



Species-specific effects of plant invasions on activity, biomass, and composition of soil microbial communities

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Abstract This study assessed the effects of *Reynoutria japonica*, *Rudbeckia laciniata*, and *Solidago gigantea* invading sites within and outside river valleys on activity, biomass, and composition of soil microbial communities. Microbial properties such as soil respiration, urease and arylsulfatase activities, microbial biomass (based on substrate-induced respiration, or SIR, and phospholipid fatty acids, or PLFA), and community composition (based on PLFA) were determined. *R. japonica* encroached on sites characterized by the lowest values of microbiological properties and *R. laciniata* on sites with the highest microbiological quality. The effect of invasion on soil microbial properties depended on the invasive plant species. *R. japonica* significantly decreased microbial biomass, determined by both SIR and total PLFA, urease activity, fungal PLFA, fungal:bacterial PLFA ratio, gram-negative bacterial PLFA, and soil respiration in comparison to soil under adjacent native plant communities. Microbial community composition also differed between soils under *R. japonica* and those under native plants. In contrast, *R. laciniata* and *S. gigantea* did not influence most microbial properties, though *S. gigantea* significantly increased fungal PLFA and *R. laciniata* and *S. gigantea* increased fungal:bacterial PLFA ratio. The effects of plant invasion on microbial properties were basically similar in soils located within and

outside river valleys, probably because initially (i.e., before invasion) soils from the two locations were largely similar in terms of basic properties such as texture, moisture, pH, C:N ratio, and most microbial properties.

Keywords Plant invasion · *Reynoutria japonica* · *Rudbeckia laciniata* · *Solidago gigantea* · Soil microbial communities · PLFA

Introduction

Invasive plants alter ecosystem structure and functioning, as they differ from natives in the physiology, leaf-area allocation, shoot allocation, growth rate, size, and fitness (Ehrenfeld 2003; Liao et al. 2008; Van Kleunen et al. 2010). Plant invasions considerably reduce the diversity and abundance, or change the composition of aboveground and belowground communities, including soil microbial communities (Belnap and Phillips 2001; Yeates and Williams 2001; Broz et al. 2007; Kappes et al. 2007; Hejda et al. 2009; Morón et al. 2009; Aguilera et al. 2010; Lenda et al. 2013). Indeed, invasive plants can change the composition or abundance of complex microbial communities and particular microbial groups, such as saprotrophic, mycorrhizal or pathogenic fungi, or ammonia-oxidizing bacteria (Kourtev et al. 2002; Hawkes et al. 2005; Batten et al. 2006; Broz et al. 2007; Niu et al. 2007; Zhang et al. 2009a, 2009b; Mincheva et al. 2014; Majewska et al. 2015). Crucial ecosystem processes, for example, organic matter decomposition and mineralization or nitrogen fixation, are also modified by invaders (Rice et al. 2004; Hawkes et al. 2005; Liao et al. 2008; Tharayil et al. 2013; Mincheva et al. 2014). These modifications may lead to changes in soil nutrient pools and

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element cycling, engendering positive feedback that potentially stabilizes current or accelerates further invasion, and prevent re-establishment of native species (Ehrenfeld 2003; Niu et al. 2007; Liao et al. 2008; Pii et al. 2015). The greater the invader-induced changes in soil, the greater the feedback that may be expected (Scharfy et al. 2010).

The magnitude and direction of changes in soil characteristics and processes brought about by invasion depend on local habitat conditions, invasive plant species traits, and/or the interaction of both (Meyerson et al. 2000; Ehrenfeld 2003; Koutika et al. 2007; Dassonville et al. 2008; Scharfy et al. 2009; Vilà et al. 2011; Hulme et al. 2013; Castro-Díez et al. 2014). Dassonville et al. (2008) reported that invasion increased nutrient concentrations of surface soils with initially low nutrient concentrations, while under the opposite conditions, a negative impact was mainly observed. Similarly, Scharfy et al. (2009) discovered that the effects of invasion on some soil physico-chemical properties depended on P availability, being more pronounced at more P-rich sites.

Reynoutria japonica, *Rudbeckia laciniata*, and *Solidago gigantea* aggressively invade anthropogenic, semi-natural, and natural habitats in Europe, forming dense, near-monoculture stands. They exert negative influence on the biodiversity of valuable natural and extensively managed habitats (Zelnik 2012). These species are considered transformers (Tokarska-Guzik et al. 2010), i.e., invasive species that “change the character, condition, form, or nature of ecosystems over a substantial area” (Pyšek et al. 2004); therefore, their effects on soil microbial processes and thus soil functioning (Nannipieri et al. 2003) require detailed investigations. Previous research has been often conducted using either one or a small number of study sites, a single invasive species/genus, and/or measuring few microbial properties, making generalizations on the impact of the invasion on soil functioning problematic (Chapuis-Lardy et al. 2006; Herr et al. 2007; Scharfy et al. 2009, 2010; Aguilera et al. 2010; Dassonville et al. 2011; Tharayil et al. 2013; Mincheva et al. 2014). To the best of our knowledge, data on the influence of *R. laciniata* invasion on soil microbial properties are lacking.

We performed an extensive investigation based on 48 independent study sites to assess the effects of *R. japonica*, *R. laciniata*, and *S. gigantea* on the activity, biomass, and composition of soil microbial communities. The study sites were located either outside or within river valleys (on floodplains); the latter were affected by fluvial processes and expected to differ from the former in terms of microclimate, the presence of alluvial materials, and soil properties. We hypothesized that the invasion would influence soil microbial properties and thus soil functioning and that the direction and magnitude of the changes would depend on the invasive species identity and location (within or outside valleys).

Materials and methods

Invasive plant species

Three invasive plant species were selected for the study: *R. japonica* Houtt. [= *Fallopia japonica* (Houtt.) Ronse Decr., = *Polygonum cuspidatum* Sieb. & Zucc.] (Polygonaceae), *R. laciniata* L. (Asteraceae), and *S. gigantea* Aiton [= *S. serotina* Aiton] (Asteraceae). These perennial herbs can reach 1.2–3 m in height. *R. japonica* is native to eastern Asia, *R. laciniata* and *S. gigantea* to North America. They invade a range of habitats such as riparian zones around standing waters or streams, floodplain woods, forest clearings, swamps, wastelands, grasslands, cultivated field margins, fallows, roadsides, and/or areas along railroad tracks (Tokarska-Guzik et al. 2010; Sudnik-Wójcikowska 2011; Bzdęga et al. 2012; Zelnik 2012).

Study sites and soil sampling

Study sites were established on ca. 7500 km² area in southern Poland (from 18° 55' E to 20° 31' E and from 49° 50' N to 50° 22' N; altitude from 180 to 320 m a.s.l.) (Fig. 1). The area lies in the transitional climate zone between a temperate oceanic climate in the west and a temperate continental climate in the east. Mean annual temperature fluctuates between 7 and 9 °C and precipitation between 700 and 900 mm. The vegetation season (days with average temperature >5 °C) spans a period between 210 and 230 days.

Forty-eight study sites were located within ($N = 24$) and outside ($N = 24$) river valleys (Fig. 1). The sites were localized relatively far from each other (a minimum of 0.4 km) and separated by areas overgrown by distinct plant communities in order to limit the possibility that the properties of one study site affect the properties of another. In other words, we did our best to have as independent study sites as possible (Fig. 1). Valley sites were localized in the floodplains of four main rivers, namely the Wisła, Raba, Skawa, and Skawinka, and their minor tributaries, at a maximum distance of ca. 10–50 m from the riverbed, depending on the size of the river. Therefore, sites within (in contrast to those outside) river valleys were potentially affected by fluvial processes. The two locations could be expected to differ in terms of microclimate and the presence of alluvial materials.

Of the forty-eight study sites, each site belonged to one of the three site types encroached by (1) *R. japonica*, Rj ($N = 16$), (2) *R. laciniata*, Rl ($N = 16$), or (3) *S. gigantea*, Sg ($N = 16$) (Fig. 1). All sites were dominated by tall herbaceous vegetation and characterized by compact and relatively large neighboring patches of invasive and native plants. At each study site, two paired plots (2 m × 2 m each) were established: one in a dense, near-monoculture (> 90 % cover) patch of the invasive plant and one in the adjacent

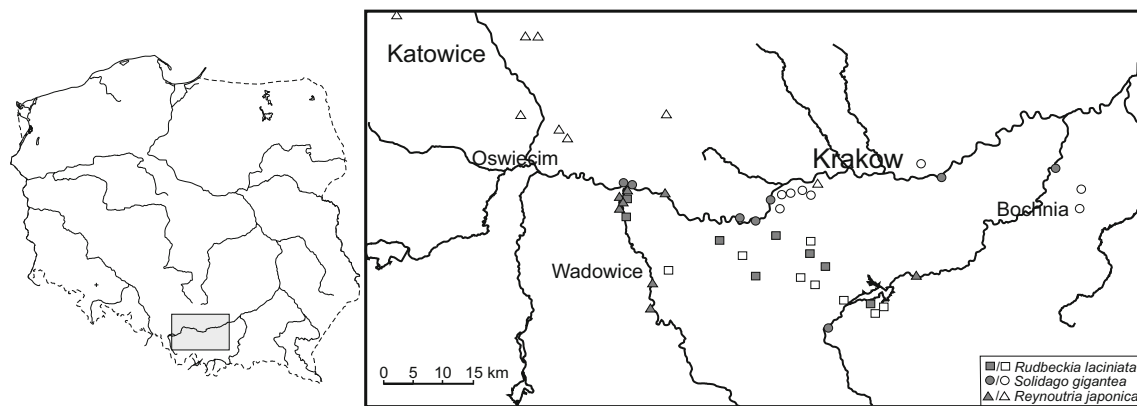


Fig. 1 Location of the study area and 48 sites within (gray symbols) and outside valleys (white symbols). Within each site, two plots (invasive vs. native) were localized

native vegetation devoid of any invasive species (control). The contrasting (invaded vs. native) plots were located as close as possible, a maximum of 15 m from each other, so as to limit differences in soil properties between the two vegetation types existing prior to the invasion event, and at least 3 m from the edge of a patch so as to minimize any effects of contrasting vegetation such as shading or litterfall. Within each plot, vascular plants and bryophytes were recorded. The 12-grade cover-abundance scale was used (1, <0.2 % cover and 1 small individual; 2, <1 % and 1–3 small individuals; 3, 1–3 % and 2–5 individuals; 4, 3–5 % and 3–8 individuals; 5, 5–12 % and 8–20 individuals; 6, 13–25 %; 7, 25–35 %; 8, 36–50 %; 9, 51–65 %; 10, 66–75 %; 11, 76–85 %; 12, 86–100 %). Uninvaded vegetation did not differ significantly in terms of plant species number and total plant cover between valleys and outside-valley locations (Table 1). The uninvaded patches of vegetation in Rj and Sg valley sites were dominated by *Phalaris arundinacea* and *Rubus caesius*, followed by *Petasites hybridus*, *Calystegia sepium*, *Aegopodium podagraria*, and *Urtica dioica* (Rj valley sites) or *Cirsium arvense* and *Tanacetum vulgare* (Sg valley sites). Rl valley sites were dominated by *Cirsium arvense*, *Galeopsis speciosa*, *Dactylis glomerata*, and *Chaerophyllum aromaticum*. *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Cirsium arvense*, and *Equisetum arvense* dominated both Rj and Sg outside-valley sites. These species were often accompanied by *Rubus caesius* (Rj outside-valley sites) or *Agropyron repens* and *Tanacetum vulgare* (Sg outside-valley sites). The patches of native vegetation in Rl outside-valley sites most often consisted of *Arrhenatherum elatius*, *Cirsium arvense*, *Holcus lanatus* and *Centaurea phrygia*.

In August 2013, three subsamples of topsoil (ca. 0–20 cm) were taken from each plot after the removal of organic layer consisting of fragmented litter and bulked to obtain one composite sample per plot. In total, 96 soil samples were collected: 3 site types (Rj vs. Rl vs. Sg) × 2 locations (within vs. outside valleys) × 8 replicates (sites) × 2 plots (invasive vs. native).

Laboratory work

Soil physicochemical properties

Soil samples were sieved (2 mm mesh) and divided into three parts that were then either dried for chemical analyses, frozen at $-20\text{ }^{\circ}\text{C}$ for phospholipid fatty acid (PLFA) analysis, or kept moist at $4\text{ }^{\circ}\text{C}$ for the other microbial analyses. Dry weight was measured after drying overnight at $105\text{ }^{\circ}\text{C}$. Maximum water-holding capacity (WHC) was assessed using a gravimetric method. Soil texture was determined through a combination of sieving and sedimentation (ISO 11277 1998). Soil pH was measured in 1:5 (w:v) water suspensions (ISO 10390 1994) with a Hach Lange HQ40D meter. Organic C was determined with a Leco RC-612 and total S with a Leco SC-144 DR dry combustion analyzer. Total N was determined by Kjeldahl method; soil was digested in H_2SO_4 with Kjeltabs ($\text{K}_2\text{SO}_4 + \text{CuSO}_4 \cdot 5\text{H}_2\text{O}$; Foss Tecator Digestor Auto) followed by distillation on a Foss Tecator Kjeltac 2300 Analyzer Unit. The available (Olsen) P was measured with an ion chromatograph (Dionex ICS-1100) following soil extraction with 0.5 M NaHCO_3 (Olsen et al. 1954, modified).

Soil microbiological properties

The soil basal respiration rate and microbial biomass, determined by substrate-induced respiration (SIR), were measured in fresh soil samples adjusted to 50 % WHC. The samples were incubated in gastight jars at $22\text{ }^{\circ}\text{C}$ for ca. 24 h; the evolved CO_2 was absorbed in 0.2 M NaOH. The excess hydroxide was titrated with 0.1 M HCl following the addition of BaCl_2 and phenolphthalein as an indicator. After the basal respiration measurements, a mixture of talcum and glucose monohydrate (4:1; $10\text{ mg glucose g}^{-1}\text{ dw soil}$) was added to the soil samples to measure substrate-induced respiration, which involves the determination of CO_2 after 4 h of incubation (Beck et al. 1996, modified).

Table 1 Basic characteristics of uninhabited plots located within and outside river valleys (mean \pm standard error, $N = 24$)

Variable	Outside valley	Valley	<i>p</i>
Sand (%)	50.6 \pm 5.2	42.5 \pm 3.5	0.39
Silt (%)	22.3 \pm 2.9	24.4 \pm 2.2	0.50
Clay (%)	27.1 \pm 2.9	33.1 \pm 2.0	0.10
Moisture (%)	14.3 \pm 1.0	15.6 \pm 1.0	0.37
pH H ₂ O	6.9 \pm 0.2	7.3 \pm 0.2	0.12
Organic C (%)	2.3 \pm 0.3	2.1 \pm 0.2	0.55
Total N (%)	0.23 \pm 0.02	0.20 \pm 0.02	0.24
Total S (g kg ⁻¹)	0.37 \pm 0.04	0.52 \pm 0.10	0.05
Olsen P (mg kg ⁻¹)	5.0 \pm 0.5	6.2 \pm 0.4	0.004
C:N	10.2 \pm 0.5	11.3 \pm 1.0	0.31
C:S	65.8 \pm 3.1	52.5 \pm 4.6	0.032
Soil respiration (μ M CO ₂ g ⁻¹ dw 24 h ⁻¹)	1.6 \pm 0.2	1.8 \pm 0.1	0.17
SIR-biomass (mg g ⁻¹ dw)	0.69 \pm 0.04	0.69 \pm 0.06	0.86
Urease activity (μ g N g ⁻¹ dw h ⁻¹)	39.5 \pm 3.4	50.8 \pm 3.9	0.040
Arylsulfatase activity (μ g pNP g ⁻¹ dw h ⁻¹)	128 \pm 12	150 \pm 15	0.35
Total PLFA (nM g ⁻¹ dw)	609 \pm 45	669 \pm 49	0.45
Bacterial PLFA (nM g ⁻¹ dw)	377 \pm 28	421 \pm 32	0.41
Gram-positive bacterial PLFA (nM g ⁻¹ dw)	234 \pm 17	255 \pm 21	0.57
Gram-negative bacterial PLFA (nM g ⁻¹ dw)	127 \pm 10	149 \pm 10	0.18
Fungal PLFA (nM g ⁻¹ dw)	20.8 \pm 3.2	20.3 \pm 2.0	0.75
Fungal:bacterial PLFA	0.05 \pm 0.01	0.05 \pm 0.004	0.86
Plant species number	11.2 \pm 0.81	11.0 \pm 0.8	0.88
Total plant cover (%) ^a	97.8 \pm 4.8	106 \pm 4.0	0.22

^a Total plant cover exceeded 100 % at some plots as plant species of different height, composing “layers” of herbaceous vegetation, were present at the same unit area. Statistically significant differences ($p < 0.05$) are shown by the italic character. Student’s *t* test was used for all variables except Olsen P and C:N ratio, for which the Mann-Whitney *U* test was employed

Urease activity was measured according to Kandeler (1996) using the unbuffered method. Soil samples were incubated at 37 °C for 2 h following the addition of urea solution. Released ammonium was extracted with KCl and determined by a modified Berthelot reaction, which is based on the reaction of sodium salicylate with ammonium in the presence of sodium dichloroisocyanurate and sodium nitroprusside at alkaline pH. Photometric measurements were performed at 690 nm with a Hach Lange DR 3800 spectrophotometer.

Arylsulfatase activity was measured according to Strobl and Traunmüller (1996). Following the addition of acetate buffer (pH = 5.8) and *p*-nitrophenylsulfate, soil samples were incubated at 37 °C for 1 h. Nitrophenol released by arylsulfatase activity was extracted, colored with NaOH, and determined at 420 nm using the Hach Lange DR 3800 spectrophotometer.

Phospholipid fatty acid (PLFA) analysis was performed according to Palojarvi (2006), with the exception of the lipid extraction, which was performed according to Macnaughton et al. (1997). Lipids were extracted from freeze-dried soil samples with a mixture of methanol:chloroform:phosphate

buffer (2:1:0.8, v:v:v) using accelerated solvent extractor ASE 200 (Dionex; two 15-min cycles, 80 °C, 1200 PSI). Following the extraction, an appropriate volume of chloroform and deionized water was added to give the correct final ratio (chloroform:methanol:phosphate buffer/water; 1:1:0.9, v:v:v) and form two phases. The chloroform layer was transferred to a new test tube, evaporated under nitrogen at 37 °C, and stored at -20 °C. The lipids were separated into neutral-, glyco-, and phospholipids in Bakerbond silica gel SPE columns (500 mg, Baker) by eluting with chloroform, acetone, and methanol, respectively. The methanol fraction was reduced to dryness under nitrogen. The phospholipids were subjected to mild alkaline methanolysis, and the resulting fatty acid methyl esters were separated and identified using a Varian GC-MS system (Varian 3900 and Saturn 2100T) and NIST library. The CP-Select CB for FAME (50 m \times 0.25 \times 0.39) column (Agilent Technologies) was used. Helium was used as a carrier gas, and injections were made in split mode (1:100). Individual fatty acids were identified relative to several standards: 37-component FAME Mix (Supelco), Bacterial Acid Methyl Ester (BAME) Mix

(Supelco), and a few additional one-component standards (Sigma-Aldrich). Methyl nonadecanoate (19:0; Fluka) was used as an internal standard.

Calculations and statistical analyses

C_{mic} was calculated according to the equation: C_{mic} ($\mu\text{g g}^{-1}$) = $40.04x + 0.37$, where x is the respiration rate given in microliters $\text{CO}_2 \text{ h}^{-1} \text{ g}^{-1}$ (Anderson and Domsch 1978).

Forty-eight PLFAs were measured in soil samples; however, most PLFAs were present in negligible amounts in soil. Eighteen fatty acids (14:0, 2OH 14:0, 15:0, a15:0, i15:0, 16:0, i16:0, 16:1 ω 7, 17:0, a17:0, i17:0, cy17:0, 17:1, 18:0, 18:1 ω 7, 18:1 ω 9, 18:1 ω 9t, 18:2 ω 6) with more than 0.5 % of the total relative abundance were present in most soils, and these fatty acids with cy19:0 were used in further calculations and statistical analyses (Bossio and Scow 1998; Moore-Kucera and Dick 2008). The sum of the above PLFAs (total PLFA) was used as a total microbial biomass indicator. PLFA 18:2 ω 6 was used as an indicator of saprophytic fungi. Bacteria were represented by 15:0, a15:0, i15:0, i16:0, 16:1 ω 7, 17:0, a17:0, i17:0, cy17:0, 18:1 ω 7, and cy19:0 (Frostegård and Bååth 1996; Ruess and Chamberlain 2010). The fatty acids a15:0, i15:0, i16:0, a17:0, and i17:0 were chosen to represent gram-positive and 16:1 ω 7, cy17:0, 18:1 ω 7, and cy19:0 gram-negative bacteria (Piotrowska-Seget and Mroziak 2003; Bardgett and Walker 2004; Moore-Kucera and Dick 2008; Cycoń et al. 2013).

Prior to statistical analyses, all variables were transformed by a logarithmic or exponential function and expressed on a 0–1 scale in order to achieve homogeneity of variances. Student's t tests or Mann-Whitney U tests were used to compare uninvaded soil properties between valley and outside-valley sites. Principal component analysis (PCA) was performed on the concentrations of individual PLFAs, expressed in mole percentages, to arrive at the minimum number of variables, called principal components (PCs), representing the composition of microbial communities. One variable (PLFA 17:1) was excluded from the PCA due to its considerable deviation from a normal distribution. Interpretation of PCs was based on factor loadings of individual PLFAs on PCs. Split-plot ANOVA was used to examine the effect of site type (3 site types—Rj, Rl, and Sg, including both invaded and native plots; whole-plot factor), location (2 locations—within and outside valleys; whole-plot factor), and invasion (2 plot types within sites—invaded vs. native; split-plot factor), or their interactions, on soil microbiological properties. Split-plot ANOVA was followed by Tukey's HSD test if any significant ($p < 0.05$) effects of site type, location, or their interactions on microbial indices were found. Contrast analysis was performed to test for differences in microbiological properties between invaded and native soils if any of the following interactions was significant: invasion \times site type,

invasion \times location, or invasion \times site type \times location. Statistical analyses employed Statistica 9 (StatSoft Inc).

Results

Seven PCs with eigenvalues >1 , explaining the highest percent of variance (a total of 77.8 % of variance in the PLFA data), were chosen to represent the microbial community composition. PC1 (19.9 % of variance) correlated mainly with i16:0 (−0.85), i17:0 (−0.74), 16:1 ω 7 (0.74), a17:0 (−0.54), cy17:0 (0.52), PC2 (15.1 %) with 16:0 (−0.84), cy17:0 (0.56), i15:0 (−0.54), a15:0 (0.53), a17:0 (0.53), PC3 (12.5 %) with 14:0 (−0.78), 15:0 (−0.76), 17:0 (−0.66), PC4 (10.3 %) with 18:2 ω 6 (0.64), a15:0 (−0.49), 18:1 ω 9t (0.45), PC5 (7.3 %) with 18:1 ω 9 (−0.49), 18:1 ω 7 (0.49), cy19:0 (0.49), PC6 (6.6 %) with 2OH 14:0 (−0.67), i17:0 (0.42), and PC7 (6.1 %) with 18:0 (0.59), cy19:0 (−0.50).

Most studied soils (70 %) were classified as clay, clay loam, or sandy clay loam. Uninvaded soils did not differ in terms of most basic physicochemical properties between valley and outside-valley sites (Table 1). Statistically significant ($p < 0.05$) differences between the locations were found only for Olsen P and C:S ratio. Uninvaded soils of the two locations were also similar in respect of nearly all microbiological properties, except urease activity (Table 1) and community composition represented by PC1 ($p = 0.015$).

Soil microbiological properties were mainly affected by two factors: site type and invasion \times site type interaction (Table 2). Effects of other factors, i.e., location, invasion, site type \times location, invasion \times location, and invasion \times site type \times location, were either rarely significant or insignificant (Table 2).

The effect of invasion on soil microbial communities depended strongly on the invasive plant species (significant effect of invasion \times site type interaction for most microbiological properties; Table 2). *R. japonica* influenced many microbial indices. SIR-biomass, urease activity, total PLFA, fungal PLFA, fungal:bacterial PLFA ratio, gram-negative bacterial PLFA, and soil respiration were significantly lower under *R. japonica* than under adjacent native plant communities (Fig. 2). Microbial community composition also differed between soils from under *R. japonica* and native plants ($p < 0.01$ for PC2 and $p < 0.001$ for PC4 and PC7). *R. laciniata* and *S. gigantea* mainly influenced the abundance of fungal community, i.e., fungal PLFA and fungal:bacterial PLFA ratio (Fig. 2) and PC4 ($p < 0.01$ for *S. gigantea*), as well as PC6 ($p < 0.05$ for *R. laciniata*) and PC7 ($p < 0.05$ for *R. laciniata* and $p < 0.01$ for *S. gigantea*). More fungi were observed under *R. laciniata* and *S. gigantea* than under native communities, in contrast to the phenomenon observed for *R. japonica*.

Table 2 Results of split-plot ANOVA for the effects of site type, location, invasion, and their interactions on soil microbial properties

Microbial variable	Site type ^a		Location ^b		Site type × location		Invasion ^c		Invasion × site type		Invasion × location		Invasion × site type × location	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Soil respiration	1.34	0.27	2.14	0.15	0.96	0.39	0.15	0.70	<i>6.24</i>	<i>0.004</i>	0.00	0.95	1.81	0.18
SIR-biomass	<i>25.00</i>	<i><0.001</i>	0.00	0.98	1.90	0.16	2.83	0.10	<i>13.77</i>	<i><0.001</i>	0.46	0.50	0.17	0.85
Urease activity	<i>13.74</i>	<i><0.001</i>	<i>6.66</i>	<i>0.013</i>	1.12	0.34	0.47	0.50	<i>13.31</i>	<i><0.001</i>	0.00	0.96	1.90	0.16
Arylsulf atase activity	<i>18.75</i>	<i><0.001</i>	1.87	0.18	1.98	0.15	<i>5.12</i>	<i>0.029</i>	0.95	0.40	0.02	0.90	3.93	<i>0.027</i>
Total PLFA	<i>3.67</i>	<i>0.034</i>	1.23	0.27	1.29	0.29	0.92	0.34	<i>4.36</i>	<i>0.019</i>	0.40	0.53	2.39	0.10
Bacterial PLFA	<i>4.13</i>	<i>0.023</i>	1.48	0.23	1.07	0.35	1.34	0.25	3.11	0.06	0.48	0.49	2.41	0.10
Fungal PLFA	2.77	0.07	0.46	0.50	2.84	0.07	0.40	0.53	<i>27.3</i>	<i><0.001</i>	0.37	0.55	2.88	0.07
Fungal:bacterial PLFA	0.05	0.96	0.05	0.83	2.18	0.13	3.75	0.06	<i>18.48</i>	<i><0.001</i>	0.00	0.97	1.79	0.18
G+ bacterial PLFA	<i>5.17</i>	<i>0.010</i>	1.17	0.29	1.28	0.29	3.10	0.09	2.25	0.12	0.92	0.34	2.21	0.12
G−bacterial PLFA	2.45	0.10	2.26	0.14	0.81	0.45	0.03	0.86	<i>3.81</i>	<i>0.030</i>	0.02	0.88	2.41	0.10
PC1	<i>6.28</i>	<i>0.004</i>	<i>4.39</i>	<i>0.042</i>	1.56	0.22	<i>12.63</i>	<i>0.001</i>	1.88	0.16	<i>4.36</i>	<i>0.043</i>	0.49	0.62
PC2	<i>5.28</i>	<i>0.009</i>	2.48	0.12	0.37	0.69	0.87	0.36	<i>6.96</i>	<i>0.002</i>	0.00	0.95	0.52	0.60
PC3	0.05	0.95	0.31	0.58	0.48	0.63	<i>6.53</i>	<i>0.014</i>	2.71	0.08	0.05	0.82	0.14	0.87
PC4	0.29	0.75	<i>5.57</i>	<i>0.023</i>	0.78	0.47	0.17	0.68	<i>15.75</i>	<i><0.001</i>	0.03	0.86	2.70	0.08
PC5	2.32	0.11	0.16	0.70	2.41	0.10	0.76	0.39	1.42	0.25	0.13	0.72	0.72	0.49
PC6	0.33	0.72	0.53	0.47	0.21	0.81	1.96	0.17	<i>4.39</i>	<i>0.019</i>	0.78	0.38	0.27	0.76
PC7	2.67	0.08	<i>4.17</i>	<i>0.05</i>	2.26	0.12	2.92	0.10	<i>13.35</i>	<i><0.001</i>	1.16	0.29	2.20	0.12

^a Three site types: encroached by *R. japonica*, *R. laciniata*, or *S. gigantea*, including both invaded and uninvaded vegetation patches (plots)

^b Two locations: within and outside valleys

^c Differences between two plot types within sites: invaded vs. native

Statistically significant effects ($p < 0.05$) are shown by the italic character

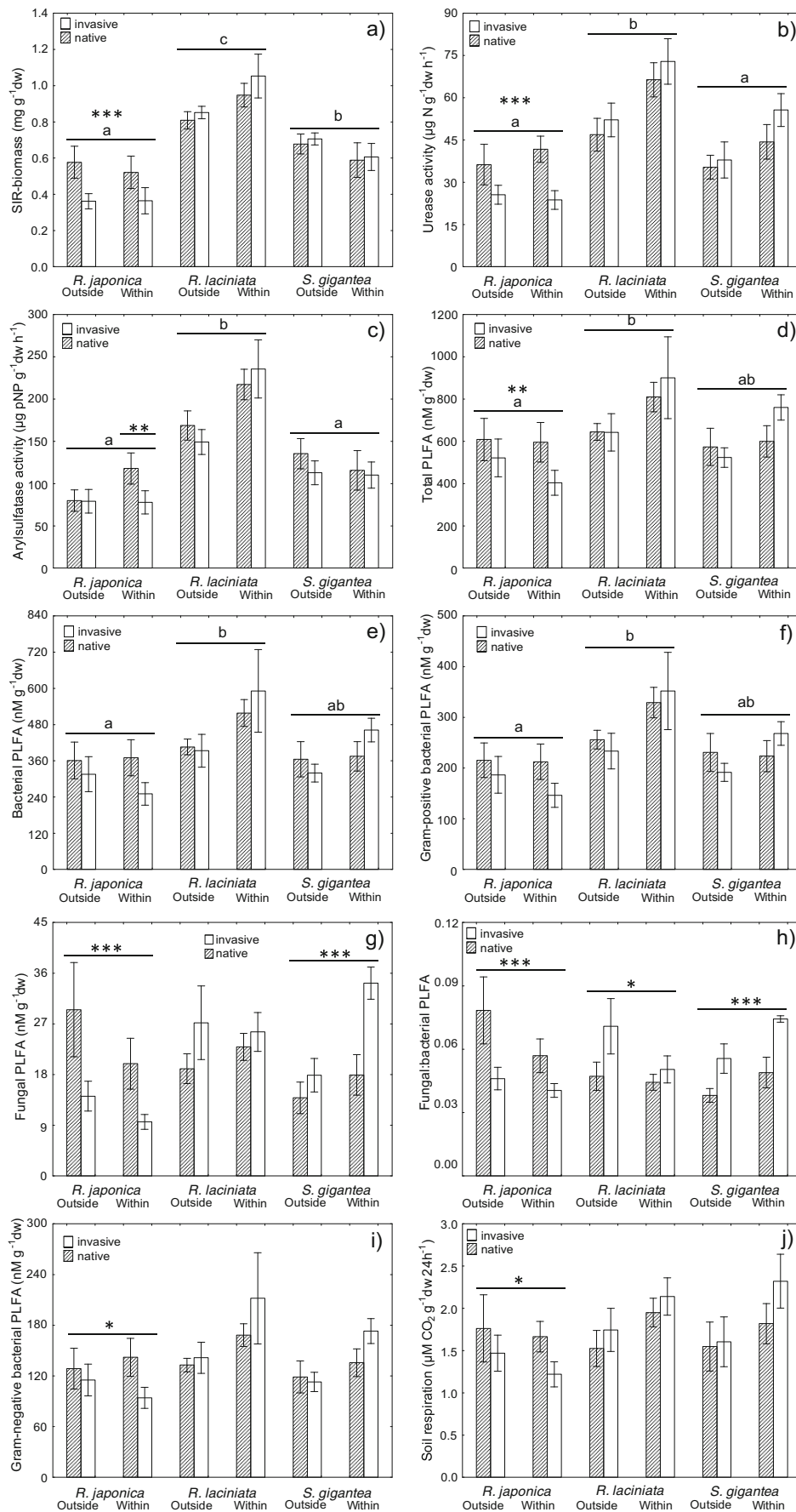
The influence of plant invasion on soil did not generally depend on location (Table 2). A significant effect of invasion × location interaction was only found in the case of PC1: microbial community composition was only influenced by invasion in outside-valley soils ($p < 0.001$). Moreover, arylsulfatase activity responded to invasion depending on both location and site type: it was significantly lower under *R. japonica* than under native plant communities in river valley soils (Table 2, Fig. 2).

The significant site type effect means that total microbial and bacterial biomass, enzyme activities, and community composition varied among sites of different invasive plant species, irrespectively of patch (plot) type, i.e., invaded vs. native; *R. japonica* encroached on sites characterized by the lowest SIR-biomass, enzyme activities, total PLFA, bacterial PLFA, and gram-positive bacterial PLFA, while the opposite was detected for *R. laciniata* (Fig. 2). Sites infested by *R. japonica* also differed from those encroached upon by *R. laciniata* in terms of the soil microbial community composition represented by PCs ($p < 0.01$ for PC1 and PC2). Most microbiological properties did not differ significantly between the locations. The only exceptions were urease activity, which was lower in outside-valley than in valley soils, and microbial community composition represented by PC1, PC4, and PC7 (Table 2).

Discussion

This study assessed the influence of three invasive plant species, *R. japonica*, *R. laciniata*, and *S. gigantea*, on activity, biomass, and composition of microbial communities in soils located within and outside river valleys. Our results clearly show that the invasion effects on soil microbes differed among the invasive plant species. *R. japonica* infestation significantly altered both the composition and the function of soil microbial communities, irrespectively of location (valley or outside valley). Specifically, its invasion reduced soil respiration, both urease and arylsulfatase activities, the abundance of fungi and gram-negative bacteria, and the fungal:bacterial ratio. The negative effects of *R. japonica* invasion on soil microbial

Fig. 2 Microbial properties of soils under invasive and native vegetation within and outside valleys (means and standard errors, $N = 8$). Different small letters above the bars denote statistically significant ($p < 0.05$) differences between three site types, i.e., sites encroached by *R. japonica*, *R. laciniata*, or *S. gigantea*, including both invaded and native plots. Asterisks indicate statistically significant effects of invasion, i.e., differences between invaded and native plots (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). The effect of invasion did not depend on location (within and outside valleys), with the exception of arylsulfatase activity. See Table 2 for results of the split-plot ANOVA



properties agree with those reported by others. Mincheva et al. (2014) discovered that *R. japonica* litter decomposed 3–4 times more slowly than the litter of native grassland species. Dassonville et al. (2011) and Tharayil et al. (2013) found that *R. japonica*, or other species of the *Reynoutria* genus, decreased enzyme activities related to N mineralization and/or denitrification, although the changes were season dependent (Tharayil et al. 2013). Our soils invaded by *R. japonica*, which is a nonmycorrhizal plant, showed a reduced abundance and species richness of arbuscular mycorrhizal fungi (AMF) (Zubek et al. unpublished). On the other hand, Aguilera et al. (2010) found no negative influence of *R. japonica* infestation on soil processes such as ammonification, nitrification, or total N mineralization.

Plants modify soil properties, including microbial processes, through deposition of litter and rhizodeposition that differ between species in terms of quantity and chemical quality (Chen et al. 2015). Invasive plants are often characterized by higher productivity than co-occurring native vegetation (Vilà et al. 2011; Jo et al. 2015). The biomass produced by *R. japonica* is 2–5 times greater and characterized by lower concentrations of essential nutrients such as N, P, K, Mg, or Mn than the biomass of native plants (Dassonville et al. 2008; Aguilera et al. 2010). Moreover, the tissues of *R. japonica* are characterized by relatively high C:N and lignin:N ratios at the time of senescence and litterfall (Aguilera et al. 2010; Mincheva et al. 2014). Hence, *R. japonica* provides the soil with huge amounts of low-quality litter (Aguilera et al. 2010; Mincheva et al. 2014), which is probably the primary reason for the severe decline in most soil microbial properties under the *R. japonica* monoculture discovered in this study. *R. japonica* invasion may have actually affected microbial properties through changes in soil chemical characteristics, as it altered the amount of soil N-NO_3^- in comparison to control soil (Stefanowicz et al. unpublished). The poor quality of litter produced by *R. japonica* and low microbial activity and decomposition rate accumulated large, undecomposed fragments of organic matter and increased the organic layer thickness under the plant (Maurel et al. 2010). The thickness of the organic layer reached ca. 20 cm at some of our study sites (data not shown).

The decomposition of detritus produced by *R. japonica*, characterized by high C:N and lignin:N ratios and relatively recalcitrant, is expected to be accomplished predominantly by soil fungi, not by bacteria (De Boer et al. 2005; Thorn and Lynch 2007). Surprisingly, our observations suggest that soil from under *R. japonica* was not beneficial to fungi, as soil fungal PLFA and fungal:bacterial ratio were considerably lower under *R. japonica* than under native plants. Previous research showed that the abundance, biomass, or composition of saprotrophic fungal communities found on decomposing litter in terrestrial and stream ecosystems differed between *R. japonica* and native plants, though it depended on study

sites or decaying tissues (leaves vs. stems) (Lecerf et al. 2007; Mincheva et al. 2014). According to Mincheva et al. (2014), there were some striking differences in fungal communities: *Phoma* sp. was isolated in very high abundance from *R. japonica* litter, whereas it was absent in native litter. The opposite observation was made for *Mucor* sp.—one of the dominant taxa in native litter.

Modifications of the soil environment by invasions can depend not only on the chemical composition of plant litter but also on the release of secondary metabolites. *R. japonica* produces numerous compounds that inhibit the growth of pathogenic bacteria and fungi (Kim et al. 2005; Zhang et al. 2013). Phenolics released by *R. japonica* can also affect seasonal patterns of soil processes such as N mineralization (Tharayil et al. 2013). Thus, these substances may also explain the low microbial activity and biomass detected in soil from under *R. japonica* in our study.

The two other invasive species, i.e., *Rudbeckia laciniata* and *Solidago gigantea*, did not influence most soil microbial properties. They significantly affected only fungi-related properties, namely fungal PLFA (*S. gigantea*) or fungal:bacterial PLFA ratio (*R. laciniata*, *S. gigantea*). Both absolute and relative abundance of soil fungi increased due to the invasion, a phenomenon which is the opposite of that found in *R. japonica*. Both plant species increased mycorrhizal frequency but decreased species richness of AMF (Zubek et al. unpublished). Our results agree with those of Scharfy et al. (2009, 2010) and Quist et al. (2014) who found that *S. gigantea* invasion had no influence or decreased soil respiration, bacterial biomass, or phosphomonoesterase activity but increased fungal biomass and/or fungal:bacterial ratio. *S. gigantea* litter may support fungal rather than bacterial growth as it has lower tissue concentrations of most nutrients and higher C:N ratio than adjacent native vegetation (Vanderhoeven et al. 2006; Thorn and Lynch 2007; Dassonville et al. 2008). However, such differences in tissue nutrient concentrations were not found by other authors (Stefanowicz et al. unpublished). High fungal biomass detected in this study may suggest that *S. gigantea* stimulates fungal pathogens in its introduced range (Scharfy et al. 2010), as shown previously for other invasive species (Nijjer et al. 2007; Mangla et al. 2008). For example, Mangla et al. (2008) found that *Chromolaena odorata*, a destructive tropical invasive weed, accumulated high concentrations of the generalist soil-borne fungi, *Fusarium semitectum*, thereby creating a negative feedback to native plant species. However, another species of the *Solidago* genus, *S. canadensis*, suppressed fungal or fungi-like pathogens (Zhang et al. 2009b). Stimulation or inhibition of soil microorganisms, including fungal pathogens, may be driven through exudation of allelochemicals (Zhang et al. 2009b). The composition of secondary metabolites, which potentially affect activity and biomass of microorganisms, differs between plant species,

including those belonging to the same genus (Kalemba and Thiem 2004). Essential oil extracted from *S. gigantea* contained 95 compounds, of which sesquiterpene (–)-cyclocolorenone was dominant; it had both antibacterial and antifungal properties (Jacyno et al. 1991; Kalemba et al. 2001; Kalemba and Thiem 2004). It is known, however, that some secondary metabolites exhibit antibacterial, but not antifungal, activity (Saeedi and Morteza-Semnani 2009), potentially altering fungi:bacteria ratio in soil.

Invasive plants may also affect activity and biomass of bacteria and fungi indirectly through changes in soil fauna that feed on microorganisms. It was proved that invasive plants can alter the abundance or species composition of soil and sediment invertebrates, including fungivorous or bacterivorous nematodes, collembola, enchytraeids, and mites (Talley and Levin 2001; Yeates and Williams 2001; Quist et al. 2014; Rusterholz et al. 2014). These changes would possibly influence microorganisms as, depending on species and grazing intensity and selectivity, soil invertebrates can inhibit or stimulate mycelial growth and alter species dominance and composition within microbial communities (Hedlund and Augustsson 1995; Crowther et al. 2011).

The lack of effects of *S. gigantea* or *R. laciniata* invasion on most soil microbial properties in our research was unexpected, as both species are considered, like *R. japonica*, “transformers” that modify ecosystems considerably (Pyšek et al. 2004; Tokarska-Guzik et al. 2010). Other studies on the influence of *S. gigantea* on soil microbial properties provided inconsistent results, with positive, negative, or no changes in soil properties due to the invasion. Chapuis-Lardy et al. (2006) and Koutika et al. (2007) found that *S. gigantea* enhanced soil respiration, C mineralization, and alkaline and acid phosphomonoesterase activities in comparison to native vegetation. Similar results were reported by Zhang et al. (2009a) for other species of the *Solidago* genus; *S. canadensis* invasion increased soil microbial biomass, basal and substrate-induced respiration, and functional diversity of microbial communities. On the other hand, Herr et al. (2007) pointed out that microbial biomass P and acid phosphomonoesterase activity did not change due to *S. gigantea* infestation, while alkaline phosphomonoesterase activity declined considerably.

Contrary to expectations, the effects of invasion on soil microbial properties did not differ between valley and outside-valley sites, probably because the two locations did not differ in terms of basic soil properties such as total C, N and S content, texture, pH, or most microbial properties. Presumably the influence of fluvial processes we had expected in the river floodplain was too weak to alter soil properties as well as plant species richness and cover considerably. Dassonville et al. (2008) and Scharfy et al. (2009) found that the direction and magnitude of changes in soil properties induced by invasion differed between study

sites, but their sites showed differences in initial (pre-invasive) soil properties. Specifically, invasion increased nutrient concentrations of surface soils with initially low nutrient concentrations, while under the opposite conditions a negative impact was mainly observed (Dassonville et al. 2008). Scharfy et al. (2009) reported that some effects of *S. gigantea* on soil depended on soil P availability, being more pronounced at P-rich sites.

In this study, soil samples were collected from paired plots, which were established in the patches of an invader and native vegetation. Such a sampling scheme did not exclude the possibility of pre-invasion differences among invaded and uninvaded plots as already mentioned by Vanderhoeven et al. (2005), Carol Adair and Burke (2010), and Dostál et al. (2013). However, our experimental plan avoided these differences since paired plots were established within one site, as close as possible to each other, in flat terrain and far enough from shrubs or trees. Experiments involving sowing, or planting, invasive and native plants in uninvaded soil should be performed in addition to field studies. Such experiments, testing the effects of *R. japonica*, *R. laciniata*, and *S. gigantea* on soil properties, are in progress.

Conclusions

Investigations concerning the effects of invasive plants on soil microbial properties are often based on only a single invasive species and sampling schemes that are affected by pseudoreplication. In contrast, our study included three invasive plant species and two locations (valleys and outside valleys) and used replicate independent study sites scattered over a vast area. The invasion of *R. japonica*, *R. laciniata*, and *S. gigantea* influenced soil microbial properties compared to native plants, but the direction and magnitude of the changes depended on the invasive species. The effects of *R. japonica* were the most pronounced: this species reduced microbial activity and biomass. Such negative effects of plant invasions on soil are not a common phenomenon as invasive plants generally increase nutrient pools, microbial activity, and rates of soil processes such as litter decomposition, N mineralization, or nitrification (Liao et al. 2008; Vilà et al. 2011). Changes in soil properties brought about by plant invasions may induce positive or negative feedback with implications for acceleration or stabilization of these invasions, re-establishment of the native flora, and the functioning of whole ecosystems. The effects of the invasive species on soil properties did not differ between valley and outside-valley locations, probably because soils of the two locations had similar initial characteristics. Further research should study the impact of plant invasions on soil microbial properties also testing seasonal effects and including ecosystems with contrasting properties.

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