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ORIGINAL PAPER

Do the impacts of alien invasive plants differ from expansive native ones? An experimental study on arbuscular mycorrhizal fungi communities

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Abstract

No studies have compared so far the effects of alien invasive and expansive native (widespread, mono-dominant) plants on arbuscular mycorrhizal fungi (AMF). Four global or European most successful invaders (*Impatiens glandulifera*, *Reynoutria japonica*, *Rudbeckia laciniata*, *Solidago gigantea*) and two expansive plants native to Europe (*Artemisia vulgaris*, *Phalaris arundinacea*) were grown in pots to elucidate the magnitude and direction of changes in AMF abundance, species richness, and species composition in soils from under multispecies native vegetation. In a second stage, the effects of these changes on a native plant, *Plantago lanceolata*, were assessed. Plant species identity had larger impact on AMF abundance, species richness, and species composition as well as on *P. lanceolata* than origin of the species (alien vs. native). This could be due to the character of AMF relationships with the plants, i.e., their mycorrhizal status and dependency on AMF. However, the alterations induced by the plant species in soil chemical properties rather than in AMF community were the major drivers of differences in shoot mass and photosynthetic performance of *P. lanceolata*. We determined that the plants produced species-specific effects on soil properties that, in turn, resulted in species-specific soil feedbacks on the native plant. These effects were not consistent within groups of invaders or natives.

Keywords Arbuscular mycorrhizal fungi (AMF) · Arbuscular mycorrhiza (AM) · Invasive plants · Expansive native plants · Plant species specificity · Soil feedback

Introduction

Plant invasions are one of the most important threats to biodiversity and significant drivers of environmental degradation and change on a global scale. However, in many cases, we do not know the direction and magnitude of invasive plant impacts on the environment, and we are also unable to elucidate which factors influence invasion processes. One of the mechanisms leading to the success of invasive plant species is that invaders change the components of soil environment due to, e.g., the release of secondary metabolites as root exudates and through deposition of litter of various quality and quantity and different uptake or immobilization of nutrients, as well as differential C provision to symbiotic fungi (Wolfe and Klironomos 2005; Stinson et al. 2006; Cantor et al. 2011; Perkins and Nowak 2012; Tanner and Gange 2013). These can modify the chemical and microbiological properties of soils (Batten et al. 2006; Shah et al. 2009; Stefanowicz et al. 2016, 2017, 2018), including the alterations in the abundance and species diversity of the most widespread and important plant symbionts—arbuscular mycorrhizal fungi (AMF) (Sanon et al. 2012; Tanner and Gange 2013; Zubek et al. 2016). These fungi inhabit the roots of a great majority of terrestrial plant species and play an important role in their

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mineral nutrition, protection against biotic and abiotic stresses, and shaping plant community by differently influencing plant species performance (Smith and Read 2008). The disturbance in the stable AMF communities as a result of invaders' colonization can decrease native and increase alien plant performance, thus facilitating plant invasions (Stinson et al. 2006; Shah et al. 2009; Xiao et al. 2014).

The investigations conducted so far have revealed species-specific effects of plant invasions on AMF abundance, species richness, and species composition. For example, the studies by Liang et al. (2004) on *Solidago canadensis* and Chen et al. (2015) on *Chromolaena odorata*, *Ageratina adenophora*, and *Flaveria bidentis* showed that the dominance of these plants increased AMF species richness. It was also found that the invasion of *A. adenophora* increased AMF abundance (Niu et al. 2007). Lekberg et al. (2013) showed that invasions of *Centaurea stoebe* and *Euphorbia esula*, but not *Bromus tectorum*, supported higher abundance and species richness of AMF than multispecies native plant communities. In contrast, the survey performed by Tanner and Gange (2013) and Zubek et al. (2016) demonstrated that *Reynoutria japonica* reduced AMF abundance and species richness. Moreover, two other alien species examined by Zubek et al. (2016), namely *Rudbeckia laciniata* and *Solidago gigantea*, decreased the number of AMF species. The changes in AMF abundance, species richness, and species composition should thus be considered as an important mechanism by which invasive plants outcompete native species (Hawkes et al. 2006; Zhang et al. 2010; Tanner and Gange 2013).

The aforementioned investigations focused on the impact of alien plants on AMF in the field. However, under controlled conditions, no studies have surveyed the influence of invaders and compared their effects with the impact of native plants, which also can be successful colonizers, forming frequently monospecific patches in the areas of their expansion. It is important to note that native plants can influence soil microbial communities using the same mechanisms as invasive ones, but the impact of invaders may be more pronounced, e.g., due to considerable differences in plant traits between invaders and natives, or a novelty of a particular mechanism to a native community (Wolfe and Klironomos 2005). Therefore, we conducted an extensive outdoor pot experiment for two consecutive growing seasons, which aimed at assessing the impact of four alien invasive plants versus two common native plant species on AMF abundance, species richness, and species composition in two soil types. Moreover, the performance of a model, native plant grown subsequently in these soils, was evaluated in the soil feedback pot experiment carried out under laboratory conditions. Understanding the interactions between invasive and native plants and AMF communities is fundamental to recognize the course and mechanisms of invasion and to yield key plant-AMF interactions necessary for the restoration of invaded areas (Busby et al. 2013).

The alien plants used in our study, namely *Impatiens glandulifera* Royle (Balsaminaceae), *Reynoutria japonica* Houtt. (Polygonaceae), *Rudbeckia laciniata* L., and *Solidago gigantea* Aiton (Asteraceae), are included in the world's (Lowe et al. 2000) and/or European (Tokarska-Guzik et al. 2012; Pyšek et al. 2012) lists of the high-impact invasive plants—the transformers, which change the character, condition, form, or nature of ecosystems (Richardson et al. 2000). *I. glandulifera* and *R. japonica* are both of Asian origin, while *R. laciniata* and *S. gigantea* are native to North America. These species were introduced to Europe as ornamental plants and escaped from cultivation into the wild. They invade natural, semi-natural, and anthropogenic habitats (Tokarska-Guzik et al. 2012). The two native species, *Artemisia vulgaris* L. (Asteraceae) and *Phalaris arundinacea* L. (Poaceae), are expansive plants that frequently co-occur with the invaders in different habitats and are their most common competitors. Moreover, they also have become successful invaders after their introduction to North America (Weston et al. 2005; Nelson et al. 2014). *I. glandulifera*, *R. laciniata*, and *S. gigantea* and both native species form arbuscular mycorrhiza (AM), whereas *R. japonica* is non-mycorrhizal (Majewska et al. 2015, 2017; Zubek et al. 2016). The plants were grown in soils representing two habitats, namely unmanaged meadow and tall herb vegetation, located outside and within river valley, respectively, which are frequently colonized by these species. We collected these soils from under multispecies native plant communities to mimic the situation that both invaders and expansive native plants encroach new area. For the laboratory soil feedback pot experiment, we used one of the native species that were present in the plant communities on both soils, *Plantago lanceolata* L. (Plantaginaceae). This model, mycorrhizal species was planted in the soils conditioned by both invaders and natives. We hypothesized that (1) both invasive and native plants significantly impact AMF community as they form monospecific patches in the colonized sites; (2) due to their novel presence in the environment, the invaders condition soils differently and exhibit different plant-soil feedback types on *P. lanceolata* performance (mycorrhizal colonization, biomass, photosynthetic index) than the native species; (3) the direction of the changes caused by the invaders and natives is also shaped by species identity as species differ in their mycorrhizal status or dependency on AM symbiosis; and (4) the effects of the invasive and native plants are also determined by the soil type.

Materials and methods

Soils

The soils for the experiment were collected from two locations: Kraków (49° 59′ 49.5″ N/19° 52′ 13.6″ E) and Zator (49° 59′ 59″ N/19° 26′ 40.5″ E), situated in southern Poland, which represent two different habitats—unmanaged meadow outside river valley

(thereafter "fallow" soil) and tall herb vegetation within river valley ("valley" soil), respectively. We chose these habitats according to the observations conducted by Kostrakiewicz-Gierałt and Zając (2014), Majewska et al. (2015), Stefanowicz et al. (2016, 2017), and Zubek et al. (2016) that the tested invasive and native plants commonly colonize them. Both soils were collected from under multispecies plant community that was devoid of alien plants. For both soil types, only the top ca. 30 cm of soil was collected. The soils were classified as loamy sand (Stefanowicz et al. 2018). The physicochemical properties, namely pH; organic C (C_{ORG}) content; total ($_T$) contents of C_T, N_T, Ca_T, K_T, and P_T; and exchangeable/available ($_{EX}$) contents of Ca_{EX}, K_{EX}, N ($N\text{-}NO_3^-$, $N\text{-}NH_4^+$), and P_{EX}, of the initial soils were examined prior to our experiment. Moreover, we conducted the same analyses at the end of the experiment to determine potential invasive/native plant-induced changes in soil properties (Stefanowicz et al. 2018).

Plants

In the outdoor experiment, we used four invasive (*I. glandulifera*, *R. japonica*, *R. laciniata*, and *S. gigantea*) and two native (*A. vulgaris* and *P. arundinacea*) plants. The seeds of five studied species and the rhizomes of *R. japonica* were gathered in October 2013 and in April 2014, respectively. We used the rhizomes of *R. japonica* in the study due to the rarity or absence of seed production of this species in southern Poland and the vegetative way of spreading (Beerling et al. 1994). Plant material was collected at the same area as soil. For the laboratory soil feedback experiment, we selected *P. lanceolata* as a representative of resident plant species on both soils. This mycorrhizal plant is commonly used in studies evaluating the impact of invasive plants on native plant performance (Lorenzo et al. 2013; Tanner and Gange 2013; Guisande-Collazo et al. 2016; Zubek et al. 2016). The seeds of *P. lanceolata* were obtained from Herbador co. (Poznań, Poland).

The outdoor experiment

Setup and maintenance The experiment was carried out for two growing seasons, from 12 April 2014 to 25 August 2015, in the Jagiellonian University Botanical Garden in Kraków (50° 3′ 57.83″ N, 19° 57′ 19.05″ E). The garden is situated in the temperate climate zone, where the mean annual temperature is 8.2 °C and the mean annual precipitation is 678 mm. The soils from two habitats were sieved through garden sieves (mesh size 1.5 cm) to remove stones, coarse roots, and other particles; then, each soil was homogenized. Six samples of each soil type were collected (initial soils). Then, the soils were put into 10-l plastic round pots (25 cm wide × 30 cm high) with drainage holes and saucer tray, one type of soil per pot. The seeds of five surveyed species were sown separately or in pairs, ca. 30 seeds per pot. In the case of *R. japonica*, one rhizome was transferred into each pot. The seeds were homogenously scattered on the soil surface and coated with 0.5 cm of soil layer (Čuda et al. 2015). In the case of annual *I. glandulifera*, we also sowed 30 seeds per pot in the second year. The following treatment configurations were established: (1) without plants (all plants that emerged from the soil seed bank were consequently thinned out), (2) *A. vulgaris*, (3) *P. arundinacea*, (4) *A. vulgaris* + *P. arundinacea*, (5) *I. glandulifera*, (6) *R. japonica*, (7) *R. laciniata*, and (8) *S. gigantea*. As we observed that *A. vulgaris* and *P. arundinacea* also form mixed patches in natural stands, we established a dual treatment of these species. For each treatment, we had six replicates, 96 pots in total (2 soil treatments × 8 plant treatments × 6 replicates). The pots were arranged in a completely random manner with ca. 50-cm distance between them and kept in open space under natural sunlight conditions. The plants were watered in the spring and summer using 1 l of water per pot, according to need. If any undesirable plant species appeared in the pots, it was immediately removed. During the winter (from October 2014 to March 2015), the plants were protected from cold using bubble wrap (the sides of every single pot were covered to 10 cm above a pot) then randomly grouped into blocks and wrapped up by nonwoven fabric. After 6 months, the cover was removed, and pots were again randomized. After 17 months, we finished the experiment. All pots were transported to the laboratory.

Material harvesting The shoots of bulked plants were harvested and top soil layer (up to 3 cm of the pot depth) was also removed. The remaining soil was removed from the pot by tapping the rim of the pot firmly against a hard surface and then the material was put into a plastic bag. From each pot, we removed 3 cm of soil layer from the sides and bottom. The roots were excavated and gently cleaned from soil residues. The shoots and roots were washed separately in tap water. The dry weight of aboveground parts of plants was measured (Stefanowicz et al. 2018). Belowground parts of plants were taken for staining in order to determine the presence of AMF. The soil from each pot was homogenized and then divided into portions: (1) ca. 100 g for AMF spore isolation, (2) ca. 500 g for establishing the soil feedback experiment, (3) ca. 100 g for PLFA analyses (see below), and (4) ca. 1000 g for physicochemical analyses (Stefanowicz et al. 2018).

Assessment of AMF root colonization Phillips and Hayman (1970) method with minor modifications (Majewska et al. 2015) was used for staining of invasive and native plant roots. The observation of AMF structures was conducted using a light microscope (Nikon Eclipse 80i with Nomarski interference contrast). Arbuscular mycorrhizal fungi colonization was determined as reported by Trouvelot et al. (1986) and the parameters analyzed were mycorrhizal frequency (*F*), relative mycorrhizal root length (*M*), and relative arbuscular richness (*A*).

Arbuscular mycorrhizal fungi spore isolation and identification The spores of AMF were isolated directly from the initial soils, at the experiment setup in 2014. At harvest (2015), we extracted spores from all pots, which represent eight treatments. The procedure of spore extraction ran as follows: ca. 100 g of soil sample was collected from homogenized soil of each pot, then put into plastic zip bag and stored in a refrigerator for a few days until analyzed. The spores were isolated from 50 g of soil by centrifugation (1389 × g for 1 min) in a sucrose solution (Brundrett et al. 1996), rinsed in water on a sieve of 50-μm mesh size, counted in a Petri dish, and mounted on slides in a drop of polyvinyl alcohol/lactic acid/glycerol (PVLG) and in a mixture of PVLG/Melzer's reagent (1:1, *v*/*v*) (Omar et al. 1979). The taxonomical classification of AMF spores was carried out using an Olympus BX light microscope as reported by Błaszkowski (2012).

Phospholipid fatty acid 16:1ω5 analysis Phospholipid fatty acid (PLFA) 16:1ω5 was used as a marker to evaluate the AMF abundance in soils (Olsson 1999). The analysis was performed according to Palojärvi (2006), excluding the lipid extraction done as reported by Macnaughton et al. (1997). The procedures and equipment used in the present study were those by Zubek et al. (2016).

The laboratory soil feedback experiment

Setup and maintenance For the estimation of the performance of the native plant in the tested soils, we conducted the experiment under laboratory conditions. We placed 450 g of the initial soils and the soils from every single pot of each treatment into 500-ml plastic round pots that were 9 cm wide and 12.5 cm high. Seeds of *P. lanceolata* were sown (10 seeds per pot). After 1 week, seedlings were manually thinned out to obtain five per pot. In total, 108 pots were established, 12 pots with the initial soils in 2014 and 96 pots from the treatments of the outdoor experiment in 2015. The plants were maintained in the open Sigma-Aldrich sun bags, which protect from potential infestation between treatments. The plant growth chamber conditions were as follows: temperature of 22 ± 2 °C and light regime 270–280 μmol PAR photons × m^{-2} × s^{-1}, 12/12 h. The pots were randomly situated. The cultures were watered once a week using 35 ml of distilled water.

Material harvesting After 7 weeks of growth, chlorophyll *a* fluorescence measurements were carried out (see below); then, the plants were harvested. The plants were rinsed with tap and then deionized water. The bulked roots of each pot were stained in order to visualize AMF mycelia for the mycorrhizal colonization assessment (see above). The shoots of each individual plant were dried at room temperature and weighed using an electronic analytical balance (Radwag, WPA 60/c/1) with a level of precision of 0.0001 g.

Evaluation of *P. lanceolata* photosynthetic performance Chlorophyll *a* fluorescence transients OJIP of intact and fully expanded leaves were measured using a Handy PEA fluorimeter (produced by Hansatech Instruments Ltd., King's Lynn, Norfolk, UK). The studied material was simultaneously dark-adapted for 30 min before measuring using leaf clips. We carried out the measurements on six leaves of randomly chosen plants of each pot. The data from each individual pot were averaged. The measurements were conducted as reported by Strasser et al. (2004) and Tsimilli-Michael and Strasser (2008). For each pot (sample), the average OJIP fluorescence transients were calculated according to the JIP test (Strasser et al. 2004), with "Biolyzer" software (Laboratory of Bioenergetics, University of Geneva, Switzerland). The performance index (PI_{ABS}), which evaluates the overall photosynthetic performance, was chosen for presentation. The description of this parameter was given by Tsimilli-Michael and Strasser (2008).

Statistical analysis

Two-way analysis of variance (plant × soil type) followed by Tukey's (HSD) test was performed to reveal significant differences in the mycorrhizal parameters (*F*, *M*, *A*), photosynthetic parameter (PI_{ABS}), shoot mass, AMF spore and AMF species numbers, and 16:1ω5 PLFA concentrations in the soils across all treatments. Prior to the analysis, the distribution normality was verified using the Lilliefors test. Levene's test was performed to assess the equality of variances.

The arbuscular mycorrhizal community attributes (i.e., AMF spore number, the number of AMF species, the concentration of 16:1ω5 PLFA) and soil chemical parameters (i.e., pH, C_T, C_{ORG}, N_T, N-NO_3^-, N-NH_4^+, P_T, P_{EX}, K_T, K_{EX}, Ca_T, Ca_{EX}; Stefanowicz et al. 2018) were used to run a canonical discriminant analysis (CDA) to identify which attribute was the most important for separation of particular plant treatments and to verify how well discriminatory variables distinguish particular plant treatments. Due to large differences in soil chemical properties between two soil types, this analysis was applied separately for the "fallow" and "valley" soil treatments, with respect to "predictor" variables. Forward stepwise analysis was used. Discriminatory power was expressed by Wilks' lambda statistic. Before the analysis, the correlation between all variables was checked in order to avoid the matrix ill-conditioning problem.

Two-way permutational multivariate analysis of variance (PERMANOVA) was used to analyze the differences in AMF species composition between the plant and soil treatments (Anderson 2001). The analysis was based on the matrix of species presence/absence in particular treatments using Jaccard coefficient, with 9999 permutations.

We also aimed to investigate which soil properties could have been causal drivers of the feedback effect. As the mycorrhizal parameters (*F*, *M*, and *A*) strongly correlated with each

other ($R > 0.9$), only the relative mycorrhizal root length (M) was incorporated in further analysis. The effect of soil chemical properties (Stefanowicz et al. 2018) and AMF community properties on *M*, shoot mass, and PI_{ABS} of *P. lanceolata* was evaluated by separate stepwise multiple linear regressions using forward variable selection with a threshold of $p < 0.05$ to entry. Strongly correlated independent variables ($R > 0.95$) were removed prior to the analysis. A detailed residual analysis was performed in order to obtain reliable regression coefficients and detect potential outliers (extreme cases).

The analyses were carried out using STATISTICA v. 12 (Statsoft, Tulsa, OK, USA) and PAST v. 3.10 (Hammer et al. 2001).

Results

The outdoor experiment

AMF colonization of invasive and native plants

The roots of all surveyed plant species were colonized by AMF except those of *R. japonica*. The mycorrhizal frequency (*F*) was influenced by both plant species and soil type (significant plant × soil interaction; Table 1, Fig. 1), with the lowest *F* values for *A. vulgaris* + *P. arundinacea* in the fallow soil. The highest mean values of relative mycorrhizal root length (*M*) and relative arbuscular richness (*A*) were observed in *A. vulgaris*, *R. laciniata*, and *S. gigantea*, and the lowest in *A. vulgaris* + *P. arundinacea*, *P. arundinacea*, and *I. glandulifera* (significant plant effect). Mean values of these parameters were higher in the river valley than in the fallow soil (significant soil effect; Table 1, Fig. 1).

AMF abundance assessed by PLFA marker

The 16:1ω5 PLFA concentration was influenced by both plant and soil type (significant plant × soil interaction; Table 1). The highest mean values of this parameter were observed in the soil from under *A. vulgaris*, whereas the lowest in the treatment without plants. *A. vulgaris* also increased 16:1ω5 PLFA concentrations in comparison to the initial soils. The decreased values of this marker in comparison to both initial soils were found for soil without plants, *I. glandulifera*, and *R. japonica* in the valley soils, as well as *S. gigantea* in the fallow soil (Fig. 2).

AMF spore number, species richness, and species composition

The highest mean values of AMF spore number were recorded in the case of *R. laciniata*, independent of soil type, and for *S. gigantea* growing in the fallow soil (significant plant × soil interaction; Table 1). In these cases, both plant species increased the number of AMF spores in comparison to their numbers in other treatments (Fig. 2).

In total, the spores of 20 AMF species were isolated from all treatments. The spores of *Septoglomus constrictum*, *Acaulospora paulinae*, *Diversispora epigaea*, and *Funneliformis mosseae* were most frequent, being found in 39, 21, 21, and 19 samples (pots) (Table S1). The number of AMF species (species richness) was influenced by the plant species (Table 1). It was higher under *R. laciniata* and

Table 1 The results of two-way ANOVA for the effects of plant, soil type, and their interaction on plant and soil parameters in the outdoor and laboratory soil feedback experiments

Parameters		Plant			Soil			Plant × soil			Error
		F	*p*	df	*F*	*p*	df	*F*	*p*	df	df
Outdoor experiment											
Mycorrhizal parameters	*F*—mycorrhizal frequency	*5.42*	*< 0.001*	5	*13.88*	*< 0.001*	1	*2.64*	*0.032*	5	60
	M—relative mycorrhizal root length	*18.55*	*< 0.001*	5	*8.31*	*0.005*	1	1.79	0.129	5	60
	A—relative arbuscular richness	*18.79*	*< 0.001*	5	*8.20*	*0.006*	1	1.63	0.165	5	60
Concentration of 16:1ω5 PLFA		*27.49*	*< 0.001*	8	0.07	0.798	1	*6.83*	*< 0.001*	8	90
Number of AMF spores		*27.03*	*< 0.001*	8	0.83	0.365	1	*2.72*	*0.010*	8	90
Number of AMF species (species richness)		*7.26*	*< 0.001*	8	0.05	0.949	1	1.58	0.142	8	90
Laboratory soil feedback experiment											
Mycorrhizal parameters	*F*—mycorrhizal frequency	*17.524*	*< 0.001*	8	*51.122*	*< 0.001*	1	*2.184*	*0.036*	8	90
	M—relative mycorrhizal root length	*16.916*	*< 0.001*	8	*55.738*	*< 0.001*	1	1.502	0.168	8	90
	A—relative arbuscular richness	*15.212*	*< 0.001*	8	*46.328*	*< 0.001*	1	1.489	0.172	8	90
Shoot mass		*27.821*	*< 0.001*	8	*89.837*	*< 0.001*	1	*8.045*	*< 0.001*	8	90
PI_{ABS}—photosynthetic performance index		*9.818*	*< 0.001*	8	*82.775*	*< 0.001*	1	*5.715*	*< 0.001*	8	90

The effects in italics are statistically significant

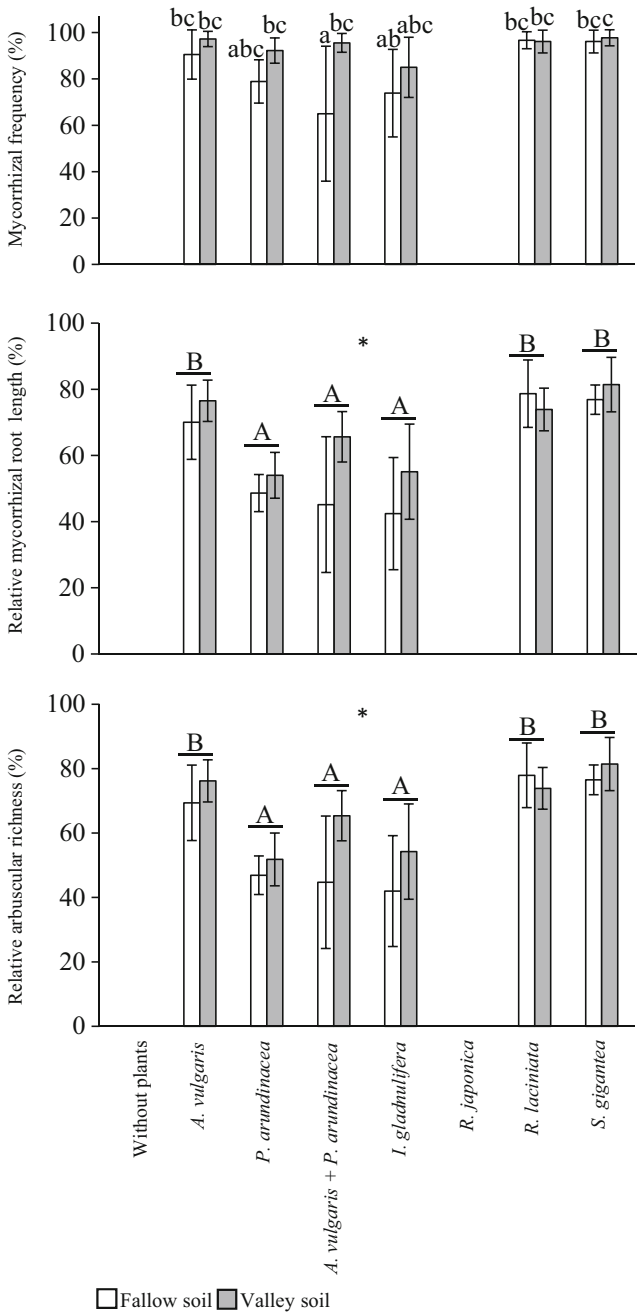

Fig. 1 Mycorrhizal frequency (*F*), relative mycorrhizal root length (*M*), and relative arbuscular richness (*A*) (means ± SD; $N = 6$) in the treatments: without plants, *Artemisia vulgaris*, *Phalaris arundinacea*, *Artemisia vulgaris* + *Phalaris arundinacea*, *Impatiens glandulifera*, *Reynoutria japonica*, *Rudbeckia laciniata*, and *Solidago gigantea* in the fallow and river valley soils. *Lowercase letters above the bars* indicate the statistically significant interaction between the plant and soil effects, *capital letters above the bars* show the significant main effect of plant, the different letters above the bars indicate statistically significant differences, and *asterisks* indicate the significant main effect of soil; for each $p < 0.05$. See Table 1 for details on the main effects and interactions

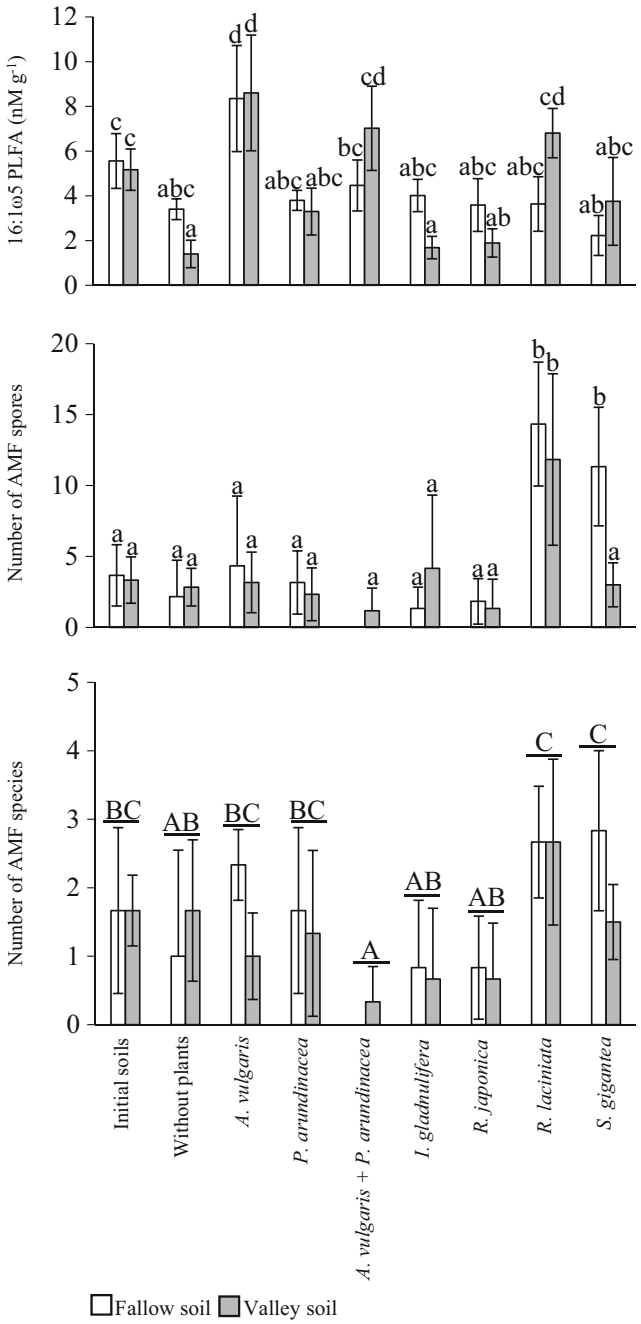

Fig. 2 The concentration of 16:1ω5 phospholipid fatty acid in soil, the number of arbuscular mycorrhizal fungi (AMF) spores in 50 g of fresh soil, and AMF species number (species richness) (means ± SD; $N = 6$) for initial soils and the treatments: without plants, *Artemisia vulgaris*, *Phalaris arundinacea*, *Artemisia vulgaris* + *Phalaris arundinacea*, *Impatiens glandulifera*, *Reynoutria japonica*, *Rudbeckia laciniata*, and *Solidago gigantea* in the fallow and river valley soils. *Lowercase letters above the bars* indicate the statistically significant interaction between the plant and soil effects, *capital letters above the bars* show the significant main effect of plant, the different letters above the bars indicate statistically significant differences, for each $p < 0.05$. See Table 1 for details on the main effects and interactions

S. gigantea in comparison to the treatments: without plants, *A. vulgaris* + *P. arundinacea*, *I. glandulifera*, and *R. japonica*. AMF species richness in the *A. vulgaris* + *P. arundinacea* treatment was also lower than those in *A. vulgaris*, *P. arundinacea*, and initial soils (Fig. 2).

PERMANOVA showed significant differences in AMF species composition between both plant ($F = 1.61$, $p < 0.05$) and soil ($F = 4.19$, $p < 0.05$) treatments. The interaction between plant treatments and soils was not significant ($F = 1.19$, $p = 0.07$; Table S2).

Factors differentiating plant treatments in the outdoor experiment

Factors differentiating plant treatments varied in particular soil type. Canonical discriminant analysis (CDA) showed that particular plant treatments on fallow soil differed significantly in terms of two mycorrhizal and six soil parameters. The remaining parameters did not have a significant discriminating power (Table S3). Standardized canonical coefficients indicated that the P_T and P_{EX} as well as K_{EX} and Ca_{EX} concentrations in soils were related to the first canonical discriminant function, along which initial soil was the most clearly separated due to low P_T and Ca_{EX} and high P_{EX} and K_{EX} concentrations. N-NH_4^+ concentration, AMF spore number, and K_T and Ca_{EX} concentrations were related to the second canonical discriminant function. In this case, invasive species, i.e., *R. laciniata*, *S. gigantea*, and *R. japonica*, were clearly separated from another invasive species *I. glandulifera* along the second canonical discriminant function due to low N-NH_4^+ and K_T concentrations as well as high AMF spore number and Ca_{EX} concentration. The same trend was found for native species, *A. vulgaris* and *P. arundinacea* (Fig. 3).

As regards treatments on valley soil, altogether, ten variables (including 2 mycorrhizal and 8 soil parameters) had the largest contribution to the discrimination of particular plant treatments, whereas the remaining parameters did not have a significant discriminating power (Table S3). P_{EX} and N-NO_3^- had the greatest contribution to separate plant treatments along the first canonical discriminant function, along which *I. glandulifera* treatments were the most clearly separated due to higher values of these parameters. Initial soil treatments were clearly separated along the second canonical discriminant function due to low Ca_{EX} and high K_{EX} and N-NH_4^+ concentrations. Analogously to the case of initial soil treatments, native plant species treatments and soil without plants were separated from invasive plant species treatments along this canonical discriminant function (Fig. 3).

The laboratory soil feedback experiment

AMF colonization of *P. lanceolata*

The mycorrhizal frequency (*F*) of *P. lanceolata* was influenced by both plant and soil type (significant plant × soil interaction; Table 1). The lowest mean values of *F* parameter were observed for fallow soils in the case of the soil without plants and *R. japonica*. They were also significantly lower than in the initial soil of this type. The mean value of this parameter was also decreased in *R. japonica* valley soil in comparison to initial soil of this type (Fig. 4). *P. lanceolata* individuals growing in the soil from treatments without plants and *R. japonica* were characterized by lowest mean values of relative mycorrhizal root length (*M*) than in the other treatments (significant plant effect). Similar trends were found for relative arbuscular richness (*A*), with the lack of differences between *I. glandulifera* and *R. japonica* (Fig. 4). The *M* and *A* parameters were higher in the river valley soil than in the fallow (significant soil type effect; Table 1, Fig. 4).

P. lanceolata shoot mass

The shoot mass of *P. lanceolata* individuals was influenced by both plant and soil types (significant plant × soil interaction; Table 1). The higher mean values of this parameter were observed for plants growing in the fallow than in valley soil in the case of *A. vulgaris*, *P. arundinacea*, *A. vulgaris* + *P. arundinacea*, and *S. gigantea*. *P. lanceolata* shoot mass was significantly increased in the treatments without plants (fallow), *A. vulgaris*, *P. arundinacea*, *A. vulgaris* + *P. arundinacea* (fallow), *I. glandulifera*, *R. laciniata* (fallow), and *S. gigantea* (fallow) in comparison to both initial soils. In the case of valley soil, the higher shoot mass was also found for soil without plants, *R. japonica*, *R. laciniata*, and *S. gigantea* in comparison to the initial soil of this type (Fig. 5).

Photosynthetic performance index of *P. lanceolata*

Photosynthetic performance index (PI_{ABS}) of *P. lanceolata* was affected by both plant species and soil type (significant plant × soil interaction; Table 1). The mean value of this parameter was lowest for the initial fallow soil in comparison to all other treatments. The higher values of PI_{ABS} in fallow than in valley soil were also found for soil without plants and *S. gigantea* (Fig. 5).

Effect of AMF community and soil chemical parameters on *P. lanceolata* (drivers of the soil feedback effect)

The selection models in linear regression analyses are presented in Table 2. Forward stepwise regression analysis with soil and AMF community predictor variables and the relative mycorrhizal root length (*M*) of *P. lanceolata* as the dependent variable showed that this parameter was significantly influenced by 16:1ω5 PLFA and the concentrations of N-NH_4^+ and P_T. Four soil chemical factors proved to have significant impact on shoot mass, which was positively associated with the N-NO_3^- and Ca_{EX} concentrations as well as pH, whereas negatively with the concentration of K_{EX}. From the 15 evaluated soil and AMF factors, only three soil properties proved to be significantly associated with photosynthetic performance

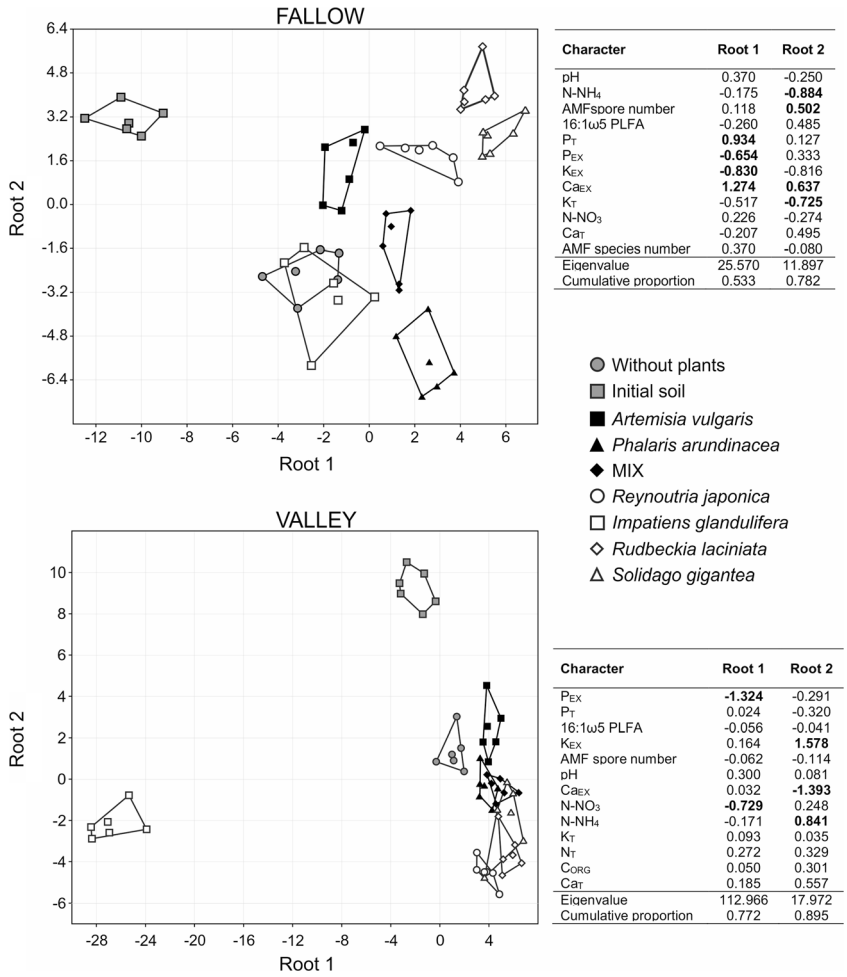

Fig. 3 Scatterplot presenting the results of canonical discriminant analysis of treatments representing different plant species for two soil types separately onto the first and second discriminant functions (canonical roots). Standardized coefficients for canonical variables are also provided. See the "Materials and methods" section for a description of variables

(PI_{ABS}) of *P. lanceolata*, i.e., the concentration of Ca_{EX} and K_{EX} as well as pH (Table 2).

Discussion

Our investigation is the first study on the influence of four most successful and high-impact global or European invaders, i.e., *I. glandulifera*, *R. japonica*, *R. laciniata*, and *S. gigantea*, on AMF abundance, species richness, and species composition in the pot experiment. Moreover, we compared for the first time the effects of invasive and expansive native plants on the aforementioned AMF community attributes and the performance of a native plant grown in soils conditioned by both groups of plants.

In line with our first and third hypotheses, but contrary to the second one, both invasive and native plants had significant impact on AMF community; however, the direction and magnitude of these effects depended on plant species identity rather than being consistent within groups of invaders and natives. Low AMF abundance, spore number, and species richness in the soils from under *R. japonica* confirmed earlier reports from the field investigations on the effects of this non-mycorrhizal species (Tanner and Gange 2013; Zubek et al. 2016). Detrimental effects on AMF community seem to be a rule for AMF non-hosts as similar trends were also showed for other non-mycorrhizal species, i.e., *Alliaria petiolata* and *Brassica nigra* (Brassicaceae), the invaders of North America that decreased AMF abundance and diversity (Callaway et al. 2008) and reduced spore germination rates (Pakpour and Klironomos 2015), respectively. However, similarly to *A. petiolata* and *B. nigra*, *R. japonica* did not eliminate AMF from soil, as revealed by the presence of spores, the concentrations of AMF-PLFA marker, and the colonization of *P. lanceolata* grown subsequently in these soils. The abundance of AMF propagules under *R. japonica* in our experiment could be due to the persistence of spores from the initial soils and/or the growth of AMF in symbioses with liverworts and mosses that occurred in the pots. These seem to be supported by the comparable level of propagules in the treatment without plants.

The reduced AMF-PLFA abundance in comparison to some other treatments was also found in the case of *I. glandulifera*. Similarly, Ruckli et al. (2014) and Tanner and Gange (2013) showed that *I. glandulifera* reduced AMF abundance in soils as revealed by decreased colonization of

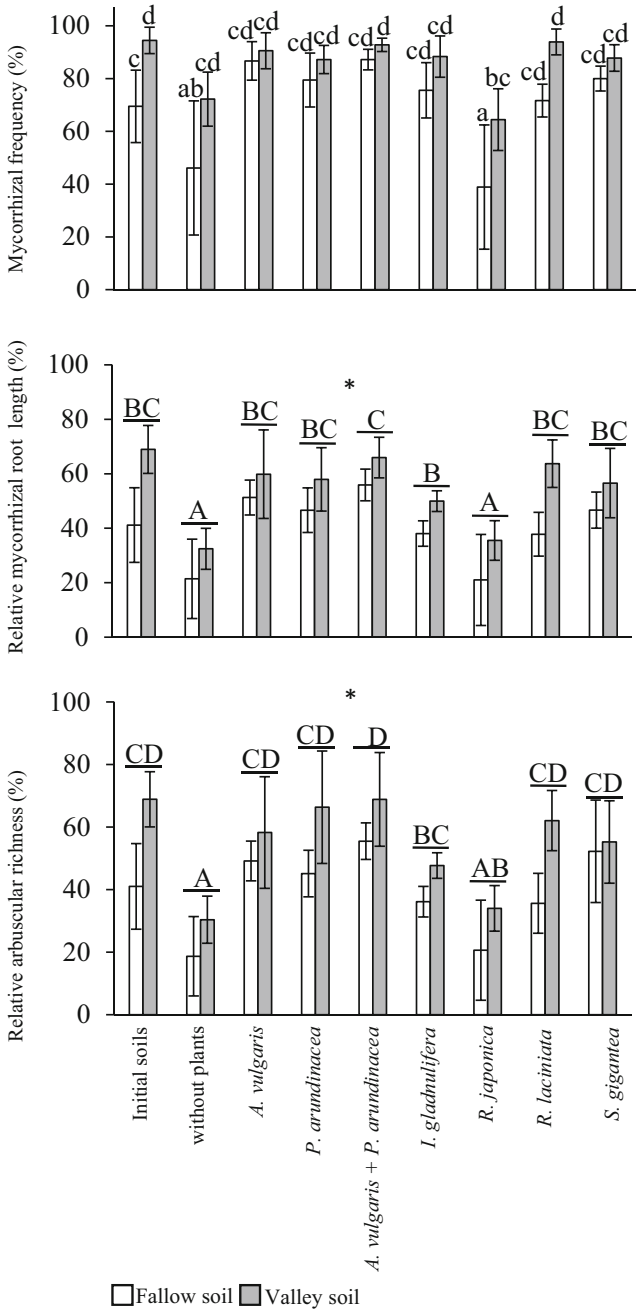

Fig. 4 Mycorrhizal colonization (means ± SD; $N = 6$) of *Plantago lanceolata* grown in the fallow and river valley initial soils and the soils from the treatments: without plants, *Artemisia vulgaris*, *Phalaris arundinacea*, *Artemisia vulgaris* + *Phalaris arundinacea, Impatiens glandulifera*, *Reynoutria japonica*, *Rudbeckia laciniata*, and *Solidago gigantea*. *Lowercase letters above the bars* indicate the statistically significant interaction between the plant and soil effects, *capital letters above the bars* show the significant main effect of plant, the different letters above the bars indicate statistically significant differences, and *asterisks* indicate the significant main effect of soil; for each $p < 0.05$. See Table 1 for details on the main effects and interactions

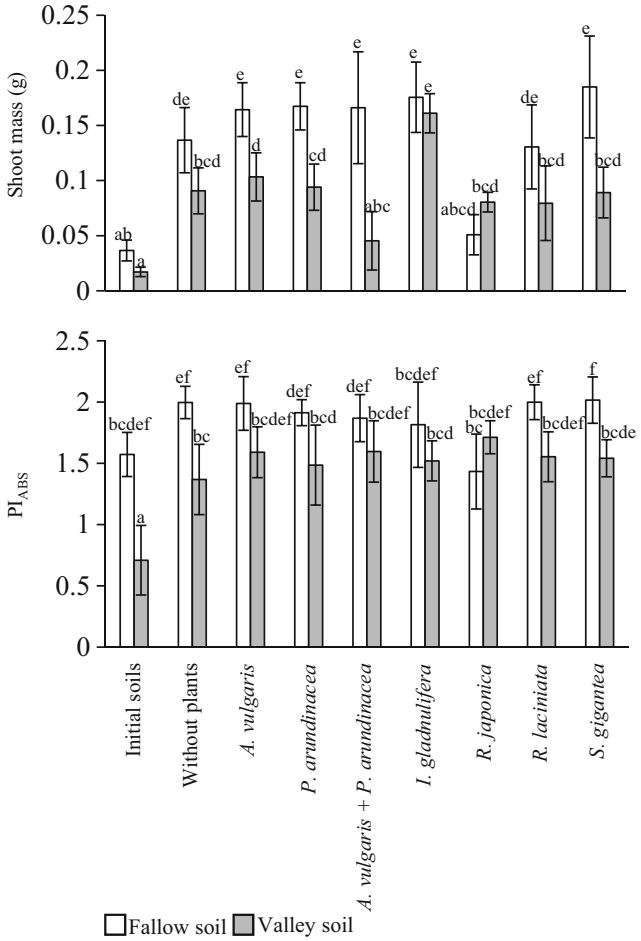

Fig. 5 Shoot mass and photosynthetic performance index (PI_{ABS}) of *Plantago lanceolata* (means ± SD; $N = 6$) grown in the initial soils and in the soils from the treatments: without plants, *Artemisia vulgaris*, *Phalaris arundinacea*, *Artemisia vulgaris* + *Phalaris arundinacea*, *Impatiens glandulifera*, *Reynoutria japonica*, *Rudbeckia laciniata*, and *Solidago gigantea*. *Lowercase letters above the bars* indicate the statistically significant interaction between the plant and soil effects and the different letters above the bars indicate statistically significant differences; for each $p < 0.05$. See Table 1 for details

native plants grown subsequently in these soils. Species from this genus are reported to be facultatively mycorrhizal, having usually low mycorrhizal dependencies (Chmura and Gucwa-Przepióra 2012; Tanner and Gange 2013). As AMF contribute to the maintenance of proper soil quality due to particle-binding properties of hyphae and their exudates (Smith and Read 2008), it is possible that the negative effect on AMF community induced by *I. glandulifera* observed in this and the aforementioned studies may in addition be a factor contributing to soil erosion caused by this species (Greenwood and Kuhn 2014).

The species specificity in the impact on AMF community characteristics was further confirmed even within one family, Asteraceae; however, in this case, the effects were relatively consistent, being neutral or positive. Increased concentrations of AMF-PLFA marker were found for *A. vulgaris*, whereas higher number of spores and higher species richness were detected for *R. laciniata* and *S. gigantea* in comparison with

Table 2 Result of stepwise multiple regression analysis for the effect of AMF community and soil parameters on relative mycorrhizal root length (*M*), shoot mass, and photosynthetic performance index (PI_{ABS}) of *Plantago lanceolata*. See the "Materials and methods" section for a description of variables

Variable	Standardized β coefficient	SE	*t*	*p*
M—$R^2 = 0.51$				
Intercept			0.044	0.965
16:1ω5 PLFA	*0.457*	*0.076*	*6.010*	*< 0.001*
$N\text{-}NH_4^+$	*0.303*	*0.078*	*3.882*	*< 0.001*
P_T	*0.225*	*0.109*	*2.053*	*0.043*
The number of AMF spores	0.139	0.079	1.753	0.083
Ca_T	− 0.292	0.196	− 1.488	0.140
K_{EX}	0.398	0.315	1.264	0.209
$N\text{-}NO_3^-$	− 0.138	0.117	− 1.177	0.242
K_T	0.320	0.351	0.910	0.365
Shoot mass—$R^2 = 0.67$				
Intercept			*− 3.790*	*< 0.001*
$N\text{-}NO_3^-$	*0.643*	*0.096*	*6.688*	*< 0.001*
Ca_{EX}	*0.310*	*0.077*	*4.042*	*< 0.001*
K_{EX}	*− 0.991*	*0.261*	*− 3.801*	*< 0.001*
pH	*0.723*	*0.264*	*2.741*	*0.007*
P_{EX}	0.140	0.073	1.924	0.057
16:1ω5 PLFA	0.125	0.068	1.851	0.067
Ca_T	0.278	0.169	1.649	0.103
The number of AMF species	− 0.095	0.061	− 1.554	0.124
P_T	0.130	0.095	1.368	0.175
PI_{ABS}—$R^2 = 0.57$				
Intercept			*2.454*	*0.016*
K_{EX}	*− 1.638*	*0.223*	*− 7.336*	*0.000*
Ca_{EX}	*0.253*	*0.079*	*3.213*	*0.002*
pH	*0.645*	*0.286*	*2.254*	*0.026*
16:1ω5 PLFA	0.132	0.070	1.882	0.063
The number of AMF spores	− 0.117	0.074	− 1.572	0.119
N_T	− 0.313	0.236	− 1.322	0.189
$N\text{-}NH_4^+$	− 0.089	0.075	− 1.193	0.236

The results in italics are statistically significant

some other treatments. Plants from Asteraceae, including invasive ones, are usually highly mycorrhizal and dependent on AM for their growth and/or element acquisition (Shah et al. 2008; Lekberg et al. 2013; Majewska et al. 2015, 2017; Zubek et al. 2016). Therefore, attaining local dominance, they may have no effect or can enhance AMF abundances relative to native mixed plant communities or monospecific patches of non-mycorrhizal/less AM-dependent plants.

The dual-species treatment with *A. vulgaris* and *P. arundinacea* had in some cases detrimental effect on AMF community characteristics, namely the number of AMF species and spores, when comparing to both single treatments of these two plants and other tested species. The mechanisms are difficult to explain, but it is possible that this is due to interspecific competition between these two expansive plants. De Deyn et al. (2010) found that the effect of particular plant species on AMF abundance in mixed plant communities depends on their abundance and/or interactions with other plant species.

Various effects of plant species on AMF abundance, species richness, and species composition could be due to several mechanisms. First, a non-mycorrhizal plant, such as *R. japonica*, can reduce AMF abundance by the lack of organic C inputs to fungi (Tanner and Gange 2013; Zubek et al. 2016). Second, plants may impact AMF community due to production of secondary metabolites that either suppress AMF development, as in the case of AMF non-host *A. petiolata* (Stinson et al. 2006; Callaway et al. 2008; Cantor et al. 2011), or selectively modify composition of AMF community by enhancing the most beneficial AMF and inhibiting less favorable ones, as it was suggested for a mycorrhizal invader *S. canadensis* (Yuan et al. 2014). Third, plants through their influence on soil

physicochemical properties may indirectly affect AMF communities (Shah et al. 2009). As revealed in our field investigations (Stefanowicz et al. 2017) and also further supported in this experiment (Stefanowicz et al. 2018), the plants under study significantly changed some chemical soil properties. This was illustrated by CDA which revealed that soil chemical properties played an important role in the differentiation of particular treatments in our experiment.

We found that changes in AMF species composition can occur under plant monoculture even after two growing seasons. Similarly, Zhang et al. (2010) showed that the composition of AMF community changed in response to *S. canadensis* invasion in the same timescale. In contrast, Day et al. (2015) revealed that decades of invasion by *Vincetoxicum rossicum* resulted in alterations in AMF community composition but these changes did not occur over the course of one growing season. *R. japonica*, *R. laciniata*, and *S. gigantea* were found not to change AMF community composition in the field (Zubek et al. 2016). The present study was based on spore assays; therefore, molecular tools need to be applied on soil samples to elucidate if these are a result of differences in sporulation or that some AMF species decline or are eliminated by the plants under study (Oehl et al. 2017; Turrini et al. 2016, 2018). Nevertheless, Bunn et al. (2015) found that AMF community composition was altered in invaded areas in the case of 78% of the studies examined in the meta-analysis. This could be due to a change in host identity as plant species can harbor different AMF taxa (Bunn et al. 2015; Turrini et al. 2016, 2018).

The effects of plant species identity on AMF abundance, species richness, and species composition were also influenced by soil type, which is in line with our fourth hypothesis. Therefore, the strength and direction of the impact of plants on these soil microorganisms can differ among sites due to various edaphic conditions.

Different effects on the performance of several native plant species were found on soils overgrown by alien plants in comparison to soils from under native vegetation, with the dominance of negative (Ruckli et al. 2014; Sanon et al. 2012; Zhang et al. 2010; Stinson et al. 2006; Callaway et al. 2008; Vogelsang and Bever 2009; Wilson et al. 2012; Zubek et al. 2016) over neutral and positive (Shannon et al. 2014; Zubek et al. 2016) feedbacks. For example, Shannon et al. (2014) found that two invaders, *Lonicera maackii* and *Ligustrum vulgare*, decreased, whereas *Elaeagnus umbellata* invasion increased AMF colonization of the native community; however, these effects did not impact the biomass of native plants. The decreased levels of AMF colonization and/or biomass of *P. lanceolata*, *Trifolium pratense*, and *Lotus corniculatus* in the field-collected soil conditioned by *R. japonica* and *I. glandulifera* were found by Tanner and Gange (2013). Zubek et al. (2016) observed that field-collected soils from under *R. japonica*, *R. laciniata*, and *S. gigantea* had no effect on the AMF colonization rate and biomass, but affected the photosynthetic performance and/or element concentrations of *P. lanceolata* and *Trifolium repens*. However, the directions and magnitude of their response depended on both species identity and the mycorrhizal status of invaders. As far as the soil feedbacks on *P. lanceolata* in this experiment are concerned, the decreased AMF colonization rates in the soil without plants and *R. japonica* treatments, but increased biomass in most treatments and enhanced photosynthetic performance index in the valley soil in comparison to the initial soils, were found. Plant species identity and soil type interactions had significant effects on *P. lanceolata*. However, as revealed by stepwise multiple regression analysis, these effects were largely driven by soil chemical properties. AMF abundance in the soil along with the concentrations of N-NH_4^+ and total P had significant effect on the degree of *P. lanceolata* colonization. However, for the shoot mass and photosynthetic performance index, only chemical properties played a significant role. Thus, possible alterations in soil chemical properties caused by plants attaining local dominance, rather than in AMF community, may be major drivers of differences in native plant performance grown subsequently on these soils. The fluctuations of element availability in soils conditioned by the plant species might be responsible for the enhanced shoot mass and photosynthetic performance index of *P. lanceolata* in comparison to the effects of initial soils. Furthermore, the effects of soil microorganisms other than AMF on *P. lanceolata* parameters cannot be ruled out.

Except for *R. japonica*, which originated from rhizomes, the shoot mass from other treatments in our pot experiment was comparable (Stefanowicz et al. 2018). In nature, however, *S. gigantea*, *R. japonica*, *R. laciniata*, and *I. glandulifera* can reach ca. 2 m and produce higher biomass per particular area/soil volume in comparison to *A. vulgaris* and *P. arundinacea*. The increased biomass of the invaders over native plants in the field can enhance the effects observed in this experiment.

Conclusions

Plant species identity had a larger impact on AMF abundance, species richness, and species composition as well as the effects on plants grown subsequently in the soils than origin of the species (alien vs. native). This could be due to the character of the relationship with plants, i.e., their mycorrhizal status and their dependency on AMF. However, alterations in soil chemical properties caused by plants attaining local dominance rather than in AMF community may be major drivers of differences in biomass and photosynthetic performance of native plants grown subsequently in these soils. The changes caused by the invasive/expansive plants in soil properties develop over such a short period as two growing seasons. More studies are needed to reveal if soil properties altered by the invasive/native plants may contribute to the competitive

ability of these species in colonizing new areas over other plants. Mechanisms responsible for the effects observed need to be elucidated, including studies in secondary metabolites that may be related to the modifications of soil environment.

From the conservational point of view, our study showed that not only invasive but also expansive native plants forming monospecific patches can affect AMF community. It thus seems to be important to monitor changes in soils also under native plants attaining local dominance. Nevertheless, the effects of plants under study on AMF attributes and the model plant performance were not drastic, even in the case of a non-mycorrhizal plant. Moreover, they were positive for *P. lanceolata* growth and photosynthetic performance in some cases. This seems to be promising for restoration of sites after removal of these plants.

Authors' contributions S.Z. and M.L.M. planned and designed the research. M.L.M., S.Z., A.M.S., and M.N. performed the experiments; JB identified AMF species; M.L.M., K.R., and S.Z. analyzed the data and prepared figures and tables; and M.L.M. and S.Z. wrote the paper with the input of other co-authors.

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