



Fallopia japonica and *Impatiens glandulifera* are colonized by species-poor root-associated fungal communities but have minor impacts on soil properties in riparian habitats

Daniel Schmitz · Johanna Girardi · Eva Ullrich · Katherine Muñoz-Sepulveda · Mirco Bundschuh · Kai Riess · Jens Schirmel

Received: 8 April 2022 / Accepted: 23 February 2023 / Published online: 16 March 2023
© The Author(s) 2023

Abstract *Fallopia japonica* and *Impatiens glandulifera* are major plant invaders on a global scale that often become dominant in riparian areas. However, little is known about how these species affect interactions in soil–plant systems. The aim of this study was to investigate the impact of both species on abiotic and biotic soil properties, with a special focus on fungi. We investigated eight sites along small streams invaded by *F. japonica* and *I. glandulifera*, respectively, and compared each with nearby sites dominated by the native species *Urtica dioica*. Three different types of samples were collected: bulk soil, rhizosphere soil and roots from invasive and native stands at each site. Bulk soil samples were analysed for soil physicochemical, microbial properties (soil

microbial respiration and ergosterol) and soil arthropod abundance (Acari and Collembola). Soil respiration was also evaluated in rhizosphere samples. The fungal community composition of both bulk soil and roots were analysed using a metabarcoding approach. Soil physicochemical properties as well as soil microbial activity, fungal biomass and soil fungal operational unit taxonomic unit (OTU) richness did not differ between invaded and native riparian habitats, indicating only minor belowground impacts of the two invasive plant species. Soil microbial activity, fungal biomass and soil fungal OTU richness were rather related to the soil physicochemical properties. In contrast, Acari abundance decreased by 68% in the presence of *F. japonica*, while Collembola abundance increased by 11% in *I. glandulifera* sites. Moreover, root-associated fungal communities differed between the invasive and native plants. In *F. japonica* roots, fungal OTU richness of all investigated ecological groups (mycorrhiza, endophytes, parasites, saprobes) were lower compared to *U. dioica*. However, in *I. glandulifera* roots only the OTU richness of mycorrhiza and saprobic fungi was lower. Overall, our findings show that *F. japonica* and *I. glandulifera* can influence the abundance of soil arthropods and are characterized by lower OTU richness of root-associated fungi.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-023-03034-2>.

D. Schmitz (✉) · J. Girardi · E. Ullrich · K. Muñoz-Sepulveda · M. Bundschuh · K. Riess · J. Schirmel

iES Landau, Institute for Environmental Sciences, RPTU University of Kaiserslautern-Landau, Landau, Germany
e-mail: daniel.schmitz@rptu.de

M. Bundschuh
Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

J. Schirmel
Eusserthal Ecosystem Research Station, RPTU University of Kaiserslautern-Landau, Landau, Germany

Keywords Acari · Collembola · *Fallopia japonica* · *Impatiens glandulifera* · Metabarcoding · *Urtica dioica*

Introduction

Invasive alien plants are widely accepted as a major cause of biodiversity loss in native communities, which, in turn, can negatively affect the entire ecosystem (Hooper et al. 2012). Besides effects on above-ground compartments, invasive plants also impact belowground compartments (Liao et al. 2007; Abgrall et al. 2019) altering resources and ecosystem functions and processes (Crooks 2002; Ehrenfeld 2003; Liao et al. 2008; Waller et al. 2020).

Invasive plants can impact soil physicochemical properties, e.g. by increasing pH and water content (*Leucanthemum vulgare*, Ahmad et al. 2020) or lowering pH and increasing water content (*Carpobrotus edulis*, Novoa et al. 2014). Invasive plants also have various effects on the soil nutrient status. For example, invasion by *Spartina alterniflora* can increase nitrogen and organic carbon levels (Liao et al. 2007) or increase phosphorus storage while having no effect on C and N (Wang et al. 2019). Soil functions can be affected in terms of decreased litter decomposition and increased microbial activity (Liao et al. 2007; Vilà et al. 2011) or reduced soil biological activity (Pehle and Schirmel 2015). Soil microbial communities, including fungi, are influenced by plant invasion with respect to biomass (e.g. increasing biomass with woody plant invasion; Liao and Boutton 2008) and shifts in the community composition and diversity (Ravit et al. 2003; Wolfe and Klironomos 2005; Si et al. 2013; Sapsford et al. 2022). Plant invasions can further influence the soil fauna (Belnap et al. 2005; Biederman and Boutton 2009; Abgrall et al. 2019), which support important soil functions such as decomposition (de Deyn et al. 2003; Tresch et al. 2019). For example, Collembola and Acari, often the dominant arthropod groups in soil (Petersen and Luxton 1982; Deharveng 1996; Behan-Pelletier 2003) respond to changes in the vegetation, including plant invasion (Salamon et al. 2004; Wissuwa et al. 2012). Altering the vegetation composition by replacing native plant species, could thus negatively affect soil arthropod abundance and diversity (Salamon et al. 2004; Wissuwa et al. 2012; Rusterholz et al. 2014). However, impacts of invasive plants on soil fauna are highly variable and depend on the habitat type (Abgrall et al. 2019), since many soil arthropod species are also dependent on abiotic soil properties (Cassagne et al. 2003; Bedano 2004).

Fallopia japonica (Houtt.) Ronse Decr., Polygonaceae and *Impatiens glandulifera* Royle, Balsaminaceae are highly abundant invasive plant species in many areas worldwide (Beerling and Perrins 1993; Beerling et al. 1994). Although their effects on soil physicochemical and biological properties are well studied, their impacts on fungal communities under field conditions are not well understood, especially due to the lack of studies using modern molecular analyses (metabarcoding). Soil fungi have important roles in ecosystem functioning (Öpik et al. 2006). Symbionts such as mycorrhizal species interact with plants through their roots by providing water and nutrients, and are essential for survival and health of most plant species (Smith and Read 2008; Kivlin et al. 2011; Tedersoo et al. 2014). In contrast to mycorrhizal fungi, root endophytes only interact with plant roots during a part of their life cycle. Mycorrhizal and endophytic fungi are especially beneficial under stressful environmental conditions and can enhance the performance, stress tolerance and disease resistance of plants (Smith and Read 2008; Rodriguez et al. 2009; Kivlin et al. 2011; Redman et al. 2011; Riess et al. 2014; Tedersoo et al. 2014). The community of mycorrhizal, endophytic as well as parasitic fungi, which also occur on living tissue, depends on the plant species and may thus be modified by invasion (Knogge 1996; Christian et al. 2016). In contrast to mycorrhizal and endophytic fungal groups, saprobic fungi are involved in the decomposition of particulate organic matter (Duguay and Klironomos 2000) and, hence, may be less affected by plant invasion.

The Asian knotweed, *F. japonica*, is a perennial, rhizome-forming species and one of the most invasive plants in Europe due to its ability to quickly produce high biomass (Beerling et al. 1994). It can affect soil characteristics (e.g., increasing mineral modifying soil nutrient stocks; Dassonville et al. 2007; Stefanowicz et al. 2017), C and N dynamics in soil (Koutika et al. 2007) or increase soil pH compared to adjacent non-invaded sites (Čerevková et al. 2019). *Fallopia japonica* shows allelopathic effects (Murrell et al. 2011; Parepa and Bossdorf 2016) with significant impacts on the soil food web structure (Abgrall et al. 2018), decreasing abundance and diversity of soil fungi, such as mycorrhizal fungi (Zubek et al. 2016). Another highly invasive plant in Europe is the Himalayan balsam, *I. glandulifera* (Beerling and Perrins 1993). This annual herb has strong dispersal

capabilities with masses of floatable seeds. *Impatiens glandulifera* is known for its impact on native communities with positive effects on soil fauna abundance (Tanner et al. 2013; Rusterholz et al. 2014), modifying soil fungal community composition by increasing fungal diversity and lowering arbuscular mycorrhizal fungal root colonization (Pattison et al. 2016; Gaggini et al. 2018, 2019).

In this study, we investigated riparian sites invaded by both species (*F. japonica* or *I. glandulifera*) and corresponding control sites dominated by the native common nettle, *Urtica dioica* L., Urticaceae. We aimed to investigate the chemistry of soil and effects on soil bacterial activity, soil arthropod abundance as well as soil fungal biomass, diversity and composition in both soil and root samples. For the fungi, we used a metabarcoding approach where sequences were assigned to operational taxonomic units (OTU). We assessed the following research questions: (1) Are soil physicochemical parameters (organic carbon content, pH value, water content) different between riparian sites invaded by *F. japonica* or *I. glandulifera* compared to native sites with *U. dioica*? (2) How does plant invasion by both species and soil physicochemical parameters affect soil microbial activity and soil arthropod abundance (Acari and Collembola)? (3) How is the biomass, OTU richness, and composition of fungi in the bulk soil affected by *F. japonica* and *I. glandulifera* invasion and related to soil physicochemical parameters? (4) How does the richness and composition of root-associated fungal OTUs differ in the presence of invasive and native plant species?

Materials and methods

Study area and target plant species

Study sites were located along small streams in forests around Landau (study area ~ 1000 km²), Rhineland-Palatinate, Germany (Online Resource 1). Sixteen riparian sites containing either sites dominated by *Fallopia japonica* and *Urtica dioica* (N=8 site pairs) or *Impatiens glandulifera* and *U. dioica* (N=8 site pairs) were selected (Online Resource 2). The perennial herb *Urtica dioica* was selected as a reference species because it is a highly abundant, naturally occurring species at riparian floodplains in Central Europe (Edwards et al. 1998). Stands

between the invasive and native plant species of each site pair were in direct vicinity (maximum distance up to 10 m), to minimize differences in soil conditions. All sites were at least 10 m² and characterized by homogenous vegetation and a cover of > 80% by their respective target species. Other common plants within the sites were *Glechoma hederacea* and *Rubus* subg. *Rubus*. In the sites dominated by *F. japonica*, an average of 3.4 plant species were identified, while in corresponding *U. dioica* sites, the average was 3.9. In sites dominated by *I. glandulifera*, the average number of species was 4.8 and in corresponding *U. dioica* sites, the average was 3.3. The forests around the target sites can be assigned to the phytocoenology classes Alnetea glutinosae and Querceteta robori-petraea according to Schubert. (2010), with *Alnus glutinosa* as the dominant tree species. Details of the vegetation at each site can be found in Online Resource 1.

Sampling

In each site, plant-specific samples were collected, namely bulk soil, rhizosphere soil and plant roots. Sampling was performed during September to October 2019. Bulk soil samples were randomly collected at the topsoil (0 to – 10 cm) using a bulb planter from three plant-specific stands and subsequently pooled and homogenized to one composite sample. Roots were taken from four randomly chosen individuals of each species using a shovel and homogenized to a composite sample by species and site. The soil attached to the roots after shaking the collected plant was separated from the plants by hand and collected as rhizosphere soil, in total 4 replicates, which were subsequently homogenized to a composite sample per species and site. Roots were further rinsed first with tap water, and finally with autoclaved water. A part of each soil type was frozen at – 20 °C and stored for analysis of soil microbial activity. The remaining bulk soil samples, rhizosphere soil samples and individual root samples were subsequently dried at 50 °C for 48 h.

Soil physicochemical properties

The bulk soil samples were used for analyses of soil physicochemical properties. Soil pH was measured

using a pH meter (pH 3110 SET 2, Xylem Analytics, Weilheim, Germany) in a 0.01 molar CaCl₂ solution (DIN EN 15933:2012-11) with field moist soil. Water content in bulk and rhizosphere soil was determined gravimetrically according to ISO 11465:1993. Samples were further analysed for organic carbon (DIN ISO 10694:1996-08) by dry burning and total nitrogen (VDLUF A I, A2.2.5:2012) via thermal conductivity. These analyses were performed by Speyer Agricultural Research Institute (Speyer, Germany).

Soil microbial activity

Soil microbial activity was investigated separately for the bulk soil and the rhizosphere soil. Basal and glucose-induced soil microbial activity were assessed by the MicroResp™ method (Campbell et al. 2003). The evolved CO₂ after incubation is indicative for soil respiration, which is an expression of soil microbial activity (Creamer et al. 2016a, b). The frozen samples were thawed at 6 °C and sieved to 2 mm. Then, they were adjusted to 45% of water holding capacity, following the recommendations of the producer. The substrates (water or glucose) were added to the soil samples followed by an incubation of 6 h at 21 °C. CO₂ was measured by a shift of the cresol red colour in the deep well plate system at 572 nm (Nanophotometer Infinite® M200, Tecan, Switzerland). Quantitative analysis was done using known concentrations of sodium bicarbonate and an excess of hydrochloric acid (Campbell et al. 2003) by interpolation of data in the calibration curve.

Soil arthropod abundance

We focussed on the highly abundant and functionally important soil arthropod taxa Acari and Collembola. We combined two methods, pitfall traps and Berlese funnels, for sampling. Four pitfall traps (plastic cups with an opening diameter of 6.5 cm) were placed one meter apart in each sampling site. Traps were set between 24th August and 15th September 2019 and were emptied and refilled every ten days. A 1:4 propylene glycol:water solution with some drops of detergent was used as a trapping liquid. Captured individuals were stored in 70% ethanol. Soil organisms were additionally extracted from the soil bulk samples using Berlese funnels. 200 ml of fresh soil per site from the collected bulk soil was filled into a

Berlese funnel for one week (4–11th September). A constant light source was attached to the top of the funnel to induce downward movement for the soil organisms. Organisms were collected at the bottom of the funnel in vials containing 20 ml of 70% ethanol and the collected invertebrates were identified to class level. The abundance of Acari and Collembola individuals from pitfall traps and Berlese funnels were combined for the analyses.

Fungi

Soil fungal biomass

Ergosterol was used as a proxy of soil fungal biomass in bulk soil samples, based on the method of Gong et al. (2001). 4 g of air-dried and milled soil (Planetary Micro Mill PULVERISETTE 7 premium line, Fritsch, Idar-Oberstein, Germany) was extracted with 12 ml of methanol for 60 min on a horizontal shaker (Kreisschüttler 3015, GFL, Burgwedel, Germany). The mixture was sonicated for 10 min (DT 514H, Bandelin electronics, Berlin, Germany) and centrifuged for 10 min at 2000 g (Universal 320, Hettich Lab Technology, Tuttlingen, Germany). The supernatant was ultra-centrifuged for 3 min at 7270 g (Micro centaur, MSE, London, UK) prior to high-performance liquid chromatography (HPLC) analysis. An aliquot of 20 µL of the supernatant was analysed via HPLC with UV detection at 282 nm (HPLC 1200 series, Agilent technologies, Santa Clara, CA, USA), equipped with a C18 LiChrospher® column (LiChrospher RP-18e, 5 µm, 100 Å, 250×4.6 mm, Merck, Darmstadt, Germany). Methanol (flow rate 1.7 ml min⁻¹) was used as a mobile phase under isocratic condition. The temperature of the column was set at 38 °C. The limit of detection (LOD) of the method was 0.06 mg kg⁻¹ (Meyer et al. 2021).

Soil and root fungal OTU richness and ecological groups

Fungal operational taxonomic unit (OTU) richness was analysed separately for bulk soil and root samples of the investigated plant species. Next-generation sequencing was carried out by the company Advanced Identification Methods (AIM) (Munich, Germany). For detailed processing of sequences, see Online Resource 3. In short, the internal transcribed

spacer 2 region of the nuc-rDNA (ITS2) was amplified using the primers ITS3tagmix/ITS4ngs (Tedersoo et al. 2014, 2015). Quality filtering reduced the initial 3,287,492 full sequences to a final dataset with 241,258 unique, non-singleton sequences. Clustering with a threshold of 2% and de novo chimera detection resulted in 6,468 OTUs (Online Resource 4). OTUs were matched against NCBI GenBank database (ncbi.nlm.nih.gov; October 2019; see Online Resource 5). Only 5,012 OTUs matched with sequences assigned to Fungi with more than 95% identity and were used for further analysis. In general, there is a large discrepancy between the described and the estimated number of species (Hawksworth and Rossman 1997). Hence, some OTUs cannot be assigned to any taxon or only at a higher taxonomic level. To increase the quality of database labelling, ambiguously attributed OTUs (e.g., "uncultured eukaryote" or "fungal endophyte") were checked manually and assigned to phyla using MycoBank (mycobank.org; Robert et al. 2013) as a reference database.

Prior to the statistical analysis, four main fungal ecological groups were identified: (1) Mycorrhiza is a widespread well-known symbiotic formation supporting both fungal and plant partner (Smith and Read 2008). In our study area, two main mycorrhizal groups are common: the arbuscular mycorrhizal fungi (AMF) comprising only Glomeromycota (Parniske 2008) and the ectomycorrhizal fungi (ECM) including mainly Basidiomycota, e.g. the large genus *Cortinarius* (Garnica et al. 2016), and Ascomycota, e.g. the species-rich order Helotiales (Tedersoo et al. 2009). In Europe, AMF typically occurs in herbaceous plants whereas ECM is usually found in woody species. (2) Root endophytes include phylogenetically diverse fungi and occurs ubiquitously in terrestrial plants across a variety of ecosystems. At some stage of their complex life cycle, they inhabit plant tissues without causing any obvious disease symptoms (Rodriguez et al. 2009). Species-rich endophytic fungal taxa are for example *Trichoderma* (Harman et al. 2004) and many members of the Sebaciales (Oberwinkler et al. 2013). (3) Saprobic fungi break down energy-rich organic substances from tissue of dead organisms or soil, where they play a key role beside bacteria (Lebreton et al. 2021). Typical saprobic fungi are representatives of the genera *Peziza* (Hansen et al. 2011) and *Mortierella* (Spatafora et al. 2016). (4) Parasitic fungi occur on living tissue and harm their

hosts. Typical examples are *Taphrina* (Ascomycota; Rodrigues and Fonseca 2003) and *Ustilago* (Bauer et al. 1997). Annotation of fungal OTUs to the ecological groups was realized in a two-step process: First, a literature search for taxa with well-known ecology was carried out. This is reasonable on genus or higher taxonomical range (Pölme et al. 2020). In a subsequent second step, a screening for OTU ecology was carried out using information deposited in metadata in the NCBI database (Online Resource 6). This approach allowed us to assess the fungal OTU richness of soil and root-associated fungi as well as the OTU richness in the respective ecological group (Zanne et al. 2020).

Data analysis

The data was analysed using R version 4.0.5 (R Core Team 2021). The package glmmTMB version 1.0.2.1 was used to create generalized linear mixed models (Brooks et al. 2017). The models were run separately for the site pairs of *F. japonica* / *U. dioica* and *I. glandulifera* / *U. dioica*, respectively. For the comparison of soil properties (organic carbon, total nitrogen, pH value, water content) between invaded and native sites, only plant species (factor with the two levels "invasive" [either *F. japonica* or *I. glandulifera*] and "native" [*U. dioica*]) was included as an explanatory variable and a Gaussian distribution was used. The study site was included as a random effect to account for our paired study design. The models for questions 2–4 incorporated plant species (factor with two levels), pH value (continuous), organic carbon content (continuous), and water content (continuous) as explanatory variables, and study site as a random effect. We decided on these variables by investigating the intercorrelation of the different explanatory variables (Online Resource 7). For example, organic carbon and total nitrogen content ($r=0.89$) were highly correlated. This allowed us to simplify the model by excluding nitrogen content. The response variables used were the soil microbial activity in bulk and rhizosphere soil, soil organism abundance, fungal biomass, total fungal OTU richness, and the OTU richness of the different fungal ecological groups (analysed separately for soil fungi and plant-associated fungi). Depending on the analysed variables, different family functions for the models were used. For the fungal OTU richness and the abundance of

soil organisms, a negative binomial model for over-dispersed count data was applied (Lindén and Mäntyniemi 2011). For the fungal biomass and both soil microbial activities, a gaussian model was used. The model results are presented by showing the estimate (Est.), z-value and P-value.

To reveal differences in the fungal OTU composition between invaded (either *F. japonica* or *I. glandulifera*) and native (*U. dioica*) sites and between fungi associated with invasive and native plants, permutational multivariate analyses of variances (PERMANOVA) were performed (command `adonis2` in the package ‘vegan’, Oksanen et al. 2019). The parameters organic carbon content, pH value and water content were used as further environmental variables to correspond to the previous models. Because of the paired study design, the study sites were used as strata in the formula. The PERMANOVA were based on presence-absence data for fungal OTUs occurring in more than one site or plant and the Jaccard index was used as a similarity measure. PERMANOVA were performed for soil fungal OTU composition (question 3) and root associated fungal OTU composition (question 4). Variation of fungal OTU compositions were visualized using nonmetric multidimensional scaling (NMDS) with the command ‘`metaMDS`’ in R package ‘vegan’.

Results

Soil physicochemical properties between invaded and native riparian vegetation

Soil properties (organic carbon content, nitrogen content, pH value and water content) did not significantly differ between sites invaded by *Fallopia japonica* or *Impatiens glandulifera* and the paired sites dominated by native *Urtica dioica* (Table S1).

Relations of soil microbial activity to riparian plant invasion and soil physicochemical properties

Water content and soil organic carbon were significantly related to bulk soil microbial activity in *F. japonica* site pairs. The basal soil respiration decreased with increasing water content (Est. = -0.04, $z = -2.91$, $P = 0.004$) and increased with increasing soil organic carbon (Est. 0.59,

$z = 2.86$, $P = 0.004$). However, the glucose-induced respiration was not affected by soil physicochemical parameters (Table S2). We did not find significant effects in basal and glucose-induced soil respiration for bulk soils from the *I. glandulifera* site pairs. Moreover, no significant effects were found for rhizosphere soils from both *F. japonica* or *I. glandulifera* site pairs (Table S2).

Soil invertebrates in relation to riparian plant invasion and soil physicochemical properties

Acari abundance was over three times higher in *U. dioica* (96 ± 99.7) than *F. japonica* (30 ± 21.6) soils (Est. = 1.33, $z = 3.77$, $P < 0.001$). Moreover, Acari abundance decreased with increasing pH (Est. = -0.55, $z = -2.91$, $P = 0.004$). When comparing *I. glandulifera* with *U. dioica* sites, Acari abundance was not different between invaded and native sites (Table S2). However, abundances slightly increased with increasing pH (Est. = 0.54, $z = 2.82$, $P = 0.005$). Collembola abundance was not affected by the presence of *F. japonica* compared to *U. dioica* (Table S2) but increased with elevated pH (Est. = 0.43, $z = 2.85$, $P = 0.004$) and organic carbon content (Est. = 0.17, $z = 2.19$, $P = 0.029$). However, when comparing *I. glandulifera* with *U. dioica*, Collembola abundance increased under presence of the invasive species (Est. = -0.33, $z = -2.61$, $P = 0.009$). Additionally, Collembola were less abundant in soils with higher organic carbon content (Est. = -0.32, $z = -3.70$, $P < 0.001$), whereas an increase in their abundance was still associated with higher pH (Est. = 0.43, $z = 2.52$, $P = 0.012$).

Soil fungi in relation to plant invasion and soil physicochemical properties

Analysis of bulk soil samples from the site pairs of *F. japonica* / *U. dioica* revealed no differences in total fungal biomass measured as ergosterol. Fungal biomass was positively correlated with organic carbon content (Est. = 0.88, $z = 2.56$, $P = 0.010$) while pH and water content had no influence (Table S3).

The general fungal OTU richness and OTU richness of three out of the four ecological fungal groups (endophytes, mycorrhiza, parasites) did not differ between *F. japonica* and *U. dioica* sites (Table S3, Fig. 1). The only exception was the OTU richness

of saprobes, which was 20% higher in *F. japonica* (103 ± 35.3) relative to *U. dioica* (82 ± 33.5) (Est. = -0.27 , $z = -3.71$, $P < 0.001$). In our model, all soil parameters were significantly related to the OTU richness of fungi: OTU richness of all fungi decreased with increasing organic carbon (Est. = -0.11 , $z = -3.01$, $P = 0.003$) and increased with increasing pH (Est. = 0.06 , $z = 2.60$, $P = 0.009$). The latter was also observed with OTU richness of endophytes (Est. = 0.23 , $z = 2.72$, $P = 0.007$), saprobes (Est. = 0.15 , $z = 2.15$, $P = 0.032$), and parasites (Est. = 0.18 , $z = 1.98$, $P = 0.048$). OTU richness of mycorrhizal fungi decreased with increasing organic carbon (Est. = -0.18 , $z = -2.06$, $P = 0.039$) and water content (Est. = -0.04 , $z = -3.73$, $P < 0.001$). In contrast to OTU richness, the composition of the soil fungal community did not differ between *F. japonica* and *U. dioica* sites and was not affected by any of the other soil characteristics (Table 1, Fig. 2a).

Regarding the site pairs of *I. glandulifera* and *U. dioica*, neither fungal biomass nor fungal OTU richness were different between the invaded and uninvaded sites (Table S3). However, fungal biomass increased with increasing organic carbon content (Est. = 1.59 , $z = 6.15$, $P < 0.001$) but decreased with higher soil water content (Est. = -0.11 , $z = -2.52$, $P = 0.012$). In terms of the fungal OTU richness, only soil water content was found to have effects (Table S3). Specifically, the OTU richness of endophytes (Est. = -0.02 , $z = -2.06$, $P = 0.039$), saprobes (Est. = -0.02 , $z = -2.66$, $P = 0.008$) and parasites (Est. = -0.02 , $z = -2.17$, $P = 0.030$) decreased with higher water content. The soil fungal community did not differ between *I. glandulifera* and *U. dioica* sites and none of the soil parameters had a significant effect (Table 1, Fig. 2b). For details of the most common fungi taxa found in soil samples of both *F. japonica* and *I. glandulifera* site pairs, see Online Resource 8.

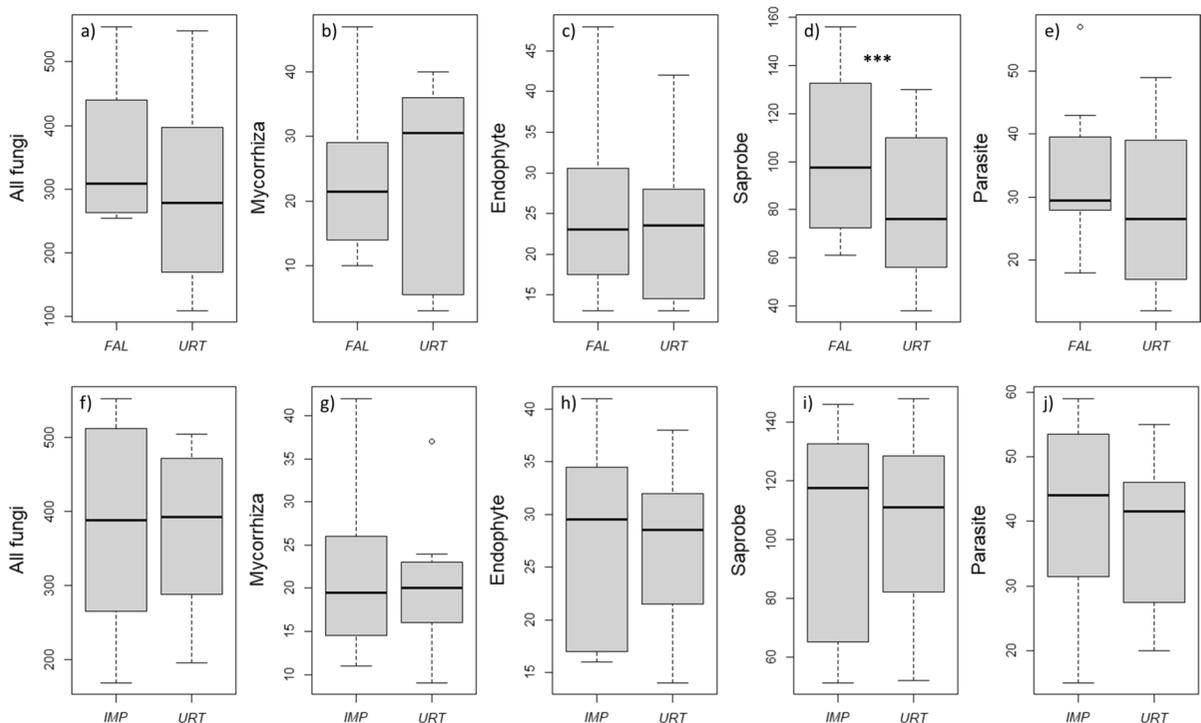


Fig. 1 Comparisons of bulk soil fungal ecological group operational taxonomic unit (OTU) richness in riparian habitats invaded by *Fallopia japonica* (FAL, a–e) or *Impatiens glandulifera* (IMP, f–j) compared to native *Urtica dioica* (URT) sites. OTU richness for all fungi and ecological groups (mycorrhiza,

endophytes, saprobes, and parasitic fungi) are compared. Boxplots show the median (thick black line), interquartile range (grey box), whiskers and outliers (circles). Significances are indicated by asterisks (***) ($P \leq 0.001$)

Table 1 Bulk soil and root fungal operational taxonomic units (OTU) composition in relation to plant species (invasive *Fallopia japonica* or *Impatiens glandulifera* vs. native *Urtica dioica*), soil organic carbon, pH value, and water content. Shown are R^2 , pseudo F-ratios and P values based on permutational multivariate analyses of variance for presence-absence data. Significant values at the 0.05 threshold are given in bold are marked with asterisks as (** $P \leq 0.01$, * $P \leq 0.05$)

	R^2	F	P
Bulk soil samples			
<i>Fallopia japonica</i> / <i>Urtica dioica</i> site pairs			
Plant species	0.05	0.83	0.109
Organic carbon	0.06	0.86	0.539
pH value	0.10	1.56	0.215
Water content	0.09	1.41	0.336
<i>Impatiens glandulifera</i> / <i>Urtica dioica</i> site pairs			
Plant species	0.05	0.74	0.563
Organic carbon	0.09	1.41	0.563
pH value	0.09	1.50	0.395
Water content	0.08	1.30	0.785
Root samples			
<i>Fallopia japonica</i> / <i>Urtica dioica</i> site pairs			
Plant species	0.21	3.77	0.009 **
Organic carbon	0.05	0.93	0.734
pH value	0.07	1.27	0.148
Water content	0.07	1.36	0.063
<i>Impatiens glandulifera</i> / <i>Urtica dioica</i> site pairs			
Plant species	0.09	1.43	0.016 *
Organic carbon	0.07	1.05	0.555
pH value	0.07	1.17	0.320
Water content	0.07	1.03	0.563

Root-associated fungi in relation to plant invasion and soil physicochemical properties

The overall root-associated fungal OTU richness was almost six times higher in *U. dioica* (63 ± 31.3) than in *F. japonica* (11 ± 4.9) (Est. = 1.75, $z = 7.57$, $P < 0.001$). Similar patterns were found for mycorrhizal OTU richness (*U. dioica*: 8 ± 5.4 , *F. japonica*: 1 ± 1.4) (Est. = 3.57, $z = 4.99$, $P < 0.001$), endophytes (*U. dioica*: 7 ± 3.3 , *F. japonica* 0 ± 0.5) (Est. = 2.74, $z = 4.53$, $P < 0.001$), saprobes (*U. dioica*: 14 ± 11.6 , *F. japonica* 4 ± 3.6) (Est. = 1.24, $z = 3.22$, $P = 0.001$) and parasites (*U. dioica*: 7 ± 4.5 , *F. japonica* 1 ± 0.9) (Est. = 2.46, $z = 4.72$, $P < 0.001$) (Fig. 3). Higher soil water content was related to a decrease in OTU richness of mycorrhiza (Est. = -0.01 , $z = -2.07$,

$P = 0.038$) and an increase in OTU richness of endophytes (Est. = 0.02, $z = 2.15$, $P = 0.031$) and parasites (Est. = 0.02, $z = 2.50$, $P = 0.013$). Additionally, the OTU richness of mycorrhiza decreased with increasing organic carbon content (Est. = -0.30 , $z = -2.01$, $P = 0.045$) and pH (Est. = -1.01 , $z = -3.07$, $P = 0.002$). The root associated fungal community differed between *F. japonica* and *U. dioica* ($R^2 = 0.21$, $P = 0.008$) (Fig. 4a). In contrast, soil parameters did not affect root colonizing fungal communities (Table 1).

Plant invasion effects were much less obvious for *I. glandulifera* compared to *F. japonica*. Only OTU richness of mycorrhiza (*U. dioica*: 6 ± 3.8 , *I. glandulifera*: 3 ± 1.2) (Est. = 0.60, $z = 2.29$, $P = 0.022$) and saprobes (*U. dioica*: 21 ± 15.9 , *I. glandulifera* 9 ± 3.6) (Est. = 0.64, $z = 2.04$, $P = 0.042$) were lower in *I. glandulifera* stands compared to *U. dioica* (Fig. 3). Moreover, the overall plant associated fungal OTU richness (pH: Est. = -0.10 , $z = -2.66$, $P = 0.008$; water content: Est. = -0.03 , $z = -2.19$, $P = 0.028$) and the richness of mycorrhizal OTU (pH: Est. = -0.36 , $z = -2.26$, $P = 0.024$; water content: Est. = -0.03 , $z = -2.30$, $P = 0.021$) decreased with increasing pH and water content. OTU richness of parasites decreased with increasing water content (Est. = -0.03 , $z = -2.05$, $P = 0.041$). While *I. glandulifera* and *U. dioica* showed distinct root associated fungal OTU compositions ($R^2 = 0.091$, $P = 0.016$), the soil parameters were not related to the fungal community composition (Table 1, Fig. 4b). For an overview over the most common fungi taxa found in root samples of both *F. japonica* and *I. glandulifera* site pairs, see Online Resource 8.

Discussion

In this study we analysed the impact of riparian plant invasions on soil, arthropods, and fungi by comparing sites invaded by *Fallopia japonica* or *Impatiens glandulifera* to corresponding sites inhabited by the native *Urtica dioica*. We found that both invasive species had only minor effects on soil physicochemical properties, soil microbial activity, soil arthropod abundance and soil fungal biomass, OTU richness, and composition. We further investigated root-associated fungal communities of the three plant species. As a key finding, we observed strong reductions in

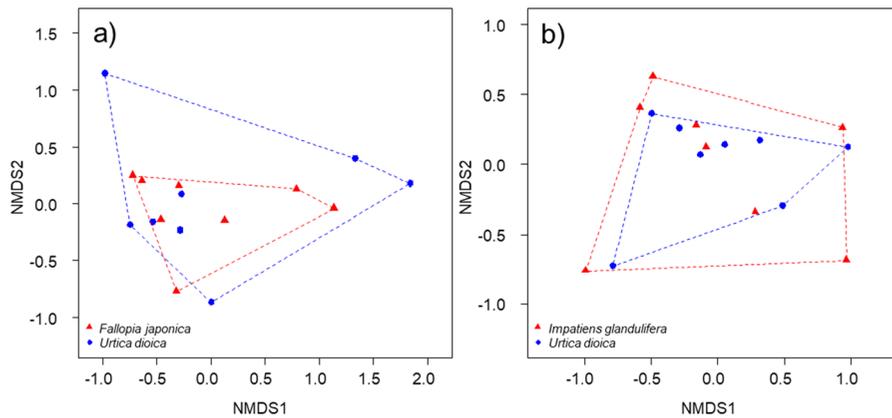


Fig. 2 Nonmetric multidimensional scaling (NMDS) ordination for the bulk soil fungal operational taxonomic units (OTU) composition of riparian site pairs of **a** *Fallopia japonica*/*Urtica dioica* and **b** *Impatiens glandulifera*/*Urtica dioica*. Boundaries indicate the OTU composition of native

(blue) and invaded (red) sites. Relations between soil fungal OTU composition and environmental variables were not significant (tested with permutational multivariate analyses of variances, see Table 1)

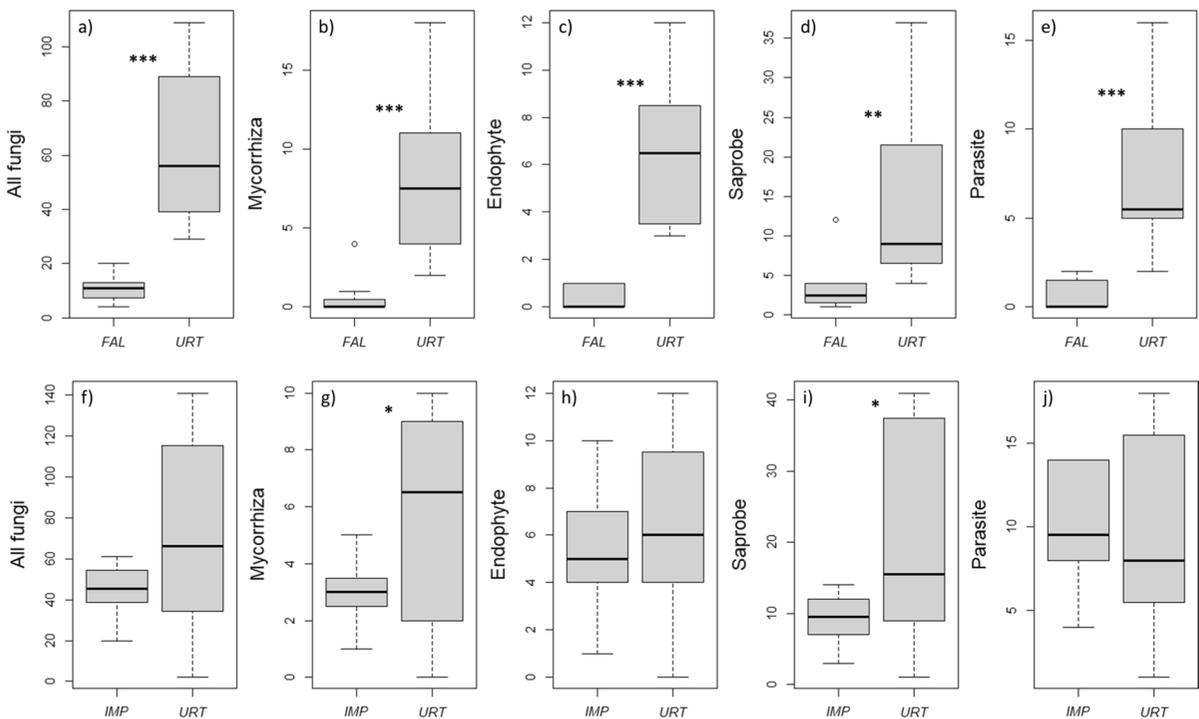


Fig. 3 Comparisons of root fungal ecological group operational taxonomic unit (OTU) richness in riparian habitats invaded by *Fallopia japonica* (FAL, **a–e**) or *Impatiens glandulifera* (IMP, **f–j**) compared to native *Urtica dioica* (URT) sites. OTU richness for all fungi and ecological groups (mycorrhiza,

endophytes, saprobes, and parasitic fungi) are compared. Boxplots show the median (thick black line), the interquartile range (grey box), whiskers and outliers (circles). Significances are indicated by asterisks (** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$)

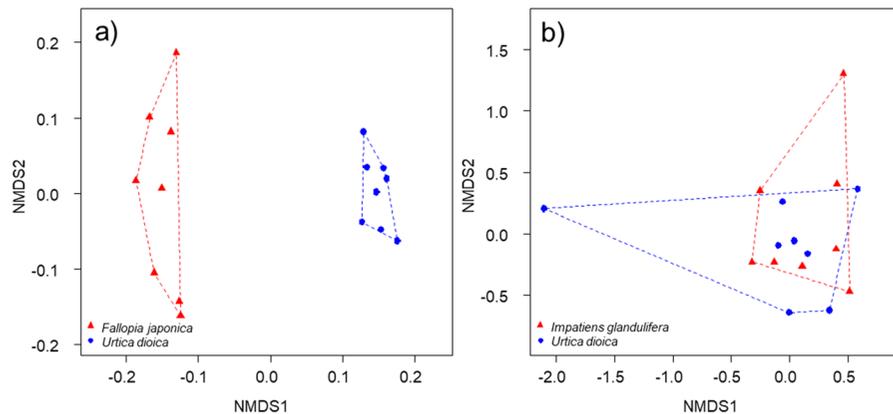


Fig. 4 Nonmetric multidimensional scaling (NMDS) ordination showing significant differences in the root fungal operational taxonomic units (OTU) composition between riparian site pairs of **a** *Fallopia japonica*/*Urtica dioica* and **b** *Impatiens glandulifera* / *Urtica dioica*. Boundaries indicate the OTU

fungal OTU richness in roots of *F. japonica* and, to a lesser extent, in roots of *I. glandulifera* compared to *U. dioica*.

Riparian plant invasion has low impact on soil physicochemical properties and soil microbial activity

None of the investigated soil physicochemical parameters (organic carbon content, pH, water content) nor soil microbial activity were significantly affected by the presence of an invasive plant invader investigated here. While soil organic carbon content seems to be less influenced (Aguilera et al. 2010), previous studies have found that micronutrient levels can increase in presence of *F. japonica*, especially under poor nutrient conditions (Dassonville et al. 2007). We studied riparian and relatively nutrient-rich habitats along streams, which could be one reason why we did not detect an impact of *F. japonica* on soil physicochemical parameters. Moreover, impacts of plant invasions often change over time (Strayer et al. 2006; Dostál et al. 2013), but information about the age of our studied plant stands was not available. For *I. glandulifera*, our results conform with findings of Čuda et al. (2017) who also found only minor impact of this species on soil physicochemical properties. Since root traits such as root exudation can influence soil functions (Bardgett 2018), the lack of an effect on soil microbial activity (measured by soil respiration) was

unexpected. Both *F. japonica* and *I. glandulifera* have also been shown to negatively impact soil microbial activity (Stefanowicz et al. 2016). However, *Fallopia* spp. may mainly affect anaerobic respiration through root exudates (for example procyanidins), while aerobic respiration is less impacted (Bardon et al. 2016, 2017). This observation might be directly linked to the lack of effects in the fungal community and biomass among sites (see below), as fungi are considered a main driver of microbial activity in soils (Žifčáková et al. 2016; Xu et al. 2019).

Fallopia japonica and *I. glandulifera* affect soil arthropod abundance

The analysed soil arthropods Acari and Collembola were strongly affected by the presence of the invasive plants, though in contrasting ways. The abundance of Collembola significantly increased in *I. glandulifera* stands but was not affected by *F. japonica*. While the impact of *I. glandulifera* was previously linked to its annual life cycle, which leads to a higher availability of food for collembolan herbivores (Tanner et al. 2013), the lack of an effect by *F. japonica* was unexpected due to its known allelopathic impacts (Kato-Noguchi 2021) on soil microfauna (Abgrall et al. 2018). However, detritivores are often less affected by invasive plants than other trophic groups, which might be explained by often increased plant

productivity in invaded habitats (Liao et al. 2008; Ehrenfeld 2010; Schirmel et al. 2016).

In our study, invasion by *F. japonica* negatively impacted Acari abundance while *I. glandulifera* had no significant effect. For *I. glandulifera*, this is in accordance with earlier reports, where its presence had differential effects on different groups of Acari, which lead to no effect in total abundances (Rusterholz et al. 2014). The lower Acari abundances in *F. japonica* sites may be explained by its phenolic compounds in the leaf litter, which have negative impacts on saprobic species (Skubala and Mierny 2009; Abgrall et al. 2018). Moreover, reduced Acari abundances under *F. japonica* might be a result of changes in the soil food web (Abgrall et al. 2018), although this was not demonstrated in our study.

In the case of *F. japonica*, we uncovered a positive and negative relationship between Collembola abundances and organic carbon contents and pH, respectively. For *I. glandulifera* sites, the opposite patterns for both variables were observed. This supports previous studies that have documented the importance of soil organic matter for shaping soil fauna communities (Rendoš et al. 2016). The influence of pH might also be indirect, by altering the soil microbial community (Fierer et al. 2009). Acari abundances were also affected by soil pH. The abundances increased with pH value in *F. japonica* site pairs but decreased in *I. glandulifera* site pairs. The effect of pH value on Acari abundance may be explained by the fact that pH differences are associated with different microhabitats, which influence Acari abundance and communities (Nielsen et al. 2010; Wissuwa et al. 2013).

Soil physicochemical properties are more influential for soil fungi than the presence of invasive plants

The presence of invasive plant species had little effect on the soil fungal biomass, OTU richness and composition in the context of this study. We only found an increase in saprobic fungi richness in soils from *F. japonica* sites compared to those from *U. dioica*. Saprobian fungi may be promoted by increased amounts of litter introduced by *F. japonica* which is degraded by saprobes (Lebreton et al. 2021). This finding is unexpected and contrasts with earlier studies, where plant invasion induced changes in fungal diversity and function (Wolfe and Klironomos 2005; Si et al. 2013). One explanation might be that the plant invasions did

not significantly alter physicochemical properties compared to the uninvaded sites, which are known to strongly influence soil fungi abundances and diversity (for example Lauber et al. 2008; Wakelin et al. 2016; Yang et al. 2017). This indicates that plant invasion may only affect the soil fungi community if it alters the physicochemical properties of the habitat. Consequently, the soil physicochemical properties were much more important in explaining soil fungi biomass and OTU richness. It is well known that water availability, organic carbon and pH have major effects on the fungal species composition (Li et al. 2015; Xiao et al. 2018). Here, the fungal biomass was affected by the soil organic carbon content providing more resources for saprobic fungal species supporting their development (Bossio and Scow 1998; Yao and Wilson 2000; Drenovsky et al. 2004). However, increased organic carbon also leads to a reduction in overall as well as mycorrhizal OTU numbers in the *F. japonica* site pairs in our study. Contrary to this observation, Zhu et al. (2020) showed that mycorrhizal species richness increases with organic carbon content. Other studies observed a decrease in fungal diversity along a gradient of the same variable (Liu et al. 2015). This might be because the interaction of mycorrhizal taxa and organic carbon in the soil is dependent on the local conditions (Hanson et al. 2008; Wei et al. 2019).

At *F. japonica* site pairs, pH value was associated with an increase of fungal OTU richness in all ecological groups except mycorrhiza (endophytes, parasites, and saprobes). In contrast, at *I. glandulifera* site pairs, pH had no significant influence on fungal OTU richness. Moreover, we did not observe an effect of pH on fungal community composition. Our findings are thus surprising, because pH value is known to affect especially mycorrhizal species richness and composition in various habitats (Porter et al. 1987; An et al. 2008; Garnica et al. 2013; Davison et al. 2015; Řezáčová et al. 2019). One possible explanation for this contradictory result might be that the differences in the pH values across our study sites were too small (on average 5.7–6.2; Table S1) to impact the fungal OTU richness and composition. In other studies, these pH ranges were much wider, for example between 4.8 and 7.5 (Porter et al. 1987) or 4.0 and 7.6 (Řezáčová et al. 2019). Increasing soil water content negatively affected mycorrhizal fungal OTU richness in the *F. japonica* site pairs and fungal biomass as well as

fungal OTU richness of endophytes, parasites, and saprobes in the *I. glandulifera* site pairs. Fungi have a lower moisture optimum than other soil microbes and have a lower competitive ability under high soil moisture conditions (Kouyeas 1964). This has also been shown by Cavagnaro (2016), where higher soil moisture negatively impacted mycorrhizal growth and colonization of plants, and Deepika and Kothamasi (2015) who found lower levels of arbuscular mycorrhizal fungi (AMF) diversity in flooded soils.

Invasive plant species are characterised by low OTU richness of root fungal communities

The root-associated fungal communities were composed of low phylogenetic OTU richness in the invasive species, and were remarkably distinct to the native counterpart *U. dioica*. Irrespective of the fungal ecological group, significantly fewer root-associated OTUs were found for *F. japonica* compared to *U. dioica*. The second species investigated, *I. glandulifera*, was also characterized by reduced root-associated fungal OTUs, however significant reductions compared to *U. dioica* were observed only for mycorrhiza and saprobic taxa. The lower endophyte and mycorrhizal OTU richness in *F. japonica* and *I. glandulifera* roots were likely caused by changes in host-symbiont interactions. Symbionts are often not host specific but functional variability between different plant-mycorrhiza combinations have been observed (Klironomos 2000). Therefore, an invasive plant species may not be able to benefit from local soil fungi which might reduce mycorrhizal and root endophytic diversity (Čuda et al. 2020). This is in line with Callaway et al. (2011) who reported that AMF from a native range stimulated stronger positive feedbacks in invasive *Robinia pseudoacacia* than AMF from an invasive range. On the other hand, root endophytes of *Centaurea stoebe* were reported to directly increase the competitive effects of the introduced plant species (Aschehoug et al. 2012). Root endophytes of two *Centaurea* species (one invasive and one native) were also found to be different, indicating that endophytes may not be able to form associations with a variety of plants (Geisen et al. 2017). Garnica et al. (2022) reported a strong colonization rate for the root endophytic species *Serendipita herbamans* in *F. japonica* in a lab study, especially in low-nutrient conditions. Secondary metabolites inhibit the growth

of especially mycorrhizal fungi (Pinzone et al. 2018), which might also explain the lower number of root-associated fungi found in *F. japonica* compared to *I. glandulifera*. Moreover, *I. glandulifera* is able to associate to some degree with AMF (Tanner et al. 2014) and according to Pattison et al. (2016), *I. glandulifera* can affect the AMF and fungal endophyte diversity.

The lower number of mycorrhizal OTUs in roots of both *F. japonica* and *I. glandulifera* compared to native *U. dioica* indicates reduced symbiotic interactions. The root associated fungi in the invasive species include no AMF, which indicates that these species may not be able to associate well with symbiotic fungi in the invasive range. Some Glomeromycota were however detected in *U. dioica* roots (*Rhizophagus* spp., see Online Resource 8). Root endophytic OTUs were lower in *F. japonica*, which might be caused by the absence of the most common and diverse genus *Trichoderma* (Harman et al. 2004). One reason might be due to the secondary metabolites utilized by *F. japonica*. We also found reduced numbers of parasitic fungal OTUs in root samples of *F. japonica* compared to *U. dioica*. The most common genus in *U. dioica*, *Fusarium*, was absent in *F. japonica*. The absence of directly associated major fungal parasites inhibiting its growth in the invasive range might contribute to the invasion success of *F. japonica*. This is in accordance with the enemy release hypothesis, which states that invasive species have increased success because of lower numbers of natural enemies (Mitchell and Power 2003). Root associated OTUs classified as saprobic were lower in both invasive species compared to the native species. Saprobian fungi may enter tissue to break down dead matter (Lebreton et al. 2021). The reduced number of OTUs in the invasive species might indicate that a smaller subset of species is able to metabolize the tissue of the two invasive plant species. Mincheva et al. (2014) showed that *F. japonica* is a low-quality food source and had a different fungal composition compared to litter from native sites.

Like the soil fungal OTU abundances, root associated fungi were affected by some soil parameters as well. The most important factor was soil water content, having a predominantly negative effect on the overall fungal OTU richness as well as the ecological groups mycorrhiza and parasites in the *I. glandulifera* site pairs. In *F. japonica* site pairs, only the number of mycorrhizal OTUs was negatively associated with

increasing water content, while higher water content was positively correlated with OTU richness in endophytes and parasites. The negative effect of higher moisture on mycorrhiza has previously been shown by Cavagnaro (2016) and Deepika and Kothamasi (2015). Tree root associated saprotrophic and parasitic community structure has also previously been shown to correlate with soil moisture, where higher soil moisture benefited only some species (Burke et al. 2009).

Conclusion

We observed only minor effects of the investigated plant invasive species *Fallopia japonica* and *Impatiens glandulifera* on soil physicochemical properties, soil microbial activity, soil fungal biomass and OTU richness. In contrast, the abundances of Acari and Collembola were impacted, indicating that both species can have direct impacts on soil biota. However, these impacts were not uniform between *F. japonica* and *I. glandulifera*, which implies that these effects are species-specific and may depend on the local soil biota composition. Looking at tissue-entering fungi, *F. japonica* clearly had lower fungi OTU richness while *I. glandulifera* was characterized only by fewer mycorrhizal and saprobic OTUs. This was further related to soil characteristics, especially water content and pH decreased fungal OTU richness. Overall, our findings indicate that *F. japonica* and *I. glandulifera* invasions may have various and partly contrasting impacts to previous studies on belowground ecosystem compartments such as soil invertebrates and fungi. Therefore, effects of these plant invaders seem to be highly context-dependent and site-specific. Furthermore, our results are in line with the enemy release hypothesis, indicating that these invasive species, especially *F. japonica*, may be less associated with fungal parasites in the invasive range, allowing them to perform better than native species.

Conflicts of interest

The authors declare that they have no conflict of interest.

Acknowledgements We also acknowledge the support of all members of the SystemLink project of the research training group 2360 of RPTU University of Kaiserslautern-Landau.

Funding Open Access funding enabled and organized by Projekt DEAL. This work was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—326210499/GRK2360.

Data availability The authors declare that the data supporting the findings of this study are available within the article and its supplementary information files.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abgrall C, Forey E, Mignot L, Chauvat M (2018) Invasion by *Fallopia japonica* alters soil food webs through secondary metabolites. *Soil Biol Biochem* 127:100–109. <https://doi.org/10.1016/j.soilbio.2018.09.016>
- Abgrall C, Forey E, Chauvat M (2019) Soil fauna responses to invasive alien plants are determined by trophic groups and habitat structure: a global meta-analysis. *Oikos* 128:1390–1401. <https://doi.org/10.1111/oik.06493>
- Aguilera AG, Alpert P, Dukes JS, Harrington R (2010) Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem processes. *Biol Invasions* 12:1243–1252. <https://doi.org/10.1007/s10530-009-9543-z>
- Ahmad R, Khuroo AA, Hamid M, Rashid I (2020) Plant invasion alters the physico-chemical dynamics of soil system: insights from invasive *Leucanthemum vulgare* in the Indian Himalaya. *Environ Monit Assess* 191:792. <https://doi.org/10.1007/s10661-019-7683-x>
- An G-H, Miyakawa S, Kawahara A, Osaki M, Ezawa T (2008) Community structure of arbuscular mycorrhizal fungi associated with pioneer grass species *Miscanthus sinensis* in acid sulfate soils: Habitat segregation along pH gradients. *Soil Sci Plant Nutr* 54(4):517–528. <https://doi.org/10.1111/j.1747-0765.2008.00267.x>
- Aschehoug ET, Metlen KL, Callaway RM, Newcombe G (2012) Fungal endophytes directly increase the competitive effects of an invasive forb. *Ecology* 93:3–8. <https://doi.org/10.1890/11-1347.1>

- Bailey JP (1994) Reproductive biology and fertility of *Fallopia japonica* (Japanese knotweed) and its hybrids in the British Isles. In: de Waal LC, Child LE, Wade PM, Brock JH (eds) Ecology and management of invasive riverside plants. Wiley, Chichester, pp 141–158
- Bardgett RD (2018) Plant trait-based approaches for interrogating belowground function. *Biol Environ* 117B(1):1–13. <https://doi.org/10.3318/bioe.2018.05pr>
- Bardon C, Piola F, Bellvert F, Haichar FEZ, Comte G, Meiffren G, Pommier T, Pujalon S, Tsafack N, Poly F (2014) Evidence for biological denitrification inhibition (BDI) by plant secondary metabolites. *New Phytol* 204:620–630. <https://doi.org/10.1111/nph.12944>
- Bardon C, Poly F, Piola F, Pancton M, Comte G, Meiffren G, Haichar FEZ (2016) Mechanism of biological denitrification inhibition: procyanidins induce an allosteric transition of the membrane-bound nitrate reductase through membrane alteration. *FEMS Microbiol Ecol*. <https://doi.org/10.1093/femsec/fiw034>
- Bardon C, Poly F, Haichar FEZ, Le Roux X, Simon L, Meiffren G, Comte G, Rouified S, Piola F (2017) Biological denitrification inhibition (BDI) with procyanidins induces modification of root traits, growth and N status in *Fallopia x bohemica*. *Soil Biol Biochem* 107:41–49. <https://doi.org/10.1016/j.soilbio.2016.12.009>
- Bauer R, Oberwinkler F, Vánky K (1997) Ultrastructural markers and systematics in smut fungi and allied taxa. *Can J Bot* 75:1273–1314. <https://doi.org/10.1139/b97-842>
- Bedano JC (2004) Soil prostigmatid mites (Acari: *Prostigmata*) of Argentina: an annotated checklist. *Syst Appl Acarol* 9:45. <https://doi.org/10.11158/saa.9.1.9>
- Beerling DJ, Perrins JM (1993) *Impatiens glandulifera* Royle (*Impatiens roylei* Walp.). *J Ecol* 81:367. <https://doi.org/10.2307/2261507>
- Beerling DJ, Bailey JP, Conolly AP (1994) *Fallopia Japonica* (Houtt.) Ronse Decraene. *J Ecol* 82:959. <https://doi.org/10.2307/2261459>
- Behan-Pelletier VM (2003) Acari and Collembola biodiversity in Canadian agricultural soils. *Can J Soil Sci* 83:279–288. <https://doi.org/10.4141/S01-063>
- Belnap J, Phillips SL, Sherrad SK, Moldenke A (2005) Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* 86:3007–3017. <https://doi.org/10.1890/05-0333>
- Biederman LA, Boutton TW (2009) Biodiversity and trophic structure of soil nematode communities are altered following woody plant invasion of grassland. *Soil Biol Biochem* 41:1943–1950. <https://doi.org/10.1016/j.soilbio.2009.06.019>
- Blume E, Bischoff M, Reichert JM, Moorman T, Konopka A, Turco RF (2002) Surface and subsurface microbial biomass, community structure and metabolic activity as a function of soil depth and season. *Appl Soil Ecol* 20:171–181. [https://doi.org/10.1016/S0929-1393\(02\)00025-2](https://doi.org/10.1016/S0929-1393(02)00025-2)
- Bossio S, Scow KM (1998) Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. *Microb Ecol* 35:265–278. <https://doi.org/10.1007/s002489900082>
- Bradford MA, Tordoff GM, Eggers T, Jones TH, Newington JE (2002) Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99:317–323. <https://doi.org/10.1034/j.1600-0706.2002.990212.x>
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. <https://doi.org/10.3929/ethz-b-000240890>
- Buée M, Reich M, Murat C, Morin E, Nilsson RH, Uroz S, Martin F (2009) 454 pyrosequencing analyses of forest soils reveal an unexpectedly high fungal diversity. *New Phytol* 184:449–456. <https://doi.org/10.1111/j.1469-8137.2009.03003.x>
- Burke DJ, López-Gutiérrez JC, Smemo KA, Chan CR (2009) Vegetation and Soil Environment Influence the Spatial Distribution of Root-Associated Fungi in a Mature Beech-Maple Forest. *Appl Environ Microbiol* 75(24):7639–7648. <https://doi.org/10.1128/AEM.01648-09>
- Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. *Nature* 427:731–733. <https://doi.org/10.1038/nature02322>
- Callaway RM, Bedmar EJ, Reinhart KO, Silvan CG, Klironomos J (2011) Effects of soil biota from different ranges on Robinia invasion: acquiring mutualists and escaping pathogens. *Ecology* 92:1027–1035. <https://doi.org/10.1890/10-0089.1>
- Campbell CD, Chapman SJ, Cameron CM, Davidson MS, Potts JM (2003) A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. *Appl Environ Microbiol* 69:3593–3599. <https://doi.org/10.1128/AEM.69.6.3593-3599.2003>
- Canini F, Zucconi L, Pacelli C, Selbmann L, Onofri S, Geml J (2019) Vegetation, pH and water content as main factors for shaping fungal richness, community composition and functional guilds distribution in soils of Western Greenland. *Front Microbiol* 10:2348. <https://doi.org/10.3389/fmicb.2019.02348>
- Cantarel AAM, Rouified S, Simon L, Bourg J, Gervais J, Blazère L, Poussineau S, Des Creuzé Châtelliers C, Piola F (2020) In nitrate-rich soil, *Fallopia x bohemica* modifies functioning of N cycle compared to native monocultures. *Diversity* 12:156. <https://doi.org/10.3390/d12040156>
- Cassagne N, Gers C, Gauquelin T (2003) Relationships between Collembola, soil chemistry and humus types in forest stands (France). *Biol Fertil Soils* 37:355–361. <https://doi.org/10.1007/s00374-003-0610-9>
- Cavagnaro TR (2016) Soil moisture legacy effects: impacts on soil nutrients, plants and mycorrhizal responsiveness. *Soil Biol Biochem* 95:173–179. <https://doi.org/10.1016/j.soilbio.2015.12.016>
- Čerevková A, Bobuřská L, Miklisová D, Renčo M (2019) A case study of soil food web components affected by *Fallopia japonica* (Polygonaceae) in three natural habitats in Central Europe. *J Nematol* 51(1):1–16. <https://doi.org/10.21307/jofnem-2019-042>
- Chagnon M, Paré D, Hébert C, Camiré C (2001) Effects of experimental liming on collembolan communities and soil microbial biomass in a southern Quebec sugar maple

- (*Acer saccharum* Marsh.) stand. *Appl Soil Ecol* 17:81–90. [https://doi.org/10.1016/S0929-1393\(00\)00134-7](https://doi.org/10.1016/S0929-1393(00)00134-7)
- Chauvat M, Forey E (2021) Temperature modifies the magnitude of a plant response to Collembola presence. *Appl Soil Ecol* 158:103814. <https://doi.org/10.1016/j.apsoil.2020.103814>
- Christian N, Sullivan C, Visser ND, Clay K (2016) Plant host and geographic location drive endophyte community composition in the face of perturbation. *Microb Ecol* 72:621–632. <https://doi.org/10.1007/s00248-016-0804-y>
- Clavel J, Lembrechts J, Alexander J, Haider S, Lenoir J, Milbau A, Nuñez MA, Pauchard A, Nijs I, Verbruggen E (2021) The role of arbuscular mycorrhizal fungi in non-native plant invasion along mountain roads. *New Phytol* 230:1156–1168. <https://doi.org/10.1111/nph.16954>
- Creamer RE, Stone D, Berry P, Kuiper I (2016a) Measuring respiration profiles of soil microbial communities across Europe using MicroResp™ method. *Appl Soil Ecol* 97:36–43. <https://doi.org/10.1016/j.apsoil.2015.08.004>
- Creamer RE, Hannula SE, Leeuwen JPV, Stone D, Rutgers M, Schmelz RM, Rüter PCd, Hendriksen NB, Bolger T, Bouffaud ML, Buee M, Carvalho F, Costa D, Dirilgen T, Francisco R, Griffiths BS, Griffiths R, Martin F, da Silva PM, Mendes S, Morais PV, Pereira C, Philippot L, Plassart P, Redecker D, Römbke J, Sousa JP, Wouterse M, Lemanceau P (2016b) Ecological network analysis reveals the inter-connection between soil biodiversity and ecosystem function as affected by land use across Europe. *Appl Soil Ecol* 97:112–124. <https://doi.org/10.1016/j.apsoil.2015.08.006>
- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166. <https://doi.org/10.1034/j.1600-0706.2002.970201.x>
- Čuda J, Vítková M, Albrechtová M, Guo WY, Barney JN, Pyšek P (2017) Invasive herb *Impatiens glandulifera* has minimal impact on multiple components of temperate forest ecosystem function. *Biol Invasions* 19:3051–3066. <https://doi.org/10.1007/s10530-017-1508-z>
- Čuda J, Skálová H, Pyšek P (2020) Spread of *Impatiens glandulifera* from riparian habitats to forests and its associated impacts: insights from a new invasion. *Weed Res* 60:8–15. <https://doi.org/10.1111/wre.12400>
- Custer GF, van Diepen LTA (2020) Plant invasion has limited impact on soil microbial α -diversity: a meta-analysis. *Diversity* 12:112. <https://doi.org/10.3390/d12030112>
- Dassonville N, Vanderhoeven S, Gruber W, Meerts P (2007) Invasion by *Fallopia japonica* increases topsoil mineral nutrient concentrations. *Ecoscience* 14:230–240. [https://doi.org/10.2980/1195-6860\(2007\)14\[230:IBFJIT\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2007)14[230:IBFJIT]2.0.CO;2)
- Dassonville N, Vanderhoeven S, Vanparys V, Hayez M, Gruber W, Meerts P (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157:131–140. <https://doi.org/10.1007/s00442-008-1054-6>
- Davison J, Moora M, Öpik M, Adholeya A, Ainsaar L, Bá A, Burla S, Diedhiou AG, Hiiesalu I, Jairus T, Johnson NC, Kane A, Koorem K, Kochar M, Ndiaye C, Pärtel M, Reier Ü, Saks Ü, Singh R, Vasar M, Zobel M (2015) Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. *Science* 349:970–973. <https://doi.org/10.1126/science.aab1161>
- de Deyn GB, Raaijmakers CE, Zoomer HR, Berg MP, de Ruiter PC, Verhoef HA, Bezemer TM, van der Putten WH (2003) Soil invertebrate fauna enhances grassland succession and diversity. *Nature* 422:711–713. <https://doi.org/10.1038/nature01548>
- Deepika S, Kothamasi D (2015) Soil moisture—A regulator of arbuscular mycorrhizal fungal community assembly and symbiotic phosphorus uptake. *Mycorrhiza* 25:67–75. <https://doi.org/10.1007/s00572-014-0596-1>
- Deharveng L (1996) Soil Collembola diversity, endemism, and reforestation: a case study in the Pyrenees (France). *Conserv Biol* 10:74–84. <https://doi.org/10.1046/j.1523-1739.1996.10010074.x>
- Díaz-Raviña M, Acea MJ, Carballas T (1995) Seasonal changes in microbial biomass and nutrient flush in forest soils. *Biol Fertil Soils* 19:220–226. <https://doi.org/10.1007/BF00336163>
- Dostál P, Müllerová J, Pyšek P, Pergl J, Klinerová T (2013) The impact of an invasive plant changes over time. *Ecol Lett* 16:1277–1284. <https://doi.org/10.1111/ele.12166>
- Drenovsky RE, Vo D, Graham KJ, Scow KM (2004) Soil water content and organic carbon availability are major determinants of soil microbial community composition. *Microb Ecol* 48:424–430. <https://doi.org/10.1007/s00248-003-1063-2>
- Duguay KJ, Klironomos JN (2000) Direct and indirect effects of enhanced UV-B radiation on the decomposing and competitive abilities of saprobic fungi. *Appl Soil Ecol* 14:157–164. [https://doi.org/10.1016/S0929-1393\(00\)00049-4](https://doi.org/10.1016/S0929-1393(00)00049-4)
- Edwards SC, MacLeod CL, Lester JN (1998) The bioavailability of copper and mercury to the common nettle (*Urtica dioica*) and the earthworm *Eisenia fetida* from contaminated dredge spoil. *Water Air Soil Pollut* 102:75–90. <https://doi.org/10.1023/A:1004993912639>
- Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523. <https://doi.org/10.1007/s10021-002-0151-3>
- Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Ann Rev Ecol Evol Syst* 41:59–80. <https://doi.org/10.1146/annurev-ecolsys-102209-144650>
- Fierer N, Strickland MS, Liptzin D, Bradford MA, Cleveland CC (2009) Global patterns in belowground communities. *Ecol Lett* 12:1238–1249. <https://doi.org/10.1111/j.1461-0248.2009.01360.x>
- Gaggini L, Rusterholz HP, Baur B (2018) The invasive plant *Impatiens glandulifera* affects soil fungal diversity and the bacterial community in forests. *Appl Soil Ecol* 124:335–343. <https://doi.org/10.1016/j.apsoil.2017.11.021>
- Gaggini L, Rusterholz HP, Baur B (2019) The annual invasive plant *Impatiens glandulifera* reduces hyphal biomass of soil fungi in deciduous forests. *Fungal Ecol* 39:242–249. <https://doi.org/10.1016/j.funeco.2018.12.004>
- Garnica S, Riess K, Bauer R, Oberwinkler F, Weiß M (2013) Phylogenetic diversity and structure of sebacinoic fungi associated with plant communities along an altitudinal gradient. *FEMS Microbiol Ecol* 83:265–278. <https://doi.org/10.1111/j.1574-6941.2012.01473.x>

- Garnica S, Liao Z, Hamard S, Waller F, Parepa M, Bossdorf O (2022) Environmental stress determines the colonization and impact of an endophytic fungus on invasive knotweed. *Biol Invas.* <https://doi.org/10.1007/s10530-022-02749-y>
- Garnica S, Schön ME, Abarenkov K, Riess K, Liimatainen K, Niskanen T, Dima B, Soop K, Frøslev TG, Jeppesen TS, Peintner U, Kuhnert-Finkernagel R, Brandrud TE, Saar G, Oertel B, Ammirati JF (2016) Determining threshold values for barcoding fungi: lessons from *Cortinarius* (Basidiomycota), a highly diverse and widespread ectomycorrhizal genus. *FEMS Microbiol Ecol* 92:fiw045. <https://doi.org/10.1093/femsec/fiw045>
- Geisen S, Kostenko O, Cnossen MC, ten Hooven FC, Vreš B, van der Putten WH (2017) Seed and root endophytic fungi in a range expanding and a related plant species. *Front Microbiol* 8:1645. <https://doi.org/10.3389/fmicb.2017.01645>
- Gerber E, Krebs C, Murrell C, Moretti M, Rocklin R, Schaffner U (2008) Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biol Conserv* 141:646–654. <https://doi.org/10.1016/j.biocon.2007.12.009>
- Gong P, Guan X, Witter E (2001) A rapid method to extract ergosterol from soil by physical disruption. *Appl Soil Ecol* 17:285–289. [https://doi.org/10.1016/S0929-1393\(01\)00141-X](https://doi.org/10.1016/S0929-1393(01)00141-X)
- Greenwood P, Kuhn NJ (2014) Does the invasive plant, *Impatiens glandulifera*, promote soil erosion along the riparian zone? An investigation on a small watercourse in northwest Switzerland. *J Soils Sediments* 14:637–650. <https://doi.org/10.1007/s11368-013-0825-9>
- Hansen K, Læssøe T, Pfister DH (2001) Phylogenetics of the Pezizaceae, with an emphasis on *Peziza*. *Mycologia* 93:958–990. <https://doi.org/10.1080/00275514.2001.12063229>
- Hanson CA, Allison SD, Bradford MA, Wallenstein MD, Treseder KK (2008) Fungal taxa target different carbon sources in forest soil. *Ecosystems* 11:1157–1167. <https://doi.org/10.1007/s10021-008-9186-4>
- Harman GE, Howell CR, Viterbo A, Chet I, Lorito M (2004) Trichoderma species—opportunistic, avirulent plant symbionts. *Nat Rev Microbiol* 2:43–56. <https://doi.org/10.1038/nrmicro797>
- Hawksworth DL, Rossman AY (1997) Where are all the undescribed fungi? *Phytopathology* 87:888–891. <https://doi.org/10.1094/PHYTO.1997.87.9.888>
- Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108. <https://doi.org/10.1038/nature11118>
- Huenneke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71:478–491. <https://doi.org/10.2307/1940302>
- Jobbágy EG, Jackson RB (2004) The uplift of soil nutrients by plants: biogeochemical consequences across scales. *Ecology* 85:2380–2389. <https://doi.org/10.1890/03-0245>
- Kato-Noguchi H (2021) Allelopathy of knotweeds as invasive plants. *Plants* 11:3. <https://doi.org/10.3390/plants11010003>
- Kivlin SN, Hawkes CV, Treseder KK (2011) Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biol Biochem* 43(11):2294–2303. <https://doi.org/10.1016/j.soilbio.2011.07.012>
- Klironomos JN (2000) Host-specificity and functional diversity among arbuscular mycorrhizal fungi. *Microbial Biosyst: New Front* 1:845–851
- Knogge W (1996) Fungal infection of plants. *Plant Cell* 8:1711–1722. <https://doi.org/10.1105/tpc.8.10.1711>
- Koutika L-S, Vanderhoeven S, Chapuis-Lardy L, Dassonville N, Meerts P (2007) Assessment of changes in soil organic matter after invasion by exotic plant species. *Biol Fertil Soils* 44(2):331–341. <https://doi.org/10.1007/s00374-007-0210-1>
- Kouyeas V (1964) An approach to the study of moisture relations of soil fungi. *Plant Soil* 20:351–363
- Lauber CL, Strickland MS, Bradford MA, Fierer N (2008) The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biol Biochem* 40:2407–2415. <https://doi.org/10.1016/j.soilbio.2008.05.021>
- Lebreton A, Zeng Q, Miyauchi S, Kohler A, Dai YC, Martin FM (2021) Evolution of the mode of nutrition in symbiotic and saprotrophic fungi in forest ecosystems. *Annu Rev Ecol Evol Syst* 52:385–404. <https://doi.org/10.1146/annurev-ecolsys-012021-114902>
- Lehmann A, Rillig MC (2015) Understanding mechanisms of soil biota involvement in soil aggregation: a way forward with saprobic fungi? *Soil Biol Biochem* 88:298–302. <https://doi.org/10.1016/j.soilbio.2015.06.006>
- Li X, Zhu T, Peng F, Chen Q, Lin S, Christie P, Zhang J (2015) Inner Mongolian steppe arbuscular mycorrhizal fungal communities respond more strongly to water availability than to nitrogen fertilization. *Environ Microbiol* 17:3051–3068. <https://doi.org/10.1111/1462-2920.12931>
- Liao JD, Boutton TW (2008) Soil microbial biomass response to woody plant invasion of grassland. *Soil Biol Biochem* 40:1207–1216. <https://doi.org/10.1016/j.soilbio.2007.12.018>
- Liao C, Luo Y, Jiang L, Zhou X, Wu X, Fang C, Chen J, Li B (2007) Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze estuary, China. *Ecosystems* 10:1351–1361. <https://doi.org/10.1007/s10021-007-9103-2>
- Liao C, Peng R, Luo Y, Zhou X, Wu X, Fang C, Chen J, Li B (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* 177:706–714
- Lindén A, Mäntyniemi S (2011) Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology* 92:1414–1421. <https://doi.org/10.1890/10-1831.1>
- Liu J, Sui Y, Yu Z, Shi Y, Chu H, Jin J, Liu X, Wang G (2015) Soil carbon content drives the biogeographical distribution of fungal communities in the black soil zone of northeast China. *Soil Biol Biochem* 83:29–39. <https://doi.org/10.1016/j.soilbio.2015.01.009>
- Marulanda A, Azcon R, Ruiz-Lozano JM (2003) Contribution of six arbuscular mycorrhizal fungal isolates to water

- uptake by *Lactuca sativa* plants under drought stress. *Physiol Plant* 119:526–533. <https://doi.org/10.1046/j.1399-3054.2003.00196.x>
- Meyer M, Diehl D, Schaumann GE, Muñoz K (2021) Agricultural mulching and fungicides-impacts on fungal biomass, mycotoxin occurrence, and soil organic matter decomposition. *Environ Sci Pollut Res* 28:36535–36550. <https://doi.org/10.1007/s11356-021-13280-3>
- Minasny B, McBratney AB, Brough DM, Jacquier D (2011) Models relating soil pH measurements in water and calcium chloride that incorporate electrolyte concentration. *Eur J Soil Sci* 62:728–732. <https://doi.org/10.1111/j.1365-2389.2011.01386.x>
- Mincheva T, Barni E, Varese GC, Brusa G, Cerabolini B, Siniscalco C (2014) Litter quality, decomposition rates and saprotrophic mycoflora in *Fallopia japonica* (Houtt.) Ronse Decraene and in adjacent native grassland vegetation. *Acta Oecologica* 54:29–35. <https://doi.org/10.1016/j.actao.2013.03.010>
- Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature* 421:625–627. <https://doi.org/10.1038/nature01317>
- Murrell C, Gerber E, Krebs C, Parepa M, Schaffner U, Bossdorf O (2011) Invasive knotweed affects native plants through allelopathy. *Am J Bot* 98:38–43. <https://doi.org/10.3732/ajb.1000135>
- Nielsen UN, Osler GHR, Campbell CD, Burslem DFRP, van der Wal R (2010) The influence of vegetation type, soil properties and precipitation on the composition of soil mite and microbial communities at the landscape scale. *J Biogeogr* 37:1317–1328. <https://doi.org/10.1111/j.1365-2699.2010.02281.x>
- Novoa A, Rodríguez R, Richardson D, González L (2014) Soil quality: a key factor in understanding plant invasion? The case of *Carpobrotus edulis* (L.) N.E.Br. *Biol Invasions* 16:429–443. <https://doi.org/10.1007/s10530-013-0531-y>
- Oberwinkler F, Riess K, Bauer R, Selosse M-A, Weiß M, Garnica S, Zuccaro A (2013) Enigmatic Sebaciales. *Mycol. Prog. Mycol Prog* 12:1–27. <https://doi.org/10.1007/s11557-012-0880-4>
- Oksanen J, Blanchet FGF, Michael Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos PH, Stevens MH, Szoecs E, Wagner H (2019) Vegan: community ecology package, vol. 2, p. 5. <https://CRAN.R-project.org/package=vegan>
- Öpik M, Moora M, Liira J, Zobel M (2006) Composition of root-colonizing arbuscular mycorrhizal fungal communities in different ecosystems around the globe. *J Ecol* 94:778–790. <https://doi.org/10.1111/j.1365-2745.2006.01136.x>
- Parepa M, Bossdorf O (2016) Testing for allelopathy in invasive plants: it all depends on the substrate! *Biol. Invasions* 18:2975–2982. <https://doi.org/10.1007/s10530-016-1189-z>
- Parniske M (2008) Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nat Rev Microbiol* 6:763–775. <https://doi.org/10.1038/nrmicro1987>
- Pattison Z, Rumble H, Tanner RA, Jin L, Gange AC (2016) Positive plant-soil feedbacks of the invasive *Impatiens glandulifera* and their effects on above-ground microbial communities. *Weed Res* 56:198–207. <https://doi.org/10.1111/wre.12200>
- Pehle A, Schirmel J (2015) Moss invasion in a dune ecosystem influences ground-dwelling arthropod community structure and reduces soil biological activity. *Biol Invasions* 17:3467–3477. <https://doi.org/10.1007/s10530-015-0971-7>
- Petersen H, Luxton M (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* 39:288. <https://doi.org/10.2307/3544689>
- Pinzone P, Potts D, Pettibone G, Warren R (2018) Do novel weapons that degrade mycorrhizal mutualisms promote species invasion? *Plant Ecol* 219:539–548. <https://doi.org/10.1007/s11258-018-0816-4>
- Pöhlme S, Abarenkov K, Henrik Nilsson R, Lindahl BD, Clemmensen KE, Kauserud H, Nguyen N, Kjäller R, Bates ST, Baldrian P, Frøselev TG, Adojaan K, Vizzini A, Suija A, Pfister D, Baral H-O, Järv H, Madrid H, Nordén J, Liu J-K, Pawlowska J, Pöldmaa K, Pärtel K, Runnel K, Hansen K, Larsson K-H, Hyde KD, Sandoval-Denis M, Smith ME, Toome-Heller M, Wijayawardene NN, Menolli N, Reynolds NK, Drenkhan R, Maharachchikumbura SSN, Gibertoni TB, Læssøe T, Davis W, Tokarev Y, Corrales A, Soares AM, Agan A, Machado AR, Argüelles-Moyao A, Detheridge A, de Meiras-Ottoni A, Verbeken A, Dutta AK, Cui B-K, Pradeep CK, Marín C, Stanton D, Gohar D, Wanasinghe DN, Otsing E, Aslani F, Griffith GW, Lumbsch TH, Grossart H-P, Masigol H, Timling I, Hiiesalu I, Oja J, Kupagme JY, Geml J, Alvarez-Manjarrez J, Ilves K, Loit K, Adamson K, Nara K, Küngas K, Rojas-Jimenez K, Bitenieks K, Irinyi L, Nagy LG, Soonvald L, Zhou L-W, Wagner L, Aime MC, Öpik M, Mujica MI, Metsoja M, Ryberg M, Vasar M, Murata M, Nelsen MP, Cleary M, Samarakoon MC, Doilom M, Bahram M, Hagh-Doust N, Dulya O, Johnston P, Kohout P, Chen Q, Tian Q, Nandi R, Amiri R, Perera RH, dos Santos CR, Mendes-Alvarenga RL, Garibay-Orijel R, Gielen R, Phookamsak R, Jayawardena RS, Rahimlou S, Karunarathna SC, Tibpromma S, Brown SP, Sepp S-K, Mundra S, Luo Z-H, Bose T, Vahter T, Netherway T, Yang T, May T, Varga T, Li W, Coimbra VRM, de Oliveira VRT, de Lima VX, Mikryukov VS, Lu Y, Matsuda Y, Miyamoto Y, Kõljalg U, Tedersoo L (2020) FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Div* 105:1–16. <https://doi.org/10.1007/s13225-020-00466-2>
- Porter WM, Robson AD, Abbott LK (1987) Factors controlling the distribution of vesicular-arbuscular mycorrhizal fungi in relation to soil pH. *J Appl Ecol* 24:663. <https://doi.org/10.2307/2403901>
- Pyšek P, Prach K (1993) Plant invasions and the role of riparian habitats: a comparison of four species alien to Central Europe. *J Biogeogr* 20:413. <https://doi.org/10.2307/2845589>
- Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob Chang Biol* 18:1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>

- R Core Team (2021) R: a language and environment for statistical computing
- Ravit B, Ehrenfeld JG, Haggblom MM (2003) A comparison of sediment microbial communities associated with *Phragmites australis* and *Spartina alterniflora* in two brackish wetlands of New Jersey. *Estuaries* 26:465–474. <https://doi.org/10.1007/BF02823723>
- Redman RS, Kim YO, Woodward CJDA, Greer C, Espino L, Doty SL, Rodriguez RJ (2011) Increased fitness of rice plants to abiotic stress via habitat adapted symbiosis: a strategy for mitigating impacts of climate change. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0014823>
- Reinhart KO, Callaway RM (2006) Soil biota and invasive plants. *New Phytol* 170:445–457. <https://doi.org/10.1111/j.1469-8137.2006.01715.x>
- Rendoš M, Raschmanová N, Kováč L, Miklisová D, Mock A, Luptáček P (2016) Organic carbon content and temperature as substantial factors affecting diversity and vertical distribution of Collembola on forested scree slopes. *Eur J Soil Biol* 75:180–187. <https://doi.org/10.1016/j.ejsobi.2016.06.001>
- Řezáčová V, Slavíková R, Konvalinková T, Zemková L, Řezáč M, Gryndler M, Šmilauer P, Gryndlerová H, Hřelová H, Bukovská P, Jansa J (2019) Geography and habitat predominate over climate influences on arbuscular mycorrhizal fungal communities of mid-European meadows. *Mycorrhiza* 29:567–579. <https://doi.org/10.1007/s00572-019-00921-2>
- Riess K, Oberwinkler F, Bauer R, Garnica S (2014) Communities of endophytic Sebaciniales associated with roots of herbaceous plants in agricultural and grassland ecosystems are dominated by *Serendipita herbamans* sp. nov. *PLOS ONE*. <https://doi.org/10.1371/journal.pone.0094676>
- Robert V, Vu D, Amor ABH, van de Wiele N, Brouwer C, Jabas B, Szoke S, Dridi A, Triki M, Ben Daoud S, Chouchen O, Vaas L, de Cock A, Stalpers JA, Stalpers D, Verkley GJM, Groenewald M, Dos Santos FB, Stegehuis G, Li W, Wu L, Zhang R, Ma J, Zhou M, Gorjón SP, Eurwilaichitr L, Ingsriswang S, Hansen K, Schoch C, Robbertse B, Irinyi L, Meyer W, Cardinali G, Hawksworth DL, Taylor JW, Crous PW (2013) MycoBank gearing up for new horizons. *IMA Fungus* 4:371–379. <https://doi.org/10.5598/ima fungus.2013.04.02.16>
- Rodrigues MG, Fonseca Á (2003) Molecular systematics of the dimorphic ascomycete genus *Taphrina*. *Int J Syst Evol Microbiol* 53:607–616. <https://doi.org/10.1099/ijs.0.02437-0>
- Rodriguez RJ, White JF, Arnold AE, Redman RS (2009) Fungal endophytes: diversity and functional roles. *New Phytol* 182:314–330. <https://doi.org/10.1111/j.1469-8137.2009.02773.x>
- Rousk J, Bååth E, Brookes PC, Lauber CL, Lozupone C, Caporaso JG, Knight R, Fierer N (2010) Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J* 4:1340–1351. <https://doi.org/10.1038/ismej.2010.58>
- Ruckli R, Rusterholz H-P, Baur B (2013) Invasion of *Impatiens glandulifera* affects terrestrial gastropods by altering microclimate. *Acta Oecologica* 47:16–23. <https://doi.org/10.1016/j.actao.2012.10.011>
- Ruckli R, Rusterholz H-P, Baur B (2014) Invasion of an annual exotic plant into deciduous forests suppresses arbuscular mycorrhiza symbiosis and reduces performance of sycamore maple saplings. *For Ecol Manag* 318:285–293. <https://doi.org/10.1016/j.foreco.2014.01.015>
- Rusterholz H-P, Salamon J-A, Ruckli R, Baur B (2014) Effects of the annual invasive plant *Impatiens glandulifera* on the Collembola and Acari communities in a deciduous forest. *Pedobiologia* 57:285–291. <https://doi.org/10.1016/j.pedobi.2014.07.001>
- Salamon J-A, Schaefer M, Alpei J, Schmid B, Scheu S (2004) Effects of plant diversity on Collembola in an experimental grassland ecosystem. *Oikos* 106:51–60. <https://doi.org/10.1111/j.0030-1299.2004.12905.x>
- Sapsford SJ, Wakelin A, Peltzer DA, Dickie IA (2022) Pine invasion drives loss of soil fungal diversity. *Biol Invasions* 24:401–414. <https://doi.org/10.1007/s10530-021-02649-7>
- Schardl CL, Craven KD (2003) Interspecific hybridization in plant-associated fungi and oomycetes: a review. *Mol Ecol* 12:2861–2873. <https://doi.org/10.1046/j.1365-294X.2003.01965.x>
- Schirmel J, Bundschuh M, Entling MH, Kowarik I, Buchholz S (2016) Impacts of invasive plants on resident animals across ecosystems taxa and feeding types: a global assessment. *Glob Chang Biol* 22(2):594–603. <https://doi.org/10.1111/gcb.13093>
- Schubert R (2010) *Bestimmungsbuch der Pflanzengesellschaften Deutschlands*, 2nd edn. Spektrum, Akad. Verl., Heidelberg
- Seifert EK, Bever JD, Maron JL (2009) Evidence for the evolution of reduced mycorrhizal dependence during plant invasion. *Ecology* 90:1055–1062. <https://doi.org/10.1890/08-0419.1>
- Shen C, Wang J, He J-Z, Yu F-H, Ge Y (2021) Plant diversity enhances soil fungal diversity and microbial resistance to plant invasion. *Appl Environ Microbiol*. <https://doi.org/10.1128/AEM.00251-21>
- Si C, Liu X, Wang C, Wang L, Dai Z, Qi S, Du D (2013) Different degrees of plant invasion significantly affect the richness of the soil fungal community. *PLOS ONE* 8:e85490. <https://doi.org/10.1371/journal.pone.0085490>
- Skubala P, Mierny A (2009) Invasive *Reynoutria* taxa as a contaminant of soil. Does it reduce abundance and diversity of microarthropods and damage soil habitat? *Pestycydy* 1–4:57–62
- Smith SE, Read DJ (2008) *Mycorrhizal symbiosis*, 3rd edn. Academic Press, New York
- Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, Berbee ML, Bonito G, Corradi N, Grigoriev I, Gryganskyi A, James TY, O'Donnell K, Roberson RW, Taylor TN, Uehling J, Vilgalys R, White MM, Stajich JE (2016) A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia* 108:1028–1046. <https://doi.org/10.3852/16-042>
- Stefanowicz AM, Stanek M, Nobis M, Zubek S (2016) Species-specific effects of plant invasions on activity, biomass, and composition of soil microbial communities. *Biol Fertil Soils* 52:841–852. <https://doi.org/10.1007/s00374-016-1122-8>

- Stefanowicz AM, Stanek M, Nobis M, Zubek S (2017) Few effects of invasive plants *Reynoutria japonica*, *Rudbeckia laciniata* and *Solidago gigantea* on soil physical and chemical properties. *Sci Total Environ* 574:938–946. <https://doi.org/10.1016/j.scitotenv.2016.09.120>
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends Ecol Evol* 21:645–651. <https://doi.org/10.1016/j.tree.2006.07.007>
- Tanner RA, Jin L, Shaw R, Murphy ST, Gange AC (2014) An ecological comparison of *Impatiens glandulifera* Royle in the native and introduced range. *Plant Ecol* 215:833–843. <https://doi.org/10.1007/s11258-014-0335-x>
- Tanner RA, Varia S, Eschen R, Wood S, Murphy ST, Gange AC (2013) Impacts of an invasive non-native annual weed, *Impatiens glandulifera*, on above- and below-ground invertebrate communities in the United Kingdom. *PLOS ONE* 8:e67271. <https://doi.org/10.1371/journal.pone.0067271>
- Taylor K (2009) Biological Flora of the British Isles: *Urtica dioica* L. *J Ecol* 97:1436–1458. <https://doi.org/10.1111/j.1365-2745.2009.01575.x>
- Tedersoo L, Pärtel K, Jairus T, Gates G, Põldmaa K, Tamm H (2009) Ascomycetes associated with ectomycorrhizas: molecular diversity and ecology with particular reference to the *Helotiales*. *Environ Microbiol* 11:3166–3178. <https://doi.org/10.1111/j.1462-2920.2009.02020.x>
- Tedersoo L, Bahram M, Pölme S, Kõljalg U, Yorou NS, Wijesundera R, Villarreal Ruiz L, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME, Sharp C, Saluveer E, Saitta A, Rosas M, Riit T, Ratkowsky D, Pritsch K, Põldmaa K, Piepenbring M, Phosri C, Peterson M, Parts K, Pärtel K, Otsing E, Nouhra E, Njouonkou AL, Nilsson RH, Morgado LN, Mayor J, May TW, Majuakim L, Lodge DJ, Lee SS, Larsson K-H, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo L, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, de Kesel A, Dang T, Chen X, Buegger F, Brearley FQ, Bonito G, Anslan S, Abell S, Abarenkov K (2014) Global diversity and geography of soil fungi. *Science* 346:1256688. <https://doi.org/10.1126/science.1256688>
- Tedersoo L, Anslan S, Bahram M, Pölme S, Riit T, Liiv I, Kõljalg U, Kisand V, Nilsson H, Hildebrand F, Bork P, Abarenkov K (2015) Shotgun metagenomes and multiple primer pair-barcode combinations of amplicons reveal biases in metabarcoding analyses of fungi. *MycKeys* 10:1–43. <https://doi.org/10.3897/mycokeys.10.4852>
- Tresch S, Frey D, Le Bayon R-C, Zanetta A, Rasche F, Fließbach A, Moretti M (2019) Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. *Sci Total Environ* 658:1614–1629. <https://doi.org/10.1016/j.scitotenv.2018.12.235>
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Wakelin SA, Gerard E, van Koten C, Banabas M, O'Callaghan M, Nelson PN (2016) Soil physicochemical properties impact more strongly on bacteria and fungi than conversion of grassland to oil palm. *Pedobiologia* 59:83–91. <https://doi.org/10.1016/j.pedobi.2016.03.001>
- Waller LP, Allen WJ, Barratt BIP, Condron LM, França FM, Hunt JE, Koele N, Orwin KH, Steel GS, Tilyanakis JM, Wakelin SA, Dickie IA (2020) Biotic interactions drive ecosystem responses to exotic plant invaders. *Science* 368:967–972. <https://doi.org/10.1126/science.aba2225>
- Wang W, Sardans J, Wang C, Zeng C, Tong C, Chen G, Huang J, Pan H, Peguero G, Vallicrosa H, Peñuelas J (2019) The response of stocks of C, N, and P to plant invasion in the coastal wetlands of China. *Glob Chang Biol* 25:733–743. <https://doi.org/10.1111/gcb.14491>
- Wei L, Vosátka M, Cai B, Ding J, Lu C, Xu J, Yan W, Li Y, Liu C (2019) The role of arbuscular mycorrhiza fungi in the decomposition of fresh residue and soil organic carbon: a mini-review. *Soil Sci Soc Am J* 83:511–517. <https://doi.org/10.2136/sssaj2018.05.0205>
- Wilson D (1995) Endophyte: the evolution of a term, and clarification of its use and definition. *Oikos* 73:274. <https://doi.org/10.2307/3545919>
- Wissuwa J, Salamon J-A, Frank T (2012) Effects of habitat age and plant species on predatory mites (Acari, Mesostigmata) in grassy arable fallows in Eastern Austria. *Soil Biol Biochem* 50:96–107. <https://doi.org/10.1016/j.soilbio.2012.02.025>
- Wissuwa J, Salamon J-A, Frank T (2013) Oribatida (Acari) in grassy arable fallows are more affected by soil properties than habitat age and plant species. *Eur J Soil Biol* 59:8–14. <https://doi.org/10.1016/j.ejsobi.2013.08.002>
- Wolfé BE, Klironomos JN (2005) Breaking new ground: soil communities and exotic plant invasion. *Bioscience* 55:477. [https://doi.org/10.1641/0006-3568\(2005\)055\[0477:BNGSCA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0477:BNGSCA]2.0.CO;2)
- Wu Q-S, Xia R-X (2006) Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well-watered and water stress conditions. *J Plant Physiol* 163:417–425. <https://doi.org/10.1016/j.jplph.2005.04.024>
- Xiao D, Huang Y, Feng S, Ge Y, Zhang W, He X, Wang K (2018) Soil organic carbon mineralization with fresh organic substrate and inorganic carbon additions in a red soil is controlled by fungal diversity along a pH gradient. *Geoderma* 321:79–89. <https://doi.org/10.1016/j.geoderma.2018.02.003>
- Xu H, Shao H, Lu Y (2019) Arbuscular mycorrhiza fungi and related soil microbial activity drive carbon mineralization in the maize rhizosphere. *Ecotoxicol Environ Saf* 182:109476. <https://doi.org/10.1016/j.ecoenv.2019.109476>
- Yang Y, Dou Y, Huang Y, An S (2017) Links between soil fungal diversity and plant and soil properties on the Loess Plateau. *Front Microbiol* 8:2198. <https://doi.org/10.3389/fmicb.2017.02198>
- Yao He, Wilson C (2000) Microbial biomass and community structure in a sequence of soils with increasing fertility and changing land use. *Microb Ecol* 40:223–237. <https://doi.org/10.1007/s002480000053>
- Zanne AE, Abarenkov K, Afkhami ME, Aguilar-Trigueros CA, Bates S, Bhatnagar JM, Busby PE, Christian N, Cornwell WK, Crowther TW, Flores-Moreno H, Floudas D, Gazis

- R, Hibbett D, Kennedy P, Lindner DL, Maynard DS, Milo AM, Nilsson RH, Powell J, Schildhauer M, Schilling J, Treseder KK (2020) Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biol Rev* 95:409–433. <https://doi.org/10.1111/brv.12570>
- Zhang Q, Yang R, Tang J, Yang H, Hu S, Chen X (2010) Positive feedback between mycorrhizal fungi and plants influences plant invasion success and resistance to invasion. *PLOS ONE* 5:e12380. <https://doi.org/10.1371/journal.pone.0012380>
- Zhu X, Yang W, Song F, Li X (2020) Diversity and composition of arbuscular mycorrhizal fungal communities in the cropland black soils of China. *Glob. Ecol. Conserv.* 22:e00964. <https://doi.org/10.1016/j.gecco.2020.e00964>
- Žifčáková L, Větrovský T, Howe A, Baldrian P (2016) Microbial activity in forest soil reflects the changes in ecosystem properties between summer and winter. *Environ Microbiol* 18:288–301. <https://doi.org/10.1111/1462-2920.13026>
- Zubek S, Majewska ML, Błaszczkowski J, Stefanowicz AM, Nobis M, Kapusta P (2016) Invasive plants affect arbuscular mycorrhizal fungi abundance and species richness as well as the performance of native plants grown in invaded soils. *Biol Fertil Soils* 52:879–893. <https://doi.org/10.1007/s00374-016-1127-3>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.