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Above- and Belowground Trophic Interactions on Creeping Thistle *(Cirsium arvense)* in High- and Low-Diversity Plant Communities: Potential for Biotic Resistance?

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Abstract: **The capacity of local communities to control introduced plants is called biotic resistance. Biotic resistance has been almost exclusively tested for plant competition and aboveground herbivores and pathogens, while neglecting root herbivores and soil pathogens. Here, we present biotic resistance by above- and belowground herbivores in concert, and relate the abundance of the plant enemies to the species diversity of the local plant communities. The study was carried out in a 7-year-old biodiversity field experiment. We used creeping thistle *(Cirsium arvense)* as a model, and quantified sap-sucking herbivores: aboveground aphids, their antagonists, and root-feeding nematodes. As plant diversity treatments, we used field plots sown with high (15 plant species, HSD) or low (4 plant species, LSD) diverse seed mixtures in 1996 and that were not weeded. Creeping thistle became established spontaneously at the start of the experiment. In 2002, in HSD plots, 90% of the plant community was made up by 11 species, compared to seven species in LSD plots. No differences were found for *C. arvense* abundance or biomass. Aboveground, three aphid species were found on *C. arvense–Uroleucon cirsii, Aphis fabae,* and *Macrosiphum euphorbiae,* but the latter was found only in low densities. Significantly more aphid species were found on individual plants in HSD plots. Moreover, in HSD plots, on average 10% of aphids were parasitized, while no parasitism was observed in LSD plots. In the root zone of *C. arvense,* significantly more nematodes were found in HSD than in LSD plots, and a significantly higher proportion of those nematodes were plant parasites. The dominant plant parasitic nematode in both treatments was *Paratylenchus.* We conclude that biotic resistance by natural enemies may be enhanced by plant species diversity, but that above- and belowground sap-sucking herbivores do not necessarily have to respond similarly to the diversity of the surrounding plant community.**

Key words: *Aphis fabae, Macrosiphum euphorbiae,* nematode, *Paratylenchus, Uroleucon cirsii.*

Abbreviations:

HSD:	high-sown plant diversity
LSD:	low-sown plant diversity

Introduction

The"biotic resistance hypothesis" states that the establishment of an introduced species into a recipient community can be prevented by the negative impacts of interactions between native biota (Elton, 1958). These negative impacts may be realized not only via competition with local plant species (Davis et al., 2000), but also by herbivores or pathogens already present in the environment, that may act as natural enemies of the introduced plant species (Maron and Vila, 2001). Herbivore and pathogen abundance is generally thought to be related to the plant species diversity of the recipient community (e.g., Elton, 1958; Root, 1973; Southwood et al., 1979; May, 1990), suggesting that plant community diversity may influence the biotic resistance of that community because of a higher probability of harbouring effective natural enemies. Most of the data considered in formulating this viewpoint originates from aboveground interactions (Mitchell and Power, 2003). In this study, we consider the possibility of biotic resistance originating from both the above- and belowground natural enemies associated with the species diversity of the recipient vegetation.

Plant diversity may influence aboveground herbivore abundance in different ways. For example, various studies have shown that more diverse plant communities support higher total numbers of aboveground insects, as well as more insect species (e.g., Siemann et al., 1998; Koricheva et al., 2000; Knops et al., 1999; Mulder et al., 1999; Haddad et al., 2001; Mortimer et al., 2002). This positive effect of plant species richness on insect herbivore abundance may be the result of greater plant biomass, greater availability of alternative plant resources, or a more complex vegetation structure (Haddad et al., 2001). Higher insect herbivore diversity may, in turn, lead to higher abundance of antagonists such as parasitoids and predators (Siemann et al., 1998). Increasing plant diversity may also increase the diversity or abundance of higher trophic levels directly, by increasing the diversity of floral resources used by the antagonists for nutrients, energy, and other purposes (Root, 1973; Jervis et al., 1993).

The "resource concentration hypothesis", on the other hand, raises the possibility of plant diversity having a negative effect on aboveground herbivore abundance. The hypothesis predicts that communities with fewer plant species will have higher abundances of the preferred host plant species and therefore higher abundances of herbivores (Root, 1973).

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Effects of plant species diversity on the diversity or abundance of soil-dwelling organisms are relatively unknown (Wardle et al., 1999; Hooper et al., 2000; Korthals et al., 2001). Soil-borne organisms, however, exert important control on the composition of plant communities (e.g., De Deyn et al., 2003). Higher plant diversity may influence soil biota by increasing the diversity of litter, the heterogeneity of soil microhabitats and energy and material flows from the vegetation to the soil (Spehn et al., 2000; Stephan et al., 2000; Wardle and Van der Putten, 2002). The few studies that have examined the influence of plant diversity on root herbivore abundance or diversity found little effect. This has been attributed to the generalist feeding behaviour and dispersal constraints of root herbivores (Wardle et al., 1999), to the delayed response of aboveground plant diversity on soil characteristics (Korthals et al., 2001), or to a dominance of plant-specific effects over plant diversity effects (Wardle and Van der Putten, 2002).

In this study we explore the interactions between creeping thistle (*Cirsium arvense* [L.]), aboveground insect herbivores (and their antagonists), and nematodes inhabiting the root zone. The plants were not sown, but had established in plots where plant species diversity had been manipulated at the start of land abandonment in 1996 (Van der Putten et al., 2000; Lepš et al., 2001). In contrast to other biodiversity experiments (e.g. Tilman et al.,1996; Hector et al., 1999), experimental plots have not been weeded to maintain original species numbers. *C. arvense* is an important weed of pasture, arable land and conservation areas (Harris and Shorthouse, 1996). It is a clonal perennial species that can express strong vegetative reproduction by means of its extensive root system (Edwards et al., 2000). Here, we report differences in plant diversity occurring 6 years after initiation of the experiment and describe the performance of *C. arvense,* as well as the associated diversity and abundance of insect herbivores and parasitoids aboveground and nematodes belowground. We consider whether differences in the number and abundance of above- and belowground natural enemies, and the degree of parasitization aboveground, may be related directly, or indirectly via changes in soil characteristics, to the plant diversity treatments.

Materials and Methods

Site description and experimental design

The experimental field was created in spring 1996, on former arable land where maize had been grown in a rotation with sugar beet, potatoes, barley, and, occasionally, *Lolium perenne.* The site was situated on sandy loam soil with the following particle size distribution: < 2 µm 3.4%; 2 – 63 µm 17.3%; > 63 µm 79.7%.

The experiment compared sowing of low (4) and high (15) species diversity seed mixtures of mid-successional plant species, natural plant colonization, and continued agriculture, using a randomized block design with five blocks. Each replicate plot measured 10 × 10 m^2 and each block contained one replicate of each treatment. Within each block the plots were separated by 2-m-wide paths.

Table 1 Plant species sown in the different high-sown diversity (HSD) and low-sown diversity (LSD) plots. All five HSD replicate plots were sown with the same mixture of 15 plants, while each LSD plot was sown with a different subsample of the HSD mixture

	High-sown diversity	Low-sown diversity				
		1	2	3	4	5
Grasses	*Festuca rubra*	×	×			
	Phleum pratense	×				×
	Poa pratensis		×	×		
	Agrostis capillaris				×	×
	Anthoxanthum odoratum			×	×	
Legumes	*Lotus corniculatus*	×				
	Trifolium pratense			×		
	Trifolium dubium				×	
	Trifolium arvense					×
	Vicia cracca		×			
Other Forbs	*Plantago lanceolata*	×				
	Tanacetum vulgare			×		
	Hypericum perforatum				×	
	Hypochaeris radicata		×			
	Linaria vulgaris					×

In this study, we limit our comparison to the high-sown diversity (HSD) and low-sown diversity (LSD) treatments. All replicates of the high diversity plots were sown with the same combination of 15 species (5 grasses, 5 legumes, and 5 other forbs), while each of the low diversity replicates contained a different subset of the high diversity mixture (2 grasses, 1 legume, 1 other forb; Table **1**). The different subsets in the LSD replicates prevented confusion between the LSD treatment and plant species-specific traits (Van der Putten et al., 2000). The high and low diversity mixtures consisted of the same number of seeds (grasses: 2500 seeds m^{-2}; legumes 500 seeds m^{-2}; other forbs 500 seeds m^{-2}). Plots were not weeded and annually, in September, all plots were mown and the aboveground biomass removed. Further details are provided by Van der Putten et al. (2000).

Plot measurements

Vegetation recording: In early August 2002, plant species occurrence and abundance was recorded in 12 permanent quadrats of 1 m^2 each in each replicate plot of 100 m^2. For each plot, the mean number of plant species per m^2 was then calculated. The low diversity plots were dominated by a few plant species that were accompanied by a number of other plant species occurring at low densities. For each plot, we also ranked plant species according to their abundance and calculated the number of plant species that made up 90% (abundance) of the community. In each permanent quadrat, percentage cover of grasses, legumes and other forbs, and vegetation height were also estimated.

Aboveground biomass: In late August 2002, aboveground biomass was clipped at 2 cm above the soil surface in 0.25 × 0.25 m^2 subplots adjacent to each of the permanent quadrats. Plant material was oven dried at 75 °C and dry weight determined.

Table 2 Aboveground vegetation characteristics for high-sown diversity (HSD) and low-sown diversity (LSD) plots. Means are shown (± SE), and results of ANOVA. NS indicates not significantly different

Variable	HSD	LSD	$F_{1,4}$	p
Plant species (number m^{-2})	12.2 ± 0.4	10.1 ± 0.8	5.2	< 0.05
90% dominance (number m^{-2})	11.0 ± 0.6	7.2 ± 1.0	10.8	< 0.01
Grasses (%)	43.2 ± 3.4	45.9 ± 10.3	0.03	NS
Other forbs (%)	33.9 ± 3.8	37.2 ± 10.9	0.06	NS
Legumes (%)	22.9 ± 1.9	16.9 ± 4.7	1.7	NS
Height (cm)	67.8 ± 6.4	69.0 ± 12.3	0.5	NS
Total biomass (g m^{-2})	971.2 ± 105.6	732.8 ± 145.6	3.4	NS

Soil characteristics: At the start of the experiment, in April 1996, 1600 randomly selected cores of 3 cm diameter and 15 cm depth were taken from the experimental field (50 × 100 m^2). Chemical analyses were performed according to Novozamsky et al. (1984). In August 2002, soil chemical analyses were repeated. At this time, 24 similarly-sized cores were taken from each individual 10 × 10 m^2 plot following a stratified random sampling pattern. The soil was homogenized and chemical properties analysed. In 2002, nitrogen mineralization rates and short-term nitrification activity were also determined according to the procedure described in Malý et al. (2000).

Measurements on Cirsium arvense

The percentage cover of *C. arvense* was estimated in each permanent 1 m^2 quadrat in each plot in early August 2002. From these data the average percentage cover per plot was calculated. In each plot, at four pre-determined points, the nearest *C. arvense* plant was clipped 2 cm above the soil surface. Plant material was oven dried at 75 °C and weighed to estimate average aboveground biomass of a *C. arvense* plant.

Towards the middle of June 2002, at a fixed point in two randomly chosen permanent quadrats in each plot, the nearest *C. arvense* plant was selected and two soil cores (17 mm diameter, 10 cm depth) were taken from its root zone. The plant was then clipped 2 cm above the soil surface, placed in a sealed plastic bag and stored at 4 °C in the laboratory. For each plant, all aphids present were identified using a stereo-microscope and the abundance of aphids, the number of aphid species, and the number of parasitized aphids (mummies) determined. To estimate aphid infestation levels on *C. arvense,* in each plot all *C. arvense* plants were individually checked for aphid presence and the percentage of aphid infested plants calculated.

Nematode sampling

After the soil of the two cores (see above) had been homogenized, 100 g were sub-sampled for nematode extraction using an Oostenbrink elutriator (Oostenbrink, 1960). The total number of nematodes and the number of plant parasitic nematodes were counted, and expressed per g dry soil. The nematodes were then heat-killed and fixed in 4% formalin and plant parasitic nematodes were identified to genus, according to Bongers (1988), using a stereo microscope at 400 – 1000 ×.

Statistical analyses

Replicated measurements taken for any parameter within one plot are in fact pseudoreplicates and were, therefore, averaged prior to statistical analyses. Data were analysed using ANOVA, with treatment and block as main factors, with five replicates per treatment and one block containing one replicate of both treatments (LDS and HDS). Percentage data were arc-sine transformed before analyses to achieve a normal distribution. Linear regression analysis was used to test for relationships between plant parasitic nematode or aphid abundance and plant diversity.

Results

Plot measurements

Vegetation: There were no significant differences in plant height, or aboveground biomass, although, on average, there was a trend for lower biomass in LSD plots (Table **2**). As expected, there was more variation between replicates of LSD than between HSD plots; the LSD replicates were initially sown with mixtures of different subsets from the total species pool present in the HSD plots. Although the sown plant communities in the LSD and HSD plots were not maintained by hand weeding, 6 years after sowing HSD plots still contained significantly more plant species than LSD plots (Table **2**). The difference was even more apparent when the number of plant species that made up 90% cover of the community was compared (Table **2**). There were no significant differences in the mean percentage cover of different functional groups between the two diversity treatments. For HSD and LSD plots, the functional groups, however, consisted of different plant species (Table **3**). In HSD plots, on average 79% (SE 2%) of the vegetation cover consisted of species that were sown in 1996, while for LSD plots this was 64% (SE 5%). Nevertheless, the relative abundance of the individual sown plant species differed. In HSD plots *Festuca rubra, Lotus corniculatus* and, to a lesser extent, *Tanacetum vulgare* were abundant in all blocks. In LSD plots, dominance differed between replicates (Table **3**). Although most LSD plots were still dominated by sown species, in block 3 *Leucanthemum vulgare,* a species that had not been sown, had become the most abundant plant species (Table **3**).

Soil: In 2002, total P levels were significantly higher in LSD than in HSD plots (Table **4**). While there was no difference between LSD and HSD plots in total N, available NO_3 was significantly higher in HSD plots, possibly due to the higher relative abundance of legumes (Table **2**). Levels of available Na were also significantly higher in HSD plots. Relative to 1996, the amount of organic matter in the soil had increased in 2002, while pH and levels of total N and P and available P (Olson P) had decreased since the start of the experiment (Table **4**).

Measurements on Cirsium arvense

The percentage cover of *C. arvense* did not differ between HSD and LSD plots (mean [SE] HSD: 3.7% [0.6]; LSD: 6.4% [4.4]; $F_{1,4} = 0.12$; $p = 0.9$). Abundance varied from 1 to 6%, with the exception of the LSD Block 1 (24%; Table **3**). Aboveground biomass of individual plants did not differ between treatments (mean plant biomass [SE] HSD: 5.7 g [0.6]; LSD: 4.5 [0.9]; $F_{1,4} = 1.16$; $p = 0.4$).

Table 3 Estimated percentage cover in each of five replicate plots sown with 15 plant species (high-sown diversity) or 4 plant species (low-sown diversity). Plant species are shown with > 5% cover in at least one plot, independent of whether they have been sown or not sown. Sown plant species were sown in all high-sown diversity plots. For low-sown diversity plots the sown species are indicated by an asterisk (*)

	Plant species	Sown	High-sown diversity					Low-sown diversity				
			1	2	3	4	5	1	2	3	4	5
Grasses	*Agrostis capillaris*	+	0	0	0	3	2	0	0	2	41*	48*
	Anthoxanthum odoratum	+	1	2	3	3	2	0	0	12*	28*	1
	Festuca rubra	+	43	45	50	34	46	37*	80*	0	0	0
	Holcus lanatus	–	2	13	9	0	1	0	3	0	1	0
	Phleum pratense	+	1	3	3	6	2	5*	0	2	1	36*
	Poa pratensis	+	4	6	5	5	2	0	0*	13*	1	1
Legumes	*Lotus corniculatus*	+	33	26	25	30	31	57*	0	2	4	0
	Trifolium arvense	+	0	0	1	0	0	0	0	0	0	10*
	Trifolium pratense	+	0	0	0	0	0	0	2	5*	1	0
	Vicia cracca	+	1	0	2	2	2	0	17*	1	1	1
	Vicia hirsuta	–	0	0	1	0	0	0	5	0	19	0
Other forbs	*Achillea millefolium*	–	0	2	4	1	3	0	0	3	7	0
	Cirsium arvense	–	4	2	3	3	6	24	2	1	3	2
	Crepis capillaris	–	1	0	0	0	0	1	6	0	1	0
	Hypericum perforatum	+	2	2	4	2	5	0	0	0	7*	0
	Leucanthemum vulgare	–	2	3	1	1	3	0	0	60	2	1
	Linaria vulgaris	+	4	6	8	4	13	0	0	0	0	6*
	Plantago lanceolata	+	2	6	5	5	5	4*	1	0	1	1
	Senecio jacobea	–	22	5	8	3	13	36	7	4	7	4
	Tanacetum vulgare	+	16	4	17	5	8	0	2	55*	2	0

Table 4 Abiotic soil characteristics in 1996 and 2002. For 2002, means are shown (± SE) for high-sown diversity (HSD) and low-sown diversity (LSD) plots. Asterisks indicate a significant difference between HSD and LSD plots in 2002 based on ANOVA. nd indicates not determined in 1996

Soil characteristic	1996	2002		$F_{1,4}$	*p*
		HSD	LSD		
Organic matter (%)	4.5	5.0 ± 0.05	4.9 ± 0.08	0.2	NS
pH (H_2O)	6.4	6.1 ± 0.04	6.1 ± 0.09	0.5	NS
pH (KCl)	5.8	5.3 ± 0.05	5.3 ± 0.08	0.06	NS
pH ($CaCl_2$)	5.9	5.4 ± 0.04	5.4 ± 0.06	0.3	NS
$CaCO_3$ (%)	0.15	0.10 ± 0.02	0.04 ± 0.01	8.9	< 0.05
N total (mg kg^{-1})	1330	1297 ± 61	1291 ± 59	0.01	NS
N mineralization ($\mu g\ g^{-1}\ wk^{-1}$)	nd	3.4 ± 0.2	2.7 ± 0.4	4.8	NS
Olson P (mg kg^{-1})	110	82 ± 2	86 ± 2	1.5	NS
P total (mg kg^{-1})	1127	929 ± 26	1054 ± 42	45.3	< 0.01
0.01 M $CaCl_2$ extraction					
Available P (mg kg^{-1})	5.1	4.6 ± 0.4	5.4 ± 0.6	5.9	NS
Available Na (mg kg^{-1})	8.2	9.0 ± 0.7	6.7 ± 0.5	7.3	< 0.05
Available K (mg kg^{-1})	75.1	83.2 ± 4.1	100.6 ± 28.7	0.4	NS
Available Mg (mg kg^{-1})	62.9	58.2 ± 3.0	59.4 ± 6.0	0.1	NS
Available NH_4 (mg kg^{-1})	nd	4.9 ± 1.0	3.6 ± 0.4	1.5	NS
Available NO_3 (mg kg^{-1})	nd	7.6 ± 0.5	3.1 ± 1.8	8.9	< 0.05

Aphids: The percentage of aphid-infested *C. arvense* plants per plot did not differ between treatments, but for LSD, variation between plots was larger than for HSD (Fig. **1a**). This may be attributable to the plant characteristics of the surrounding community in LSD plots influencing aphid infestation levels on *C. arvense*. The average number of aphids per plant also did not differ between treatments ($F_{1,4} = 0.58$; $p = 0.5$; Fig. **1b**). Three different aphid species were found on *C. arvense*: *Uroleucon cirsii* (L.) (a specialist herbivore on *Cirsium*), *Aphis fabae cirsiiacanthoidis* (Scopoli) and *Macrosiphum euphorbiae* (Thomas), the latter two species are both generalists. Across both HSD and LSD plots, *U. cirsii* and *A. fabae cirsiiacanthoidis* occurred in densities of about 60 per plant; the density of *M. euphorbiae* was much lower (2 per plant) (Table **5**). While, for all three aphid species, average densities did not differ between treatments, the number of aphid species per plant was significantly higher in HSD plots ($F_{1,4} = 36.0$; $p < 0.01$; Fig. **1 c**). Parasitism, measured as the number of mummies, was only observed in HSD plots (Fig. **1 d**). On average, 10% of the aphids in HSD plots were parasitized.

There was a positive relationship between abundance of *C. arvense* and density of the specialist aphid *Uroleucon cirsii* ($F_{1,8} = 8.2$; $p < 0.05$; $R^2 = 0.50$), but not for the generalist aphid *Aphis fabae*. There was no relationship, however, between the abundance of either aphid species and plant diversity.

Nematodes: Significantly more nematodes occurred in the root zone of *C. arvense* plants in HSD than in LSD plots ($F_{1,4} = 9.19$; $p < 0.05$; Fig. **2 a**). In particular, the abundance of plant parasitic nematodes was higher in the HSD plots ($F_{1,4} = 59.37$; $p < 0.01$; Fig. **2 b**); there was also a significant difference in the proportion of plant parasitic nematodes between the two diversity treatments ($F_{1,4} = 12.58$; $p < 0.05$; Fig. **2 c**). The majority (> 80%) of plant parasitic nematodes belonged to the genus *Paratylenchus*. Nematodes belonging to the genera *Tylenchorhynchus*, and *Tylenchus* were also found but at relatively low densities (Table **5**). There were more *Pratylenchus* in HSD than in LSD plots (Table **5**). There was a positive relationship between the abundance of the dominant plant parasitic nematode *Paratylenchus* and the number of plant species per m^2 (Fig. **3**).

There were no major significant relationships between aphid and nematode densities. Nevertheless, while higher plant species diversity enhanced the numbers of plant parasitic nematodes in the soil, the number of plant parasitic nematodes, in turn, was positively related to the number of aphid species above ground ($F_{1,9} = 7.7$; $p < 0.05$; $R^2 = 0.49$).

Discussion

The results indicate that, in this study, *C. arvense* has a higher diversity and abundance of associated above- and belowground herbivores and enemies of the aphids aboveground in a more diverse plant community than in a plant community with lower species diversity. On *C. arvense* plants in HSD plots we found, on average, more aphid species and higher numbers of plant parasitic nematodes. Moreover, in the HSD plots, aphids were parasitized, whereas this was not observed at all in the LSD plots.

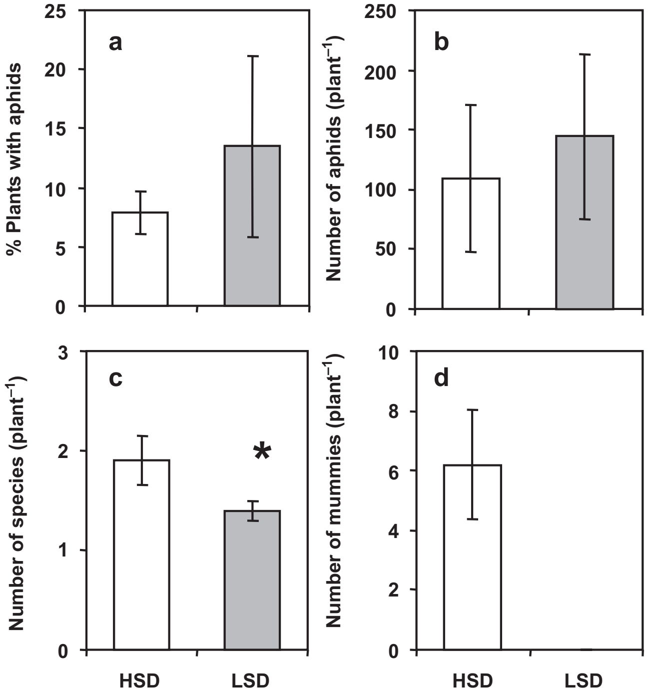

Fig. 1 Aboveground trophic interactions on *C. arvense*. Shown are mean (± SE) (**a**) percentage of aphid-attacked plants, (**b**) aphid number per plant, (**c**) aphid species per plant, and (**d**) the number of parasitized aphids (mummies) per plant, in plots sown in 1996 with 15 (HSD) or four (LSD) plant species. * $p < 0.05$.

Aboveground effects

Uroleucon cirsii is a specialist aphid on *Cirsium* species (Kluth et al., 2002). We did not observe differences in abundance for this aphid species between the two diversity treatments. The resource concentration hypothesis implies that herbivores, and in particular specialists, will be more abundant when the host plant is more abundant (Root, 1973; Koricheva et al., 2000). We observed a positive relationship between *U. cirsii* density per plant and the abundance of *C. arvense*. *C. arvense* abundance, however, appeared to be unrelated to the diversity of the surrounding community. We also did not find a direct effect of plant diversity treatments on aphid abundance, as observed by Koricheva et al. (2000). Both *Aphis fabae* and *Macrosiphum euphorbiae* are polyphagous herbivores and other studies have suggested that polyphagous herbivores should be relatively non-responsive to variation in plant diversity, as these herbivores depend less on concentration of one particu-

Table 5 Plant parasitic nematodes and aphid species found on *C. arvense* plants growing in high-sown diversity (HSD) and low-sown diversity (LSD) plots. Means are shown (± SE) and results of an ANOVA test. NS indicates not significantly different

		HSD	LSD	$F_{1,4}$	*p*
Nematodes (number g soil^{-1})	*Paratylenchus*	8.6 ± 1.7	3.2 ± 1.4	83.2	< 0.001
	Tylenchorhynchus	0.9 ± 0.4	0.01 ± 0.01	0.2	NS
	Tylenchus	0.10 ± 0.06	0.07 ± 0.05	4.5	NS
Aphids (number plant^{-1})	*Uroleucon cirsii*	57.2 ± 50.1	72.3 ± 50.1	0.6	NS
	Aphis fabae	47.7 ± 17.9	71.4 ± 31.3	3.0	NS
	Macrosiphum euphorbiae	4.3 ± 3.0	0.6 ± 0.6	1.3	NS

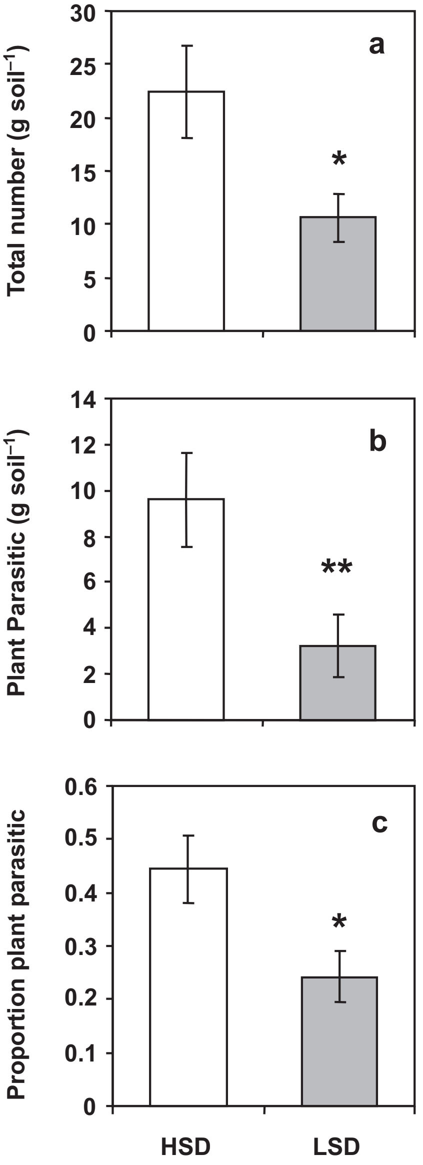

Fig. 2 Belowground trophic interactions on *C. arvense.* Shown are the mean (± SE) (**a**) number of nematodes, (**b**) plant parasitic nematodes and (**c**) the proportion of plant parasitic nematodes in soil taken from the root zone of *C. arvense* growing in plots sown in 1996 with 15 (HSD) or four (LSD) plant species. * $p < 0.05$; ** $p < 0.01$.

lar host plant compared to mono- or oligophagous herbivores (e.g., Sieman et al., 1998). In our study, specialist aboveground herbivores were influenced not by plant diversity but by host plant abundance and, therefore, for specialist herbivores plant diversity will not influence biotic resistance against an invading plant. The abundance of generalist aphids appears to be independent of the surrounding vegetation. These results suggest that there was no aboveground biotic resistance against *C. arvense.*

Aphid parasitism was only observed in HSD plots. This may be due to the increased diversity and concentration of floral resources in these plots (T. M. Bezemer, pers. observation). Many arthropod parasites and predators depend on nectar, such as from floral resources, for their survival (Jervis et al., 1993).

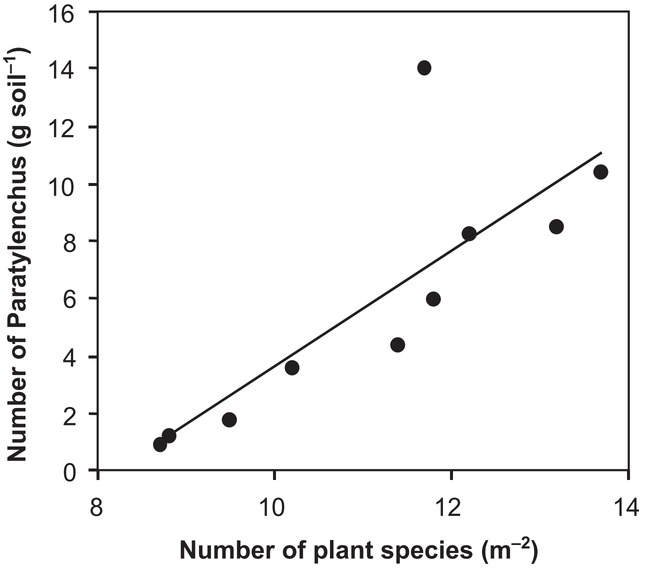

Fig. 3 Relationship between plant species diversity and number of plant parasitic nematodes *(Paratylenchus)* found in the root zone of *C. arvense* plants.

The increased importance of the third trophic level in the high-diversity plots may result in a reduced impact of the herbivore on the invading plant.

Belowground effects

Although we did not find evidence for the biotic resistance hypothesis above ground, the density of the generalist plant parasitic nematode *Paratylenchus* increased linearly with increasing numbers of plant species. We believe this result is not due to the absolute number of plant species present, but rather the abundance, or presence or absence, of particular plant species. It is important to note that since soil organisms, such as nematodes, have low dispersal capacities, nematode densities in 2002 in HSD and LSD plots are the result of accumulative increases in numbers since 1996 (Korthals et al., 2001; Van der Putten et al., 2001). A number of studies have shown that plant parasitic nematodes can reduce plant growth and productivity (Stanton, 1988; De Deyn et al., 2003). Consequently, higher numbers of plant parasitic nematodes in plots with high plant diversity would imply that these communities may have higher biotic resistance to invading plant species. Our results, therefore suggest that belowground there may be stronger biotic resistance against *C. arvense* in high-diverse than in low-diverse plant communities. However, to test whether biotic resistance is real in this system, additional work needs to be carried out to test whether the generalist plant parasitic nematodes have a more significant effect on *C. arvense* than on the plant species already present in the community.

C. arvense is a persistent perennial with recruitment of new plants via seed and small root fragments and, once established, one plant can infest large areas by recruitment of shoots from adventitious buds on a creeping root system. Root herbivory might, therefore, potentially be more effective in reducing thistle abundance, relative to shoot feeding herbivores. Other studies have also shown that both nematode diversity (Bardgett and Cook, 1998) or abundance (Yeates et al., 1999) can increase with increasing plant diversity, possibly due to a greater abundance of resources (Bardgett et al., 1998). There is also some evidence that the richness or abundance of soil organisms, such as arbuscular mycorrhizal fungi, soil bacteria, or earthworms, can be positively related to plant species diversity (e.g., Stephan et al., 2000; Spehn et al., 2000; Burrows and Pfleger, 2002). However, in these studies the differences in diversity between the experimental plant communities were much larger, as a result of hand weeding, than in our case.

Above- and belowground interactions

There is evidence that above- and belowground communities on a shared host plant may interact (Brown and Gange, 1990; Bardgett et al., 1998; Van der Putten et al., 2001). Root herbivory, for example, has been reported to enhance the performance of foliar feeding insects (Gange and Brown, 1989; Masters and Brown, 1992; Masters et al., 1993, 2001; Masters, 1995; Gange, 2001), while in the presence of foliar feeders, the performance of belowground herbivores may be reduced (Masters and Brown, 1992; Moran and Whitham, 1990; Salt et al., 1996). Above- and belowground interactions can occur via, for example, re-allocation from root to shoot of primary metabolites such as nitrogen and carbohydrates from the host plant following exposure to root herbivory (Gange and Brown, 1989; Masters et al., 1993), or the induction of secondary plant metabolites across compartments (Bezemer et al., 2003, 2004; Van Dam et al., 2003).

Most work on above- and belowground interactions has been carried out with individual plants and under controlled conditions. Little is known about the importance of such interactions under field conditions, although some studies do provide evidence that such interactions do occur in the field (e.g., Moran and Whitham, 1990; Masters, 1995; Masters et al., 2001). Other work has shown that nematode population densities can be enhanced in grasslands exposed to aboveground grazing (reviewed in Bardgett et al., 1998). Our results are a first attempt to quantify biotic resistance by both above- and belowground herbivores in concert in relation to the species diversity of the surrounding plant community.

In conclusion, our study did not show a relationship between nematode and aphid abundance on *C. arvense,* but we have shown that the species diversity of the surrounding plant community can influence both the above- and belowground community of sap sucking herbivores. The level of parasitization aboveground was also highest in the high-diversity plant community. This study highlights that linkages between above- and belowground herbivores may depend critically on the species diversity of the surrounding plant community, and that this may have differential effects above and below ground. The implication is that the analysis of the biotic resistance of a plant community against the establishment of plant species in a plant community may be dependent on both above- and belowground herbivores. Subsequent studies should also include other feeding guilds of above- and belowground herbivores, as well as their antagonists, in order to produce a more complete analysis of biotic resistance against introduced plants in relation to the local plant species diversity.

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