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Vertebrate herbivores influence soil nematodes by modifying plant communities

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Abstract. Abiotic soil properties, plant community composition, and herbivory all have been reported as important factors influencing the composition of soil communities. However, most studies thus far have considered these factors in isolation, whereas they strongly interact in the field. Here, we study how grazing by vertebrate herbivores influences the soil nematode community composition of a floodplain grassland while we account for effects of grazing on plant community composition and abiotic soil properties. Nematodes are the most ubiquitous invertebrates in the soil. They include a variety of feeding types, ranging from microbial feeders to herbivores and carnivores, and they perform key functions in soil food webs.

Our hypothesis was that grazing affects nematode community structure and composition through altering plant community structure and composition. Alternatively, we tested whether the effects of grazing may, directly or indirectly, run via changes in soil abiotic properties. We used a long-term field experiment containing plots with and without vertebrate grazers (cattle and rabbits). We compared plant and nematode community structure and composition, as well as a number of key soil abiotic properties, and we applied structural equation modeling to investigate four possible pathways by which grazing may change nematode community composition.

Aboveground grazing increased plant species richness and reduced both plant and nematode community heterogeneity. There was a positive relationship between plant and nematode diversity indices. Grazing decreased the number of bacterial-feeding nematodes, indicating that in these grasslands, top-down control of plant production by grazing leads to bottom-up control in the basal part of the bacterial channel of the soil food web.

According to the structural equation model, grazing had a strong effect on soil abiotic properties and plant community composition, whereas plant community composition was the main determinant of nematode community composition. Other pathways, which assumed that grazing influenced nematode community composition by inducing changes in soil abiotic properties, did not significantly explain variation in nematode community composition.

We conclude that grazing-induced changes in nematode community composition mainly operated via changes in plant community composition. Influences of vertebrate grazers on soil nematodes through modification of abiotic soil properties were of less importance.

Key words: above–belowground interactions; community ecology; floodplain grassland; grazing; nematodes; soil biota; structural equation modeling (SEM); The Netherlands; top-down–bottom-up control; vertebrate herbivores.

INTRODUCTION

Grazing by aboveground vertebrate herbivores, abiotic soil properties, and plant community composition all have been reported to determine soil community composition, function, and diversity (see, e.g., Stanton 1988, Yeates 1999, Wardle 2002, Bardgett 2005). Most studies have considered the effects of herbivores (e.g., Wall-Freckman and Huang 1998, Guitian and Bardgett

2000, Mikola et al. 2001), plant species (e.g., De Deyn et al. 2004b, Salamon et al. 2004, Viketoft et al. 2005), and soil abiotic properties (e.g., Sarathchandra et al. 2001, Housman et al. 2007) on soil biota independently, while their interactions rarely have been examined. One of the major complications in unraveling the individual effects and their interactions is that effects of grazing, soil abiotic properties, and plant community composition are not independent. Therefore, it is still poorly understood whether effects of grazing on soil communities operate via plant community changes (e.g., Bardgett et al. 1998, Wardle et al. 2001, Bardgett and Wardle 2003) or altered soil abiotic properties (e.g., Bazot et al. 2005). Previous studies on determinants of

soil community composition were carried out under controlled experimental conditions, i.e., common garden or pot experiments (e.g., Wardle et al. 1999, De Deyn et al. 2004b, Viketoft 2008); thus little is known about field situations (Casper and Castelli 2007).

The aim of our study was to examine if grazing effects on soil biota operate through modification of soil abiotic properties, through altered plant community composition, or through more complicated routes, for example when grazing causes plant-induced changes in soil abiotic properties. We collected plant and soil data from a long-term grazing exclusion experiment in the field and assessed the relative importance of alternative causal pathways by structural equation modeling (SEM). We used SEM because it can test the fit of data to a priori causal hypotheses when a particular organization among variables is assumed (Shipley 2000, Grace 2006). It allows testing of multivariate hypotheses in which some variables can act as predictor and response variables at the same time.

To characterize the soil community, we focused on nematode community composition, because this taxonomic group includes a wide variety of feeding types, including bacterial feeders, fungal feeders, plant feeders, omnivores, and carnivores (Yeates et al. 1993). Consequently, the nematode community serves as a proxy for community composition of other groups of soil organisms at different trophic levels. Considering the variety of nematode feeding types in the soil, the possible limiting resources will also be variable, including plant roots, bacteria, fungi, mosses, other nematodes, and insects. In general, lower trophic level organisms in soil food webs are supposed to be controlled by top-down forces, whereas higher trophic level organisms are controlled by bottom-up forces (de Ruiter et al. 1995). However, resource selectivity probably plays a more important role in soil food webs than previously supposed (Ruess et al. 2000, De Deyn et al. 2004b). Therefore, we considered that a myriad of bottom-up, top-down, and competitive control factors, as well as resource specificity, may be involved in determining the nematode community composition. We analyzed main pathways that could hypothetically orchestrate grazing effects on this myriad of nematode control factors.

In order to test the hypothetical pathways that may explain grazing effects on nematode community composition, we constructed four competing conceptual models (Fig. 1) and determined the closest fit with the best model resulting from the SEM analysis. The hypothetical pathways of grazer effects on nematode community composition were based on information in the literature. (1) Soil abiotic conditions can affect nematode community composition (Yeates and Bongers 1999) and can be changed by herbivore activities. For example, grazers change soil bulk density as a result of trampling and they locally alter soil pH, nutrient availability, and N mineralization rates by dung and urine deposition (e.g., Ruess and McNaughton 1987,
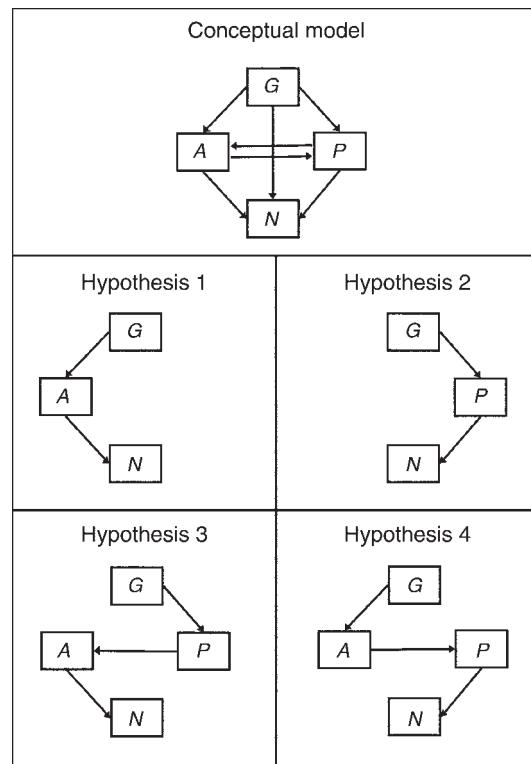

FIG. 1. The top panel shows the conceptual model of pathways via which grazing may affect nematode community composition and diversity. The four bottom panels show the models for the four alternative hypotheses outlining how aboveground grazing may affect nematode community composition. Variables are: G, grazing treatment (grazed or ungrazed); A, soil abiotic properties; P, plant community composition; and N, nematode community composition. The four hypotheses are (1) grazing alters soil abiotic properties, which directly affect nematode community composition; (2) grazing changes plant community composition, which alters nematode community composition; (3) grazing changes plant community composition, which affects nematode community composition indirectly by changing soil abiotic properties; and (4) grazing changes soil abiotic properties, which affect nematode community composition indirectly by changing plant community composition.

Steinauer and Collins 1995, Hobbs 1996, McNaughton et al. 1997, Frank et al. 2000, Bakker et al. 2004). (2) Grazing-induced nematode community changes can be mediated by changes in plant community composition. As a result of selective removal of plants, herbivores alter the extinction–colonization balance and competitive interactions between plants (e.g., Milchunas and Lauenroth 1993, Olff and Ritchie 1998). Altered plant community composition may lead to a different nematode community composition, because nematodes are able to respond differently to specific plants (van der Putten and van der Stoel 1998, De Deyn et al. 2007). Consequently, plant community composition, rather than plant diversity, determines community composition of soil nematodes (De Deyn et al. 2004b, Viketoft et al. 2005). (3) Grazing can also affect nematode community composition by altering soil abiotic properties indirectly

via plant responses and changes in plant community composition. This, in turn, influences the amount and quality of resources entering the soil via plant nutrient allocation and root exudation (Holland and Detling 1990, Bardgett et al. 1998, Guitian and Bardgett 2000). Moreover, altered plant community composition often results in a different structural and chemical composition of plant litter returned to the soil, and in different depletion patterns of soil resources such as water and nutrients (Yeates 1999, Wardle 2002). (4) Finally, the nematode community composition can be altered because grazers change soil abiotic properties, which change plant community composition, leading to changes in nematode community composition.

To analyze the relative importance of the different pathways (Fig. 1), we excluded aboveground vertebrate grazers (cattle and rabbits) from a species-rich floodplain grassland and compared plant and nematode community composition, as well as various soil abiotic properties, between the grazed and ungrazed plots. We expected the effects of grazing by large aboveground vertebrate herbivores, soil abiotic properties, and plant community composition on nematode community composition to be hierarchically structured according to the size of the organisms involved: grazers > plants > soil biota (Bradford et al. 2002, Ettema and Wardle 2002, Bardgett et al. 2005). Therefore, the four alternative pathways proposed include unidirectional effects only. Although there may be feedback effects of the soil community on the plant and herbivore community (e.g., Blomqvist et al. 2000, Bardgett and Wardle 2003, De Deyn et al. 2004a), we did not include these effects in our analysis.

METHODS

Site description

The study was conducted in the Junner Koeland area, a 100-ha nature reserve along the river Overijsselse Vecht in the northeast of The Netherlands (52°32′ N, 6°36′ E). The area includes a 50-ha floodplain, where we carried out our experiment. This site used to be flooded regularly until canalization of the river Vecht (around 1910) and regulation of the water level. The Junner Koeland was common grazing land, used by farmers from the village Junne, and has been grazed by livestock for centuries. Nowadays, it is managed as a nature reserve by the National Forestry Service (Staatsbosbeheer), and is grazed by cattle (*Bos taurus*) from April until November at stocking rates of about 0.3 animals/ha. The most abundant natural vertebrate herbivores in the area are European rabbits (*Oryctolagus caniculus*) and common voles (*Microtis arvalis*). Dominant plant species in the grasslands are the graminoids *Agrostis capillaris*, *Festuca rubra*, *Holcus lanatus*, and *Luzula campestris*. Frequently occurring dicots are *Rumex acetosa* and *Trifolium repens*. Also, the grasslands locally host several endangered plant species, such as *Dianthus deltoides*, *Succisa pratensis*, *Thymus serpyllum*, and *Mentha pulegium* (nomenclature follows van der Meijden 2005).

Experimental design

In 1994, a long-term exclosure experiment was set up consisting of five randomly established blocks, each containing a fenced exclosure plot of 12 × 12 m from which cattle and rabbits were excluded ("Ungrazed" treatment) and at 2 m distance an adjacent plot of 12 × 12 m to which cattle and rabbits had free access ("Grazed" treatment). Within each plot, four permanent subplots of 2 × 2 m were established to record long-term vegetation and abiotic responses to cattle and rabbit grazing. All 40 subplots were positioned at least 1 m from the fences to avoid edge effects.

Measurements

In each of the 40 subplots of 2 × 2 m, we recorded plant species composition in July 2006 at peak standing biomass. We estimated cover of each plant species visually according to the decimal Londo scale (Londo 1976). In the first week of November 2006 we randomly selected three locations per subplot, from each of which we collected 2 kg of soil from the top 15 cm using a hand shovel. After gentle homogenization and removal of stones, we collected two subsamples of 100 g each. We used one sample to isolate, identify, and count nematodes and the other to measure soil organic matter content (SOM) and soil texture. We extracted nematodes using Oostenbrink elutriators (Oostenbrink 1960). A subsample of 10% of the extraction was preserved and the nematodes were heat-killed and fixed (35% formaldehyde diluted to 4%). In each sample we counted the total number of nematodes and identified a minimum of 150 nematodes to family, genus, or species level according to Bongers (1988). Nematodes were classified into feeding types according to Yeates et al. (1993): plant feeders, fungal feeders, bacterial feeders, carnivores, and omnivores. The nematodes were distributed into c-p (colonizer-persister) classes to calculate a maturity index, MI (Bongers 1990).

We determined soil organic matter content (SOM) of dry soil samples (achieved by drying for 24 h at 105°C) by loss-on-ignition at 550°C for 3 h. SOM was expressed as the relative difference in mass before and after ignition. We determined soil texture in freeze-dried soil as the percentage contribution to total volume of each of the particle size classes. The freeze-dried soil was first dispersed by ultrasonification and was subsequently analyzed with a coulter counter LS230 (fluid module; Beckman Coulter, Fullerton, California, USA).

Additionally, per subplot we collected two PVC cylinders filled with soil (diameter 4.3 cm, length 16 cm) to measure potential nitrogen (N) mineralization rates. We homogenized soil from half of all tubes within 24 h after collection to measure soil moisture content (%), pH, and extractable concentrations of inorganic nitrogen (NO_3^- and NH_4^+). The remaining tubes were kept at 21°C and constant soil moisture levels for 6 weeks. After 6 weeks the soil was homogenized and extractable levels of NO_3^- and NH_4^+ were measured

again. The differences between the first and second analysis yield potential mineralization rates per subplot (Olff et al. 1994). To determine NO_3^- and NH_4^+ concentrations, we dissolved 25 g of soil in 60 mL 1 mol/L KCl. Concentrations were determined colorimetrically with a Flow Solution Autoanalyzer (Skalar Analytical, Breda, The Netherlands). We determined soil moisture content as the loss in mass after drying soil at 105°C for 24 h. To measure pH we dissolved 15 g of soil in 20 mL of demineralized water and measured the samples with a Sentron pH meter (Sentron, Roden, The Netherlands).

Data analysis

To characterize plant and nematode community structure in each subplot ($n = 40$), we calculated plant species and nematode taxon richness (S, the total number of plant species or nematode taxa per subplot), Shannon's diversity index ($H' = -\sum p_i \ln(p_i)$, where p_i is the relative cover or abundance of species i; Magurran 2003), and evenness ($E = H'/\ln(S)$). We calculated plant and nematode community dissimilarity from Euclidian Distance (ED) using the percentage cover of each plant species or the abundance of each nematode taxon, respectively, according to the following formula:

$$ED = \sqrt{\sum_{i=1}^{S} (x_{i1} - x_{i2})^2}$$

where S is species/taxon richness, x_{i1} is the percentage cover or abundance of species i in plot 1, and x_{i2} is the percentage cover or abundance of species i in plot 2. We calculated ED by comparing all four subplots within one plot. Thus, in total we had five replicated dissimilarity values for grazed areas and five for ungrazed areas. We tested community structure and soil abiotics data for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). When necessary, data were $\log(x + 1)$-transformed.

We tested grazing effects on plant and nematode community structure (S, H', E, ED, and MI) and soil abiotic properties using mixed-model ANOVAs with the metrics of community structure or soil abiotics as response variables. Grazing was used as a fixed factor and block as a random factor. We tested the relationship between nematode and plant community structure (S, H', E, ED) using ANCOVA with metrics for nematode community structure as response variables, grazing as a fixed factor, and metrics for plant community structure as continuous predictor variables.

To analyze via which of the four hypothetical pathways grazing was affecting nematode community composition (i.e., taxon and feeding type composition), we used structural equation modeling (SEM). Prior to the SEM procedure we reduced the number of variables for abiotic soil properties, plant community composition, and soil nematode community composition through principal component analyses (PCA) on each group of variables separately. For each group the first principal component (PC) was used in the subsequent SEM analysis to represent soil abiotic properties (PC1 explained ~70% of variation), plant community composition (PC1 explained ~30% of variation), and soil nematode community composition (PC1 explained ~25% of variation), respectively. All variables used in the SEM analysis were observed variables. We started the SEM procedure with the specification of a conceptual model of relationships in our system (Fig. 1), based on a priori and theoretical knowledge. In this model we hypothesized that grazing may alter soil abiotic properties and plant community composition, which in turn may affect nematode community composition. Soil abiotic properties and plant community composition could influence each other as well. The conceptual model provided a framework for the actual SEM analysis and test of our four alternative pathways. The subplots in the grazing experiment were grouped into blocks (see experimental design) to account for unmeasured variation due to the position of the plots on an environmental gradient which was determined by the distance to the river. In the SEM analysis we were not able to include the factor "block." To account for potential unmeasured effects of the block structure, we added the variable "distance" (DIST; Fig. 3) to the model. This variable describes the distance of each subplot to the river, therefore serving as an indicator for subplot position on the gradient, which corresponds to the blocking structure in the experiment. As minimum sample size in SEM, Bentler and Chou (1987) recommend using 15 cases per measured variable, or even fewer when there are no missing values. In our study we just met these recommendations: we measured three variables and our sample size was 40 without missing values.

In the SEM analysis we compared the model-implied variance–covariance matrix against the observed variance–covariance matrix. Data were fitted to the models using the maximum likelihood estimation method. The χ^2 goodness-of-fit statistic and its associated P value were used to judge the model fit to the data. A large P value associated with the χ^2 value indicates that the covariance structure of the data does not differ significantly from expected, based on the model. By stepwise removal of nonsignificant paths from the initial model (i.e., the model closest to our conceptual model), we selected the model that best fitted our data. We compared this SEM model to the conceptual models describing our hypothetical pathways (Fig. 1). This procedure enabled us to determine which proposed pathways best explained grazing effects on nematode community composition. We also tested the models with direct effects of grazing on nematode community composition included to see whether this effect would explain significant amounts of variation in nematode community composition.

All univariate statistical analyses were performed using STATISTICA (release 7.1, StatSoft, Tulsa,

TABLE 1. Overview of effects of grazing treatment (ungrazed or grazed) on soil abiotic properties, plant community structure, and nematode community structure (mean ± SEM).

Variable	Ungrazed	Grazed	$F_{1,30}$†	P
Soil abiotic properties				
pH	4.48 ± 0.15	4.85 ± 0.10	24.2	**0.008**
Soil organic matter (g/100 g)	7.58 ± 0.85	8.65 ± 1.07	5.38	0.081
Soil moisture (g/100 g)	25.3 ± 1.21	23.4 ± 1.41	2.29	0.205
Potential NO_3^- mineralization rate (mg/kg)	42.7 ± 4.00	14.7 ± 3.55	23.0	**0.009**
Potential NH_4^+ mineralization rate (mg/kg)	0.83 ± 1.24	8.09 ± 2.86	6.63	0.062
Clay (%)	4.32 ± 0.28	3.95 ± 0.52	0.44	0.546
Silt (%)	25.6 ± 1.86	24.9 ± 2.27	0.05	0.831
Sand (%)	70.0 ± 2.12	71.0 ± 2.79	0.09	0.778
Plant community structure				
Species richness (S)	8.00 ± 1.06	13.0 ± 0.73	11.3	**0.028**
Evenness (E)	0.66 ± 0.05	0.55 ± 0.03	3.45	0.137
Diversity (H')	1.33 ± 0.06	1.41 ± 0.08	0.80	0.422
Heterogeneity (ED)	53.7 ± 10.01	21.7 ± 3.94	7.02	0.057
Vegetation height (cm)	24.01 ± 2.68	5.61 ± 0.60	48.6	**0.002**
Nematode community structure				
Species richness (S)	25.8 ± 1.81	24.2 ± 2.01	1.96	0.234
Evenness (E)	0.76 ± 0.02	0.75 ± 0.04	0.07	0.805
Diversity (H')	2.45 ± 0.12	2.38 ± 0.17	0.69	0.454
Heterogeneity (ED)	19.1 ± 2.06	12.2 ± 1.58	13.7	**0.021**
Maturity index (MI)	2.06 ± 0.30	1.51 ± 0.13	4.93	0.091

† Degrees of freedom were 1 and 30, except for ED, for which they were 1 and 4.

Oklahoma USA). Multivariate statistical analyses (PCA) were performed using CANOCO for Windows (version 4.5; ter Braak and Šmilauer, Wageningen-UR, The Netherlands). SEM analyses were performed using AMOS 5.0.1 student version (Amos Development, Spring House, Pennsylvania, USA).

RESULTS

Grazing effects on plant community composition, soil abiotic properties, and nematodes

In grazed plots we found a significantly higher pH, whereas potential NH_4^+ mineralization rates and soil organic matter content tended to be increased. However, potential NO_3^- mineralization rates were significantly lower in grazed plots (Table 1). Grazing decreased heterogeneity (ED) in nematode communities and caused a nearly significant reduction of heterogeneity in plant communities. In the grazed plots, the vegetation was lower and plant species richness was higher than in the plots where grazing was excluded. The grazing regime did not influence taxon richness in the nematode community. Grazing influenced neither evenness (E) nor diversity (H') in both plant and nematode communities. The maturity index (MI) for the nematode community tended to be lower in the grazed plots (Table 1). The grazed plots had significantly fewer numbers of bacterial-feeding nematodes (Fig. 2; $F_{1,30} = 10.26$, $P = 0.033$); other nematode feeding groups showed the same tendency, although not significant ($P > 0.05$).

Nematode community diversity (H') was positively related to plant community diversity ($P = 0.006$, $F_{1,37} = 8.54$), and this relationship was not different between grazed and ungrazed plots ($P = 0.307$, $F_{1,37} = 1.07$). However, there was neither a relationship between plant species richness and nematode taxon richness ($P = 0.159$, $F_{1,37} = 2.07$), nor between indices of plant and nematode evenness (E) ($P = 0.129$; $F_{1,37} = 2.40$) and heterogeneity (ED; $P = 0.181$, $F_{1,7} = 2.20$).

Effects of grazers on nematodes: alternative pathways

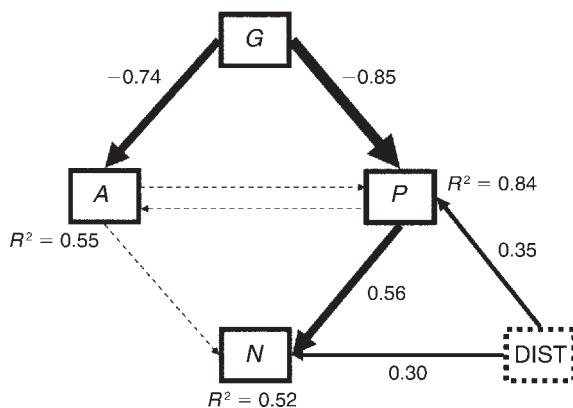The SEM that we finally selected and used for interpretation explained 52% of the variation in nematode

FIG. 2. Final model results of SEM analysis ($\chi^2 = 0.57$, $P = 0.989$, df = 5). Square boxes display variables included in the model: G, grazing treatment (grazed or ungrazed); A, soil abiotic properties (PC1); P, plant community composition (PC1); N, nematode community composition (PC1); and DIST, distance to river, used as an indicator for position on the environmental gradient. Solid arrows indicate significant effects (at the level $P < 0.05$); dashed arrows represent effects that were not significant. Arrow width corresponds directly to the standardized path coefficient. R^2 values associated with response variables indicate the proportion of explained variation by relationships with other variables. Values associated with solid arrows represent standardized path coefficients.
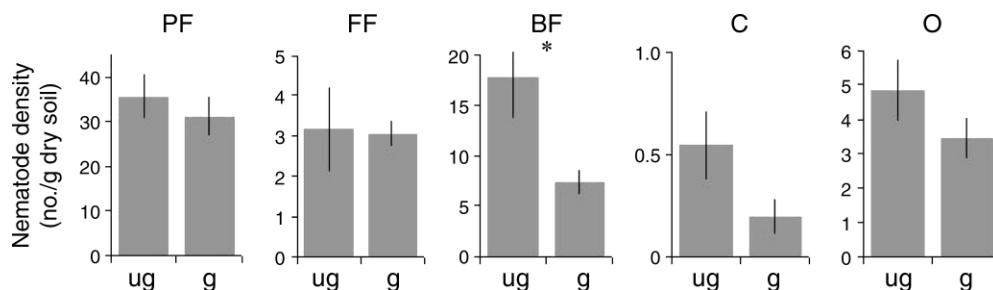
Fig. 3. Density of nematodes (mean ± SE) per feeding type in each grazing treatment. Grazing treatments are plotted on the x-axis (ug, ungrazed; g, grazed). The different graphs represent different nematode feeding types (PF, plant-feeding nematodes; FF, fungal-feeding nematodes; BF, bacterial-feeding nematodes; C, carnivorous nematodes; O, omnivorous nematodes). The asterisk indicates a significant difference at $P < 0.05$.

community composition by grazers, plant community composition, soil abiotic factors, and distance to the river ($\chi^2 = 0.568$, $P = 0.989$, df = 5; Fig. 3). Grazing had strong pathways to soil abiotic properties ($P < 0.001$) and plant community composition ($P < 0.001$). However, plant community composition was the only factor that was associated significantly with nematode community composition ($P < 0.001$). The non-recursive (i.e., reciprocal) paths between soil abiotic properties and plant community composition, as well as the path from soil abiotic properties to nematode community composition, were not significant ($P > 0.05$). Therefore, we found the strongest evidence for hypothetical pathway 2, that grazing alters plant community composition, which in turn alters nematode community composition (Fig. 1). The other pathways, which assumed that grazing influences nematode community composition by inducing direct and indirect changes in soil abiotic properties, were less important in explaining variation in nematode community composition. Within the context of our SEM analysis, we did not find a direct effect of aboveground grazing on nematode community composition ($P = 0.926$). Distance to the river (DIST) significantly affected both nematode and plant community composition (Fig. 3), and therefore was kept in the model.

DISCUSSION

Twelve years of excluding cattle and rabbits from an extensively managed grassland changed soil abiotic properties and the structure of plant and nematode communities. Aboveground grazing decreased the abundance of nematodes, specifically bacterial feeders. Grazing reduced spatial heterogeneity (ED) in both plant and nematode communities. Diversity indices in both plant and nematode communities were positively related, indicating structural linkages between plants and nematodes. SEM revealed that grazing by cows and rabbits most likely influenced nematode community composition by altering plant community composition instead of by altering soil abiotic properties. Therefore, our SEM approach supports conclusions from plant addition experiments (De Deyn et al. 2004b, Viketoft et

al. 2005) and plant removal studies (Wardle et al. 1999) that nematode community composition depends on plant community composition. One previous study that also tried to tease apart the effects of plant community composition and soil abiotic properties on soil microbial community composition and structure (Broughton and Gross 2000) was constrained by plant community composition changing with soil fertility. This will be a usual limitation when performing field sampling along environmental gradients. Our SEM approach, based on a long-term grazing exclusion experiment, is the first to our knowledge to tease apart the effects of grazing, plant communities, and soil abiotic properties on soil community composition.

The effects of plant community composition on nematode community composition may result from effects directly related to living plant roots and indirect effects as a result of root exudates and inputs of detritus and leaf litter into the soil food web (Wardle et al. 2004). Direct effects will work mostly through root-feeding nematodes. Because root-feeding nematodes may be host specific (van der Putten and van der Stoel 1998), a change in plant species composition will directly alter nematode composition in this feeding group (Yeates and Bongers 1999). De Deyn et al. (2004b) showed that particular plant species enhanced the abundances of specific plant-feeding nematode types. Other nematode feeding types, such as bacterial and fungal feeders, are affected indirectly by plant community change through altered inputs of root exudates and plant litter, which first influence the soil microbial community and then the bacterial- and fungal-feeding nematodes (Stanton 1988, Wardle et al. 2004).

We found higher numbers of bacterial-feeding nematodes in ungrazed plots, which could result from an altered microbial community composition due to changed plant species composition. Plant species may discharge different root exudates, resulting in plant-specific microbial communities (Grayston et al. 1998, Johnson et al. 2003, Marschner et al. 2004). Relatively little is known about feeding selectivity of bacterial- and fungal-feeding nematodes, but considering the variety in mouth parts, it is possible that these nematodes have

some degree of resource specialization or preference (Ruess et al. 2000). Therefore, altered bacterial community composition can be expected to result in a change in bacterial-feeding nematode composition. Indeed, preliminary analysis of the microbial community in our study system revealed that aboveground vertebrate grazing reduced bacterial activity, which may explain the lower numbers of bacterial-feeding nematodes in grazed plots. Moreover, bacterial activity tended to be positively related to the number of bacterial-feeding nematodes in a plot (G. F. Veen, *unpublished data*). Previous studies on the consequences of aboveground vertebrate grazing for microbial biomass or activity reported both positive (e.g., Bardgett et al. 1998, 2001, Wang et al. 2006) and negative effects (e.g., Stark and Grellmann 2002, Sankaran and Augustine 2004). A reduction in microbial activity by aboveground vertebrate grazing can be explained as a result of lower plant litter quality due to grazing-induced dominance of unpalatable species (Bardgett and Wardle 2003) or a result of lower plant litter quantity due to decreased litter production under cattle grazing (Bakker 2003).

The quality and quantity of plant litter input to the soil is affected by plant community composition. High litter quality and inputs from herbivore droppings will promote the bacterial decomposition chain of the soil food web, whereas lower quality litter and the absence of droppings may enhance the fungal decomposition chain (Wardle et al. 2004). Interestingly, in our case, grazing reduced the number of bacterivorous nematodes, suggesting that the grazing pressure was too high to promote the bacterial food chain. Omnivores may be influenced similarly to the herbivores and bacterial- and fungal-feeding nematodes, whereas carnivores will be affected more indirectly, i.e., via other nematode feeding groups, mites, collembolans, or altered insect communities in the soil (Yeates et al. 1993). Because carnivores tended to be reduced as well in the grazed plots, grazing also appeared to influence organisms at higher trophic levels in the soil food web.

Conclusion

We conclude that effects of grazing by aboveground vertebrate herbivores on soil nematode community diversity, heterogeneity, and composition mainly operate via altering plant community structure and composition. Abiotic soil properties had less influence on nematode community composition. Grazing effects showed up at various positions in the soil food web, reducing the numbers of bacterivorous and carnivorous nematodes. Grazing effects on the soil community as a result of altered plant community composition may be mediated by altered quality, quantity, and distribution of resources in the soil.

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