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Impact of the invasive plant *Solidago gigantea* on soil nematodes in a semi-natural grassland and a temperate broadleaved mixed forest

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Abstract

Relationships between alien plant species and their aboveground effects have been relatively well studied, but little is known about the effects of invasive plants on belowground faunal communities. Nematodes are abundant, ubiquitous and diverse soil biota, and alterations of their community compositions can illustrate changes in belowground ecosystems. In 2016 and 2017, we determined the response of species diversity, community composition and trophic composition of the soil nematode communities to invasion by the alien plant *Solidago gigantea* in two ecosystems, forest and grassland, where invasion takes place. Nematode abundance was higher and number of identified nematode species was lower at invaded than uninvaded sites, indicated by lower species diversity, regardless of ecosystem. Herbivorous nematodes were the most affected trophic group. Herbivore abundance was higher at invaded than uninvaded sites and in grassland than forest. The herbivorous species *Boleodorus thylactus*, *Geocenamus* sp., *Helicotylenchus* spp., *Paratylenchus bukowinensis*, *Pratylenchoides crenicauda* and *Rotylenchus robustus* were more abundant at the invaded sites. Abundances of nematodes in the other tropic groups were limited or not affected. The invasion did not significantly affect the ecological and functional indices, except for the Channel Index in 2016. Differences were observed in values of Enrichment Index (indicator of resource availability), Channel Index (indicator of ascendant bacterial/fungal decomposition channel) and Basal Index (indicator of depleted-perturbed soil food webs) between grassland and forests. We can thus conclude that invasion by *S. gigantea* significantly alters nematode community indicators (abundance, species diversity and specific trophic groups); however, this effect seems to be significantly influenced by the type of ecosystem where invasion takes place.

Introduction

Invasive species have recently become a large international concern of ecologists, representing the second most important cause of species extinction globally after habitat destruction (Fitoussi *et al.*, 2016). The giant goldenrod, *Solidago gigantea* Ait. (Asteraceae), a perennial herb native to North America, is a common, widespread and important invasive species in most European countries (Weber, 1998). *Solidago gigantea* often forms dense monospecific stands in a broad range of habitats (Weber & Jakobs, 2005; De Groot *et al.*, 2007) and substantially changes the physicochemical and biological properties of the soil (Liao *et al.*, 2013), confirmed by many studies, published in the last decade, on the effect of *S. gigantea* on the belowground which has increasing trend in the last decade. For example, Chapuis-Lardy *et al.* (2006) mentioned that *S. gigantea* enhances soil phosphorus turnover rates, Sterzyńska *et al.* (2017) reported increase in soil acidity and Baranová *et al.* (2014) found changes in soil moisture in invaded ecosystems. *Solidago gigantea* invasion negatively affected plant diversity and average plant cover (Moroń *et al.*, 2009) and significantly decreased bacterial and increased fungal biomass in soil (Scharfy *et al.*, 2010). Invasion of *S. gigantea* had a very strong negative effect on diversity and abundance of wild pollinator (Moroń *et al.*, 2009) and ants (Lenda *et al.*, 2013), but Baranová *et al.* (2014) mentioned significant changes in Coleoptera families and Carabidae assemblages, but not necessarily reduction in their diversity. Soil nematodes are ubiquitous and numerous and constitute an informative bioindicator group for the functioning of soil food webs due to their trophic diversity and extensive interconnectedness within the soil food web (Neher *et al.*, 2005). The analysis of the composition of nematode fauna serves as a basis for the ecological assessment of soil (De Goede & Bongers, 1994). These authors reported that nematode communities could be defined for a range of terrestrial habitats and that these communities could be associated with characteristics of the soil and vegetation. Plants, as primary producers and providers of resources to soil food webs, are of vital importance for the composition, structure and functioning of soil communities,

including nematodes (De Deyn *et al.*, 2004). So far, the impact of invasive plants on soil free living and plant parasitic nematodes has received little attention (Chen *et al.*, 2007; Renčo & Baležentiené, 2015; Renčo *et al.*, 2019), and to our knowledge only one recent study from Germany is available about the impact of invasive *S. gigantea* on soil nematofauna (Quist *et al.*, 2014). *Solidago gigantea* as well as other invasive species are known to invade a wide range of ecosystems which can have specific community compositions of soil nematodes. Therefore, estimating the status of, and associated changes in, the structures of soil nematode communities after the establishment of invasive plants must thus include the assessment of different habitats (Renčo & Baležentiené, 2015).

Our objective was to assess and compare the nematode communities in areas invaded and uninvaded by *S. gigantea* in two types of ecosystem: a lowland semi-natural grassland and a temperate broadleaved mixed forest. We hypothesized that changes caused by the *S. gigantea* in native habitats would affect soil physical properties, reduce nematode abundance and species diversity, and affect the trophic structure and selected ecological and functional indices of the nematode communities. We studied the impact of *S. gigantea* on the nematode communities in these two semi-natural ecosystems by analysing the communities at the species level and calculating diversity, ecological and functional indices to characterize the condition of the soil food webs in both invaded and uninvaded soils.

Material and methods

Study sites and area

Sites invaded by *S. gigantea* were found by actively searching a suitable area. We established sites across the entire range of habitats and environmental conditions in which the species occurred. Invaded sites had at least 80% coverage of *S. gigantea*, and uninvaded sites did not contain this species. The study was carried out in a region of the Košice Basin in the lowlands of south eastern Slovakia (48°42′N″, 21°18′E″). This region has a warm climate; winter and summer temperatures range from −1 to −3 °C and from 18 to 20 °C, respectively, and mean annual precipitation is 600 mm. The soil is classified as a Haplic Cambisol (Miklós, 2002).

The characteristics of the sites were:

Uninvaded forest (F): ten study sites in stands dominated by *Quercus*, *Fagus*, *Carpinus* and *Betula* (deciduous forests). Mean soil organic carbon content C_{org} was 2.79% (2.29–3.18), and mean soil nitrogen (N) content was 0.24% (0.19–0.26).

Uninvaded grassland (G): ten study sites with indigenous multispecies vegetation dominated by *Dactylis glomerata*, *Lolium perenne*, *Trifolium pratense*, *Capsella bursa-pastoris* and *Taraxacum officinale*. Mean C_{org} was 3.30% (2.27–4.29), and mean N was 0.36% (0.25–0.47).

Invaded forest (FS): ten nearly monospecific stands of *S. gigantea* on forest edges, with an estimated time of invasion of 10–15 years. Mean C_{org} content was 2.31% (1.54–3.12), and mean N content was 0.22% (0.17–0.30).

Invaded grassland (GS): ten study sites in nearly monospecific stands of *S. gigantea* on grassland edges, with an estimated time of invasion of 10–20 years. Mean C_{org} content was 3.27% (2.38–4.18), and mean N content was 0.34% (0.26–0.43).

The C_{org} and N data from obtained soil samples were provided by the National Agriculture and Food Centre, Slovakia. The sites were within an area of 20×15 km and separated by a mean distance of 3.5 km. Elevation at the sites ranged from 192 to 380 m a.s.l. (Miklós, 2002). The uninvaded and invaded sites were adjacent to each other (mean distance between the invaded and uninvaded sites was 50 m; range 30–80 m). The uninvaded sites were assumed to represent sites prior to invasion by *S. gigantea*. Invaded and uninvaded sites had highly similar overall habitat conditions. Pairs of invaded and uninvaded sites did not differ in elevation, inclination, exposition, type or management.

Sampling and processing

Composite soil samples consisted of five subsamples that were collected in September 2016 and September 2017 in the 10–20 cm layer in each site using a hand spade. A total of 80 composite samples (20 sites (ten in forest and ten in grassland) × two invasion states (invaded and uninvaded areas) × two sampling dates) were collected. The samples were transferred to the laboratory in plastic bags. Each sample was gently homogenized manually before processing. Soil-moisture content was measured gravimetrically after the soil had been dried to a constant weight in an oven at 105 °C for 24 h. Soil pH was determined for air-dried soil samples in a 1:3 solution of soil: 0.01 M CaCl$_2$. All determinations were performed in triplicate.

Nematodes were isolated from 100 g of the composite soil samples by a combination of Cobb sieving and decanting (Cobb, 1918) and a modified Baermann technique (Van Bezooijen, 2006). Nematodes were extracted from aqueous soil suspensions using a set of two cotton-propylene filters. Subsamples were removed after extraction at room temperature for 24 h. The aqueous suspensions containing nematodes were examined under a stereomicroscope, excessive water was removed and the nematodes were fixed in a formalin/alcohol/acetic acid solution and evaluated on permanent glycerine slides (Southey, 1986). All isolated nematodes were microscopically identified to species, or juveniles to genus using an Eclipse 90i light microscope (Nikon, Japan), with original species descriptions and several taxonomic keys: Brzeski (1998), Loof (1999), Siddiqi (2000), Andrássy (2005, 2007, 2009) and Geraert (2008, 2010).

The total number of species, nematode abundance, abundance of nematodes per trophic group and a species diversity index (Shannon & Weaver, 1949) were determined. Nematode species were assigned to five trophic groups: bacterivores, fungivores, herbivores, omnivores and predators (Yeates *et al.*, 1993; Wasilewska, 1997). Ecological indices such as the Maturity Index (MI) for free living taxa, and the Plant Parasite Index (PPI) for plant parasitic taxa were used to assess the status of the soil ecosystems using nematode communities (Bongers, 1990). Both maturity indices (MI, PPI) were calculated using a c-p value that represented the life history characteristics of the nematode taxa associated with r- and K-selection. Species with c-p values of 1 or 2 are r-selected or colonisers. These species are very tolerant to disturbances due to their short generation times, large population fluctuations and high fecundities. Species with a c-p value of 5 are K-selected, or persisters, with long life cycles, low reproductive rates, low metabolic activities and slow movement; they are thus very sensitive to disturbances. Lower c-p values are indicative of more disturbed environments, and higher values are characteristic of less disturbed environments (Bongers, 1990).

Functional indices, such as the Enrichment Index (EI), Structure Index (SI) and Channel Index (CI) (Ferris *et al.*,

2001), and the Basal Index (BI) (Ferris *et al.*, 2001; Berkelmans *et al.*, 2003) associated with development of the maturity indices led to a functional guild classification of nematodes as a basis for studying and comparing ecosystem processes. Considering soil nematode taxa as representatives of functional guilds generates an indicator profile that is not constrained by population distribution patterns and microenvironment effects (Ferris & Bongers, 2006). Indices of soil food webs such as the EI, SI, CI and BI are used to infer food web complexity and the main pathways of organic matter decomposition (Ferris *et al.*, 2004). EI is based on the abundance of enrichment opportunistic nematodes, and indicates rapid decomposition of low C:N organic matter mediated by bacteria. EI thus suggest whether the soil environment is nutrient enriched (high EI) or depleted (low EI). SI weights the prevalence of omnivore and predatory nematodes in the soil food web as an indicator of long and complex soil food webs with high connectance and numerous trophic links, and indicates if the soil ecosystem is structured with more trophic links (high SI) or degraded with fewer trophic links (low SI). The CI, in contrast, is based on the abundance of fungal feeding opportunistic nematodes and indicates slower decomposition of high C:N organic matter mediated by fungi. A high CI (>50%) indicates a higher proportion of fungal decomposition while low CI (<50%) suggests bacterial decomposition channels (Ferris *et al.* 2001). The BI is derived from the abundance of persistent microbial feeding nematodes; high BI values indicate short and depleted soil food webs. All community indices were calculated using the online programme 'NINJA: An automated calculation system for nematode-based biological monitoring' (Sieriebriennikov *et al.*, 2014; http://spark.rstudio.com/bsierieb/ ninja).

Statistical analysis

Soil pH, soil-moisture content, mean nematode abundance, mean abundance of nematodes per trophic group, nematode cp1-5 groups and the diversity, ecological and functional indices (the Shannon–Weaver species diversity index and the MI, PPI, EI, SI, CI and BI) were analysed using Statistica (StatSoft Inc. 2013).

The data were analysed with a repeated, two-way ANOVA, with 'ecosystem' (F, G), 'invasion status' (invaded, uninvaded), 'year' (as a repeated measure) and their interactions as factors. Box–Cox transformation was applied to satisfy the assumptions of these parametric tests using maximum likelihood and the Golden Search iteration on all variables except those that were normally distributed (mean nematode abundance and the BI and MI). The factor 'year' strongly influenced the majority of the variables tested, so the data set was split to investigate the effects of 'ecosystem' and 'invasion status' separately with two-way ANOVAs for the samples from 2016 and 2017. A main-factor ANOVA (factors 'ecosystem', 'invasion status' and no interaction) was used if 'ecosystem' and 'invasion status' did not interact. *t*-tests were applied separately for each ecosystem to determine the effect of 'invasion status' if 'ecosystem' and 'invasion status' interacted.

A redundancy analysis (RDA) was used on the nematode community data for the two years separately, with explanatory variables soil pH, soil-moisture content, 'ecosystem' and 'invasion status' to identify the relationships between the nematode taxa and soil properties. All data were log-transformed. The entire data set was first included in the RDA, and the analysis was then repeated with the 71 (of 90) and 57 (of 70) most abundant

genera for 2016 and 2017, respectively, which covered >99% of the total abundance, to obtain a clear ordination site (see Results). The effects of the explanatory variables were quantified by automatic forward selection. These ordination analyses were performed in Canoco 5 for Windows (Ter Braak & Šmilauer, 2012).

Results

Soil acidity and moisture content

Soil pH was higher at the invaded than the uninvaded sites, but differed significantly only in 2017 ($P < 0.001$), not taking the 'ecosystem' into account. pH was significantly higher in the grassland than the forest ($P < 0.001$) in both years. The interaction of 'ecosystem' × 'invasion status' had a significant impact on pH in 2016 ($P < 0.001$), and subsequent *t*-tests confirmed a significant effect of 'invasion status' on pH for both grassland and forest ($P < 0.05$ and <0.01, respectively). Soil-moisture content was slightly higher at the invaded than the uninvaded sites ($P < 0.001$) and at the forest than the grassland sites ($P < 0.05$), but both only in 2016 (tables 1 and 2).

Soil nematode abundance, species diversity and species composition

Mean nematode abundance and species diversity were distinct between invaded and uninvaded soils. While *S. gigantea* invasion significantly increases nematode abundance (both years $P < 0.001$) the species diversity was significantly lower ($P < 0.05$ or <0.01) at the invaded than the uninvaded sites in both years (tables 1 and 2), not taking 'ecosystem' into account. The bi-factorial interaction 'ecosystem' × 'invasion status' significantly influenced mean nematode abundance and species diversity ($P < 0.05$ and <0.01, respectively) in 2017 only. Subsequent *t*-tests confirmed a significant effect of 'invasion status' for both variables only at the forest sites ($P < 0.01$ and <0.001).

A total of 91 nematode species were recorded in study sites. The number of identified nematode species was highest in G (2016 and 2017: 68 and 55), followed by F (60 and 49), GS (62 and 56) and FS (53 and 48) (table 3). *Aulolaimus costatus* and *Plectus longicaudatus* were observed only in FS and GS. *Anaplectus granulosus*, *Aulolaimus oxycephalus*, *Ceratoplectus assimilis*, *Microdorylaimus parvus*, *Tylencholaimus minimus*, *Trophurus sculptus* and *Tylenchus arcuatus* were exclusively in GS, and *Dorylaimoides limnophilus* was exclusively in FS.

The RDA ordinations of the selected nematode species (containing 99% of total nematode abundance) for 2016 and 2017 are presented in figs 1 and 2, respectively. The two values of both nominal variables, 'ecosystem' and 'invasion status', differed from each other. For 2016, interactive forward selection indicated that pH (explaining 19.7% of the variance, *P* (adjusted) = 0.002), 'ecosystem' (7.1%, *P* (adjusted) = 0.002), soil-moisture content (6.7%, *P* (adjusted) = 0.002) and 'invasion status' (5.4%, *P* (adjusted) = 0.002) were significant. Monte Carlo permutation tests confirmed the significance of all constrained axes (pseudo $F = 5.6$, $P = 0.002$).

The results were similar for 2017: pH (explaining 20.9% of the variance, *P* (adjusted) = 0.003) 'ecosystem' (6.4%, *P* (adjusted) = 0.002), moisture content (6.1%, *P* (adjusted) = 0.002) and 'invasion status' (4.5%, *P* (adjusted) = 0.002) were significant. Monte Carlo permutation tests confirmed the significance of all

Table 1. F values from two-way ANOVAs in the samples from 2016 with 'ecosystem' (Forest, Grassland) 'invasion status' (Invaded, Uninvaded) and their interactions as factors from analysis of soil pH, soil moisture, total nematode abundance, species diversity index, abundance in trophic groups, abundance in cp value, particular ecological and functional indices with associated probabilities (P) and degree of freedom reported.

							Ecosystem				Invasion Status			
							Forest		Grassland		Uninvaded		Invaded	
	Ecosystem		Invasion Status		Ecosystem × Invasion Status									
Year 2016	F(1,36)	P	F(1,36)	P	F(1,36)	P	A	SD	A	SD	A	SD	A	SD
pH	124.70	***	2.35	ns	20.94	***	5.3	0.6	6.6	0.3	5.8	1.0	6.0	0.6
Soil moisture	6.15	*	19.67	***	1.88	ns	12.3	1.1	11.5	1.3	12.6	1.1	11.2	1.1
Nematode abundance	0.59	ns	15.24	***	2.40	ns	648.7	365.4	713.6	258.2	516.8	213.3	845.5	316.3
Species diversity index	0.002	ns	5.47	*	2.52	ns	2.5	0.2	2.5	0.4	2.6	0.2	2.4	0.4
Bacterivores	1.08	ns	0.08	ns	2.63	ns	290.4	237.5	171.2	66.4	198.2	90.8	263.4	240.4
Fungivores	1.54	ns	18.00	***	1.56	ns	171.5	133.2	114.2	68.4	86.2	40.2	199.5	125.6
Herbivores	36.89	***	8.56	**	0.26	ns	120.9	95.2	379.7	230.3	178.8	143.3	321.8	257.0
Predators	0.45	ns	6.34	*	0.45	ns	24.8	38.8	18.5	22.7	9.7	7.1	33.6	41.1
Omnivores	1.45	ns	3.19	ns	0.22	ns	41.2	37.0	30.1	20.4	43.9	36.5	27.4	19.3
cp1	15.02	***	0.26	ns	0.01	ns	137.1	145.5	37.5	27.9	68.2	52.6	106.4	153.7
cp2	0.24	ns	8.64	**	12.24	**	340.3	274.2	297.8	91.3	248.3	128.9	389.8	239.4
cp3	35.08	***	7.66	**	0.55	ns	83.2	74.8	308.1	204.8	125.2	101.5	266.0	231.1
cp4	0.29	ns	0.24	ns	0.04	ns	69.6	51.0	55.8	36.8	66.5	44.9	59.0	44.8
cp5	0.27	ns	0.004	ns	0.06	ns	18.6	40.0	14.5	20.3	8.7	10.0	24.4	42.3
Maturity Index	2.70	ns	0.16	ns	0.02	ns	2.2	0.4	2.4	0.3	2.3	0.3	2.3	0.4
Plant Parasite Index	1.63	ns	0.58	ns	1.14	ns	2.7	0.4	2.8	0.2	2.8	0.4	2.7	0.2
Channel Index	10.02	**	5.95	*	3.35	ns	26.8	22.4	45.0	24.3	29.2	25.3	42.5	23.1
Basal Index	13.96	***	0.37	ns	11.28	**	19.4	9.5	28.8	8.1	23.3	11.3	24.9	8.6
Enrichment Index	27.97	***	0.40	ns	9.64	**	70.2	13.6	50.1	12.8	61.4	20.0	59.0	12.7
Structural Index	0.85	ns	0.99	ns	7.70	**	60.1	19.7	56.8	15.2	61.2	15.7	55.7	19.0

***0.001; **0.01; *0.05.

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Table 2. F values from two-way ANOVAs in the samples from 2017 with 'ecosystem' (Forest, Grassland)', invasion status' (Invaded, Uninvaded) and their interactions as factors from analysis of soil pH, soil moisture, total nematode abundance, species diversity index, abundance in trophic groups, abundance in cp value, particular ecological and functional indices with associated probabilities (P) and degree of freedom reported.

	Ecosystem		Invasion Status		Ecosystem × Invasion Status		Ecosystem				Invasion Status			
							Forests		Grassland		Uninvaded		Invaded	
Year 2017	F(1,36)	P	F(1,36)	P	F(1,36)	P	A	SD	A	SD	A	SD	A	SD
pH	156.56	***	32.45	***	2.90	ns	5.3	0.5	6.6	0.4	5.7	0.8	6.2	0.7
Soil moisture	3.54	ns	3.74	ns	0.42	ns	12.2	1.8	13.1	1.7	13.2	2.0	12.1	1.4
Nematode abundance	0.66	ns	15.93	***	5.17	*	467.7	217.6	504.0	112.5	396.7	152.8	575.0	143.6
Species diversity index	3.38	ns	11.43	**	9.02	**	2.3	0.4	2.5	0.3	2.6	0.3	2.3	0.4
Bacterivores	0.48	ns	1.95	ns	0.43	ns	223.8	176.1	167.0	97.6	163.1	106.8	227.7	169.2
Fungivores	0.63	ns	2.50	ns	0.26	ns	77.0	52.2	81.9	45.9	65.8	34.4	93.1	57.2
Herbivores	12.80	**	15.18	***	4.81	*	136.9	118.2	224.3	94.4	135.2	114.8	226.0	96.9
Predators	0.09	ns	0.97	ns	11.98	**	8.3	6.1	9.1	12.8	7.3	6.4	10.1	12.5
Omnivores	0.002	ns	2.42	ns	1.50	ns	21.9	15.0	21.7	14.6	25.3	15.5	18.2	13.1
cp1	7.28	*	1.85	ns	0.84	ns	144.7	135.2	77.6	100.9	85.6	99.2	136.7	140.0
cp2	0.17	ns	3.43	ns	1.01	ns	196.9	125.3	209.6	70.3	174.4	81.3	232.1	111.2
cp3	18.41	***	12.50	**	1.24	ns	85.3	90.3	169.6	76.5	90.1	85.8	164.8	86.4
cp4	0.52	ns	4.37	*	6.34	*	35.7	19.3	39.3	14.8	42.6	17.6	32.4	15.3
cp5	0.03	ns	0.74	ns	2.78	ns	5.2	6.3	8.0	13.1	4.0	5.5	9.2	13.1
Maturity Index	1.05	ns	1.99	ns	3.81	ns	2.0	0.5	2.2	0.4	2.2	0.3	2.0	0.5
Plant Parasite Index	3.52	ns	0.12	ns	0.33	ns	2.5	0.3	2.7	0.1	2.6	0.3	2.7	0.2
Channel Index	8.15	**	0.03	ns	0.02	ns	11.2	6.0	32.9	25.4	21.6	17.9	22.6	24.6
Basal Index	12.45	**	0.72	ns	0.15	ns	13.8	6.9	23.0	9.3	19.5	9.8	17.3	9.0
Enrichment Index	12.25	**	1.14	ns	0.17	ns	80.2	9.2	62.0	19.6	68.8	17.4	73.4	18.2
Structural Index	0.44	ns	2.10	ns	4.84	*	60.2	21.9	56.6	13.5	62.3	17.2	54.5	18.4

***0.001; **0.01; *0.05.

Table 3. Check-list of nematode species in trophic groups, cp value and mean total abundance (A) (individual/100 g soil) and standard deviation (SD) in two years 2016 and 2017; in 'ecosystem' (Forest, Grassland) and 'invasion status' (Invaded, Uninvaded).

Species		Cp	Forest 2016				Forest 2017				Grassland 2016				Grassland 2017			
			Invaded		Uninvaded		Invaded		Uninvaded		Invaded		Uninvaded		Invaded		Uninvaded	
			A	SD	A	SD	A	SD	A	SD	A	SD	A	SD	A	SD	A	SD
Bacterivores																		
Acrobeles ciliatus	Acil	2	-	-	-	-	-	-	-	-	-	-	1.4	2.8	-	-	-	-
Acrobeles cylindricus	Acyl	2	1.3	4.1	1.8	3.4	0.3	0.7	0.9	1.9	0.3	0.9	0.9	1.1	-	-	0.4	1.3
Acrobeloides nanus	Anan	2	90.5	102.0	34.3	30.8	25.3	34.5	28.9	25.3	21.9	11.9	49.8	24.9	15.2	16.6	17.8	15.5
Alaimus primitivus	Apri	4	7.7	7.9	11.1	6.2	1.6	1.6	7.4	6.6	8.3	8.5	4.4	6.3	3.7	3.3	3.1	4.1
Amphidelus coronatus	Acon	4	-	-	0.7	1.6	-	-	-	-	-	-	0.1	0.3	-	-	0.1	0.3
Anaplectus granulosus	Agra	2	-	-	-	-	-	-	-	-	0.4	1.0	-	-	-	-	-	-
Aulolaimus oxycephalus	Aoxy	3	-	-	-	-	-	-	-	-	2.2	3.6	-	-	0.7	1.6	-	-
Aulolaimus costatus	Acos	3	-	-	-	-	0.2	0.6	-	-	0.5	1.6	-	-	0.1	0.3	-	-
Cephalobus persegnis	Cper	2	39.0	22.0	4.8	4.8	16.5	22.2	6.0	4.5	26.0	18	36.8	18.0	27.7	7.8	24.4	17.8
Ceratoplectus assimilis	Cass	2	-	-	-	-	-	-	-	-	1.9	3.9	-	-	-	-	-	-
Cervidellus hamatus	Cham	2	-	-	-	-	-	-	-	-	-	-	0.2	0.6	-	-	-	-
Cervidellus vexilliger	Cvex	2	0.1	0.3	6.0	3.6	3.1	6.5	3.2	3.1	0.9	1.9	0.3	0.7	0.2	0.6	1.2	1.8
Ereptonema arcticum	Earc	2	-	-	-	-	-	-	-	-	-	-	1.2	1.9	-	-	-	-
Eucephalobus striatus	Estr	2	45.5	43.0	16.3	17.3	16.6	29.6	9.0	5.3	24.0	15.7	46.4	25.5	38.1	15.3	22.7	14.4
Heterocephalobus elongatus	Helo	2	-	-	0.5	1.6	-	-	-	-	-	-	-	-	-	-	-	-
Chiloplacus propinquus	Cpro	2	3.9	4.9	-	-	0.4	0.8	0.2	0.6	3.4	4.6	9.2	15.1	1.4	2.0	2.3	3.7
Panagrolaimus rigidus	Prig	1	-	-	0.5	1.0	-	-	0.3	0.9	0.6	1.9	2.7	5.5	0.3	0.9	-	-
Paramphidelus dolichurus	Pdoi	4	-	-	0.2	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Plectus geophilus	Pgeo	2	-	-	-	-	-	-	-	-	3.6	4.1	4.6	3.8	2.7	2.4	7.1	8.1
Plectus longicaudatus	Plon	2	-	-	-	-	6.6	9.0	-	-	-	-	-	-	0.2	0.6	-	-
Plectus parietinus	Ppar	2	5.9	5.9	3.7	4.1	5.0	3.7	7.0	6.0	5.6	6.6	3.7	3.6	1.8	3.2	1.8	2.8
Plectus parvus	Ppai	2	13.7	8.5	11.4	10.3	5.9	11.2	5.1	5.2	2.1	2.4	2.5	2.7	1.6	2.2	1.9	2.2
Prismatolaimus dolichurus	Pdol	3	0.6	1.6	3.1	5.9	-	-	0.2	0.6	-	-	-	-	-	-	-	-
Prismatolaimus intermedius	Pint	3	2.3	3.7	1.0	1.2	5.6	9.4	2.0	2.4	2.1	2.7	2.4	3.7	0.9	1.7	0.8	1.1
Teratocephalus terrestris	Tter	3	-	-	0.3	0.7	-	-	0.5	1.6	-	-	-	-	-	-	0.3	0.9
Wilsonema schuurmansstekhoveni	Wsch	2	-	-	0.3	0.9	0.3	0.7	0.4	0.8	0.2	0.6	0.1	0.3	0.3	0.7	0.4	0.8
Zeldia punctata	Zpun	2	-	-	0.5	0.8	-	-	-	-	-	-	-	-	-	-	-	-
Rhabditis spp. juv.	Rspp	1	174.9	197.0	98.8	52.3	204.0	168.0	85.1	50.5	37.3	27.5	34.3	30.1	69.1	55.6	85.7	135.2

Fungivores

Aphelenchoides composticola	Acom	2	37.3	40.0	5.1	8.2	3.5	4.7	-	-	2.7	8.5	0.4	1.3	0.3	0.9	-	-
Aphelenchoides parietinus	Apar	2	41.5	49.0	3.7	4.8	1.0	2.0	-	-	4.3	2.8	2.6	3.6	0.5	1.1	1.6	2.6
Aphelenchoides ritzemabosi	Arit	2	3.6	8.8	0.2	0.6	2.9	5.1	4.9	8.6	6.1	9.0	4.6	4.6	1.9	2.3	2.2	3.7
Aphelenchoides saprophilus	Asap	2	25.2	37.0	1.2	2.9	27.3	34.8	5.8	7.7	4.4	6.1	0.1	0.3	1.0	1.6	0.6	1.3
Aphelenchus avenae	Aave	2	23.9	42.0	0.8	1.6	7.2	8.9	0.5	0.8	63.9	35.7	27.9	14.2	50.1	44.2	26.9	21.6
Diphtherophora communis	Dcom	3	2.3	4.4	12.4	12.3	-	-	14.5	14.1	27.6	43.2	1.8	3.1	12.2	15.5	0.7	1.3
Ditylenchus sp.	Dsp.	2	1.4	4.4	-	-	-	-	-	-	2.5	4.7	0.5	1.6	-	-	-	-
Dorylaimoides limnophilus	Dlim	4	0.9	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dorylaimoides micoletzkyi	Dmic	4	1.3	2.3	-	-	2.8	4.8	-	-	1.1	1.4	1.0	2.2	0.8	1.4	-	-
Doryllium zeelandicum	Dzee	4	10.4	14	12.4	9.5	1.9	3.3	4.2	4.3	13.1	28	6.1	4.9	9.0	13.9	6.0	5.9
Filenchus hamatus	Fham	2	-	-	9.8	26.1	-	-	-	-	-	-	-	-	-	-	-	-
Filenchus misellus	Fmis	2	22.4	31.0	15.4	23.4	4.7	10.4	16.7	18.4	-	-	-	-	-	-	-	-
Filenchus vulgaris	Fvul	2	36.9	44.0	30.6	25.0	19.0	11.8	22.4	16.6	21.0	16.7	27.4	17.9	23.6	11.7	17.3	7.3
Paraphelenchus pseudoparietinus	Ppse	2	43.3	58.0	-	-	12.1	20.9	0.2	0.6	-	-	5.6	10.3	-	-	1.5	2.4
Tylencholaimus minimus	Tmin	4	-	-	-	-	-	-	-	-	0.8	2.5	-	-	1.1	2.3	-	-
Tylencholaimus mirabilis	Tmir	4	0.4	0.8	-	-	1.8	3.4	-	-	0.6	1.6	1.4	3.8	1.5	3.2	3.5	5.4
Tylencholaimus stecki	Tste	4	-	-	0.5	1.6	-	-	0.5	1.6	-	-	0.9	2.8	-	-	1.5	4.7

Herbivores

Aglenchus agricola	Aagr	2	2.3	3.5	1.1	3.5	3.7	3.9	8.8	7.6	7.2	4.2	20.5	25.9	9.9	9.7	6.8	6.2
Amplimerlinius macrurus	Amac	3	-	-	-	-	-	-	-	-	-	-	0.3	0.9	-	-	-	-
Axonchium coronatum	Acor	5	-	-	0.8	1.8	-	-	-	-	0.4	0.7	1.5	3.2	1.3	1.3	0.1	0.3
Basiria gracilis	Bgra	2	1.6	4.1	1.8	3.1	2.9	4.8	-	-	36.6	38.8	29.7	34.9	20.4	10.6	7.9	8.3
Bitylenchus dubius	Bdub	2	0.7	2.2	-	-	-	-	1.6	4.1	6.9	11.7	2.7	4.6	-	-	0.8	1.8
Boleodorus thylactus	Bthy	2	16.5	33.0	-	-	29.9	54.4	-	-	19.0	27.6	6.0	9.0	13.2	7.1	15.1	10
Coslenchus costatus	Ccos	2	-	-	0.1	0.3	-	-	-	-	0.1	0.3	0.1	0.3	0.2	0.6	-	-
Criconemoides curvatum	Ccur	3	1.0	2.2	1.9	2.5	0.1	0.3	1.4	3.0	1.0	1.8	1.5	2.4	0.6	1.0	0.4	0.8
Gracilacus straeleni	Gstr	2	1.5	3.2	7.0	9.4	4.1	3.0	5.9	7.4	5.3	9.6	17	32.1	5.2	8.2	26.2	28.2
Geocenamus sp.	Gsp.	3	-	-	-	-	-	-	-	-	33.3	42.7	18.5	15.4	18.2	12.8	9.6	13.9
Helicotylenchus digonicus	Hdig	3	57.3	89.0	0.9	1.3	97.7	105	2.7	5.6	312.0	249.0	144	83.0	135.0	50.5	85.5	63.9
Helicotylenchus dihystera	Hdih	3	1.4	3.8	-	-	10.1	15.1	-	-	-	-	3.3	8.3	-	-	16.5	23.7
Helicotylenchus multicinctus	Hmul	3	0.2	0.6	-	-	-	-	-	-	1.9	4.3	3.5	10.1	1.6	3.9	-	-
Heterodera sp. juv.	Hsp.	3	-	-	1.4	2.5	-	-	-	-	-	-	0.1	0.3	1.4	4.4	-	-

(Continued)

Table 3. (*Continued.*)

Species		Cp	Forest 2016				Forest 2017				Grassland 2016				Grassland 2017			
			Invaded		Uninvaded		Invaded		Uninvaded		Invaded		Uninvaded		Invaded		Uninvaded	
			A	SD	A	SD	A	SD	A	SD	A	SD	A	SD	A	SD	A	SD
Longidorus elongatus	Lelo	5	0.2	0.6	1.9	2.5	1.2	3.8	2.9	3.0	0.2	0.4	5.3	7.4	0.2	0.6	1.4	3.7
Malenchus exiguus	Mexi	2	7.6	8.0	25.3	25.8	8.1	7.7	22.5	12.4	7.5	3.3	10.3	10.7	6.5	4.2	7.1	6.5
Meloidogyne sp.	Mlsp	3	0.2	0.6	25.6	34.9	-	-	0.3	0.9	-	-	-	-	-	-	-	-
Paratylenchus bukowinensis	Pbuk	2	33.2	51.0	-	-	34.9	46.1	2.4	5.1	0.1	0.3	2.4	5.1	0.8	1.8	2.4	6.3
Pratylenchoides crenicauda	Pcre	3	24.9	30.0	1.6	3.0	4.2	7.1	9.2	11.2	26.6	81.3	0.6	1.9	18.5	15.0	5.6	8.6
Pratylenchus penetrans	Ppen	3	-	-	-	-	-	-	-	-	-	-	0.2	0.6	-	-	2.1	6.6
Pratylenchus pratensis	Ppra	3	3.6	8.4	0.4	0.8	1.5	2.3	0.2	0.6	1.8	5.7	4.3	2.5	1.5	4.1	16.6	26.3
Pratylenchus thornei	Ptho	3	-	-	0.8	2.5	-	-	-	-	-	-	-	-	-	-	-	-
Rotylenchus robustus	Rrob	3	14.8	17.0	0.7	1.1	13.4	21.6	0.9	2.2	13.5	19.8	10.6	17	4.6	5.0	4.0	4.4
Trichodorus sparsus	Tspa	4	-	-	1.9	3.5	-	-	2.7	4.9	-	-	-	-	-	-	-	-
Trophurus sculptus	Tscu	3	-	-	-	-	-	-	-	-	0.8	2.5	-	-	0.8	1.7	-	-
Tylenchorhynchus cylindricus	Tcyl	3	-	-	-	-	-	-	-	-	-	-	0.5	1.6	-	-	0.4	1.3
Tylenchus arcuatus	Tarc	2	-	-	-	-	-	-	-	-	2.8	7.0	-	-	-	-	-	-
Xiphinema diversicaudatum	Xdiv	5	-	-	1.5	2.3	-	-	0.4	1.3	-	-	-	-	-	-	-	-
Omnivores																		
Aporcelaimellus obtusicaudatus	Aobt	5	1.9	3.5	2.1	3.5	0.5	1.3	1.1	2.3	-	-	0.4	0.8	-	-	-	-
Ecumenicus monohystera	Emon	4	-	-	0.5	1.6	-	-	-	-	3.7	6.2	9.6	12.5	1.2	3.8	2.2	5.2
Enchodelus macrodorus	Emac	4	15.8	18.0	3.9	4.1	5.8	6.0	9.0	6.3	1.3	1.9	3.4	7.1	3.7	4.3	7.3	9.0
Eudorylaimus opistohystera	Eopi	4	-	-	0.2	0.6	-	-	0.9	1.5	-	-	0.7	1.3	-	-	-	-
Eudorylaimus silvaticus	Esil	4	10.1	9.2	36.2	43.8	1.6	2.1	13.7	9.8	11.1	7.6	20.5	19.9	9.6	9.4	2.1	3.0
Mesodorylaimus bastiani	Mbas	4	1.3	2.0	0.2	0.6	-	-	0.5	1.1	0.4	0.7	-	-	0.5	1.1	0.4	0.8
Mesodorylaimus centrocercus	Mcen	4	-	-	2.5	5.4	-	-	-	-	-	-	-	-	-	-	-	-
Microdorylaimus parvus	Mpar	4	-	-	-	-	-	-	-	-	0.4	0.8	-	-	0.4	1.3	-	-
Paraxonchium laetificans	Plae	5	-	-	-	-	-	-	0.7	1.5	-	-	-	-	-	-	-	-
Prodorylaimus longicaudatoides	Ploi	4	2.4	4.2	-	-	1.0	1.3	-	-	0.7	1.5	0.8	1.9	-	-	1.6	3.5
Pungentus silvestris	Psil	4	-	-	-	-	-	-	-	-	-	-	0.4	1.3	-	-	-	-
Thonus ettersbergensis	Tett	4	3.6	5.4	1.7	3.5	6.6	10.0	2.3	2.7	2.0	4.7	4.7	7.1	5.5	6.4	8.8	9.4

Predators																		
Anatonchus tridentatus	Atri	4	0.5	1.3	0.6	0.1	0.3	2.2	3.1	1.0	2.0	1.2	2.8	0.5	1.1	0.2	0.6
Clarkus papillatus	Cpap	4	-	-	0.6	0.3	0.9	-	-	0.2	0.6	0.2	0.6	-	-	-	-
Coomansus parvus	Cpar	4	9.2	15.0	0.4	-	-	-	-	4.2	4.6	2.2	4.0	0.8	1.9	0.3	0.7
Discolaimus texanus	Dtex	5	-	-	-	-	-	-	-	2.8	5.1	2.1	2.9	1.9	2.6	0.2	0.6
Mylonchulus brachyuris	Mbra	4	1.1	2.1	0.9	0.9	1.9	3.6	3.2	4.3	3.4	0.8	1.2	2.0	3.6	1.1	1.4
Oxydirus oxycephalus	Ooxy	5	28.5	55	0.2	3.1	4.9	0.5	1.3	14.7	26.4	1.5	3.4	10.1	14.6	0.7	2.2
Tripyla setifera	Tset	3	0.6	1.6	7.0	0.4	1.0	5.4	4.8	-	-	1.7	2.6	-	-	0.4	1.3
Total number of species			53	60	48	49	62	56	55								

constrained axes (pseudo $F = 5.3$, $P = 0.002$). Soil pH was the most important factor in both years, explaining >50% of the total variance (50.6, and 55.1% for 2016 and 2017, respectively), and the other factors explained between 11% and 18%. The general trends were similar for both years: forest and uninvaded sites were associated with soil-moisture content whereas grassland and invaded sites were associated with soil acidity. RDA analysis indicated that species diversity tends to be higher in uninvaded habitats, which is also supported by table 3. Several nematode species were found to be in positive correlation with *S. gigantea* invaded habitat, e.g. *Aphelenchoides parietinus*, *Aphelenchus avenae*, *Boleodorus thylactus*, *Coomansus parvus*, *Diphtherophora communis*, *Dorylaimoides micoletzkyi*, *Oxydirus oxycephalus*, *Pratylenchoides crenicauda* and *Thonus ettersbergensis*. In contrast, *Anatonchus tridentatus*, *Cervidellus vexilliger*, *Eudorylaimus opistohystera*, *E. silvaticus*, *Malenchus exiguus* and *Tripyla setifera* were more abundant in the uninvaded sites. Bacterivore *Plectus geophilus*, fungivore *A. avenae* and herbivore *Helicotylenchus digonicus* tend to have higher abundance at higher pH, while *T. setifera*, *C. vexilliger* and *Rhabditis* spp. negatively correlated with soil acidity. In contrast, clear relation of species to soil moisture was not confirmed, different patterns were observed for different years, e.g. *H. digonicus* is at once positively (fig. 2) and once negatively (fig. 1) associated with soil moisture.

Nematode trophic groups and evaluation of the ecological and functional indices

Bacterivores were the most abundant trophic group at the forest sites, followed by fungivores and herbivores in 2016 and by herbivores and fungivores in 2017. In contrast, herbivores were most abundant at the grassland sites in both years, followed by bacterivores and fungivores (tables 1 and 2). The only trophic group significantly affected by both invasion status and ecosystem was herbivores. Their numbers were higher at the invaded than the uninvaded sites ($P < 0.01$; $P < 0.001$) and at the grassland than the forest sites ($P < 0.001$; $P < 0.01$). Besides herbivores, *S. gigantea* invasion significantly influenced the abundance of fungivores and predators in 2016; both were more abundant at the invaded than the uninvaded sites mostly due to the high abundances of *Aphelenchoides* spp. and *O. oxycephalus*. The bi-factorial interaction 'ecosystem' × 'invasion status' did not show significant impact on nematode trophic groups in 2016. A similar trend was recorded in 2017; however, two trophic groups, herbivores ($P < 0.05$) and predators ($P < 0.01$), were significantly affected by 'ecosystem' × 'invasion status'. A subsequent t-test confirmed an invasion effect for both herbivores and predators ($P < 0.001$ and $P < 0.01$, respectively) at the forest sites, but only for predators ($P < 0.05$) at the grassland sites.

Only nematodes of cp3 group were significantly affected by both ecosystem and invasion status in both years (tables 1 and 2). Their numbers, mainly plant parasitic nematodes *Helicotylenchus*, *Geocenamus* and *Pratylenchus*, were significantly higher at the grassland than at the forest sites ($P < 0.001$) and at the invaded than at the uninvaded sites ($P < 0.01$) in both years. *Solidago gigantea* invasion also significantly affects the abundance of cp2 nematodes in 2016 and cp4 nematodes in 2017; however, while cp2 increased, cp4 decreased under invasive plant in comparison to uninvaded control sites ($P < 0.01$; $P < 0.05$). The number of cp1 nematodes was significantly higher at the forest than the grassland sites; mainly bacterivores ($P < 0.001$; $P < 0.05$) represented by *Rhabditis* spp.
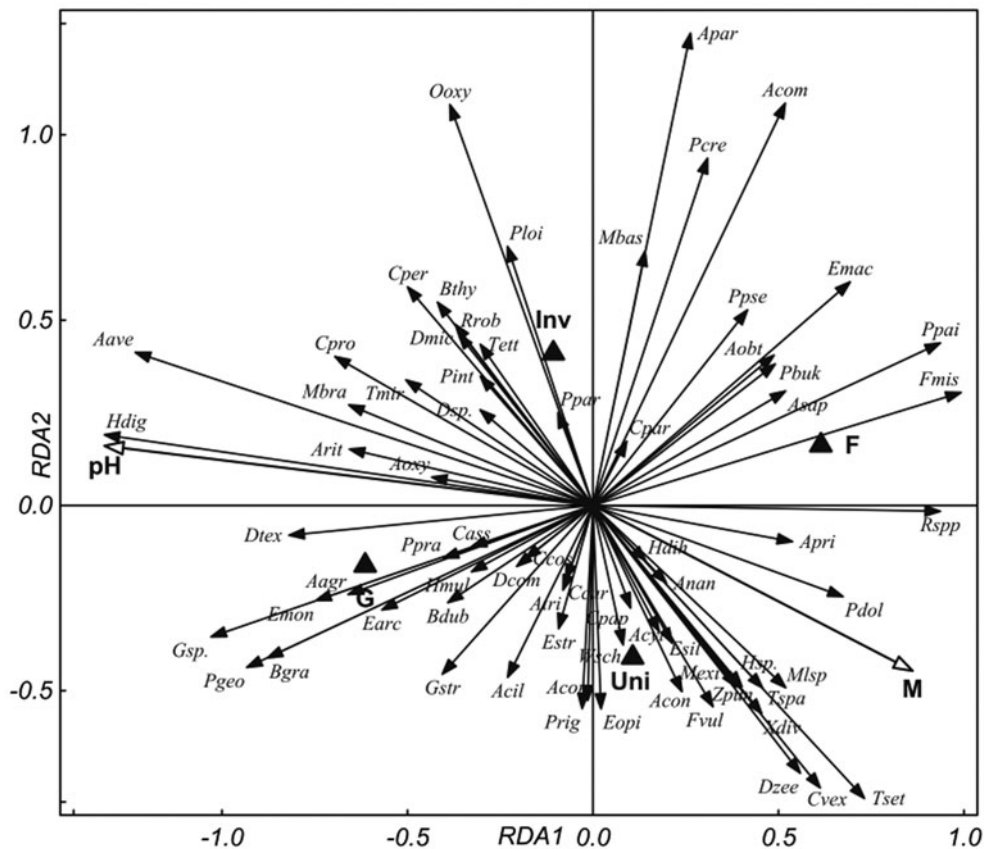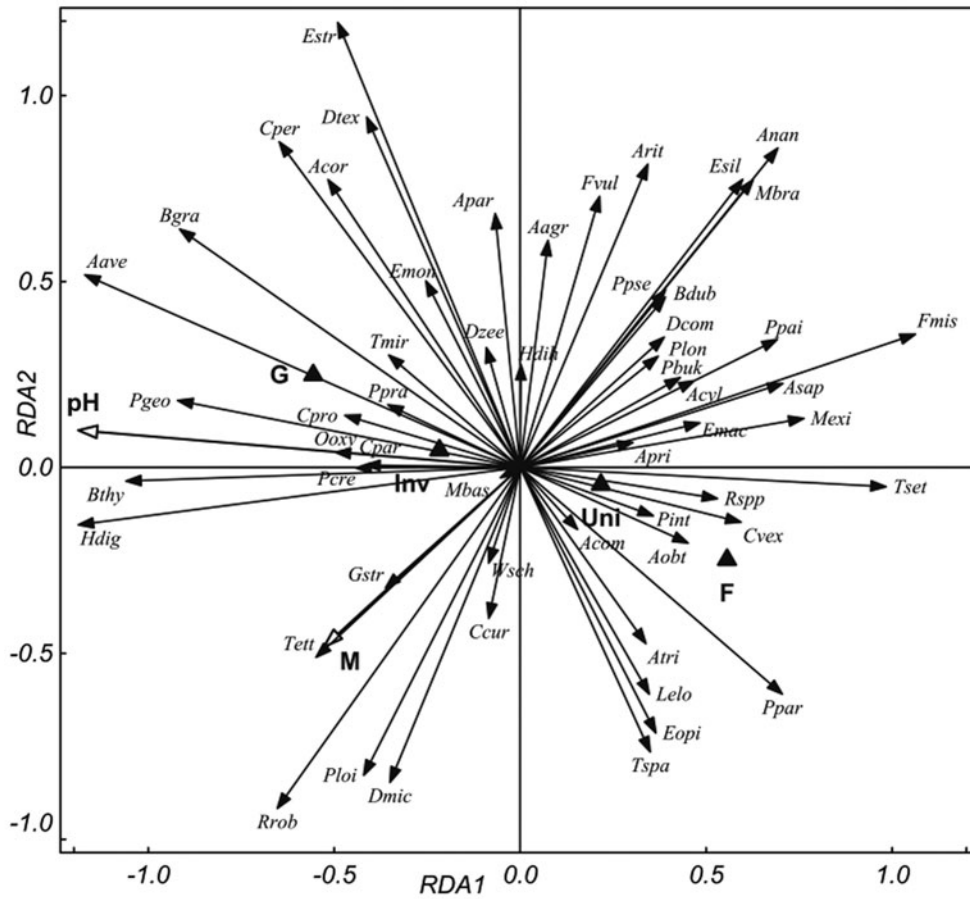
Fig. 1. RDA ordination diagram of the nematode communities in the samples from 2016 with explanatory variables: soil pH; M, soil moisture; 'ecosystem' and 'invasion status'. Ecosystem: F, forest; G, grassland. Invasion status: Inv, Invaded; Uni, Uninvaded. Quantitative variables are plotted as arrows with white heads, nominal variables as black triangles. Nematode genera are plotted as arrows with black heads (for abbreviations see table 3). The eigenvalues of the first two axes are 0.21 and 0.07 and they explain 55.2% and 19.3% of the fitted variation, respectively.

MI, PPI, BI, EI and SI were not significantly different between the invaded and uninvaded sites. Only the CI differed significantly between the invaded and uninvaded sites in 2016 ($P < 0.05$) (tables 1 and 2). The CI and BI were significantly higher at the grassland than the forest sites in both years ($P < 0.001$; $P < 0.01$). On the other hand, the EI was lower at the grassland than the forest sites in both years ($P < 0.001$ or $P < 0.01$). The interaction of 'ecosystem' × 'invasion status' differed significantly for the BI, EI and SI in 2016 (all $P < 0.01$) (table 1) and only for the SI in 2017 ($P < 0.05$) (table 2). Subsequent *t*-tests confirmed the invasion effect for all these cases only for the forest sites ($P < 0.05$).

The results of the EI and SI plotted 95% of the forest soil samples in Quadrat B (figs 3 and 4), which characterized the soil food web as N-enriched, with bacterial pathways of decomposition, a low C:N ratio and a regulated food web. Most samples from G or GS were plotted in Quadrat B (25% or 45%) or C (40% or 30%), which characterized the soil as N-enriched, with bacterial and fungal pathways of decomposition channel, and a maturing or structured food web. Samples from FS were allocated in 50% in Quadrat A, which characterized a disturbed soil food web, with a lower C:N ratio and bacterial pathways of decomposition.

Discussion

The investigation of the belowground effects of *S. gigantea* invasion in two semi-natural habitats, grassland and forest, on soil

properties such as soil-moisture content and pH was ambiguous. Lower soil-moisture content at the invaded sites in one year was probably due more to the season than plant invasion. Grassland soils tend to be less acidic than forest soils (Tisdale *et al.*, 1985), as we also observed ($P < 0.001$). pH was significantly higher at the invaded sites only in one of the two years. The effect of *S. gigantea* on soil pH was similarly inconsistent in other studies. Sterzyńska *et al.* (2017) and Zhang *et al.* (2009) reported that invasion by *S. gigantea* significantly increased soil pH, but Herr *et al.* (2007) and Quist *et al.* (2014) reported the opposite trend, slightly lower pH where *S. gigantea* had invaded. Invasions by different alien plants often, but not always, alter soil properties, as recently reported by Ehrenfeld & Scott (2001), Ehrenfeld (2003) and Gaggini *et al.* (2018).

Soil nematode abundance, diversity and species composition

Our results demonstrated that nematode abundance and diversity in soils invaded by *S. gigantea* differed significantly from neighbouring soils with native flora, regardless of ecosystem. We assumed that invasive plant *S. gigantea* would decrease both nematode abundance and diversity, which have been reported previously in surveys with some other invasive plants, e.g. *Heracleum sosnowskyi* (Renčo & Baležentiené, 2015; Renčo *et al.*, 2019), *Spartina alterniflora* (Zhang *et al.*, 2018) or *Bromus tectorum* (Belnap *et al.*, 2005), but our hypothesis was

Fig. 2. RDA ordination diagram of the nematode communities in the samples from 2017 with explanatory variables: soil pH; M, soil moisture; 'ecosystem' and 'invasion status'. Ecosystem: F, forest; G, grassland. Invasion status: Inv, Invaded; Uni, Uninvaded. Quantitative variables are plotted as arrows with white heads, nominal variables as black triangles. Nematode genera are plotted as arrows with black heads (for abbreviations see table 3). The eigenvalues of the first two axes are 0.23 and 0.07 and they explain 60.9% and 19.1% of the fitted variation, respectively.
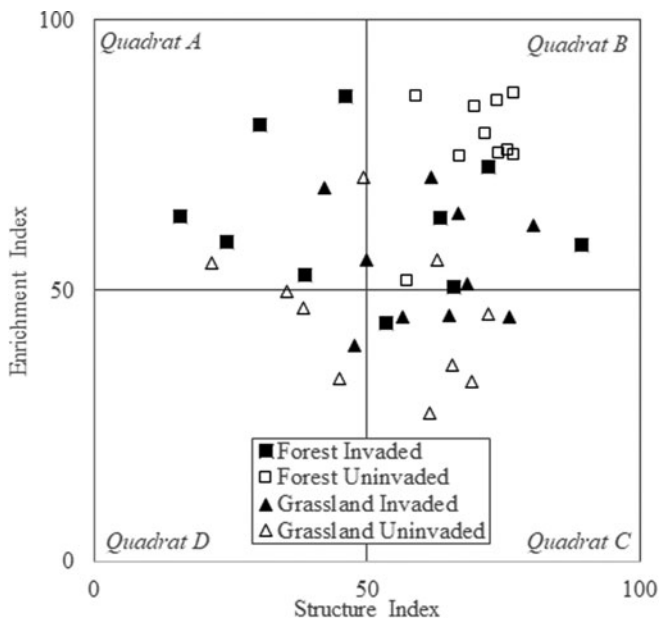
Fig. 3. Food web condition in soil (forest and grassland) invaded and uninvaded by *Solidago gigantea* in 2016. The evaluation is based on nematode faunal analysis according to Ferris *et al.* (2001).
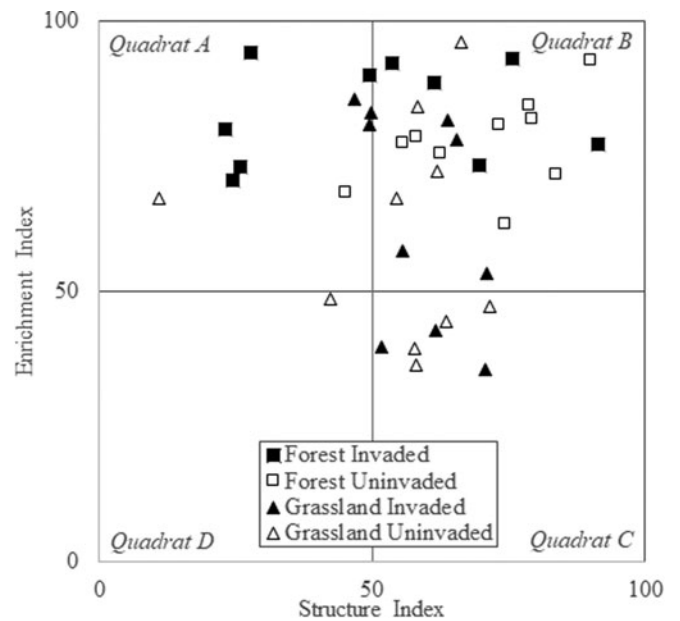
Fig. 4. Food web condition in soil (forest and grassland) invaded and uninvaded by *Solidago gigantea* in 2017. The evaluation is based on nematode faunal analysis according to Ferris *et al.* (2001).

only partly supported. Nematode diversity was lower at the sites invaded by *S. gigantea* than at both uninvaded grassland and forests ecosystems. On the other hand, we observed higher nematode abundance at invaded than uninvaded sites; however, abundance was higher only for some species from herbivore trophic group as *B. thylactus*, *Geocenamus* sp., *Helicotylenchus* spp., *Paratylenchus bukowinensis*, *P. crenicauda* and *Rotylenchus robustus*.

Yeates (1999) reported that lower diversities of plant species in ecosystems negatively affected the populations of herbivorous nematodes, and Bongers (1990) indicated that herbivores depended on the establishment of higher plants with root systems that could serve as food sources. *S. gigantea* often grows in clumps, forming mostly monospecific stands. Therefore, the abundance of some herbivorous species in our study may have been higher because nutrient-use efficiency and biomass production are high in sites with *S. gigantea* (Vanderhoeven *et al.*, 2006; Scharfy *et al.*, 2009), which has a well-developed root system on which some plant parasitic nematodes can feed. Invasive plants are also generally exposed to more favourable plant soil feedback interactions than are their native neighbours (Klironomos, 2002; Quist *et al.*, 2014). Similar, a higher abundance of herbivorous nematodes has been reported in the woody legume mesquite (*Prosopis glandulosa*) in its historical habitats (playas and arroyos) than in recently invaded desertified perennial grasslands in the Chihuahuan Desert, USA (Virginia *et al.*, 1992), or in sites invaded with *Ambrosia trifida* than in sites with native *Chenopodium serotinum* (Liang *et al.*, 2007). Yeates & Williams (2001) found seven additional taxa of herbivorous nematodes in areas invaded by the weed *Tradescantia fluminensis* than in reference locations in New Zealand. In contrast, Renčo & Baležentiené (2015) found significantly fewer plant parasites, e.g. *Gracilacus straeleni*, *H. digonicus*, *P. bukowinensis*, *Pratylenchus pratensis* and *R. robustus*, under invasive *H. sosnowskyi* than uninvaded control sites in three different habitats, suggesting a high sensitivity to accumulated toxic compounds. A similar lower abundance of herbivores was observed by Zhang *et al.* (2018). Scharfy *et al.* (2010) studied the effect of *S. gigantea* on soil microbes in typical wetland soils (Gleysols and a gleyic Cambisol) under controlled mesocosmic conditions and observed a significant decrease in bacterial biomass and an increase in fungal biomass in plant communities dominated by *S. gigantea*. Bacterivorous nematode taxa that feed on soil microbes in our study did not have a clear response to invasion, but the abundance of fungivorous nematodes that feed on fungal biomass was higher at the invaded sites. Quist *et al.* (2014) used a quantitative PCR-based method and determined 11 nematode taxa, also observed a higher abundance of fungivorous nematodes, but only of one family, Aphelenchoididae, in invaded sites in two contrasting habitats in riparian zones and semi-natural grasslands invaded by *S. gigantea*, but nematode families Aphelenchidae and Diphtherophoridae were unaffected. In our study we observed higher abundance of nematodes *Aphelenchoides composticola*, *A. parietinus*, *A. ritzemabosi*, *A. saprophilus* (Aphelenchoididae) and *A. avenae* (Aphelenchidae) and lower abundance of *D. communis* (Diphtherophoridae) in invaded than uninvaded sites (table 3). Other trophic groups such as omnivores and predators that tend to be sensitive to environmental changes (Bongers, 1990; Yeates *et al.*, 1993, Ferris *et al.*, 2001) were slightly or not affected by ecosystem or invasion status. Quist *et al.* (2014), Renčo & Baležentiené (2015) and Fitoussi *et al.* (2016) reported similar results.

Evaluation of the nematode ecological and functional indices

Nematodes possess the most important attributes among soil organisms of any prospective bioindicator (Cairns *et al.*, 1993), due to their high abundance, diversity and trophic structure in soil (Bongers, 1990). Several attempts have been made to identify relationships between nematode community structure and the succession of natural ecosystems or environmental disturbances (De Goede *et al.*, 1993; Yeates, 1999). The MI and PPI have also been used to infer the position of nematode communities along ecological successions (Bongers, 1990; Korthals *et al.*, 1996). The MI, used as a measure of the ecological successional status of soil communities (Bongers, 1990), was generally low in our study (mean MI 2.0–2.4), regardless of ecosystem or invasion status, indicating a disturbed and stressed environment (Bongers & Bongers, 1998). The MI is based on the principle that different taxa have contrasting sensitivities to stress or disruption of the successional sequence because of their life-history characteristics expected by cp1-5 values. Cp1 nematodes represent colonisers with short generation times, large population fluctuations and high fecundity, and cp5 nematodes represent persisters, produce few offspring and generally appear later in succession (Bongers & Bongers, 1998; Bongers & Ferris, 1999). The abundances of cp1 and cp2 nematodes were higher at the invaded than the uninvaded sites, but not significantly.

The EI is a measure of opportunistic bacterivorous and fungivorous nematodes present in the soil ecosystem (Ferris *et al.*, 2001). The mean EI value for all sites was higher than 50%, which indicates that the soil ecosystem was nutrient-enriched with prevailed bacteria-mediated, organic matter decomposition. Comparing ecosystems, EI was lower at the grassland than the forest sites in both years, but EI did not differ significantly between the invaded and uninvaded sites. The SI is the relative contribution of nematodes with higher cp-value (3–5) and indicates the state of food webs affected by stress or disturbance (Ferris *et al.*, 2001). The value of SI can also specify the possibility of control of predators, but in our study did not differ significantly between invaded and uninvaded sites or ecosystems, confirming the findings by Renčo *et al.* (2019).

The CI indicates the predominant pathways of decomposition in soil food webs; values <50% indicate pathways dominated by bacteria, and values >50% indicate a higher proportion of fungal decomposition (Ferris, *et al.*, 2001). The CI in our study was higher at the grassland than the forest sites ($P < 0.01$ both years) and at the invaded than the uninvaded sites ($P < 0.05$ only in 2016) but was below 50% in both cases, indicating that the decomposition was dominated by bacterial pathways. A similar value of CI under invasive *H. sosnowskyi* in the several different ecosystems with a monoculture was observed by Renčo *et al.* (2019). The BI provides information about the relative proportion of the basal (cp2) component of all nematodes present (Berkelmans *et al.*, 2003) and was higher at the grassland than the forest sites, but did not differ significantly between the invaded and uninvaded sites. In conclusion, the colonization of *S. gigantea* in Europe represents a hazard at the scales of plant community and landscape (Quist *et al.*, 2014) and may greatly affect aboveground–belowground feedback, especially, when the invading species has vastly different physiological trays from native flora (Wardle *et al.*, 2004).

This study provides insights into the impact of invasion by *S. gigantea* on the variation of soil nematode communities in grassland and forest ecosystems it invades. Our results

demonstrated that *S. gigantea* invasion affected the soil nematode communities positively by increasing their total abundance (mainly herbivores), but negatively by decreasing their diversity relative to neighbouring soil with native flora. The higher abundance of plant parasitic nematodes observed in both years at the invaded grasslands suggested that *S. gigantea* can serve as a potential reservoir of plant nematode pests, which can make recovery of these ecosystems more difficult. Maturity indices (MI, PPI) and SI were not able to distinguish the differences in the nematode communities between invaded and uninvaded sites in both ecosystems. Relative low values of MI, PPI and CI, moderate values of SI and high values of EI however suggest prevailing bacterial decomposition pathways in the soil food web of habitats studies, indicating disturbed and stressed environment.

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