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REGULAR ARTICLE

Plant–soil feedback in native *vs.* invasive populations of a range expanding plant

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Abstract
Background and aims Although plant–soil feedback has been suggested as a mechanism that drives the success of invasive plants, studies that investigate differences in the intensity of plant–soil feedback among native and invasive populations of the same species are still lacking. However, such knowledge is important because it can provide an understanding of the mechanisms responsible for the spread of a species. *Rorippa austriaca* is a potentially invasive species - a successful range expander in Europe.
Methods We compared the plant–soil feedback of *R. austriaca* in populations from its native and invasive range. We explored both intraspecific feedback as well as feedback on a co-occurring grass species.
Results Our results revealed a strong negative feedback effect as a consequence of soil conditioning by *R. austriaca* from the native range. On the contrary, a negative feedback effect was not observed for invasive *R. austriaca*. Interestingly, *R. austriaca* from the invasive range had a higher biomass than native *R. austriaca*.
Conclusion Our results might be explained by pathogen accumulation and soil modification by native *R. austriaca*, which had strong intra- and interspecific effects that seemed to be lost in the invasive *R. austriaca*. The loss of negative intraspecific plant–soil feedback and the increased growth of the invasive population may contribute to its successful range expansion. In spite of its increased growth, the co-occurring grass species is expected to successfully coexist with the invasive *R. austriaca*.

Keywords Activated carbon · Biotic interactions · Brassicaceae · Plant–soil feedback · Soil community · Austrian yellowcress

Introduction

Species distributions are changing because of climate change, changes in land use and globalization (Parmesan 2006; Thuiller et al. 2008; Pereira et al. 2010). Because these moving plants may have deep-seated effects on entire ecosystems and also on agricultural production and human health, many studies have attempted to identify the factors that determine which alien species are more likely to succeed in invading and which will likely fail (Seastedt and Pyšek 2011).

A factor that strongly affects species success in a new range is the ability of the plant to modify the soil in

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which it grows and to suppress the growth of the other plants and/or support its own growth (Callaway et al. 2004; Reinhart and Callaway 2004; Zuppinger-Dingley et al. 2011). This effect can be mediated through the input of chemical compounds and organic matter from the plant to the soil, by impacting hydrological processes and surface soil temperatures and by providing habitats and/or resources for soil biota (Bardgett and Wardle 2010; Lamb et al. 2011). Changes in soil properties caused by plants, which in turn influence the performance of plants, are termed 'plant–soil feedback' (Bever et al. 1997; Van der Putten et al. 2013).

Plant–soil feedback characterized by an individual plant affecting itself or other plants of the same species is called direct (intraspecific) plant–soil feedback. It can be negative, neutral or positive depending on the net growth effect of the soil modified by the plant compared to unmodified soil (Van der Putten et al. 2013). Multiple studies (Klironomos 2002; Reinhart et al. 2003; Callaway et al. 2004; Knevel et al. 2004; Bennett et al. 2011; Yang et al. 2013) indicated that intraspecific plant–soil feedback can play an important role in the invasiveness of plant species.

It has been demonstrated that the type of intraspecific feedback can differ depending on where in an invasive species' distributional range it is studied. Specifically, it was shown that species experience stronger intraspecific negative feedback in their native range than in their invasive range (e.g., Klironomos 2002; Reinhart et al. 2003; Agrawal et al. 2005; Engelkes et al. 2008; Kulmatiski et al. 2008, but see Anacker et al. 2014). In addition to the differences between the intensity of intraspecific feedback in soils from different areas, it has also been shown that individuals of the same species originating from different areas (i.e., the native and invasive range) might experience intraspecific feedback of different intensity (Te Beest et al. 2009; Andonian and Hierro 2011; Yang et al. 2013). Although the majority of studies have shown that species experience stronger intraspecific negative feedback in their native range than in their invasive range, several recent studies have arrived at a different conclusion (Andonian et al. 2011; Birnbaum and Leishman 2013). For example, Andonian et al. (2011) found that *Centaurea solstitialis*, a globally invasive weed, generated strong negative intraspecific feedback in regions where it is the most invasive, while it generated neutral plant–soil feedback in non-invasive regions.

Differences in the intensity of plant–soil feedback between the native and invasive range could be caused by micro evolutionary changes leading to a change in a range of species traits (Bone and Farres 2001; Maron et al. 2004; Callaway and Ridenour 2004; Bossdorf et al. 2005). Most plant–soil feedback studies have focused on the impact of the soil biota on the invasive and related non-invasive plant species in the non-native range. However, very few studies have explored the differences in plant–soil feedback effects between genotypes of the same species from the native and the invasive range (Te Beest et al. 2009; Seifert et al. 2009; Andonian and Hierro 2011; Birnbaum and Leishman 2013). Theoretically, invasive genotypes could have lost the intraspecific negative feedback that may limit the populations in the native range. This loss in negative feedback compared to the native range may then contribute to the success of the plant's invasion. Alternatively, plant invasiveness may be promoted by strong interspecific plant–soil feedback. Interspecific plant–soil feedback is feedback from one plant species that affects another species. For example, invasive exotic plants can promote soil pathogens that have a more negative effect on the surrounding native plant species than on the exotics themselves (Mangla et al. 2008). They can also reduce local mycorrhizal fungi with negative consequences for native plant species (Stinson et al. 2006; Lankau and Strauss 2007; Van der Putten et al. 2013). In addition, plants can produce secondary metabolites such as allelopathic root exudates that are relatively ineffective against their natural neighbours because of adaptation but may be highly inhibitory to newly encountered plants in the invaded communities (Callaway and Ridenour 2004).

Most studies compare intraspecific and interspecific plant–soil feedback effects of invasive exotic plants that were introduced from other continents (Klironomos 2002; Knevel et al. 2004; Van Grunsven et al. 2009, but see Van Grunsven et al. 2007). However, not all exotic plants arise from other continents. In past decades, many species have moved to higher latitudes within the same continent, partly driven by climate change (Parmesan 2006; Morriën and van der Putten 2013). Recently, it has been shown that plant–soil feedback can play an important role in the spread of invasive species within continents as well (Engelkes et al. 2008; van Grunsven et al. 2010).

The aim of this study was to understand the importance of plant–soil feedback in the spread of range expanding *Rorippa austriaca* (Crantz) Besser (Austrian yellowcress). *R. austriaca* is a successful intra-continental range expander, which has spread northwards and westwards from central and south-eastern Europe within the Eurasian continent (Jonsell 1993; Tutin et al. 1993; Bleeker 2003). In the Netherlands, *R. austriaca* was first discovered around the 1920s and has strongly increased in abundance since the 1980s and particularly since 2000 (Tamis et al. 2005; Engelkes et al. 2008). Meisner et al. (2012) tested how the legacy of litter from invasive *R. austriaca* affects its own performance in comparison to that of its congeneric native *R. sylvestris*, which co-occurred in an invaded habitat in the Netherlands. Their results suggested that both invasive and native *Rorippa* species may benefit from the litter of invasive *R. austriaca*. In the closely related species *R. sylvestris* and *R. indica*, negative effects of root exudates on lettuce growth were recorded (Yamane et al. 1992a; Yamane et al. 1992b). Negative effects of root exudates of *R. austriaca* on plant growth of other co-occuring species could thus be expected. In this study, we explored differences in plant–soil feedback between native and invasive populations of *R. austriaca* and asked the following questions:

A) What are the differences in intraspecific plant–soil feedback effects between plants of *R. austriaca* from the native and invasive range?
B) Is there any interspecific plant–soil feedback effect of *R. austriaca* on co-occurring grass species and does this effect differ between *R. austriaca* from the native and invasive range?

To answer these questions, we performed two pot experiments on plant–soil feedback in the common garden in the native range of *R. austriaca*. In the first step, we conditioned the soil with native and invasive *R. austriaca* and co-occurring grass species. In the second step, this soil was used for the cultivation of native and invasive *R. austriaca* and a co-occurring grass species to test the effects of soil conditioning on different populations within the same species and on co-occurring species.

Methods

Study species

R. austriaca is a polycarpic herbaceous perennial with a semi rosette growth form and relatively deep storage roots (Oberdorfer 1990). It combines clonal growth by lateral roots with the ability to regenerate from root fragments (Dietz et al. 2002). It can also reproduce via seeds and is an obligate outcrossing species (Bleeker and Matthies 2005). Stands of *R. austriaca* can be found growing in sandy soils as well as in nutrient rich loamy soils in habitats with greatly different vegetation structures ranging from open, intensively or patchily disturbed sites to sites with dense, more successional herbaceous vegetation. In its invasive range, it predominantly occurs along riversides.

Collection of plant material

Root fragments of *R. austriaca* were collected in 5 populations in both the native range in the Czech Republic (central Europe) and the invasive range in Western Europe in the Netherlands in 2011 (Table 1). In each range and population, we took root fragments from 5 distinct rosettes of adult *R. austriaca* plants to reflect possible genotypic variability within populations. We refer to these rosettes as different individuals. The root fragments were put in 3 L pots with common garden soil mixed with sand (at a ratio of 1:1). Plants resprouting from these root fragments were subsequently cultivated for 12 months in the experimental garden.

Soil conditioning (first experimental phase)

Three root fragments of similar size (length 4 cm, diameter 0.3–0.5 cm) from each plant of *R. austriaca* cultivated in the experimental garden in 2011 were placed in the 2 L pots filled with unsterilized common garden soil that had never been exposed to *R. austriaca* mixed with steam-sterilized river sand at a ratio of 1:1. The experiment contained 150 pots in total; i.e., pots with plants from 2 ranges × 5 populations × 5 individuals × 3 clonal replicates. Because plants of *R. austriaca* were planted from root fragments and not from the seeds, it was not possible to sterilize them in the experiment. However, we grew them for 12 months in the same soil and in the same experimental garden prior to the experiment. We assumed that any possible microbial differences

Table 1 List of populations, global positioning system (*GPS*) coordinates (*WGS 84*), altitude, number of plants (*Pop size*) in 2011, substrate and site description, where root fragments of *R. austriaca* were taken for the experiments

Range	Population	GPS coordinates		Altitude	Pop size	Substrate/soil type	Description
		N	E	[m asl]			
Native	NAT1	49.046389	15.800278	449	15	Shallow infertile soil with gravel	Ditch next to the road
	NAT2	50.009722	14.414722	224	20	Deep fertile soil	City lawn
	NAT3	50.004722	14.401944	190	100	Shallow infertile soil with gravel	River bank
	NAT4	48.978056	14.444722	391	25	Shallow infertile soil with gravel	Road side
	NAT5	49.056667	14.445556	369	30	Deep fertile soil	River bank and field road
Invasive	INV1	51.966111	4.454167	−5	>1000	Sand	Road side
	INV2	51.982222	5.868889	25	>2000	Rocks, sand, sandy loam	River bank
	INV3	51.864444	5.987500	13	>2000	Sand	River bank, high dry shores
	INV4	51.954167	5.656667	7	~500	Sand/rocks	River bank, along pier, dry high shores
	INV5	51.930278	4.226944	3	>200	Loam	River bank, grassland

originating from the original soil in which the plants were naturally growing were likely to be greatly diminished or absent. However, we cannot completely exclude the possibility that beneficial or detrimental microbes were carried over from the original growth location. Additionally, we grew *Agrostis capillaris* in 2 L pots in the same soil mixture (150 pots); 0.1 g of *A. capillaris* seeds (obtained from the Planta Naturalis company, Czech Republic) were sown in each pot. *A. capillaris* is a common grass species that is easy to cultivate, often forming nearly monodominant stands that occur at the localities occupied by *R. austriaca* in both ranges.

All 150 pots of *R. austriaca* and 150 pots of *A. capillaris* were grown for 8 weeks in the experimental garden located in the Institute of Botany, the Czech Academy of Sciences in Průhonice (322 m asl, 49°99′N, 14°57′E) from late May to late July 2012, when all of the plants were harvested. The environmental conditions of experimental garden were similar to those at natural localities in the Czech Republic, in which *R. austriaca* and *A. capillaris* grow. During cultivation, both species substantially increased their aboveground and belowground biomass, but they were not limited by the 2 L pots.

At the end of this first experimental phase, we had three soil types: soil from pots with 1) *R. austriaca* from the native range (150 L) 2) *R. austriaca* from invasive range (150 L) and 3) *A. capillaris* (300 L). Soil from all pots within the three variants was mixed to create specific soil types (see Hawkes et al. 2013 and Sun et al. 2014 for similar approach). We mixed the soils because we wanted to study the overall effects of native and invasive populations of *R. austriaca*, rather than looking at the effect of individual genotypes or populations, and we wanted to keep the number of replicates reasonable. In addition, the growth of the plants in the pots was uneven (i.e., very large plants or many *A. capillaris* seedlings were present in some pots and small plants and few seedlings were present in others). By mixing the soil we thus ensured that all of the soil used in the second experimental phase experienced the same intensity of conditioning.

Plant–soil feedback (second experimental phase)

A) Plant–soil feedback on Rorippa

In the second experimental phase, we explored the differences in the intraspecific plant–soil feedback effects between populations of *R. austriaca* from the native and invasive range. We grew *R. austriaca* from the native and invasive range in 2 L pots with the soil type conditioned by *R. austriaca* from native and invasive range and the soil type conditioned by *A. capillaris*. *R. austriaca* plants were established from root fragments taken from the 5 individuals of each population grown in the first experimental phase. There were 3 soil types × 2 ranges × 5 populations × 5 individuals, i.e., 150 pots in total.

B) Plant–soil feedback on co-occurring species

In a complementary experiment, we compared the interspecific plant–soil feedback effects of populations of *R. austriaca* from native and invasive range on growth of the co-occurring species *A. capillaris*. We grew *A. capillaris* plants in 2 L pots in the three soil types from the first experimental phase (conditioned by *R. austriaca* native, *R. austriaca* invasive, *A. capillaris*). We used *A. capillaris* plants from the first experimental phase and chose plants as similar as possible for planting with leaves 4–6 cm long. After a week, dead plants of *A. capillaris* were replaced by new plants.

To check for the possible effects of allelopathic secondary metabolites of *R. austriaca* on competing plants, we included an activated carbon treatment of all three soil types by adding 20 mL of activated carbon per litre of soil (particle size <0.075 mm; Resorbent Ostrava). Activated carbon has high affinity for potentially toxic organic compounds and is commonly used to test for allelopathic effects (Callaway and Aschehoug 2000; Dostál 2011). There were 3 soil types (*R. austriaca* native, *R. austriaca* invasive, *A. capillaris*)×2 soil treatments (with and without activated carbon addition)×25 plant replicates, i.e., 150 pots with *A. capillaris* in total.

The plants from both experiments in the second experimental phase were cultivated for 8 weeks from late July to late September 2012 outdoors in the experimental garden. At the end of September, the plants were harvested and the above- and belowground biomass was separated. After drying to a constant weight (at 70 °C for 48 h), the biomass was weighed.

Data analyses

In the second experimental phase, the total biomass of *R. austriaca* was closely correlated with its aboveground and belowground biomass ($r=0.80$, $P<0.001$ and $r=0.98$, $P<0.001$, respectively) and total biomass of *A. capillaris* was closely correlated with its aboveground and belowground biomass ($r=0.95$, $P<0.001$ and $r=0.99$, $P<0.001$, respectively). Furthermore, the aboveground and belowground biomass was closely related for *R. austriaca* ($r=0.66$, $P<0.001$) and *A. capillaris* ($r=0.92$, $P<0.001$) as well. Therefore, we used only total biomass of both species in further analyses.

To explore the differences in the intraspecific plant–soil feedback effects between *R. austriaca* from the native and invasive range, the effects of range, population, individual, and soil type were tested using Generalized Linear Models (GLM). Further, we also tested the effect of the interaction between soil type and range and the interaction between soil type and population on the total biomass of *R. austriaca*. Range and soil type were fixed factors and population nested within range and individual identity nested within population were random factors. Differences between soil types within each range were tested with Tukey's HSD test.

To compare interspecific plant–soil feedback effects of populations of *R. austriaca* from the native and invasive range on the growth of co-occurring *A. capillaris* grass, the effects of soil type, activated carbon addition and their interaction on total biomass of *A. capillaris* were tested in a full factorial ANOVA. *A. capillaris* total biomass data were square root transformed to meet the assumptions of the analyses. Differences between soil types within each activated carbon treatment were tested with Tukey's HSD test.

To see how plant–soil feedback might potentially affect species interactions within the community, we further explored the strength of pairwise plant–soil feedback interactions between native and invasive *R. austriaca* and the co-occurring grass *A. capillaris* as suggested by Bever et al. (1997). The interaction coefficient, I_S, which represents the net pairwise feedback, is defined as $I_S=\alpha_A-\beta_A-\alpha_B+\beta_B$. The variables α and β represent the growth of the two plant species, respectively, and the subscripts A and B indicate which plant species was used for the soil conditioning (soil A being conditioned by species α and soil B being conditioned by species β) (Bever et al. 1997; Bever et al. 2010; Mangan et al. 2010; Shannon et al. 2011). Feedback interaction between the two species is indicated when the interaction coefficient is significantly different from 0 (by a *t* test). Because we had 25 individuals of *R. austriaca* (5 populations×5 individuals) from each range in each soil type, we were able to calculate an I_S for each individual (resulting in 25 I_S values for each pairwise comparison). We then used a *t* test to determine whether the I_S values were significantly different from zero (i.e., no feedback interaction). When I_S is positive, the feedback increases the relative performance of the locally abundant plant species generating a positive feedback dynamic that would lead to loss of diversity at a local scale. Conversely, when I_S is negative, feedback decreases the relative performance of the locally abundant plant species, leading to coexistance through net negative feedback. A negative I_S indicates net negative feedback (coexistence), and a positive Is indicates positive feedback (exclusion). The I_S was calculated for the three possible pairs of plants in our data, i.e., native *R austriaca* and *A. capillaris*, invasive *R. austriaca* and *A. capillaris*, native and invasive *R. austriaca*.

All statistical analyses were carried in R version 3.0.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Results

A) Plant–soil feedback on Rorippa

In the second experimental phase, *R. austriaca* plants from the invasive range produced 32 % more biomass than *R. austriaca* plants from the native range ($P=0.013$; Table 2a). Furthermore, the biomass of *R. austriaca* was significantly different between the three soil types conditioned by *R. austriaca* from the native and invasive range and by *A. capillaris* ($P<0.001$; Table 2a). We found a significant negative effect from soil conditioned by native *R. austriaca*, however, this effect significantly influenced the biomass of native *R. austriaca* (i.e., an average decrease of 30 % compared to soil type conditioned by *A. capillaris*) but did not affect the biomass of invasive *R. austriaca* (Fig. 1). Soil types conditioned by invasive *R. austriaca* and by *A. capillaris* were not significantly different in their effects on the biomass of both native and invasive *R austriaca* (GLM, Tukey's HSD test, $P>0.256$ in all cases; Fig. 1). The biomass was also different between individual *R. austriaca* plants within populations and marginally different between populations within ranges ($P=0.017$ and $P=0.080$, respectively; Table 2a, Fig. 2). The interactions between range and population and soil type were not significant, which indicates that the effects of soil type were similar in both ranges and all populations ($P=0.916$ and $P=0.221$, respectively; Table 2a, Fig. 2).

Table 2 A) Effects of the *R. austriaca* range (native and invasive), population nested within range, individual nested within population, soil type (soil conditioned by native and invasive *R. austriaca*, the co-occurring grass species *A. capillaris*) and their interaction on total biomass of *R. austriaca* tested by a Generalized Linear Model. B) Effects of the soil type (soil conditioned by native and invasive *R. austriaca* and the co-occurring grass species *A. capillaris*), the addition of activated carbon and their interaction on the total biomass of the co-occurring grass species *A. capillaris* tested by a factorial ANOVA. Significant values ($P<0.05$) are in bold; marginally significant ($P<0.1$) are in italics

	Df	F	*P*
A)			
Range	**1**	**10.00**	**0.013**
Population in range	*8*	*2.27*	*0.080*
Individual in population	**39**	**1.76**	**0.017**
Soil type	**2**	**12.38**	**<0.001**
Range x soil type	2	1.66	0.221
Population in range x soil type	16	0.54	0.916
Error	78		
B)			
Soil type	**2**	**18.03**	**<0.001**
Activated carbon treatment	*1*	*3.10*	*0.080*
Soil type x activated carbon treatment	2	2.16	0.120
Error	144		

B) Plant–soil feedback on co-occurring species

The biomass of *A. capillaris* differed between the soil types ($P<0.001$). Activated carbon addition had a

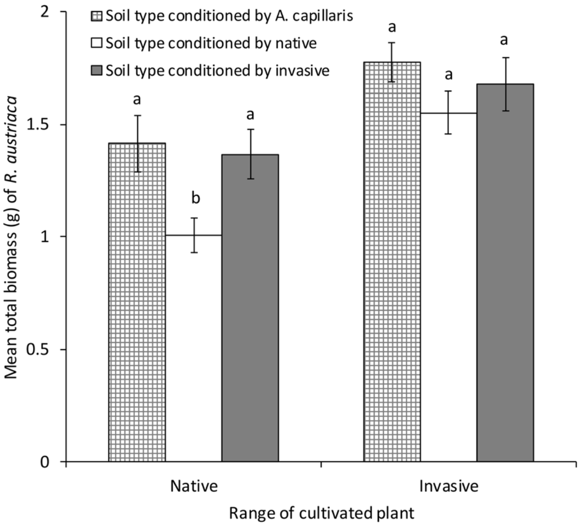

Fig. 1 Mean total biomass of *R. austriaca* from the native and the invasive range in different soil types from the plant–soil feedback experiment. Bars are means±SEM. Significant differences in *R. austriaca* biomass between the three soil types within the range are indicated by different lowercase letters (GLM, Tukey's HSD, $P<0.05$). Columns sharing the same letter are not significantly different ($P>0.05$)

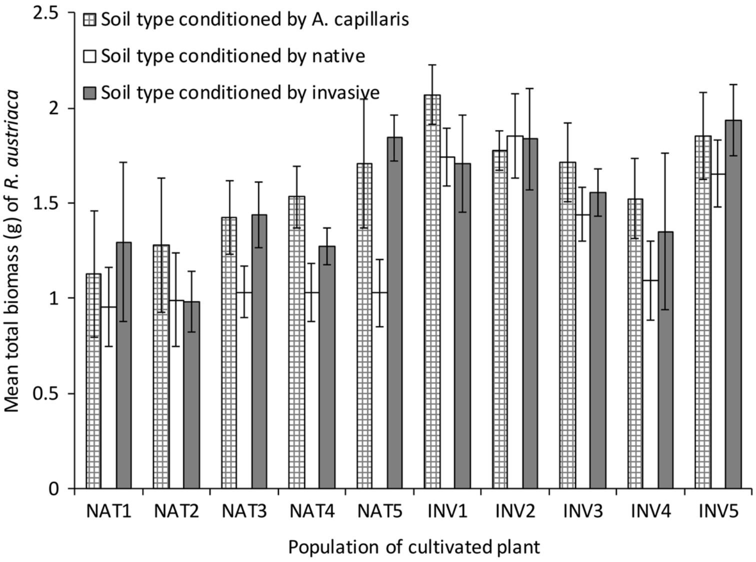

Fig. 2 Effects of different soil types on the growth of populations of native and invasive *R. austriaca*. Mean total biomass of *R. austriaca* populations from the native and the invasive range in different soil types from the plant–soil feedback experiment. Bars are means±SEM

marginally significant effect leading to a weak (12 %) overall increase in the biomass of *A. capillaris* ($P=0.080$). There was no interaction between the soil type and the addition of activated carbon ($P=0.120$; Table 2b, Fig. 3). While we recorded no differences between *A. capillaris* biomass in soil types conditioned by *A. capillaris* and invasive *R. austriaca*, we found a significant decrease of biomass in soil type conditioned by native *R. austriaca* (i.e., an average biomass decrease of 28 and 46 % compared to soil type conditioned by *A. capillaris* and invasive *R. austriaca*, respectively). The effects were similar in treatments with and without activated carbon (ANOVA, Tukey's HSD test, $P<0.05$, Fig. 3, Table 2b).

Effect of plant–soil feedback on possible interactions within the community

In the analyses of plant–soil feedback interactions between native *R. austriaca* and *A. capillaris*, we found a consistent negative effect of soil type conditioned by native *R. austriaca* with very similar negative consequences for the growth of both native *R. austriaca* and *A. capillaris*; i.e., no significant feedback interaction was evident ($I_S=-0.18$, $P=0.221$; Fig. 4a). In the comparison of plant–soil feedback of invasive *R. austriaca* and *A. capillaris*, *A. capillaris* grew better in soil type conditioned by invasive *R. austriaca* compared to its own soil. Invasive *R. austriaca* performed slightly worse in its own soil type as well, resulting in significant negative feedback interaction ($I_S=-0.41$, $P=0.005$; Fig. 4b). Both species in the community were suppressed by the negative effect of its own soil type and neither had a competitive advantage. On the contrary, in comparison of native and invasive *R. austriaca*, we found marginally significant positive plant–soil feedback interaction ($I_S=0.28$, $P=0.057$; Fig. 4c), when native *R. austriaca* grew more poorly in its own soil

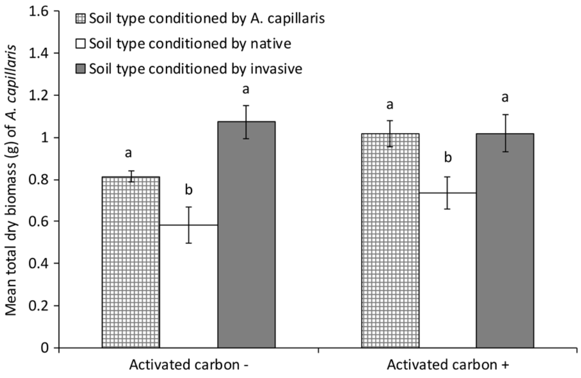

Fig. 3 Effects of different soil types conditioned by *R. austriaca* plants and by the co-occurring grass species *A. capillaris* and activated carbon addition on growth of the co-occurring grass *A. capillaris*. Significant differences (ANOVA, Tukey's HSD, $P<0.05$) between soil types within treatments with (activated carbon +) and without (activated carbon –) activated carbon are indicated by different lowercase letters. Bars are means±SEM. Columns sharing the same letter are not significantly different from each other ($P>0.05$)

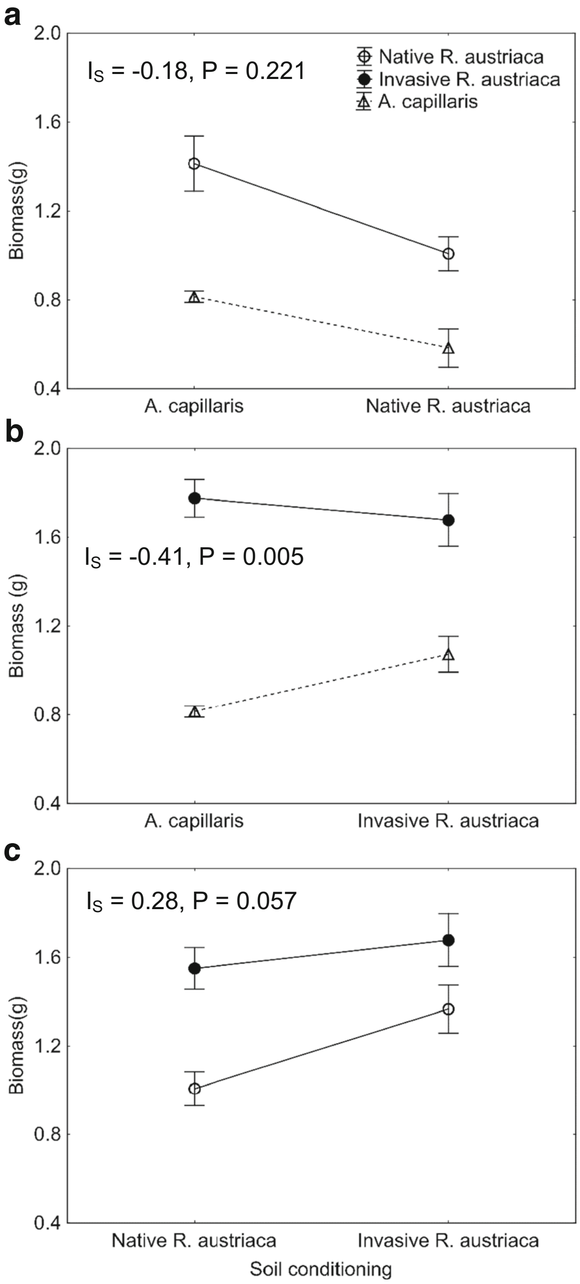

Fig. 4 Pairwise comparison of the average biomass of native and invasive *R. austriaca* and the co-occurring grass *A. capillaris* grown in the three soil types (soil conditioned by native or invasive *R. austriaca* or the co-occurring grass *A. capillaris*). The interaction coefficient I_S indicates the strength of pairwise plant–soil feedback interaction between **a**) *A. capillaris* and native *R. austriaca*, **b**) *A. capillaris* and invasive *R. austriaca* and **c**) native and invasive *R. austriaca*. Significance was tested using a *t* test to determine whether the I_S values were different from zero (i.e., no feedback interaction). A negative I_S indicates net negative feedback (coexistence), and a positive I_S indicates positive feedback (exclusion)

while no difference was noted for invasive *R. austriaca*. This ability might provide a competitive advantage to invasive *R. austriaca*, which is not limited by intraspecific negative plant–soil feedback such as native *R. austriaca*.

Discussion

Our results revealed a strong effect from soil conditioning on the biomass of native *R. austriaca* and the grass *A. capillaris*. Specifically, the plants performed more poorly in soil conditioned by native *R. austriaca* compared to soil conditioned by invasive *R. austriaca* or by *A. capillaris*. A negative effect from soil conditioned by native *R. austriaca* on the biomass of the co-occurring grass *A. capillaris* was detected both in the presence and absence of activated carbon.

Similarly to this study, it has been shown that performance of *Ailanthus altissima* was significantly different in soil conditioned by populations of single species of different origin (Felker-Quinn et al. 2011). This difference might be explained by changes in soil nutrients and/or in the composition of the soil microbial community (Seifert et al. 2009; Felker-Quinn et al. 2011). It has been repeatedly shown that plants affect soil nutrients and the soil microbial community, which affects the colonization success of conspecifics and/or heterospecifics (e.g., Klironomos 2002; Callaway et al. 2004; Jordan et al. 2008; Perkins and Nowak 2013). Perkins and Nowak (2013) found that native species produced plant–soil feedback that benefited other species more than themselves and non-native invasive species tended to produce plant–soil feedback that benefited themselves more than other species. This mechanism increases the potential of non-native species to become invasive. This is somewhat similar to our results, which indicated that invasive *R. austriaca* did not experience intraspecific negative soil feedback and may not be as limited as native *R. austriaca* when colonizing new localities. The reason for this difference between the native and invasive populations remains unknown. One explanation could be that rapid evolutionary change of the plant occurred in the new range; i.e., the plants in the new range might have evolved a different type of plant–soil feedback. For example, Seifert et al. (2009) showed that introduced North American and native European populations of *Hypericum perforatum* differed in their mycorrhizal responsiveness. North

American populations benefited less from inoculation with a cosmopolitan arbuscular mycorrhizal fungal species than did European populations. North American populations also had finer root systems, invested more in reproductive biomass and less in below-ground biomass than European populations.

The less negative intraspecific plant–soil feedback might be because invasive populations of *R. austriaca* exhibit more extensive clonal growth compared to native *R. austriaca*, i.e., invasive populations more often reproduce vegetatively rather than generatively, thus remaining closer together and more likely grow in their own soil (N. Bihler & M. Macel, unpublished data). The selection against negative plant–soil feedback could thus be stronger in the invasive range. Alternatively, there may be high variation in the intensity of plant–soil feedback in the native range (Peña et al. 2009; Felker-Quinn et al. 2011; Lankau 2013) and genotypes that have less negative intraspecific plant–soil feedback in the native range could also be the ones that are spreading or are spreading more successfully into the new range. This explanation is consistent with our results, as we also found differences among soil feedbacks of plants grown from different individuals within populations of *R. austriaca* (Table 2a). This topic, however, requires further study. There is also a possibility that *R. austriaca* from the invasive range could experience negative plant–soil feedback in soil from invasive range because local soil pathogens are adapted to the local genotypes of *R. austriaca* (Thrall et al. 2002). However, soil used in our experiment did not have any previous exposure to *R. austriaca*, and the closest populations were several tens of kilometres from the experimental garden. Unless we repeat the experiments using soil from the invasive range, we cannot exclude this option.

Negative soil feedback caused by native *R. austriaca* affected not only *R. austriaca* but also the co-occurring grass *A. capillaris*, which might be caused by production of allelopathic chemicals by native *R. austriaca* (Bais et al. 2003). Previous studies on related *Rorippa* species (Yamane et al. 1992a; Yamane et al. 1992b) revealed a negative effect on the growth of other plant species as a consequence of production of root exudates and suggested possible allelopathic effects. However, allelopathic effects are usually reported for exotic species when such effects facilitate the invasion of exotics in the new range; the so called Novel Weapons Hypothesis (Callaway and Ridenour 2004; Thorpe et al. 2009; Barto et al. 2010). Here, we show that native *R. austriaca* also negatively affects the growth of a co-occurring species. We have only recorded slight non-significant increases in *A. capillaris* biomass in soil conditioned by native *R. austriaca* after activated carbon addition (see Fig. 3). Because the effect of the activated carbon on plant growth was relatively small and non-significant, it does not seem very likely that native *R. austriaca* produced high concentrations of toxic root exudates that negatively affected *A. capillaris*. Rather, other, non-chemical, mechanisms might play a role, such as pathogen accumulation of the native *R. austriaca*. An alternative explanation may be that native *R. austriaca* takes up more nutrients from the soil than invasive *R. austriaca*, which negatively affected the growth of *A. capillaris* (Kardol et al. 2006). However, if *R. austriaca* plants from the native range took up more nutrients than *A. capillaris* and *R. austriaca* from the invasive range, it should probably grow larger than invasive *R. austriaca*, which was not the case. We did not include a fertilization treatment in our experiments so that we could control for this well-known confounding factor in plant–soil feedback experiments (see, e.g., Te Beest et al. 2009 for such an approach). Future experiments should control for the potential effect of nutrient uptake on the plant–soil feedback observed here.

Because *R. austriaca* in its invasive range does not experience negative plant–soil feedback, it may gain competitive advantage over other plants in the community in its new range and thus may become invasive. However, the co-occurring grass species *A. capillaris* also benefits from soil conditioned by invasive *R. austriaca*, compared to soil conditioned by *A. capillaris*. This is seen from the results of plant–soil feedback interactions analyses indicating that invasive *R. austriaca* gains no advantage in competition with *A. capillaris*. These two species should thus be able to coexist. However, this conclusion should be verified by an experiment in which the effect of soil conditioned by *A. capillaris* is compared to the effect of soil conditioned by both *A. capillaris* and invasive *R. austriaca*. This experiment would determine how conditioning by invasive *R. austriaca* can remove the negative home soil effect of *A. capillaris*. Moreover, further studies should also include other species occurring in the communities with *R. austriaca* so that we could generalize our results.

Our results thus indicate that other factors contribute to *R. austriaca* expansion. In this study, we found that *R. austriaca* plants from the invasive range grew significantly larger than the plants from the native range, which could confer an important competitive advantage. In agreement with this finding, Buschmann et al. (2005) compared *R. austriaca* from the introduced range in North America and from the native range (central Europe) and found that the invasive North American plants grew larger than the native plants. This also agrees with other studies that indicate that plants from the invasive range grow larger than plants from the native range (e.g., Blumenthal and Hufbauer 2007; Abela-Hofbauerová and Münzbergová 2011). For *R. austriaca*, the larger size of plants from the invasive range does not seem to be related to a shift in resource allocation from shoot defence to growth as predicted by the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995 but see Felker-Quinn et al. 2013). Native and invasive populations were equally damaged by shoot herbivores and had similar concentrations of shoot defences (Buschmann et al. 2005; Huberty et al. 2014). Currently, nothing is known about the root defences of this species.

Conclusions

We found negative intra- and interspecific plant–soil feedback in *R. austriaca* from the native range but not from the invasive range. This could be explained by pathogen accumulation by the native *R. austriaca*. In contrast, *R. austriaca* from the invasive range induced no intra- or interspecific plant–soil feedback and was less affected by soil conditioned by native *R. austriaca* than native *R. austriaca* was. Furthermore, the invasive population showed increased vigour compared to the native population. This thus suggests that, contrary to our expectation, plants from the invasive range did not increase but diminished their negative effects on other species via soil modification. The co-occurring grass species is thus likely to co-exist with *R. austriaca* in the invasive range.

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