negative impact of the aboveground herbivores was stronger in the absence of nematodes (42%) than in their presence (23%) despite the fact that nematodes by themselves reduced root

biomass by 17% (Fig. 2). This indicates that the negative effects of aboveground herbivores and soil nematodes on plant biomass were far less than additive (72, 62 and 86% less than expected for total, shoot and root biomass, respectively), i.e. we observed an antagonism between aboveground herbivores and nematodes in their negative effects on plant biomass. For total and root biomass, the strength of this antagonism between herbivores and nematodes further depended on the pres-

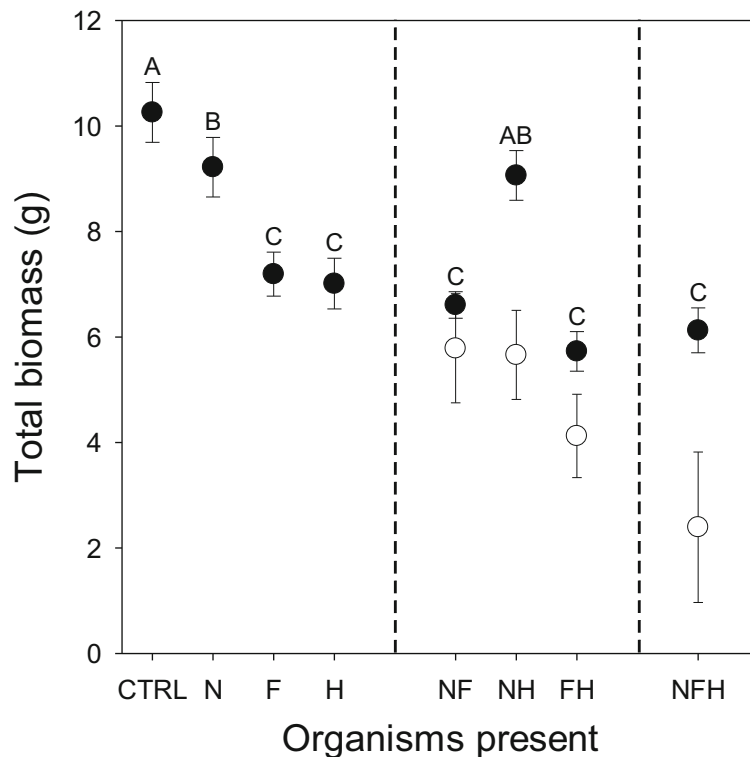
**Table 2** Results of a GLM analyzing the effects of aboveground herbivory, soil fungicide, competition, their interactions and soil source on *Triadica sebifera* root-knot nematode loads in pots in which nematicide was not applied

Effect	df	F	P
Fungi	1,49	2.5	0.1191
Herbivore	1,49	4.0	0.0513
Competition	<b>1,49</b>	<b>21.6</b>	<b>&lt;0.0001</b>
Fungi × herbivore	<b>1,49</b>	<b>5.5</b>	<b>0.0232</b>
Fungi × competition	1,49	0.7	0.4027
Herbivore × competition	1,49	0.2	0.6234
Fungi × herbivore × competition	1,49	0.9	0.3387
Soil source	7,49	0.6	0.7907

Significant results are in bold

**Table 3** Results of a GLM analyzing the effects of aboveground herbivory, soil nematodes, competition, their interactions and soil source on *Triadica sebifera* root arbuscular mycorrhizal colonization in pots in which no soil fungicide was applied

Effect	df	F	P
Nematode	1,49	0.3	0.6085
Herbivore	1,49	2.4	0.1284
Competition	1,49	1.9	0.1719
Nematode × herbivore	1,49	0.1	0.7843
Nematode × competition	1,49	0.6	0.4300
Herbivore × competition	1,49	0.2	0.6508
Nematode × herbivore × competition	1,49	0.1	0.7463
Soil source	7,49	0.6	0.7451



**Fig. 1** The dependence of *Triadica sebifera* total biomass in a pot on the presence of aboveground herbivores, soil fungi, and/or soil nematodes. Solid circles represent experimental data and open circles represent the predicted effects of multiple biotic interactions if their effects had been additive. “CTRL”: control (all biota absent, i.e. fungicide and nematicide application, no weevil addition), “N”: only soil nematodes present (fungicide application, no weevil addition); “F”: only soil fungi present (nematicide application, no weevil addition); “H”: only aboveground herbivores present (fungicide and nematicide application, weevil addition); “NF”: soil nematodes and fungi present (no fungicide or nematicide

application, no weevil addition); “NH”: soil nematodes and aboveground herbivores present (fungicide application, weevil addition); “FH”: soil fungi and aboveground herbivores present (nematicide application, weevil addition); “NFH”: soil nematodes, soil fungi, and aboveground herbivores present (no fungicide or nematicide application, weevil addition). Means  $\pm$  1 SE. Experimental means with the same letter were not significantly different in post-hoc tests. Note that the data for the competition and no-competition treatment have been averaged, since competition did not show a significant main or interaction effect in the analyses. The full dataset is presented in Fig. S1a

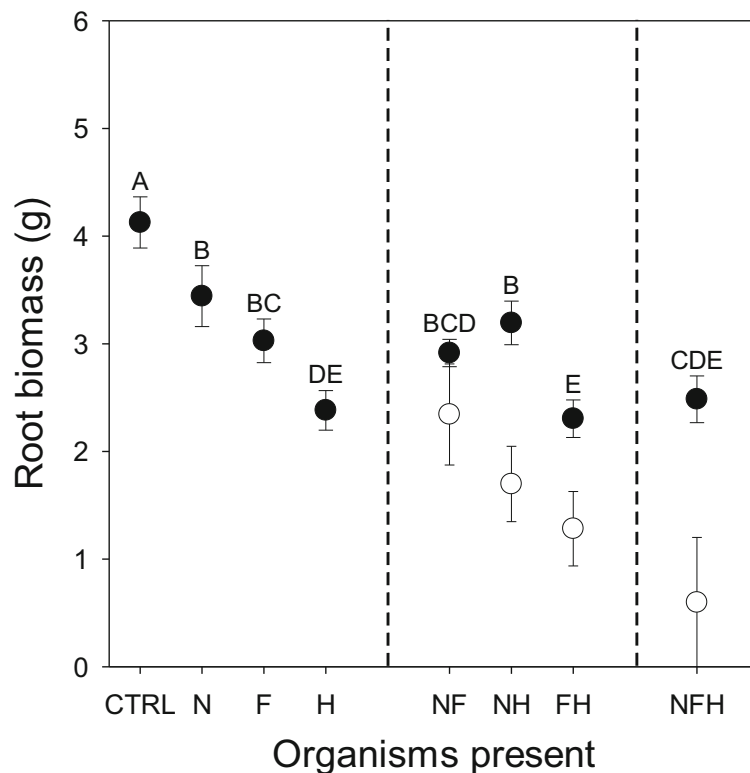
ence of soil fungi (significant “Nematode  $\times$  fungi  $\times$  herbivore” interaction, Table 1). Specifically, the antagonism between herbivores and nematodes in their effects on total and root biomass was weaker in the presence of soil fungi (48 and 35% less than expected if their effects had been additive, respectively) than in their absence (72 and 62%, respectively), indicating that herbivores and nematodes more fully exerted their negative effects on plant root and total biomass in the absence of soil fungi. By contrast, shoot biomass was consistently reduced by soil fungi, independent of the presence of soil nematodes and aboveground herbivores, so for this trait the strength of the antagonism between aboveground herbivores and nematodes was not affected by soil fungi (no significant “Nematode  $\times$  fungi  $\times$  herbivore” interaction, Table 1). A similar pattern as

observed for total and root biomass was observed for plant height at the time weevils were removed (Fig. S2). Also for this trait, the reduction by a combination of aboveground herbivores and nematodes (18%) was less than expected if their effects had been additive (30%) (“Nematode  $\times$  herbivore” interaction, Table S1) and the strength of this interactions depended on the presence of soil fungi (significant “Nematode  $\times$  fungi  $\times$  herbivore” interaction, Table S1, Fig. S2).

Plant competition (one vs. two plants per pot) slightly reduced root biomass per pot (from  $3.21 \pm 0.13$  to  $2.76 \pm 0.12$  g, Table 1, Fig. S1b), but did not show any interaction with the above- or belowground biotic factors in its effect on plant root, shoot or total biomass (Table 1). Plant competition did affect soil nematode densities (Table 2). In particular, the number of root

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**Fig. 2** The dependence of *Triadica sebifera* root biomass in a pot on the presence of aboveground herbivores, soil fungi, and/or soil nematodes. Solid circles represent experimental data and open circles represent the predicted effects of multiple biotic interactions if their effects had been additive. “CTRL”: control (all biota absent); “N”: only soil nematodes present; “F”: only soil fungi present; “H”: only aboveground herbivores present; “NF”: soil nematodes and fungi present; “NH”: soil nematodes and aboveground herbivores present; “FH”: soil fungi and aboveground

herbivores present; “NFH”: soil nematodes, soil fungi, and aboveground herbivores present (for a more complete description see legends to Fig. 1). Means  $\pm$ 1 SE. Experimental means with the same letter were not significantly different in post-hoc tests. Note that the data for the competition and no-competition treatment have been averaged, since competition did not show any interaction effects with other factors in the analyses. The full dataset is presented in Fig. S1b

knots per pot was four times as high in the competition as in the no-competition treatment (Fig. 4), whereas the total root biomass per pot in the competition treatment was only 14% lower. Nematode root-knot numbers were also enhanced by aboveground herbivores, but only in the absence of soil fungi (Fig. 4, Table 2: Fungi  $\times$  herbivore interaction). AMF colonization was not affected by aboveground herbivores, soil nematodes, competition or any of their interactions (Table 3, Fig. 5).

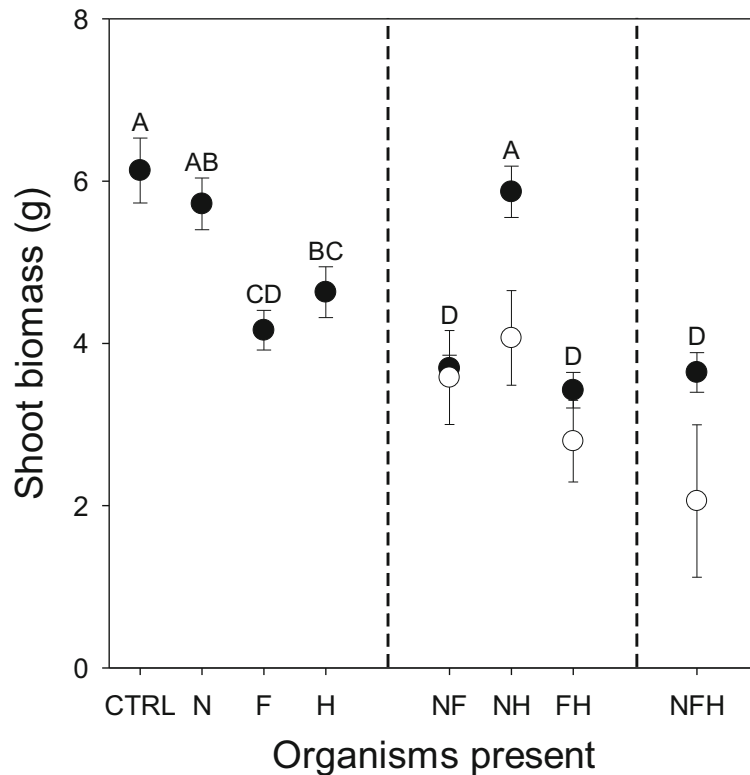
## Discussion

In this study, we explicitly tested for the interactive effects of an aboveground herbivore (weevil), soil fungi, and soil nematodes on the performance of the tallow tree. We found strong non-additive effects of these

organisms on plant biomass and these effects appeared to be predominantly mediated by antagonistic interactions between the plant-associated organisms, leading to less negative effects on plant performance than would be expected from their individual contributions. In particular, strong antagonism was observed between the effects of the aboveground herbivore and soil nematodes on plant performance, partly mitigating each other’s negative effects on plant biomass.

Antagonistic effects of soil nematodes on aboveground herbivores have been observed previously. Tomato plants infested with the root-knot nematode *M. incognita* showed reduced performance of the leaf mining lepidopteran herbivore *Tuta absoluta* (Arce et al. 2017). Similarly, performance of the lepidopteran leaf chewing herbivore *Spodoptera litura* was reduced on soybean infested with the cyst nematode *Heterodera*



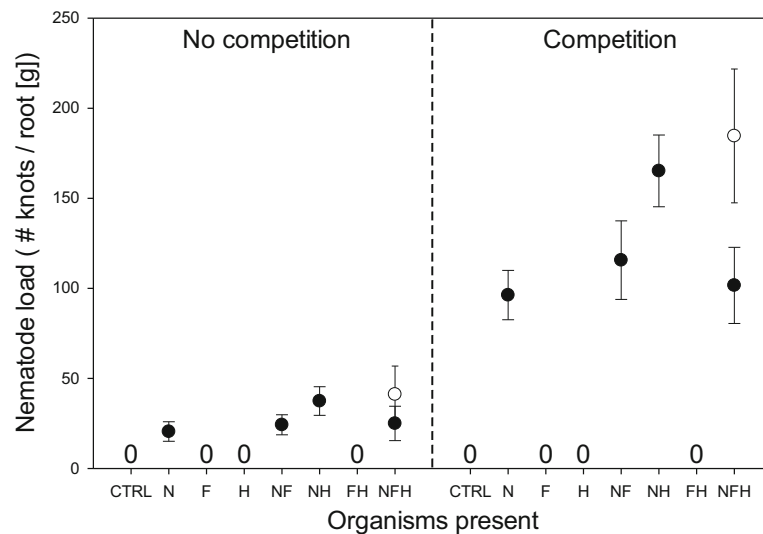


**Fig. 3** The dependence of *Triadica sebifera* shoot biomass in a pot on the presence of aboveground herbivores, soil fungi, and/or soil nematodes. Solid circles represent experimental data and open circles represent the predicted effects of multiple biotic interactions if their effects had been additive. “CTRL”: control (all biota absent); “N”: only soil nematodes present; “F”: only soil fungi present; “H”: only aboveground herbivores present; “NF”: soil nematodes and fungi present; “NH”: soil nematodes and aboveground herbivores present; “FH”: soil fungi and aboveground

herbivores present; “NFH”: soil nematodes, soil fungi, and aboveground herbivores present (for a more complete description see legends to Fig. 1). Means  $\pm$ 1 SE. Experimental means with the same letter were not significantly different in post-hoc tests. Note that the data for the competition and no-competition treatment have been averaged, since competition did not show a significant main or interaction effect in the analyses. The full dataset is presented in Fig. S1c

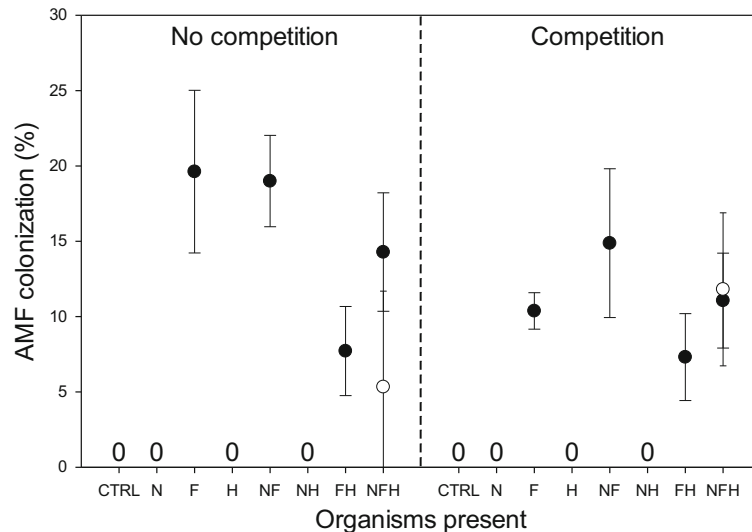
*glycines* (Li et al. 2017). However, there are also many counter-examples. For instance, in tobacco, *M. incognita* was found to reduce the synthesis or transport of root-produced nicotine, resulting in better performance of aboveground feeding larvae of the lepidopteran herbivore *Trichoplusia ni* (Kaplan et al. 2008). In fact, negative effects of plant parasitic nematodes on aboveground herbivores have been more commonly observed for sap sucking insects such as aphids than for leaf chewing insects (see reviews by Biere and Goverse 2016; Soler et al. 2012; Wondafraash et al. 2013) and these effects are usually attributed to lower levels of leaf or stem primary metabolites such as amino acids and nitrogen or enhanced leaf defense (Guo and Ge 2017). In our experiment, we did not check whether the nematodes actually reduced the performance of the weevils themselves, we rather observed that they

reduced the negative effects of weevils on plant biomass after a period of recovery from herbivory. In principle this could have been mediated either by attenuating effects of nematodes on the negative impact of herbivory itself, or by positive effects of nematodes on the ability of plants to regrow after herbivory. The data on plant height immediately following herbivory (Table S1, Fig. S2) show that the attenuating effects of nematodes on plant height could already be observed shortly after herbivory, hence that the effects already occurred during the period that both nematodes and weevils were simultaneously feeding on the plant. Since the percent leaf damage by the shoot herbivores was similar across treatments, these effects were not mediated by a lower amount of foliage removal on nematode-infested plants. Instead we speculate that the nematodes might have affected the herbivore’s spatial distribution



**Fig. 4** The dependence of *Triadica sebifera* root knot nematode numbers per pot on the presence of aboveground herbivores, soil fungi, and/or soil nematodes when plants were grown in the absence (left panel) or presence (right panel) of an intraspecific competitor. Solid-circles represent experimental data and open-circles represent the predicted effects of soil fungi and aboveground herbivores if their effects had been additive. Symbols “0” on top of the X-axis indicate that no nematodes were detected in treatment combinations receiving nematocide.

“CTRL”: control (all biota absent); “N”: only soil nematodes present; “F”: only soil fungi present; “H”: only aboveground herbivores present; “NF”: soil nematodes and fungi present; “NH”: soil nematodes and aboveground herbivores present; “FH”: soil fungi and aboveground herbivores present; “NFH”: soil nematodes, soil fungi, and aboveground herbivores present (for a more complete description see legends to Fig. 1). Means  $\pm$  1 SE. Post-hoc tests did not reveal significant differences between treatment combinations



**Fig. 5** The dependence of *Triadica sebifera* root mycorrhizal colonization levels on the presence of aboveground herbivores, soil fungi, and/or soil nematodes when plants were grown in the absence (left panel) or presence (right panel) of an intraspecific competitor. Solid-circles represent experimental data and open-circles represent the predicted effects of soil fungi and aboveground herbivores if their effects had been additive. Symbols “0” on top of the X-axis indicate that no AMF were detected in treatment combinations receiving fungicide. “CTRL”: control

(all biota absent); “N”: only soil nematodes present; “F”: only soil fungi present; “H”: only aboveground herbivores present; “NF”: soil nematodes and fungi present; “NH”: soil nematodes and aboveground herbivores present; “FH”: soil fungi and aboveground herbivores present; “NFH”: soil nematodes, soil fungi, and aboveground herbivores present (for a more complete description see legends to Fig. 1). Means  $\pm$  1 SE. Post-hoc tests did not reveal significant differences between treatment combinations

of feeding within the foliage, for instance by inducing increased defenses in young foliage (Biere and Govers 2016; Soler et al. 2012), forcing herbivores to feed on perhaps older or more basal, less defended leaves. The value of old vs. young or basal vs apical leaves for plants can be very different and any nematode-induced shifts in the spatial pattern of aboveground herbivore feeding could therefore significantly affect plant fitness (Wang et al. 2012). Alternatively, nematodes could have reduced overall leaf quality, so that a given amount of leaf loss would have resulted in a lower amount of resources lost from the plant. For instance, root-knot nematodes have been shown to reduce foliar nitrogen levels in tomato (Guo and Ge 2017) and nitrogen and phosphorus levels in cucumber (Xu et al. 2010). Regardless of the underlying cause, our finding indicates that antagonistic interactions between the aboveground insect herbivore and the belowground nematodes attenuated their negative effects on plant performance.

Interestingly, the strength of the antagonism between the weevils and soil nematodes depended on the presence of soil fungi. More specifically, soil fungi reduced the extent of antagonism between the aboveground herbivore and soil nematodes. The mechanism by which soil fungi in our experiment counteracted the antagonistic effects of nematodes on herbivores is currently unknown. AM fungi are well known antagonists of nematodes (Hol and Cook 2005), suggesting that these fungi could have suppressed the nematodes and their antagonistic effects on aboveground herbivores by controlling nematode numbers in our experiment. However, such a scenario is only partly supported by our data. Soil fungi indeed reduced nematode numbers by around 40%, but only on weevil-infested plants (Fig. 4) and not on weevil-free plants, suggesting that more complex interactions than a simple antagonistic effect of soil fungi on nematodes might play a role. Three-way interactions between nematodes, fungi, and aboveground insect herbivores have been investigated previously (e.g. De Roissart et al. 2013; McCarville et al. 2012; Zhou et al. 2016). For instance, the simultaneous presence of a cyst nematode, a leaf stem fungus, and an aphid on soybean generally reduced the performance of the aphid and the fungus compared to their presence alone, but increased the performance of the nematode (e.g. McCarville et al. 2012). However, the consequences of such interactions for plant performance have rarely been investigated, and the mechanisms underlying such effects are poorly understood. The mechanism underlying

the observed attenuating effect of soil fungi on the antagonism between the effects of nematodes and shoot herbivores therefore requires further study. Overall, our study underscores the importance of considering joint effects of different above- and/or belowground biotic interactions on plant performance in future studies.

While the effects of weevils on plant performance thus strongly depended on the presence of soil biota (nematodes and soil fungi), soil fungi had a more consistent negative effect on *T. sebifera* performance (Figs. 1, 2 and 3, compare F, NF and NHF), i.e., even though the modulation of their effects by nematodes and herbivores was statistically significant, they overall strongly decreased plant above- and belowground biomass. The predominantly negative effect of soil fungi in our experiment might indicate that the community of soil fungi mainly harbored pathogenic fungi, that were not quantified in our study. The predominantly negative effects of the soil fungi are in line with previous studies in our system that have reported strong negative effects of soil fungi on *T. sebifera* performance in its native range when plants were exposed to these fungi in the absence of aboveground herbivory (Yang et al. 2013, 2015a). Previous studies have found that soil fungi can be strong drivers of negative plant-soil feedbacks and soil biotic effects, both of which play an important role influencing community diversity and the success of biological invasions (van der Putten et al. 2013; van der Putten et al. 2016; Yang et al. 2013, 2019).

Our results show that aboveground herbivores and soil fungi alone did not significantly affect the abundance of root-knot nematodes, but that there was a strong interaction between their effects on nematode abundance. Herbivory in fact strongly increased nematode abundance, but only in the absence of soil fungi. Positive effects of aboveground herbivores on plant parasitic nematode numbers have commonly been reported (e.g. Alston et al. 1993; Kafle et al. 2017; Kaplan et al. 2009; Russin et al. 1993). However, as discussed above, only few studies have considered three-way interactions between insect herbivores, plant parasitic nematodes and soil fungi. In our study, we could speculate that AM fungi competed with nematodes for carbon or nutrients that were sequestered in roots in response to aboveground herbivory, a process known as herbivore-induced resource sequestration (Orians et al. 2011). Alternatively, the fungi could have induced signaling responses leading to induced nematode resistance, mitigating the positive effect of aboveground

herbivory on nematode numbers. In this context, unraveling the mechanism will need further studies examining root carbon, nutrients and defense chemicals and their effects on these soil organisms.

Intraspecific competition reduced root biomass and increased nematode abundance but did not change the effect of any of the biotic agents on plant biomass. The decline in root biomass under intraspecific competition shows that competition (likely for light) changed allocation of resources to shoots and roots. On the other hand, intraspecific competition did not change root AMF colonization, nor the direction of the effect of soil biota on plant biomass. Interestingly, the number of root-knot nematodes per unit root biomass increased more than four-fold under intraspecific competition, whereas root biomass was only reduced by 14%, resulting in an enormous increase in the number of root knot nematodes per pot. This suggests that root-knot nematodes prosper when plants are grown in close proximity under higher densities. Plants that grow in dense stands, such as some mustards, nettles and some trees are more easily located by herbivores, pathogens, and, over time, root antagonists such as nematodes (Bardgett and Wardle 2003; Bennett and Bever 2007; Downey et al. 2018). Not only do these plants therefore have to contend with increased intraspecific competition, but they may also harbor more above- and below-ground enemies, generating selection to disperse over time (Jing et al. 2015; Klironomos 2002; Packer and Clay 2000; van der Putten et al. 2001). Together these results suggest that intraspecific competition indirectly affects plant-soil interactions via changing plant biomass allocation patterns and by influencing plant-parasite interactions.

In conclusion, we found that soil fungi reduced the extent of antagonism between soil nematodes and the aboveground herbivore. These results show the critical importance of considering effects of plant antagonists in their full biotic context. The joint negative effects of weevils and nematodes on *T. sebifera* biomass would have been grossly overestimated based on their individual effects, i.e., they are less than would be expected from their individual effects on plant performance. Our findings indicate that the simultaneous presence of different attackers can lead to interactions that partly mitigate the negative effects of one attacker by another. This suggests that plants have developed strategies to cope with simultaneous damage by above- and below-ground attackers because plants are often attacked by a

wide diversity of above- and belowground organisms in natural ecosystems (Borgstrom et al. 2018; Erwin et al. 2014; Heinen et al. 2018a, b; Huang et al. 2014; Meier and Hunter 2018; Scherber et al. 2010). Most importantly, these results highlight the importance of considering the roles of diverse above- and belowground species and their interactions in regulating plant growth and population dynamics. We argue that it is necessary for future studies to evaluate the role of above- and below-ground biotic interactions on plant community dynamics from a system level viewpoint.

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**Authors contributions** QY, JD and ES conceived the experiments. QY carried out the experiments. QY, AB and ES carried out data analysis. QY, AB, JH, JD and ES wrote the manuscript.

#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

#### References

- Alston DG, Schmitt DP, Bradley JR, Coble HD (1993) Multiple pest interactions in soybean: effects on *Heterodera glycines* egg populations and crop yield. *J Nematol* 25:42–49
- Arce CCM, Machado RAR, Ribas NS, Cristaldo PF, Ataíde LMS, Pallini A, Carmo FM, Freitas LG, Lima E (2017) Nematode root herbivory in tomato increases leaf defenses and reduces leaf miner oviposition and performance. *J Chem Ecol* 43:1–9
- Bardgett RD, Wardle DA (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 9:2258–2268
- Bardgett RD, Wardle DA (2010) Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change. Oxford series in ecology and evolution. Oxford University Press, New York
- Barto EK, Rillig MC (2010) Does herbivory really suppress mycorrhiza? A meta-analysis. *J Ecol* 98:745–753

- Bennett AE, Bever JD (2007) Mycorrhizal species differentially alter plant growth and response to herbivory. *Ecology* 1:210–218
- Bezemer TM, Van der Putten WH, Martens H, Van de Voorde TFJ, Mulder PJJ, Kostenko O (2013) Above- and below-ground herbivory effects on below-ground plant–fungus interactions and plant–soil feedback responses. *J Ecol* 101:325–333
- Biere A, Govers A (2016) Plant-mediated systemic interactions between pathogens, parasitic nematodes, and herbivores above- and belowground. *Annu Rev Phytopathol* 54:499–527
- Borgstrom P, Bommarco R, Strengbom J, Viketoft M (2018) Above- and belowground insect herbivores mediate the impact of nitrogen eutrophication on the soil food web in a grassland ecosystem. *Oikos* 127:1272–1279
- Bowsher AW, Shetty P, Anacker BL, Siefert A, Strauss SY, Friesen ML (2017) Transcriptomic responses to conspecific and congeneric competition in co-occurring *Trifolium*. *J Ecol* 105:602–615
- Broeckling CD, Broeckling CD, Broz AK, Bergelson J, Manter DK, Vivanco JM (2008) Root exudates regulate soil fungal community composition and diversity. *Appl Environ Microbiol* 74:738–744
- Copes WE, Schem H (2005) Plant spacing effects on microclimate and *Rhizoctonia* web blight development in container grown *Azalea*. *HortScience* 40:1408–1412
- De Roissart A, de la Peña A, Van Oyen L, Van Leeuwen T, Ballhorn DJ, Bonte D (2013) The presence of root-feeding nematodes – not AMF – affects an herbivore dispersal strategy. *Acta Oecol* 52:38–44
- Downey H, Lewis OT, Bonsall MB, Fernandez DC, Gripenberg S (2018) Insect herbivory on seedlings of rainforest trees: effects of density and distance of conspecific and heterospecific neighbors. *Ecol Evol* 8:12702–12711
- Ebone LA, Kovaleski M, Deuner CC (2019) Nematicides: history, mode, and mechanism action. *Plant Sci Today* 6:91–97
- Engelkes T, Morriën WE, Verhoeven KJF, Bezemer TM, Biere A, Harvey JA, McIntyre LM, Tamis WLM, van der Putten WH (2008) Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature* 456:946–948
- Erwin AC, Züst T, Ali JG, Agrawal AA (2014) Above-ground herbivory by red milkweed beetles facilitates above- and below-ground conspecific insects and reduces fruit production in common milkweed. *J Ecol* 102:1038–1047
- Folgarait PJ, Marquis RJ, Ingvarsson P, Braker HE, Arguedas M (1995) Patterns of attack by insect herbivores and a fungus on saplings in a tropical tree plantation. *Environ Entomol* 24:1487–1494
- Geisler M, Gibson DJ, Lindsey KJ, Millar K, Wood AJ (2012) Upregulation of photosynthesis genes, and down-regulation of stress defense genes, is the response of *Arabidopsis thaliana* shoots to intraspecific competition. *Bot Stud* 53:85–96
- Guo HG, Ge F (2017) Root nematode infection enhances leaf defense against whitefly in tomato. *Arthropod Plant Interact* 11:23–33
- Hamilton EW, Frank DA (2001) Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology* 82:2397–2402
- Hauser TP, Christensen S, Heimes C, Kiaer LP (2013) Combined effects of arthropod herbivores and phytopathogens on plant performance. *Funct Ecol* 27:623–632
- Heinen R, van der Sluijs M, Biere A, Harvey JA, Bezemer TM (2018a) Plant community composition but not plant traits determine the outcome of soil legacy effects on plants and insects. *J Ecol* 106:1217–1229
- Heinen R, Biere A, Harvey JA, Bezemer TM (2018b) Effects of soil organisms on aboveground plant-insect interactions in the field: patterns, mechanisms and the role of methodology. *Front Ecol Evol* 6:106
- Hol WHG, Cook R (2005) An overview of arbuscular mycorrhizal fungi–nematode interactions. *Basic Appl Ecol* 6:489–503
- Hoysted GA, Lilley CJ, Field KJ, Dickinson M, Hartley SE, Urwin PE (2017) A plant-feeding nematode indirectly increases the fitness of an aphid. *Front Plant Sci* 8:1897
- Huang W, Siemann E, Xiao L, Yang XF, Ding JQ (2014) Species-specific defence responses facilitate conspecifics and inhibit heterospecifics in above-belowground herbivore interactions. *Nat Commun* 5:4851
- Jing J, Raaijmakers C, Kostenko O, Kos M, Mulder PJJ, Bezemer TM (2015) Interactive effects of above- and belowground herbivory and plant competition on plant growth and defence. *Basic Appl Ecol* 16:500–509
- Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ (2012) Mycorrhiza-induced resistance and priming of plant defenses. *J Chem Ecol* 38:651–664
- Kafle D, Hänel A, Lortzing T, Steppuhn A, Wurst S (2017) Sequential above- and belowground herbivory modifies plant responses depending on herbivore identity. *BMC Ecol* 17:5
- Kaplan I, Halitschke R, Kessler A, Rehill BJ, Sardanelli S, Denno RF (2008) Physiological integration of roots and shoots in plant defense strategies links above- and belowground herbivory. *Ecol Lett* 11:841–851
- Kaplan I, Sardanelli S, Denno RF (2009) Field evidence for indirect interactions between foliar-feeding insect and root-feeding nematode communities on *Nicotiana tabacum*. *Ecol Entomol* 34:262–270
- Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70
- Kong HG, Kim BK, Song GC, Lee S, Ryu C-M (2016) Aboveground whitefly infestation-mediated reshaping of the root microbiota. *Front Microbiol* 7:1314
- Koricheva J, Gange AC, Jones T (2009) Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology* 90:2088–2097
- Kos M, Tuijl MAB, de Roo J, Mulder PJJ, Bezemer TM (2015) Species-specific plant-soil feedback effects on above-ground plant-insect interactions. *J Ecol* 103:904–914
- Kostenko O, Mulder PJJ, Bezemer TM (2013) Effects of root herbivory on pyrrolizidine alkaloid content and aboveground plant-herbivore-parasitoid interactions in *Jacobaea vulgaris*. *J Chem Ecol* 39:109–119
- Li XH, Li BP, Meng L (2017) Below-ground nematode herbivory of resistant soybean cultivars impairs the performances of an above-ground caterpillar and its parasitoid. *Ecol Entomol* 42:712–720
- Liu J, Yang Q, Siemann E, Wei H, Ding JQ (2019) Latitudinal and altitudinal patterns of soil nematode communities under

- tallow tree (*Triadica sebifera*) in China. *Plant Ecol* 220:965–976
- Machado RAR, Arce CCM, McClure MA, Baldwin IT, Erb M (2018) Aboveground herbivory induced jasmonates disproportionately reduce plant reproductive potential by facilitating root nematode infestation. *Plant Cell Environ* 41:797–808
- Masters GJ, Brown VK, Gange AC (1993) Plant mediated interactions between above-and below-ground insect herbivores. *Oikos* 66:148–151
- McBride RG, Mikkelsen R, Barker KR (1999) A comparison of three methods for determining root-knot nematode infection of cotton roots. *Nematropica* 29:147–151
- McCarville MT, O'Neal M, Tylka GL, Kanobe C, MacIntosh GC (2012) A nematode, fungus, and aphid interact via a shared host plant: implications for soybean management. *Entomologia Experimentalis et Applicata* 143:55–66
- McGonigle TP, Miller MH, Evans DG, Fairchild GL, Swan JA (1990) A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytol* 115:495–501
- Meier AR, Hunter MD (2018) Arbuscular mycorrhizal fungi mediate herbivore-induction of plant defenses differently above and belowground. *Oikos* 127:1759–1775
- Mörrien E, Engelkes T, Van der Putten WH (2011) Additive effects of aboveground polyphagous herbivores and soil feedback in native and range-expanding exotic plants. *Ecology* 92:1344–1352
- Nijjer S, Rogers WE, Lee CTA, Siemann E (2008) The effects of soil biota and fertilization on the success of *Sapium sebiferum*. *Appl Soil Ecol* 38:1–11
- Orians CM, Thom A, Gómez S (2011) Herbivore-induced resource sequestration in plants: why bother? *Oecologia* 167: 1–9
- Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281
- Pangesti N, Pineda A, Pieterse CM, Dicke M, van Loon JJ (2013) Two-way plant mediated interactions between root-associated microbes and insects: from ecology to mechanisms. *Front Plant Sci* 4:414
- Pieterse CMJ, Zamioudis C, Berendsen RL, Weller DM, Van Wees SCM, Bakker PAHM (2014) Induced systemic resistance by beneficial microbes. *Annu Rev Phytopathol* 52: 347–375
- Pozo MJ, Azcon-Aguilar C (2007) Unraveling mycorrhiza-induced resistance. *Curr Opin Plant Biol* 10:393–398
- Reader RJ (1992) Herbivory, competition, plant mortality and reproduction on a topographic gradient in an abandoned pasture. *Oikos* 65:414–418
- Real-Santillan RO, del-Val E, Cruz-Ortega R, Contreras-Cornejo HA, Gonzalez-Esquivel CE, Larsen J (2019) Increased maize growth and P uptake promoted by arbuscular mycorrhizal fungi coincide with higher foliar herbivory and larval biomass of the fall armyworm *Spodoptera frugiperda*. *Mycorrhiza* 29:615–622
- Russin JS, McGawley EC, Boethel DJ (1993) Population development of *Meloidogyne incognita* on soybean defoliated by *Pseudoplusia includens*. *J Nematol* 25:50–54
- SAS Institute (2013) SAS/ACCESS® 9.4. SAS Institute Inc., Cary, NC, USA
- Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze ED, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein AM, Koller R, König S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Müller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tschamntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553–556
- Schittko C, Wurst S (2014) Above- and belowground effects of plant-soil feedback from exotic *Solidago canadensis* on native *Tanacetum vulgare*. *Biol Invasions* 16:1465–1479
- Skoneczny D, Zhu XC, Weston PA, Gurr GM, Callaway RM, Weston LA (2019) Production of pyrrolizidine alkaloids and shikonins in *Echium plantagineum* L. in response to various plant stressors. *Pest Manag Sci* 75:2530–2541
- Soler R, Van der Putten WH, Harvey JA, Vet LEM, Dicke M, Bezemer TM (2012) Root herbivore effects on aboveground multitrophic interactions: patterns, processes and mechanisms. *J Chem Ecol* 38:755–767
- Stam JM, Kroes A, Li YH, Gols R, van Loon JJ, Poelman EH, Dicke M (2014) Plant interactions with multiple insect herbivores: from community to genes. *Annu Rev Plant Biol* 65: 689–713
- van der Putten WH, Vet LE, Harvey JA, Wäckers FL (2001) Linking above-and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends Ecol Evol* 16:547–554
- van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA (2013) Plant-soil feedback: the past, the present and future challenges. *J Ecol* 101:265–276
- van der Putten WH, Bradford M, Brinkman EP, van de Voorde TFJ, Veen GF (2016) Where, when and how plant-soil feedback matters in a changing world. *Funct Ecol* 30:1109–1121
- Wang Y, Ding JQ, Wheeler GS, Purcell MF, Zhang GA (2009) *Heteropoderopsis bicallosicollis* (Coleoptera: Attelabidae): a potential biological control agent for *Triadica sebifera*. *Environ Entomol* 38:1135–1144
- Wang Y, Huang W, Siemann E, Zou JW, Wheeler GS, Carrillo J, Ding JQ (2011) Lower resistance and higher tolerance of invasive host plants: biocontrol agents reach high densities but exert weak control. *Ecol Appl* 21:729–738
- Wang Y, Siemann E, Wheeler GS, Zhu L, Gu X, Ding JQ (2012) Genetic variation in anti-herbivore chemical defences in an invasive plant. *J Ecol* 100:894–904
- Weidenhamer JD, Montgomery TM, Cipollini DF, Weston PA, Mohny BK (2019) Plant density and rhizosphere chemistry: does Marigold root exudate composition respond to intra- and interspecific competition? *J Chem Ecol* 45:525–533
- Whitehead R (1998) The UK pesticide guide. Massachusetts, CABI Publishing, Cambridge
- Wondafrahs M, Van Dam NM, Tytgat TOG (2013) Plant systemic induced responses mediate interactions between root parasitic nematodes and aboveground herbivorous insects. *Front Plant Sci* 4:87

- Xu H, Ruan WB, Gao YB, Song XY, Wei YK (2010) Effects of root-knot nematodes on cucumber leaf N and P contents, soil pH, and soil enzyme activities. *Ying Yong Sheng Tai Xue Bao* 21:2038–2044 [Article in Chinese with English abstract]
- Yang JW, Yi H-S, Kim H, Lee B, Lee S, Ghim S-Y, Ryu C-M (2011) Whitefly infestation of pepper plants elicits defence responses against bacterial pathogens in leaves and roots and changes the below-ground microflora. *J Ecol* 99:46–56
- Yang Q, Carrillo J, Jin HY, Shang L, Hovick SM, Nijjer S, Gabler CA, Li B, Siemann E (2013) Plant-soil biota interactions of an invasive species in its native and introduced ranges: implications for invasion success. *Soil Biol Biochem* 65:78–85
- Yang Q, Wei SJ, Shang L, Carrillo J, Gabler CA, Nijjer S, Li B, Siemann E (2015a) Mycorrhizal associations of an invasive tree are enhanced by both genetic and environmental mechanisms. *Ecography* 38:1112–1118
- Yang Q, Li B, Siemann E (2015b) Positive and negative biotic interactions and invasive *Triadica sebifera* tolerance to salinity: a cross-continent comparative study. *Oikos* 124:216–224
- Yang Q, Li B, Siemann E (2015c) The effects of fertilization on plant-soil interactions and salinity tolerance of invasive *Triadica sebifera*. *Plant Soil* 394:99–107
- Yang Q, Ding JQ, Siemann E (2019) Biogeographic variation of distance-dependent effects in an invasive tree species. *Funct Ecol* 33:1135–1143
- Zhang KD, Lin YT (1994) Chinese tallow. China Forestry Press, Beijing
- Zhou WQ, Starr JL, Krumm JL, Sword GA (2016) The fungal endophyte *Chaetomium globosum* negatively affects both above- and belowground herbivores in cotton. *FEMS Microbiol Ecol* 92(10):fww158

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