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Research

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Due to climate warming, many plant species shift ranges towards higher latitudes. Plants can disperse faster than most soil biota, however, little is known about how range-expanding plants in the new range will establish interactions with the resident soil food web. In this paper we examine how the soil nematode community from the new range responds to range-expanding plant species compared to related natives. We focused on nematodes, because they are important components in various trophic levels of the soil food web, some feeding on plant roots, others on microbes or on invertebrates. We expected that range expanding plant species have fewer root-feeding nematodes, as predicted by enemy release hypothesis. We therefore expected that range expanders affect the taxonomic and functional composition of the nematode community, but that these effects would diminish with increasing trophic position of nematodes in the soil food web.

We exposed six range expanders (including three intercontinental exotics) and nine related native plant species to soil from the invaded range and show that range expanders on average had fewer root-feeding nematodes per unit root biomass than related natives. The range expanders showed resistance against rather than tolerance for root-feeding nematodes from the new range. On the other hand, the overall taxonomic and functional nematode community composition was influenced by plant species rather than by plant origin. The plant identity effects declined with trophic position of nematodes in the soil food web, as plant feeders were influenced more than other feeding guilds. We conclude that range-expanding plant species can have fewer root-feeding nematodes per unit root biomass than related natives, but that the taxonomic and functional nematode community composition is determined more by plant identity than by plant origin. Plant species identity effects decreased with trophic position of nematodes in the soil food web.

Due to climate warming many plant species currently shift ranges to higher latitudes (Bakkenes et al. 2002, Walther et al. 2002, Parmesan and Yohe 2003). When plant species shift range faster than organisms occupying higher trophic levels in the aboveground and belowground food web, range shifts may disrupt the original trophic interactions (Van der Putten et al. 2004, Menendez et al. 2008, Van Grunsven et al. 2010). In their newly invaded range the range-expanding plant species can be considered exotic. Some of these range shifters originate from other continents, whereas others are native in lower latitude areas of the continent where range expansion takes place. All these plant species will establish new interactions with local above-ground and belowground biota. However, relatively little is known about the implications of plant range expansion for taxonomic and functional characteristics of food webs in the new range. Here, we study the response of nematodes from the invaded range to range expanding plant species in comparison with phylogenetically related plant species that are native in the invaded habitats.

Nematodes are important components of the soil food web, driving ecosystem processes (Ritz and Trudgill 1999, Yeates 1999, Griffiths et al. 2000), influencing crop production (Yeates et al. 2009) and plant community structure (Van der Putten and Van der Stoel 1998, Yeates 1999, Verschoor et al. 2002, De Deyn et al. 2003). Besides root-feeding nematodes, there are nematodes feeding on bacteria, protozoa, fungi, mites and other soil nematodes (Yeates et al. 1993a). As nematodes are predominantly soil inhabitants, they are supposed to have less dispersal capacity and to respond less to climate warming by range expansion than many plant species (Berg et al. 2010). Thus, when analyzing nematode community composition, an impression can be obtained of responses of the second, third, and higher

trophic levels in the soil food web to range expanding plant species. Previous studies on plants influencing nematode community composition have focused mostly on the relationship with plant species diversity and identity (Korthals et al. 2001, Hedlund et al. 2003, Wardle et al. 2003, De Deyn et al. 2004, Viketoft et al. 2005, Eisenhauer et al. 2010) and less on effects of exotic plant species (Van der Putten et al. 2005). We investigated the taxonomic and functional community composition of nematodes in the root zone of range expanding versus related native plant species and compared effects of plant origin with plant species identity.

In some studies, important effects were found of plant identity on multiple trophic levels in the soil food web and ecosystem processes (Wardle et al. 1999, 2003, Porazinska et al. 2003). Primary consumers in the soil, such as microbes and root feeders can be more responsive to plant species composition than secondary (microbial feeders) and tertiary consumers (predators) (Wardle et al. 2003, Viketoft et al. 2009). Higher-level consumers on average are less diverse, less abundant, and under stronger anthropogenic pressure than primary producers (Duffy 2002). This applies to a wide variety of above- and belowground biota (Cardinale et al. 2006, Scherber et al. 2010), including nematodes at various trophic levels in the soil food web (Scherber et al. 2010).

A reduced diversity (Brinkman et al. 2005) or density (De Rooij-Van der Goes 1995, De la Peña et al. 2008) of root-feeding nematodes can result in a lower feeding pressure on range-expanding plant species. This might explain why range expanding plants receive less negative feedback effects from the soil community of invaded habitats than phylogenetically related native plant species (Van Grunsven et al. 2007, Engelkes et al. 2008). Therefore, in the present study we also analyzed the relationship between the numbers of root-feeding nematodes per unit root biomass and the plant-soil feedback effects of range-expanding plants and plant species that are native in the invaded range. When plants perform well while suppressing root-feeding nematodes, they can be considered resistant, but it is also possible that plants perform well under high nematode densities (Trudgill 1991). In that case range-expanding plants can be considered tolerant (Strauss and Agrawal 1999). Besides these direct interactions of range expanding and native plant species with root-feeding nematodes, we also examined indirect interactions with nematodes at higher trophic levels in the soil food web. Exotic plants have been shown to alter soil biological and chemical characteristics in the rhizosphere, which can influence the structure of the microbial community (Kourtev et al. 2003). This could have an indirect effect on bacterivorous- and fungivorous nematode community and their predators, through altered resource quality and quantity (Saj et al. 2009).

We tested the hypothesis that range-expanding plant species have fewer root-feeding nematodes per unit root biomass and that the range-expanding plant species affect the taxonomic and functional composition of the nematode community different from phylogenetically related native plants. We compared plant origin effects with effects of plant species identity. We expected to find the strongest plant origin or plant identity effects on the plant feeders, and diminishing effects with increasing trophic position of nematodes in the soil food web.

Material and methods

In order to determine the effects of plant origin and plant identity, we performed a growth experiment with range-expanding plant species and phylogenetically related natives using soil inocula from the invaded habitat. At the end of the growth experiment, the taxonomic and functional composition of the nematode community was analyzed in several ways. We compared the nematode abundance of the different feeding groups (root feeders, fungal feeders and bacterial feeders, omnivores and carnivores) and of feeding types within the root feeders: root associates (least specialized), ectoparasites (generally with wide host ranges), semi-endoparasites, migratory endoparasites (more specialized, but still often polyphagous) and sedentary endoparasites (containing both polyphagous species (e.g. *Meloidogyne* spp) and more host-specific species (e.g. *Globodera* and *Heterodera* spp.) (Trudgill 1991, Yeates et al. 1993a). Functional diversity of the nematode community was analyzed by diversity indices developed for nematode community studies (Ferris et al. 2001).

Plant species, seeds and soil

We selected recently introduced range-expanding plant species and phylogenetically related natives using the National Standard List of the Dutch flora (FLORON 2003) and the updated version of this list (Tamis 2005). In this database, the Netherlands is divided in grid cells of one square kilometer. Field surveys have been made to determine whether a grid cell is occupied by a certain plant species or not. We used a scale ranging from zero (no national grid cell occupied) to ten (all national grid cells occupied) (Tamis 2005). We analyzed grid cell abundances between 1902–1950, between 1975–1988 and between 1988–2000 using four criteria: 1) range-expanding plants should have established in the Netherlands in the 20th century, and 2) they should have increased in national grid cell abundance in the last decades of the 20th century in order to have been able to respond positively to climate warming (Tamis 2005), 3) they should have related native species in the same genus and 4) all native and range-expanding plant species occur in the same habitat (riparian areas in the Rhine Delta). These four criteria enabled us to produce a phylogenetically controlled comparison of native and recently invading range-expanding plant species (Agrawal et al. 2005, Funk and Vitousek 2007) sharing the same habitat. Of those plant species, we collected seeds from the field or, in a few cases, purchased seeds through a specialized seed supplier who collects seeds from local plant populations. Some species did not germinate, which left us with fifteen plant species in total, six range expanders and nine natives.

Five out of the six range-expanding plant species belonged to the family *Asteraceae* (*Bidens frondosa, Senecio inaquidens, Artemisia biennis, Solidago gigantea* and *Centaurea stoebe)* and one to the *Apiaceae* (*Angelica archangelica*). Three range-expanding plant species originated from Eurasia: *A. biennis* (north Asia)*, C. stoebe* (central Europe) and *A. archangelica* (northeast Europe). The other three range expanders originated from other continents: *Bidens frondosa* (North America)*, Senecio inaquidens* (South Africa) and *Solidago*

gigantea (North America). We included nine related native plant species; for three genera we included two native plant species (*B. cernua, B. tripartita, S. viscosus, S. vulgaris, A. vulgaris, S. virgaurea, C. cyanus, C. jacea* and *A. sylvestris*).

Prior to germination, all seeds were surface sterilized using 100 ml diluted Loda Bleech (1% hypochlorid solution) for several minutes and then rinsing by demineralized water. Seeds were germinated on glass beads with demineralized water at day conditions of 14 h at 20°C and night conditions of 10 h at 10°C for species that flower in early season, or days of 16 h at 25°C and nights of 8 h at 15°C for species that flower in late season. Seedlings were placed at 4°C in light until all species had germinated and the experiment could start. After transplantation, dead seedlings were replaced until the third week of the experiment.

We collected soil from five random sites in the Millingerwaard, (the Netherlands; 51°87'N, 6°01'E), a nature reserve in the Geldersche Poort region where all range expanding and related native plant species co-occur. The soil samples were homogenized, as we were not interested in spatial variation in the field, and inoculated into a sterilized sandy loam soil from Mossel, Planken Wambuis (52°06'N, 5°75'E). The soil sterilization was carried out by gamma radiation (25 kGray), which eliminated all soil biota (Van der Putten et al. 2007).

Experimental setup

Phase I: soil conditioning
Seventy-five pots of 4 l were filled with a 5:1 mixture of sterilized soil and inoculum soil. We established five replicate pots of each plant species (six range expanders and nine natives, resulting in 75 pots). Each pot received four seedlings to promote soil conditioning and the experiment was carried out in a greenhouse under controlled conditions (60% RH, day: $21 \pm 2°C$; night $16 \pm 2°C$). Additional light was provided by metal halide lamps (225 μmol $^{-1}$ m^{-2} PAR) to ensure a minimum light intensity during the day. Plants were provided with demineralized water every second day to compensate for water uptake and evapotranspiration. Every week, initial soil moisture level was reset by weighing. In order to prevent plants from nutrient depletion, Hoagland solution was added at a rate of 25 ml of 0.5 strength week^{-1}, which is a dosage that does not prevent the establishment of arbuscular mycorrhizal fungi (Van der Putten et al. 2007). After eight weeks of growth, the plants were harvested and the conditioned soils were used for a second growth phase to test the feedback effect of their own soil community.

Phase II: soil feedback
The conditioned soil from every pot in phase I of the growth experiment was split into two halves. One half was placed in a 1.3 l pot to be called 'own' soil. The other half was used to create control soils. The control soil of every plant species contained soil conditioned by all other plant species, excluding plants from the same genus. Because all controls shared soil from five genera, we assumed initial soil nutrient conditions to be similar for all control pots. We established five replicates with own and five with control soils (resulting in 150 pots): each replicate was made from a separate replicate from the soil conditioning phase. We planted three seedlings per pot.

Water, light and nutrient conditions were supplied as in phase I, except that 10 ml of 0.5 Hoagland solution was added on a weekly basis because the pots were smaller, there were fewer plants and there was less water loss from the soil surface compared to the 4-l pots. After week 10, when most nematode species should have had at least one reproduction cycle the pots were harvested. From half of the soil the roots were collected, air-dried at 70°C for 48 h and weighed. The other half of the soil and roots was used for nematode extraction, and thereafter the roots were air-dried and weighed. We calculated the soil feedback as ln(total biomass in own soil)/(total biomass in control soil), which provides symmetric positive and negative values (Petermann et al. 2008, Brinkman et al. 2010).

Nematode collection

Nematodes were extracted from those pots that contained own soil using Oostenbrink elutriators (Oostenbrink 1960). The suspensions with nematodes were then led through one 75 μm sieve and three 45 μm sieves. The material, including nematodes collected from the 75 and 45 μm sieves was transferred to a double cotton filter on a sieve in a dish with a layer of tap water (Oostenbrink 1960). The nematodes were allowed to migrate through the filter into the water for 24 h at room temperature, which resulted in relatively clean suspensions for nematode counting. Suspensions were stored at 4°C until they were fixated with hot paraffin. Root-inhabiting nematodes were collected by placing the roots in a mistifier. After nematode extraction for 48 h in the mistifier the roots were dried and weighted. The total numbers of nematodes in the root and soil samples were counted, identified to genus or family level using a reverse light microscope and categorized into feeding guilds according to Bongers (1988) and Yeates et al. (1993a). The root feeders were further subdivided into five feeding types: ectoparasites, semi-endoparasites, migratory endoparasites and sedentary endoparasites (Yeates et al. 1993a). Epidermis or root hair feeders were classified as plant-associated nematodes (Yeates et al. 1993b). Total numbers of nematodes were expressed as numbers per gram root biomass and numbers per pot.

Calculations and data analyses

The number of nematode taxa as used in Table 1 consists of mainly genera and some families and corresponds with the taxa mentioned in Fig. 2, except for the five feeding types of the plant parasitic nematodes used. These were split into genera and one family (*Criconematidae*) (Table 1). Simpson's evenness was calculated to determine effects of plant identity on nematode taxonomic diversity (Magurran 2004). Plant effects on the nematode community structure were assessed via the Structure index (SI) (Ferris et al. 2001) and the Maturity index (MI) (Bongers 1990) both indicating aspects of functional diversity. SI and MI are calculated as weighted abundances of nematodes in different feeding guilds, taking their position on the coloniser–persister (cp) scale into account. This scale ranges from 1 to 5; cp-1 nematodes are the enrichment opportunists with short generation times and a high reproduction rate, while cp-5 nematodes do not tolerate disturbance but have a long life span and low reproduction rate

Table 1. Functional and taxonomic nematode diversity in pots with different plant species of native and range expanding origin (+identifies range expanding plant species). Different letters denote differences at the p < 0.05 level.

Species	Taxonomic diversity		Functional diversity	
	Number of taxa	Simpson evenness	Structure index	Maturity index
Angelica archangelica+	26.4 ab	0.025 a	84.8 b	3.14 b
Angelica sylvestris	24.3 ab	0.031 ab	81.0 ab	2.94 ab
Bidens tripartita	23.0 ab	0.028 ab	86.4 b	3.23 b
Bidens frondosa+	20.6 a	0.024 a	83.6 b	3.18 b
Bidens cernua	22.3 ab	0.029 ab	82.9 b	2.95 ab
Senecio viscosus	26.3 ab	0.032 ab	71.6 ab	2.75 ab
Senecio inaequidens+	23.8 ab	0.037 b	71.8 ab	2.82 ab
Senecio vulgaris	24.0 ab	0.032 ab	49.5 a	2.25 a
Artemisia vulgaris	25.2 ab	0.033 ab	85.2 b	3.12 b
Artemisia biennis+	26.5 ab	0.027 ab	75.9 ab	2.96 ab
Solidago virgaurea	23.8 ab	0.034 ab	84.6 b	2.46 ab
Solidago gigantea+	22.3 ab	0.035 ab	64.6 ab	2.44 ab
Centaurea stoebe+	25.0 ab	0.034 ab	87.3 b	3.15 b
Centaurea jacea	28.0 b	0.032 ab	85.8 b	3.07 ab
Centaurea cyanus	22.8 ab	0.026 ab	78.0 ab	3.05 ab
Origin				
Native	24.4 a	0.031 a	77.9 a	2.87 a
Range expander	24.1 a	0.030 a	79.1 a	2.99 a

(Bongers and Bongers 1998). The SI gives a value between 0 and 100 expressing the percentage of disturbance sensitive nematodes (mainly cp-3 values and onwards) per total nematodes (of all cp-values). The MI is calculated as the weighted mean of all cp-values from all taxa.

We analyzed the differences between origin and between plant species within origin using a nested ANOVA. All variables were considered fixed, including species, because we used all plant species that were available in our experimental site (Engelkes et al. 2008). We performed Sign tests to compare numbers of nematodes between natives and range expanders. These non-parametric Sign tests are considered to be insensitive low-power tests, which provide strong evidence that the main results from the overall analysis hold very generally across the plant species and nematode taxa within feeding guild (Siegel and Castellan 1988). In order to test for a relationship between numbers of plant parasitic nematode per gram root and soil feedback a Spearman rank order correlation was performed with the species as replicate units. The same test was used to examine the relationship between omni-carnivore nematode numbers and the fungivorous, bacterivorous and root feeding nematodes with plant species as unit of replication. The plant root biomass against the number of plant-feeding nematodes was also tested by this approach. The effect of plant species identity on the nematode taxonomic (taxa, Simpson's evenness) and functional (SI, MI) diversity was tested by nested ANOVA where plant species were nested within origin. To compare nematode diversity among plant species Tukey HSD post-hoc tests were performed. All statistical analyses were carried out in STATISTICA 9 (StatSoft, Inc. 2009). To improve normality and homogeneity of variances of residuals among groups defined by the statistical models, numbers of root-feeders, fungivorous, bacterivorous and omni-carnivorous nematodes were natural log-transformed (x + 1) prior to analysis.

Results

There were no differences in numbers of root-feeding nematodes per pot between range expanding and native plants ($F_{1,51} = 1.19$, p = 0.177) (Fig. 1a). However, because range-expanding plants overall had more root biomass than native plants ($F_{1,51} = 57.16$, p < 0.001; data not shown), they were exposed to fewer root-feeding nematodes per gram root biomass ($F_{1,51} = 15.93$, p < 0.001) (Fig. 1e). Within seven out of nine genera comparisons the range expanders had fewer root-feeding nematodes per gram root than the native plants (unpubl.). This pattern also holds when considering the five feeding types (ectoparasites, semi-endoparasites, migratory endoparasites, sedentary endoparasites and plant-associated nematodes) separately. When considering the responses of the five feeding types to the nine plant genera separately, in 34 out of 45 (nine genera × five feeding types) comparisons there were fewer root feeders per gram root of the range expanders than of the natives. (Z = 3.28, p = 0.001). The results of these 45 comparisons are not totally independent from each other, because all five feeding types occurred in each of the nine comparisons. Nonetheless, the Sign test provides additional support to the ANOVA that roots of range-expanding plants were exposed to fewer root-feeding nematodes than roots of related natives.

There were more fungivorous nematodes per pot in range expanding than in native plants ($F_{1,51} = 4.48$, p = 0.039) (Fig. 1b). Due to more root biomass in range expanders than natives, range-expanding plants had fewer fungivorous nematodes per gram root than the native plant species ($F_{1,51} = 6.03$, p = 0.018) (Fig. 1f). When compared to the pattern observed for the root feeders, difference of numbers of fungivores per gram root biomass between range expanding and native plants was less pronounced. Within plant genus only in five out of nine genera the range expanders had fewer fungivorous nematodes per gram root than native
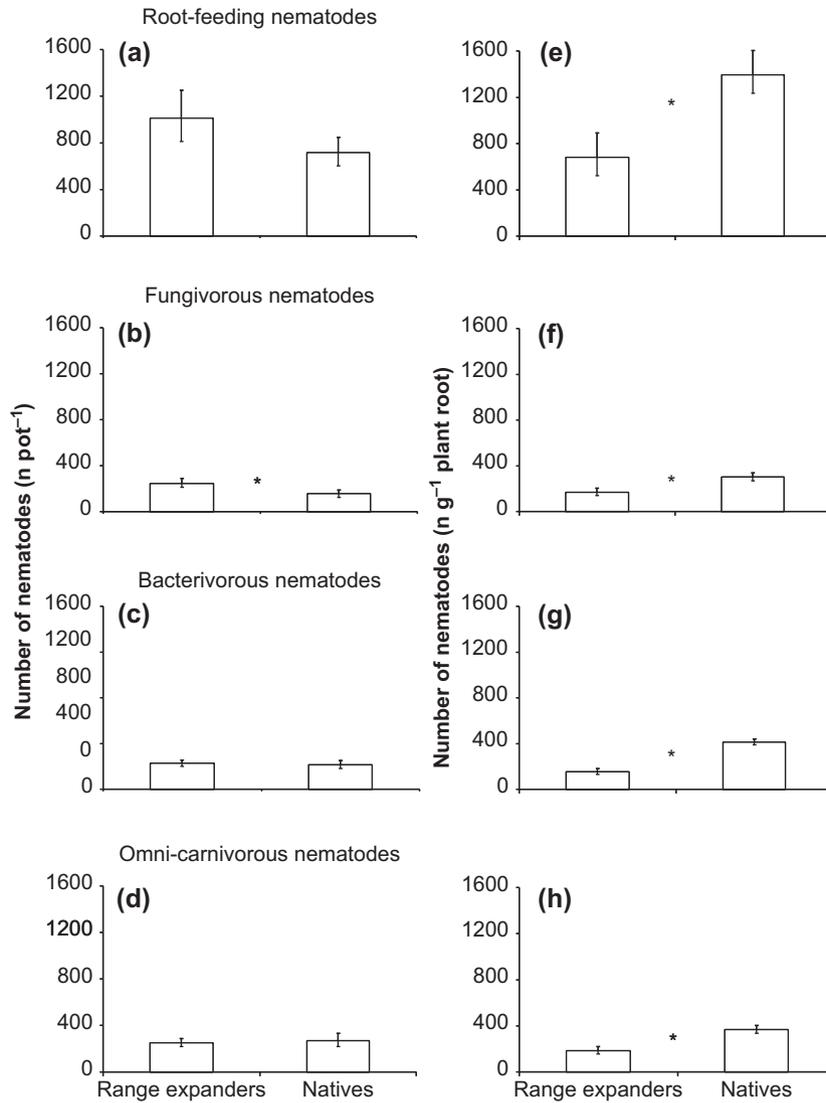
Figure 1. Panel (a–d) show mean nematode numbers per pot ± SE in native and range expanding plants. Panel (e–h) show mean nematode numbers per gram root biomass ± 1 SE in native and range expanding plants. Panel (a) and (e) represent root-feeding nematodes, (b) and (f) fungivorous nematodes, (c) and (g) bacterivorous nematodes and (d) and (h) omni-carnivorous nematodes. Bars show back-transformed means of natural log (x + 1) transformed data. * indicates significant differences at $p < 0.05$.

plants. Considering the five genera of fungivorous nematodes separately the Sign test gave no significant deviation from what could be expected by chance (unpubl.).

There were no differences in numbers of bacterivorous nematodes per pot between range expanding and native plants ($F_{1,51} = 0.08$, $p = 0.779$) (Fig. 1c). Since range expanders had more root biomass than natives, range expanders had fewer bacterivorous nematodes per gram root biomass than native plants ($F_{1,51} = 24.93$, $p < 0.001$) (Fig. 1g). Within plant genus, in seven out of nine genera the range expanders had fewer bactivorous nematodes per gram root than native plant species. Within the sixteen taxa of bacterivorous nematodes in 68 out of 111 comparisons (nine genera × 16 bacterivorous nematode taxa minus 33 taxa that were not present in all genera) there were fewer bacterivores per unit root biomass in the range expanders than in the natives. A Sign test made clear that this difference between native and range-expanding plant species is significantly greater than would be expected by chance ($Z = 3.23$, $p = 0.001$).

There were no differences in numbers of omni-carnivorous nematodes per pot between range expanding and native plants ($F_{1,51} = 0.24$, $p = 0.627$) (Fig. 1d). Since range expanders had more root biomass than natives, there were fewer omni-carnivorous nematodes per gram root biomass in the range expanders than in native plants ($F_{1,51} = 7.75$, $p = 0.008$) (Fig. 1h). When compared within plant genus, in six out of nine nematode genera range expanders had fewer omni-carnivorous nematodes than native plants. Within the thirteen taxa of omni-carnivorous nematodes in 63 out of 96 comparisons (nine genera × 13 omni-carnivorous nematode taxa minus 21 taxa that were not represented in all genera) range expanders had fewer omni-carnivores than the natives. A Sign test made clear that this difference between native and range-expanding plant species is significantly greater than would be expected by chance ($Z = 3.16$, $p = 0.002$). When we consider all feeding guilds of nematodes, we found the same trend in all guilds. Range expanders had fewer nematodes per gram root than native plants.

This was not only caused by the higher root biomass of range expanders since the root biomass did not correlate with the root-feeding nematodes (n = 27, R^2 = –0.258, p = 0.195) (unpubl.). Also the root biomass of the native plants did not correlate with the root-feeding nematodes (n = 39, R^2 = 0.193, p = 0.239) (unpubl.).

Overall, root-feeding nematodes were the most numerous nematode guild (Fig. 2). Sedentary endoparasitic nematodes (Fig. 2a) represented the majority of the plant parasites in most plant species except for *S. viscosus*, *S. inaequidens* and both the *Solidago* species. Fungivorous nematodes were represented in lower numbers (Fig. 2b), although they were relatively abundant in *S. viscosus* and *S. vulgaris*. Most fungivorous nematodes belonged to the genus *Aphelenchus*. The bacterivorous nematodes also occurred in smaller numbers than the plant parasites and were represented by a variety of different taxa (Fig. 2c). *Eucephalobus*, *Mesorhabditis* and *Acrobeloides* were the dominant bacterivorous genera. The omni-carnivorous nematodes were also represented by a broader variety of taxa of which *Microdorylaimus*, *Eudorylaimus*, *Thonus* and the *Mononchidae* were the best represented taxa (Fig. 2d). Overall, numbers of omni-carnivorous nematode per gram root biomass had a significant positive relationship with root feeders (n = 15, R^2 = 0.761, p = 0.001), fungivores (n = 15, R^2 = 0.793, p < 0.001) and bacterivores (n = 15, R^2 = 0.861, p < 0.001) (Fig. 3). Plant species that had few root feeders per gram root also had few fungivores (although not significant) (n = 15, R^2 = 0.468, p = 0.079), bacterivores (n = 15, R^2 = 0.564, p = 0.028) and omni-carnivores (n = 15, R^2 = 0.761, p = 0.001) (Fig. 3). When analyzed per pot, there was a tendency that plant species having most root-feeding nematode also had most fungivores (n = 15, R^2 = –0.157, p = 0.576), bacterivores (n = 15, R^2 = –0.45, p = 0.092) and omni-carnivores (n = 15, R^2 = 0.5, p = 0.058) (unpubl.).

The taxonomic and functional diversity of nematode communities of range-expanding plants did not differ from natives (Table 1). However, there were some significant differences among plant species, mainly because *B. frondosa* had fewer nematode taxa than *C. cyanus* (Table 1). Simpson evenness of the nematode community of *B. frondosa* and *A. archangelica* was significantly lower than of *S. inaequidens* (Table 1). *S. vulgaris* had a significantly lower SI than *A. archangelica*, *B. tripartita*, *B. frondosa*, *B. cernua*, *A. vulgaris*, *S. virgaurea*, *C. stoebe* and *C. jacea* (Table 1). *S. vulgaris* also had a significantly lower MI than *A. archangelica*, *B. tripartita*, *B. frondosa*, *A. vulgaris* and *C. stoebe* (Table 1).

There was no relationship between soil feedback and numbers of root-feeding nematodes per gram root (n = 15, R^2 = –0.1571, p = 0.576) (Fig. 4). However, the data reveal some interesting patterns. In Fig. 4, three plant species (*A. sylvestris*, *A. archangelica* and *S. gigantea*) have a positive soil feedback and relative few plant root-feeding nematodes per gram root, suggesting that these plant species are resistant against nematodes. *Bidens cernua* showed tolerance, because it had a positive soil feedback while exposed to high numbers of root-feeding nematodes per gram root (Fig. 4). *Bidens frondosa*, *B. tripartita* and *C. cyanus* had negative soil feedback coinciding with high amounts of root-feeding nematodes. These plants may be susceptible to root-feeding nematodes (Fig. 4). Most other plant species in our experiment had a

negative soil feedback while being exposed to relatively few root-feeding nematodes per gram root (Fig. 4). In those cases root-feeding nematodes might have been contributing less to the negative soil feedback effects.

Discussion

Range-expanding plant species had fewer root-feeding nematodes per gram root biomass than phylogenetically related plant species that are native in the invaded habitat. The same pattern emerged for fungivorous nematodes, bacterivorous nematodes, and omni-carnivores (Fig. 1e–h). However, the total amount of root-feeding nematodes per pot did not differ from pots with native plants, which is consistent with observations made by Porazinska et al. (2003). Since range expanders produced more root biomass per pot than their native counterparts, they had a lower exposure to nematodes per gram root biomass. During the 10 weeks of plant growth there should have been ample time for ectoparasitic root-feeding nematodes to have responded to the plant species by multiplication (De Rooij-Van der Goes 1995). On the other hand, the experimental period may have been relatively short for the sedentary endoparasites, some of which need up to 12 weeks to produce new cysts (Brinkman et al. 2005). As differences between range expanding and native plants were quite consistent across the various types of root-feeding nematodes, our results suggest that the range-expanding plants promoted numbers of root-feeding nematodes less than related natives. Alternatively, it may be that nematode numbers in the rhizosphere of range-expanding plants are more controlled by natural enemies than in the rhizosphere of natives. This possibility is less likely, as it would require that the range expanders are able to develop novel interactions with higher trophic level organisms (Verhoeven et al. 2009).

Although range expanders overall had fewer nematodes per gram root biomass than native plant species, plant identity appeared to be a stronger determinant of the numbers of root-feeding nematodes than plant origin. Within some genera, there was relatively little variation between species, such as was the case for *Bidens* spp., whereas in other genera, for example *Centaurea* spp., there was considerable variation among species (Fig. 2). Therefore, both plant genus and plant species identity may determine the root-feeding nematode community composition more than plant origin. Effects of plant identity on the nematode community were also found by Yeates (1999), De Deyn et al. (2004) and Viketoft et al. (2005), but none of these studies has considered exotic or range-expanding plant species.

A study on the foredune grass *Ammophila arenaria* in its non-native range showed that the grass had fewer specialized root-feeding nematode taxa than native grasses (Van der Putten et al. 2005). In our experiment sedentary endoparasites, which have relatively specialized interactions with their host plants, represented the majority of the root-feeding nematodes (Fig. 2). However, most these sedentary nematodes were *Meloidogyne* spp., which is a genus that contains relatively polyphagous species that can make good use of dicotyledon plants (De Deyn et al. 2007). *Meloidogyne* spp. and other sedentary endoparasites were practically absent in *S. inaequidens* and *S. gigantea*, as well as in their related
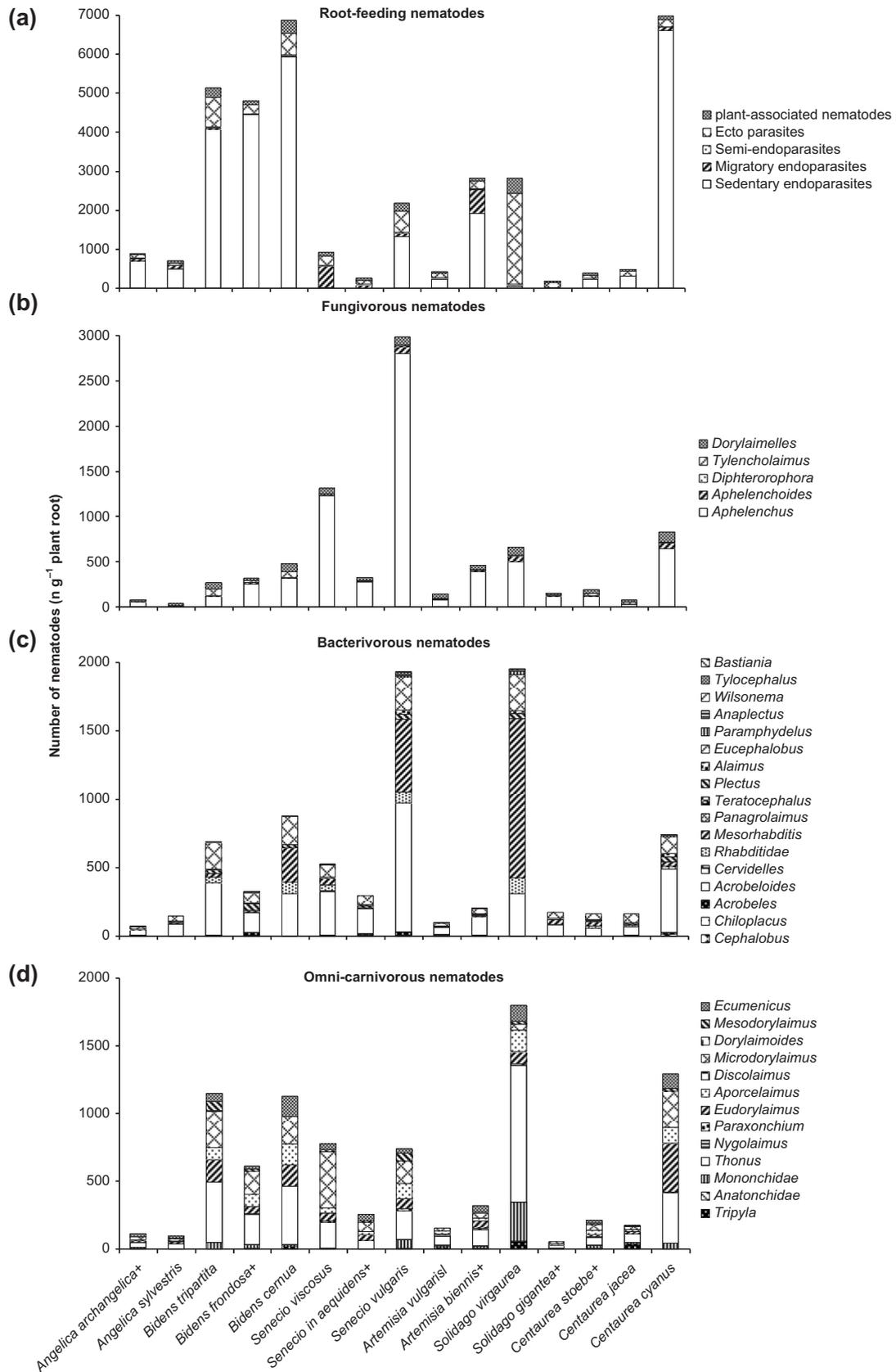
Figure 2. Panels show mean nematode numbers per gram root biomass in the different plant species of native and range expanding origin. Bars are divided into plant feeding types (panel a), or in family/genus level (panel b, c and d). +Indicates range expanding plant species.
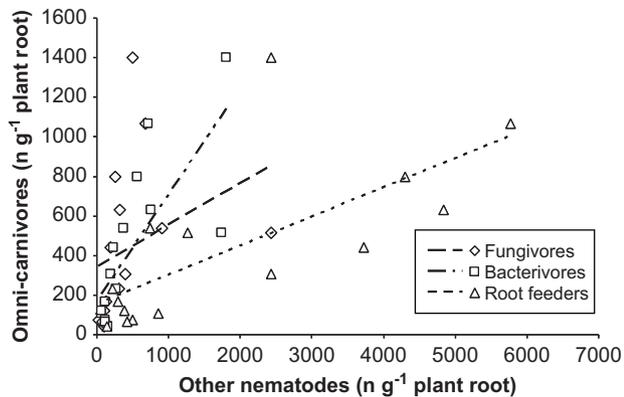
Figure 3. Relationship between the numbers of fungivores, bacterivores and root feeding nematodes per gram root biomass (x-axis) plotted against the number of omni-carnivore nematodes per gram root biomass (y-axis).

natives. In all other range-expanding plant species, there were high numbers of *Meloidogyne* spp. present, suggesting that these polyphagous root feeders perform relatively well on range-expanding plant species. On the other hand, more specialized sedentary endoparasites such as *Heterodera* were practically absent from all plant roots in our experiment, so that most feeding pressure will have been due to *Meloidogyne* spp.

Numbers of fungivorous nematodes were relatively high compared to other studies (Bardgett and Cook 1998). The fungivores either were growing on fungi that have rapidly colonized the sterilized soil during the conditioning phase, or they may have been feeding on e.g. root hairs. Numbers of bacterivorous nematodes were similar to the fungivorous nematodes and are likely determined by the resource quality of the bacteria, rather than the resource quantity of the bacteria. Thus the nutrient content of the microbes can influence the microbivorous nematode community composition (Mikola and Setälä 1998, Schmidt et al. 2000). Omni-carnivorous nematodes were represented in similar numbers as the fungivores and the bacterivores

and are determined by plant-feeding nematodes, fungivorous and bacterivorous nematodes as well as by the available microorganism community. Since many food sources are available for this group, the omni-carnivores seem to be the least responsive to the plant identity in the pot. Because of the duration of the experiment (10 weeks), we may have missed out on some taxa that have long reproduction cycles.

In order to obtain information on the effects of the range-expanding plant species on entire soil food webs, a more complete analysis of food web structure and functioning is required. Nevertheless, when we correlated the numbers of nematodes in the different feeding guilds to the numbers of omni-carnivorous nematodes bacterivorous nematodes turned out to explain more variation than fungivorous and root-feeding nematodes (Fig. 3). In spite of our partial analysis of the soil food web, the data suggest that effects of plant origin, plant genus or plant species can trickle up the belowground food chain through nematode predator–prey interactions, being stronger through the bacterial (and slightly less through the fungal) based energy channel than through the plant feeder based energy channel. However, as bacterivorous nematodes responded less strong to plant differences than root-feeding nematodes plant origin and identity effects on soil food web interactions were found to diminish with increasing trophic position of the nematodes. These results also suggest that effects of range expanders on the decomposition channel in the soil food web are less pronounced than on the root feeder-based channel. Plant origin effects were weaker than for example effects of plant diversity determined in other studies (De Deyn et al. 2004, Viketoft et al. 2005, Scherber et al. 2010, Eisenhauer et al. 2011).

There were no differences in taxonomic diversity and functional diversity between range expanders and native plant species (Table 1), however, there were some differences due to plant species identities (Table 1). Most plant species, however, did not show differences in the number of nematode taxa. In an outdoor mesocosm study that was running for several years, plant species-specific effects on
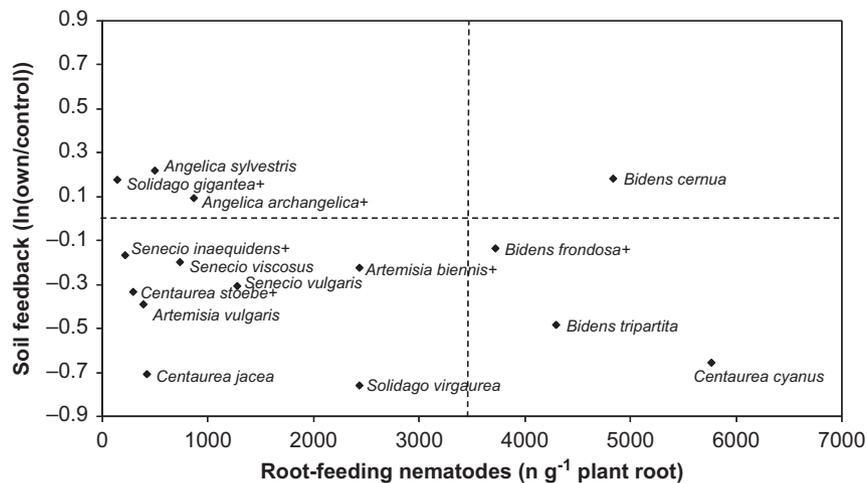

Figure 4. Mean numbers of root-feeding nematodes per gram root biomass (x-axis) plotted separately for each plant species against the soil feedback (y-axis). Soil-feedback was calculated for each replicate within plant species as ln(total biomass in own soil)/(total biomass in control soil). Plant species are divided in four quadrants. [+]Indicates range expanding plant species.

taxonomic diversity have been observed (De Deyn et al. 2004), so that such effects may require a longer duration of the experiment. There were some minor differences in Simpsons' eveness (Table 1) also implying that there were no major effects of plant species on the distribution of the nematode taxa and numbers per taxon. There were also some differences in functional diversity among plant species. Both SI and MI indicated that most nematodes in the community were somewhat disturbance sensitive, which would correspond to a grassland community with low disturbance frequency and a fungal-dominated decomposition channel (Ferris et al. 2001).

A number of plant species in our experiment had negative soil feedback while having relatively few root-feeding nematodes (Fig. 4). These plant species appear to be resistant to root-feeding nematodes, although these nematode numbers may also be low due to abundance control by competition or natural enemies (Piśkiewicz et al. 2008). Most likely, root-feeding nematodes did not play a major role in these negative soil feedback effects, but selective elimination and inoculation studies are needed in order to further determine the relationship between nematode numbers and growth reduction (De Rooij-Van der Goes 1995). Some other plant species had high amounts of root-feeding nematodes in combination with negative plant–soil feedback (Fig. 4). These plants appeared non-resistant and intolerant to root-feeding nematodes, but again selective elimination and inoculation studies are needed in order to determine the actual nematode effects on plant biomass production. Only one plant species had positive soil feedback in combination with high numbers of root-feeding nematodes (Fig. 4), which may point at tolerance (Ashton and Lerdau 2008). In any case, the range expanders did not reveal a specific strategy (tolerance or resistance), according to their scattered relationships between numbers of root-feeding nematodes and plant-soil feedback (Fig. 4). These different strategies of range-expanding plant species to root-feeding nematodes may affect the development of virulence (Trudgill 1991), which is the capacity of enemies to circumvent the resistance of the host species. Resistant plants tend to suppress the virulence of root-feeding nematodes while tolerant plants compensate biomass loss by compensatory growth (Trudgill 1991). We have performed the plant–soil feedback experiment using an own–foreign comparison, which usually results in less outspoken feedback values than when using non-sterilized and sterilized soils as a comparison (Kulmatiski et al. 2008, Brinkman et al. 2010). Our observation that range-expanding plant species may differ in their interaction with root-feeding nematodes is not influenced by the way of testing plant–soil feedback effects; it only would have magnified the differences on the y-axis of Fig. 4.

We conclude that range-expanding plant species are exposed to fewer root-feeding nematodes per unit dry root mass compared to their native congeners. However, the effects of range expanding plant species on the nematode feeding guilds at higher trophic positions in the soil food web were less strong than for root feeders. This suggests that effects of range-expanding plants diminish with trophic position of nematodes in the soil food web. Correlations between predator nematodes and their prey suggested that effects of range-expanding plant species may trickle up in the soil food web. This applies to both plant species originating from the same and other continents. The latter are being considered in most studies on invasive exotic plant species. Plant genus or plant species-specific effects on taxonomic and functional nematode community composition were stronger than plant origin effects.

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