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Selective alteration of soil food web components by invasive giant goldenrod *Solidago gigantea* in two distinct habitat types

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Apart from relatively well-studied aboveground effects, invasive plant species will also impact the soil food web. So far, most research has been focusing on primary decomposers, while studies on effects at higher trophic levels are relatively scarce. Giant goldenrod *Solidago gigantea*, native to North America, is a widespread and common invasive species in most European countries. We investigated its impact on plant communities and on multiple trophic levels of the soil food web in two contrasting habitats: riparian zones and semi-natural grasslands. In 30 pairs of invaded and uninvaded plots, floristic composition, pH, fungal biomass and the densities of 11 nematode taxa were determined by using a quantitative PCR-based method. In the two habitats, the invader outcompeted both rare and dominant plant species. Belowground, *S. gigantea* invasion reduced pH, increased overall fungal biomass as well as the density of a single lineage of fungivorous nematodes, the family Aphelenchoididae. The densities of two other, phylogenetically distinct lineages of fungivorous nematodes, Aphelenchidae and Diphtherophoridae, were unaffected by the local increase in fungal biomass. Apparently this plant species induces a local asymmetric boost of the fungal community, and only Aphelenchoididae were able to benefit from this invader-induced change. The alternative explanation – the results are explained by a subtle, *S. gigantea*-induced 0.1–0.2 units decrease of pH – seems unlikely, as pH optima for nematode taxa are relatively broad. Thus, apart from readily observable aboveground effects, the invasive plant species *S. gigantea* affects fungal biomass as well as a specific part of the fungivorous nematode community in a soil type-independent manner.

The successful establishment of exotic species in a given habitat is considered as one of the major driving forces of changes in biodiversity (Sala et al. 2000). Most naturalised exotic plants behave ecologically comparable to resident species, but a small proportion – invasive plants – can become exceptionally abundant in their new environments (for terminology see Pyšek et al. 2004). Hejda and co-workers (2009) studied the main factors determining the impact of invasive plant species on the native plant community. According to them, species identity and characteristics such as stand height and cover are major determinants for invasiveness. The number of studies focusing on belowground effects of invasive plant species has grown substantially over the last decade (Vilà et al. 2011). Most of these studies concentrate on the impact on microbial communities (reviewed by Van der Putten et al. 2007) and nutrient cycling (reviewed by Ehrenfeld 2003). From these studies it has become clear that interactions between plants and soil biota can play a decisive role with regard to the invasive success of exotic plant species. For example, the invasiveness of naturalised plant species has

been shown to be promoted by their ability to stimulate generalist soil pathogenic fungi (Mangla et al. 2008) or by the local presence of compatible mycorrhizal fungi (Nuñez et al. 2009). Selective changes in the microbial community can lead to alterations at multiple levels of the food web, and may thereby affect its stability (Dunne et al. 2002). This notion could contribute to our understanding of the ecological impact of exotic plant species. However, little attention has been paid to invader-induced changes on higher trophic levels in the soil food web so far (Belnap and Phillips 2001, Belnap et al. 2005, Chen et al. 2007).

Due to the enormous biodiversity and the high number of trophic relationships, there are myriad interactions between plants and soil microbial communities (Porazinska et al. 2003). Nematodes constitute an informative bio-indicator group for soil food web functioning, owing to their omnipresence in pores between soil aggregates, their trophic diversity, and their high degree of interconnectedness within the soil food web (Neher et al. 2005). A range of studies has focused on interactions between plant community composition and nematode assemblages

(De Deyn et al. 2004, Viketoft et al. 2005, Bezemer et al. 2010, Viketoft and Sohlenius 2011). So far, the impact of exotic plants on nematode communities has received little attention (Van der Putten et al. 2005, Morriën et al. 2011). Assemblages of this trophically diverse micro-faunal group should preferably be studied at family or genus level, and not at the level of feeding guilds, as previous reports showed that this taxonomic resolution is required for understanding the impact of plant communities or land use (Porazinska et al. 1999, Neher et al. 2005, Viketoft and Sohlenius 2011). However, for experiments with intense sampling designs, microscopy-based community analyses are (too) laborious and time-consuming. Here, we applied a recently developed set of quantitative PCR (qPCR)-based molecular assays (Vervoort et al. 2012) that allows for the analysis of nematode assemblages at or below family level in a relatively short time frame.

In the present study, giant goldenrod *Solidago gigantea*, a common invasive plant species in most European countries, was selected as a model to examine belowground effects of successful invaders. *Solidago gigantea* forms near monoculture stands in a broad range of habitats (Weber and Jakobs 2005). In recent years, several studies revealed properties of *S. gigantea* which possibly contribute to its invasiveness, e.g. high biomass production, high nutrient efficiency, alteration of nutrient turnover (Vanderhoeven et al. 2006, Scharfy et al. 2009) and the excretion of allelochemicals (Abhilasha et al. 2008). In 2010, Scharfy et al. studied the effect of *S. gigantea* on soil biota in typical wetland soils (gleysols and a gleyic cambisol) under controlled mesocosm conditions. They observed a significant decrease in bacterial and an increase in fungal biomass in soil below *S. gigantea*-dominated plant communities. However, it is hard to predict whether these are specific or more widespread consequences of invasion by *S. gigantea*, and little is known about possible follow-up changes at higher trophic levels in the soil food web.

In this study, we investigated the belowground impact of *S. gigantea* on the fungal biomass and the nematode community composition in riparian zones and semi-natural grasslands (characterised by river clay and sandy soils respectively). By including two contrasting environments, we were looking for generic effects of invasion by *S. gigantea* on multiple trophic levels of the soil food web. In a mesocosm experiment, Scharfy et al. (2010) showed both bacterial and fungal biomass to be affected by *S. gigantea*. If this were true in other soil types and under natural conditions, these shifts should be reflected in changes in the bacterivorous and fungivorous nematode community.

Material and methods

Sites of study

Within an area of approx. 200 km² covering parts of the Dutch provinces Utrecht and Gelderland, ten sites were selected from two habitat types commonly invaded by *Solidago gigantea*: riverbanks of the Rhine and the Walloon and semi-natural grasslands on Pleistocene sandy soils (Supplementary material Appendix 1 Table A1). In this area,

the presence of *S. gigantea* have been reported since 1912 (Te Linde and Van den Berg 2003). In riparian habitats, *S. gigantea* is mainly spread by surface waters, which carry (fragments of) plants that can sprout under favourable conditions elsewhere (Weber and Jakobs 2005). Beekeepers and gardeners introduced *S. gigantea* to the semi-natural grasslands under investigation. All selected sites met the following criteria: 1) *S. gigantea* occurred in well-defined patches in the plant community, 2) soil and plant communities showed no signs of disturbances caused by foraging wildlife or mowing, 3) sites that belong to the same habitat type were comparable in plant community, pH and humidity.

Soil sampling

For both invaded habitats, five sites were investigated. For each site, three separate plot pairs were defined, consisting of two directly neighbouring 4-m² (2 × 2 m) plots; one plot dominated by *S. gigantea* invaded plot and one uninvaded plot. Thus, in total 60 plots were studied. For each plot, the floristic composition was determined, and a composite soil sample was collected. Each composite soil sample consisted of a mixture of 20 randomly taken soil cores (Ø 1.5 cm, depth: 25 cm) that were homogenised thoroughly, immediately thereafter this mixture was stored at 4°C. Sampling took place during the week of 12 September 2011, when the plant community was at peak standing biomass. One month earlier, the nematode diversity of all sites of this study was assessed microscopically (for details see Supplementary material Appendix 1 Table A2).

Plant community analysis

In each plot (n = 60) a relevé was made; all species of higher plants were recorded and the proportion of each species in the vegetation was estimated according to a modified Braun-Blanquet scale (Barkman et al. 1964, Supplementary material Appendix 1 Table A3). Community characteristics were determined by calculating the species richness (*S*) and the Shannon diversity (*H'*) as described by Hejda et al. (2009).

Soil acidity and humidity

A subsample (20 g) of each composite soil sample was used to determine the moisture content and pH-H₂O. Soil moisture content was determined by weight loss after 72 h incubation at 40°C. The dried soil was sieved with a 2 mm mesh; thereupon soil pH was measured in demineralised water using a gel-electrolyte electrode.

Nematode extraction and community analysis

For each of the composite samples, a 100 g subsample was taken, and nematodes were extracted using an elutriator (Oostenbrink 1960). Nematode suspensions were analysed microscopically, or by a qPCR-based methodology (Vervoort et al. 2012, 2014).

Microscopic analysis (of samples collected in August 2011) was used to assess the nematode community

composition for invaded and uninvaded plots in each of the habitat types. Communities were characterised by the morphological identification (till genus level) of 100 individuals per sample (soil from under invaded plant communities and native plant communities was analysed separately for each site ($n = 20$; for details see Supplementary material Appendix 1 Table A1–A2). On the basis of this nematode biodiversity inventory, sets of taxon-specific PCR primer combinations were selected, hereby optimizing the coverage of the molecular assays. Within the orders Dorylaimida and Mononchida, cluster-specific primers D3 and M3 were used according to Holterman et al. (2008). For the family Plectidae, separate primers were used targeting either *Anaplectus* or Plectidae except *Anaplectus*.

For the samples collected in September 2011, overall nematode densities were determined by counting two subsamples of each of the nematode suspensions ($n = 60$). DNA extraction from nematode suspensions, lysate purification and subsequent qPCR reactions – using 11 nematode taxon-specific primer combinations – were performed as described by Vervoort et al. (2012).

Fungal biomass

Fungal biomass was determined by measuring the ergosterol content in soil samples. Ergosterol is a sterol that is present in fungal cell membranes, which does not occur in plant or animal cells (Gessner and Schmitt 1996, Stahl and Parkin 1996). This approach largely excludes arbuscular mycorrhizal fungi which are known to contain relatively low amounts of ergosterol (Olsson et al. 2003). Ergosterol was extracted from 1 g of soil using the alkaline extraction protocol described by (de Ridder-Duine et al. 2006). Subsequently, high-performance liquid chromatography was used to determine the ergosterol contents of the samples (de Ridder-Duine et al. 2006).

Data analysis

Soil properties, plant communities, and nematode densities were analyzed using mixed linear models (using PROC MIXED of the SAS software system ver. 9.2, Littell 2006). If needed, data were transformed, in order to arrive at approximately normal distributions of residuals as required for valid statistical inference. The variables soil pH, moisture content, plant-species richness, and diversity remained untransformed; nematode densities (total) were square root-transformed; and all other variables (ergosterol and nematode taxon densities) were log-transformed. The log-transformation was applied after addition of a constant (0.05 for ergosterol, and 0.5 for nematode densities with the exception of Dorylaimida D3) to push data away from the lower bound zero. Mixed linear models were used, because multiple observations from the same site and/or plot pair within sites are not necessarily uncorrelated. The fixed part of the mixed model contained main effects of habitat and invasion and their interaction. Besides the residual error, random effects are introduced for sites and for plot pairs (within sites), so that total error variance is split into variance components for sites and for plot pairs within sites, and residual variance. We present the following

results from the mixed models: 1) hypothesis tests for interaction and main effects of factors habitat and invasion and 2) back transformed 95% confidence intervals for means per habitat and invasion, and the ratios (impact (%)) of back transformed means for invaded and uninvaded plots per habitat, together with a statement about the significance of the difference between invaded and uninvaded plots.

Results

Changes in native plant communities upon *S. gigantea* invasion

In total, we identified 64 and 78 vascular plant species in riparian vegetation and semi-natural grasslands, respectively. In invaded plots, 35 and 39 vascular plant species were recorded, respectively. For invaded plant communities, plant-species richness (S) and diversity (H') were significantly lower compared to native plant communities ($p < 0.001$; Table 1, Fig. 1). Common native species largely determining the plant community (e.g. *Jacobaea vulgaris*, *Holcus lanatus*, *Achillea millefolium*, *Dactylis glomerata* and *Plantago lanceolata*; Supplementary material Appendix 1 Table A3) were nearly absent in invaded plant communities. Relatively rare species such as *Achillea ptarmica*, *Epipactis* sp., *Odontites vernus* subsp. *serotinus* (only present in riparian zones) and *Filago vulgaris* (only present in semi-natural grasslands) were completely absent in the plots invaded by *Solidago gigantea*. On the other hand, ground ivy *Glechoma hederacea* thrived rather equal in invaded patches (Supplementary material Appendix 1, Table 2).

Impact of *S. gigantea* invasion on soil acidity and moisture content

Overall, a comparison of pH of soils from uninvaded versus invaded plots revealed slight but significantly lower pH in invaded soils ($p < 0.001$; Table 1). Soil moisture content tended to be lower in invaded plots, but this effect was not significant ($p = 0.077$; Table 1). In general, the soil pH under semi-natural grasslands was ≈ 1.5 units lower (Table 2) and more variable as compared to the riparian plots ($p < 0.001$; Tables 1, 2). The average moisture content of riparian clay soils was higher, although not significantly, as compared to the sandy soils of the semi-natural grasslands (Table 1).

Impact on soil fungal biomass

Overall, soil from invaded plots contained significantly higher amounts of fungal biomass as compared to uninvaded plots ($p < 0.001$; Table 1, Fig. 1). Fungal biomass was approximately twice as high in soil collected from *S. gigantea* invaded plots, in comparison to plots with native plant communities (Table 2).

Changes in nematode assemblages upon *S. gigantea* invasion

Overall, total nematode densities (determined microscopically) were similar in neighbouring invaded and uninvaded

Table 1. Summary of ANOVA F_{df} and associated p-values, testing for differences in the variables soil pH, soil moisture content (%), total nematode density (per 100 g dry soil, analysed by microscope), fungal biomass (expressed as mg ergosterol kg⁻¹ soil), plant-species richness (S_{plant}), plant-species diversity (H'_{plant}), and the density of 11 nematode taxa (per 100 g dry soil, analysed by quantitative PCR). These variables were tested for habitat type, invasion (neighbouring invaded and un-invaded plots) and their interaction (Habitat type × Invasion), based on mixed models fitted to these variables. p-values < 0.05 are considered significant, and indicated in bold.

	Habitat type		Invasion		Habitat type × Invasion	
	$F_{1,8}$	p	$F_{1,28}$	p	$F_{1,28}$	p
Soil pH	54.64	<0.001	5.96	0.021	1.22	0.279
Soil moisture content	2.88	0.128	3.36	0.077	0.32	0.579
Nematode density	50.21	<0.001	0.43	0.518	0.01	0.924
Fungal biomass	1.89	0.207	20.48	<0.001	1.09	0.306
S_{plant}	4.45	0.068	82.02	<0.001	7.09	0.013
H'_{plant}	3.36	0.104	81.44	<0.001	2.16	0.153
Aphelenchidae	12.31	0.008	0.00	0.946	1.09	0.306
Aphelenchoididae	13.51	0.006	5.58	0.025	0.86	0.363
Diphtherophoridae	0.00	0.949	0.33	0.571	0.14	0.712
Dorylaimida D3	6.25	0.037	1.89	0.181	2.47	0.127
Mononchida M3	0.20	0.668	2.35	0.137	5.71	0.024
Cephalobidae	7.99	0.022	0.29	0.597	9.79	0.004
Plectidae (except <i>Anaplectus</i>)	0.93	0.362	0.12	0.731	1.94	0.174
<i>Anaplectus</i>	0.46	0.515	2.00	0.168	0.82	0.374
Alaimidae	7.22	0.028	2.14	0.155	3.32	0.079
Prismatolaimidae	0.02	0.879	0.11	0.740	0.65	0.426
Panagrolaimidae	6.51	0.034	0.51	0.480	0.70	0.411

^anematode taxa defined as by De Ley et al. (2006), except for Dorylaimida D3 and Mononchida M3 (Holterman et al. 2008).

soils. However, when we measured the impact of *S. gigantea* at nematode taxon level, only one family, i.e. Aphelenchoididae, showed overall higher densities in invaded plots, regardless of habitat type ($p = 0.025$; Fig. 1). Apart from fungivores, the family Aphelenchoididae includes a number of (facultative) plant parasites. The primer-combination used in this study excludes all plant parasites from this family, except for *Aphelenchoides fragariae* (Vervoort et al. 2012). The absence of this plant parasitic species was confirmed (data not shown) using an additional, *A. fragariae*-specific molecular assay (Rybarczyk-Mydlowska et al. 2012). Two other fungivorous taxa, Aphelenchidae and Diphtherophoridae (the latter represented in these two habitats by a single genus, *Diphtherophora*), did not show a difference in density between uninvaded and invaded soil (Fig. 1). For the predatory nematode family Mononchida M3 (Holterman et al. 2008) and bacterivorous Cephalobidae, a significant interaction was observed between habitat type and invasion of *S. gigantea* (Table 1), showing that the nature of their response to invasion is habitat-type dependent.

When considering the two habitat types separately, differences between uninvaded and adjacent invaded soil were more pronounced in the riparian habitats than in semi-natural grasslands (Fig. 1, Table 2). While in riparian soils the densities of four out of eleven families differed significantly between invaded and uninvaded plots, this was observed for only one taxon in semi-natural grasslands (Table 2). In invaded riparian soils, the density of Aphelenchoididae was significantly higher, as well as the density of two bacteria feeding families, Cephalobidae and Alaimidae (Fig. 1, Table 2). Other bacteria feeders did not show a consistent response. Mononchida M3, a family of predatory nematodes, was significantly more abundant

in invaded riparian plots as well. In semi-natural grasslands, we found significantly higher densities of omnivorous Dorylaimida D3 in invaded plots; other taxa did not show a significant response (Table 2).

Analysis of samples taken in August 2011 and analysed microscopically, showed that in general nematode diversity was similar for both habitats. The selection of eleven taxon-specific qPCR assays covered 26 of the 48 free-living genera shared by both habitat types. For the riparian soil, 46% of the diversity and an estimated average of 86% of the total amount of free-living nematodes were covered by these sets of primer combinations. For soil from the semi-natural grasslands, the molecular assays covered 50% of the free-living nematode diversity and an estimated 80% of the total free-living nematode community (Supplementary material Appendix 1 Table A2).

Discussion

Investigation of belowground effects of giant goldenrod *Solidago gigantea* in two (semi-) natural habitats – riverbanks and grasslands – revealed a systematic effect of invasion on soil pH, a part of the fungal community, and a single lineage of fungivorous nematodes: invaded soils of two distinct habitats contained more fungal biomass and higher densities of fungivorous Aphelenchoididae than uninvaded soils. Interestingly, the densities of two other lineages of fungivorous nematodes, members of the families Aphelenchidae and Diphtherophoridae, did not change in response to the increased fungal biomass (Fig. 1). No systematic effect was observed on the bacterivorous nematodes. These results show that – apart from aboveground effects – invasive plant species can cause significant alterations in the nematode

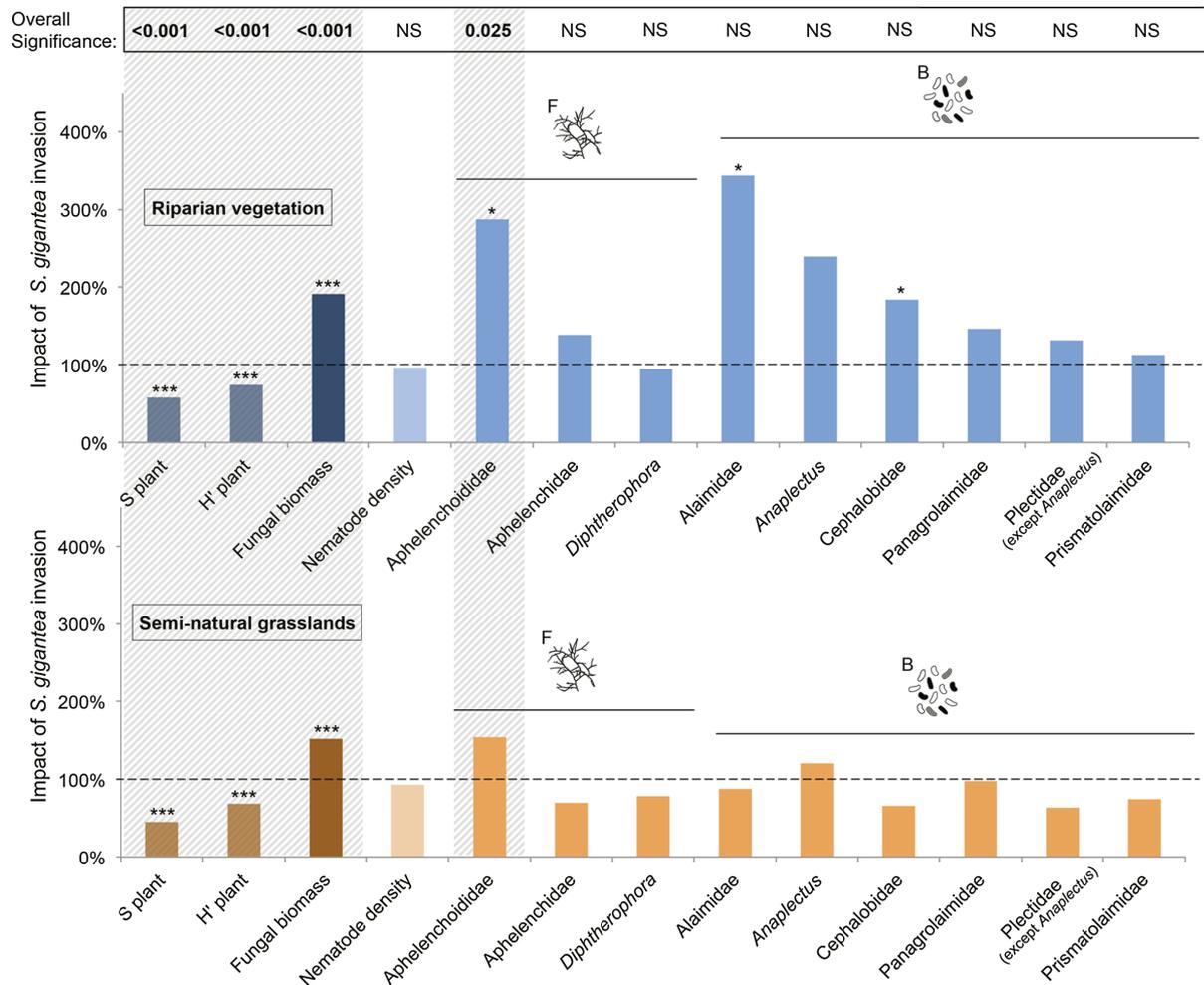


Figure 1. Impact of *Solidago gigantea* invasion in two habitat types, riparian vegetation and semi-natural grasslands, on plant-species richness (S_{plant}), plant-species diversity (H'plant), fungal biomass, total nematode density, and the densities of three fungivorous ('F') and six bacterivorous ('B') nematode taxa. Impacts are expressed as the percentage of the (back transformed) mean values in invaded plots as compared to uninvaded plots (no change = 100%). For each of the two habitats, significant differences between invaded and uninvaded plots are given by asterisks (* $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$; data extracted from the fitted mixed models). Overall significances of the effects of *S. gigantea* invasion (= data from both habitat types taken together) are given in top part of this figure (expressed as p-values). A shaded background is used to highlight significant variables.

community, which appear to be selective for specific taxa within functional groups.

Alternatively, it might be suggested that the local presence of dense *S. gigantea* stands is the result of a locally distinct fungal community. However, this would contradict the results of an extensive mesocosm experiment performed by Scharfy et al. (2010) in which *S. gigantea* was added to a number of experimentally assembled plant communities using soils that had not been covered by *S. gigantea*.

Effect of *Solidago gigantea* on soil acidity

The slightly lower pH in invaded plots (0.1–0.2 units) may be caused by acidic compounds that are released from *S. gigantea* roots into the rhizosphere (Weber and Jakobs 2005). Several studies focused on the impact of *S. gigantea* on nutrient pools, and showed a decrease (although site-dependent) in pH in combination with an enhanced P availability (Chapuis-Lardy et al. 2006, Herr

et al. 2007). In our study, only small differences in pH were measured, i.e. on average 0.1 units, which seem unlikely to explain the observed changes in soil biota, and more specifically, the increase of one of the three lineages of fungivorous nematodes (Aphelenchoididae). It is noted that a higher pH in riparian zones (appr. 1.5 units), resulted in a higher Aphelenchoididae density (Table 2). Furthermore, pH was measured in bulk soil, and more pronounced effect in the rhizosphere can not be excluded.

Solidago gigantea invaded plant communities

In *S. gigantea*-invaded plant communities, we observed a 42% and 55% reduction of plant-species richness in the riparian and semi-natural grassland habitats, respectively. This impact is relatively high; in a study of Hejda et al. (2009), an overall reduction of plant-species richness of 26% was reported in ruderal plant communities, meadows and along rivers in the Czech Republic. The authors

Table 2. The 95% confidence intervals for the estimated mean response (Est. mean) of soil variables measured in plots invaded or uninvaded by *Solidago gigantea* in two habitat types, i.e. riparian vegetation and semi-natural grasslands. Values were back transformed to the original scale if needed and are based on mixed models fitted to the (transformed) variables. Soil variables include; soil pH, soil moisture content (%), total nematode density (per 100 g dry soil, analysed by microscope), fungal biomass (expressed as mg ergosterol kg⁻¹ soil), plant-species richness (S_{plant}), plant-species diversity (H'_{plant}), and the density of 11 nematode taxa (per 100 g dry soil, analysed by quantitative PCR). Nematode taxa are defined as by De Ley et al. (2006), except for Dorylaimida D3 and Mononchida M3 (Holterman et al. 2008).

	Riparian vegetation						Semi-natural grasslands					
	Un-invaded			Invaded			Un-invaded			Invaded		
	lower	Est. mean	upper	lower	Est. mean	upper	lower	Est. mean	upper	lower	Est. mean	upper
Soil pH	7.5	7.7	7.8	7.5	7.6	7.8	5.5	6.0	6.4	5.3	5.8	6.3
Soil moisture content	15.0	18.5	21.9	13.4	16.8	20.3	10.8	14.2	17.7	9.9	13.4	16.8
Nematode density	2190	2584	3010	2104	2491	2910	967	1234	1534	891	1148	1438
Fungal biomass	0.28	0.43	0.67	0.52	0.82	1.32	0.46	0.72	1.15	0.68	1.09	1.77
S_{plant}	10.1	12.3	14.6	4.9	7.1	9.4	15.1	17.3	19.6	5.5	7.8	10.1
H'_{plant}	2.1	2.3	2.5	1.5	1.7	1.9	2.4	2.6	2.8	1.6	1.8	2.0
Aphelenchidae	15.9	33.1	69.4	22.0	45.9	96.4	6.1	12.4	25.6	4.3	8.6	17.7
Aphelenchoididae	5.8	11.0	21.6	16.1	31.8	63.2	2.5	4.5	8.5	3.7	6.9	13.3
Diphtherophoridae	1.1	2.8	9.5	1.1	2.7	9.0	1.2	3.3	11.2	1.0	2.6	8.5
Dorylaimida D3	17.1	32.5	62.4	16.4	31.2	59.9	4.8	8.9	16.7	8.4	15.9	30.2
Mononchida M3	1.7	3.9	10.3	5.8	15.9	45.4	2.7	6.9	19.2	2.1	5.1	13.9
Cephalobidae	136.2	211.6	330.4	249.3	389.9	611.2	110.9	171.8	267.7	73.2	112.4	174.1
Plectidae (except <i>Anaplectus</i>)	87.8	156.0	277.5	115.1	204.7	364.3	168.5	299.7	533.6	107.2	190.6	339.2
<i>Anaplectus</i>	3.6	10.1	29.9	8.2	24.1	73.0	3.3	9.1	27.0	3.9	11.0	32.8
Alaimidae	18.5	69.1	261.2	62.7	237.0	899.7	4.2	14.7	54.5	3.8	12.9	47.6
Prismatolaimidae	1.5	3.5	9.7	1.6	3.9	11.1	1.6	3.9	11.0	1.3	2.9	8.0
Panagrolaimidae	2.0	3.1	5.1	2.8	4.5	7.7	1.4	2.1	3.3	1.4	2.0	3.3

stated that *S. gigantea* had no decisive community-level impact, and in addition, *S. gigantea* was found to be impacted by limited extent as compared to other invasive plant species such as *Fallopia* spp. (66–86% reduction S_{plant}) and *Heracleum mantegazzianum* (53% reduction S_{plant}). Our results show that the degree of impact of *S. gigantea* in both habitat types is similar to the impact of *H. mantegazzianum* in meadows and forest edges of the Czech Republic (Hejda et al. 2009).

Solidago gigantea renders invaded plots unfit for most resident native plants. At least in part this could be attributed to the high efficiency of *S. gigantea* in the immobilization of minerals such as P and C (Vanderhoeven et al. 2006, Scharfy et al. 2009) From June onwards, the stems and leaves of *S. gigantea* can become increasingly dense and compete successfully for light (Weber and Jakobs 2005, Banta et al. 2008). Moreover, *S. gigantea* releases large amounts of furanoid compounds and acidic compounds in the rhizosphere (Weber and Jakobs 2005). In the case of *Solidago canadensis*, (Yuan et al. 2013) uncovered a relationship between the allelochemical content of the plants and their ability to compete with native plant species. Allelochemical compounds produced by *S. gigantea* may also play an important role in its competitiveness and could affect not only resident plant species but also belowground communities.

Despite the success of *S. gigantea*, not all plants were negatively affected. We observed a rare and exotic parasitic plant *Cuscuta gronovii* (originally from North America), which had strangled and hereby killed *S. gigantea* plants. It is assumed that invasive plants benefit from being released from their natural enemies (Keane and Crawley 2002). This advantage might not persist (Diez et al. 2010), and *C. gronovii* could become an important factor limiting *S. gigantea* proliferation along rivers.

Effects on soil food web components by *S. gigantea*

Despite the fact that both habitats differ in soil type, floristic composition, and land use history, we found significant overall belowground effects of *S. gigantea* on soil acidity, fungal biomass, and the density of Aphelenchoididae, a single lineage of fungivorous nematodes. The consistency of these effects suggests that they are general consequences of the dominant presence of *S. gigantea* in its invaded range.

Regarding the increase of fungal biomass and the differential shift observed for fungivorous nematodes, our results suggest that invasion of *S. gigantea* causes an asymmetric boost of the soil fungal community. In Fig. 2, the head regions of the three fungivorous nematode genera are shown. All of them are equipped with a protrusible piercing device that is used to puncture the fungal cell wall. However, the morphologies of these devices (indicated by arrows in Fig. 2) are distinct, and this could point at disparate food preferences. In vitro studies, *Aphelenchoides saprophilus* has been shown to multiply on various mycorrhizal and saprophytic fungal species, whereas *Tylolaimophorus*, a member of the Diphtherophoridae, would not survive on any of these fungi (Ruess and Dighton 1996). Another *Aphelenchoides* species, *A. hamatus*, could feed and multiply on mycelium from four plant parasitic and a range of edible fungal species (Rössner and Nagel 1984, Ruess and Dighton 1996). Among the Aphelenchidae, a family relatively unrelated to the Aphelenchoididae (Van Meegen et al. 2009), *Aphelenchus avenae* was reported to prefer plant parasitic fungi to saprophytic species (Okada and Kadota 2003). This information shows that at least some fungivorous members of the Aphelenchoididae are polyphagous, and our data suggest this could be different for the two other major lineages of fungivorous nematodes, Diphtherophoridae and Aphelenchidae.

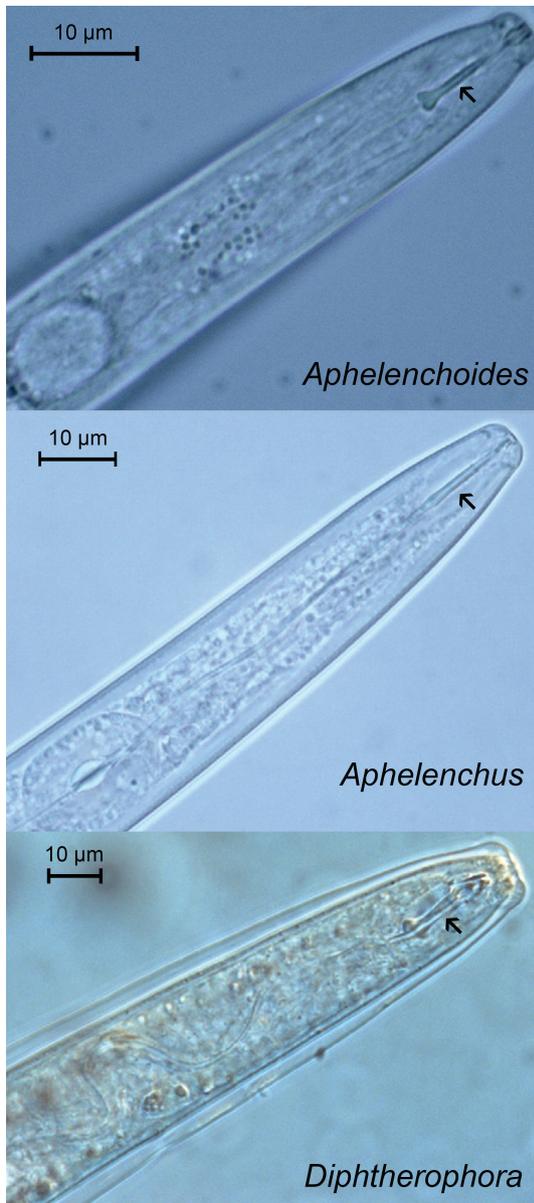


Figure 2. Pictures of the head regions of representatives of the fungivorous nematode genera *Aphelenchoides*, *Aphelenchus* and *Diphtherophora* (pictures taken at 1,000 \times magnification). To puncture the fungal cell walls, fungivores are equipped with a hardened protrusible piercing device (stylet or spear, indicated by arrows). The protrusibility is facilitated by muscles attached to the knobs or swellings at the basal part of this piercing device. The stylet of *Aphelenchoides* species is slender with easily observable basal knobs, whereas the stylet of *Aphelenchus* is characterized by slight basal swellings only. *Diphtherophora* has a short onchiostyle (different ontogeny as compared to a stylet) with a basal swelling of the onchiostyle extension.

Beside overall effects, we observed habitat-type dependent changes for some of the nematode taxa. Increased densities of two bacterivorous nematode families, Alaimidae and Cephalobidae, were exclusively observed in riparian vegetation. The over four times higher density of Alaimidae in the riparian zones as compared to the semi-natural grasslands suggests that these river clay soils are a preferred habitat for Alaimidae. Possibly, Alaimidae

under near optimal conditions are more responsive to environmental changes such as a drastic change in the plant community. Cephalobidae, a widespread and abundant family of bacterivores, significantly increased in invaded riparian vegetation whereas their numbers decreased in invaded patches in grasslands (significant interaction effect). The family Cephalobidae was represented by six identical genera in both habitats (Supplementary material Appendix 1 Table A2). The significant impact of *S. gigantea*'s presence can be explained by a change in the abundance of a single or several different genera. Interpretation of the responses for this family requires the development and use of genus-specific assays in future studies.

Conclusion

In Europe, the colonisation of *S. gigantea* represents a hazardous factor at the plant community and at the landscape scale. After all, we found that next to ruderal communities (Hejda et al. 2009), also relatively biodiverse areas are affected. Compared to most resident plant species, *S. gigantea* has a high nutrient efficiency and biomass production (Vanderhoeven et al. 2006, Scharfy et al. 2009), assumedly because invaders are generally exposed to more favourable plant–soil feedback interactions than their native neighbours (Klironomos 2002). The results reported here show that nematode communities in *S. gigantea*-invaded soils are significantly different from neighbouring soils under the native flora. Remarkably, the observed two-fold increase of fungal biomass in soil under *S. gigantea* patches, did not result in a general, more or less even density increase in fungivorous nematodes, but rather in the specific boost of a single lineage, the Aphelenchoididae. Recent experimental data point at distinct food preferences for individual lineages of fungivorous nematodes (Vervoort et al. 2012), and a specific stimulation of a part of the fungal community would be a plausible explanation for the results presented in this paper. In order to better understand the belowground effects of *S. gigantea* in Europe, we currently work on the establishment of causal links between plant invader-induced changes in the composition of bacterial and fungal communities and shifts in the composition of bacterivorous and fungivorous nematode assemblages.

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Supplementary material (available online as Appendix oik-01067 at <www.oikosjournal.org/readers/appendix>). Appendix 1.