Nematology, 2011, Vol. 13(8), 995-1008

Grassland management history affects the response of the nematode community to changes in above-ground grazing regime

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Received: 4 February 2011; revised: 8 April 2011
Accepted for publication: 10 April 2011; available online: 3 June 2011

Summary – Changes in grassland management induce disturbances that influence both soil functioning and soil fauna. This study aimed at determining the extent to which the composition of a grassland soil nematode community could be altered by a shift of grazing regime and the potential feedback that these alterations could provoke on grassland functioning. Therefore, we monitored the composition of the soil nematode community (*i.e.*, plant-, bacterial- and fungal-feeders, omnivores and carnivores) of mesocosms that were sampled from two contrasted long-term field trials (high *vs* low grazing treatments) and subsequently subjected to high or no grazing for 2 years. The soil nematofauna responded faster and more strongly to the application of an intensive grazing regime on a previously extensively exploited system than the other way round. The application of an intensive grazing regime induced a significant increase in numbers of bacterial feeders and a decrease of the relative abundance of fungal-feeding nematodes. The nematofaunal community structure was determined by both the past and current grazing regimes throughout the 2 years of monitoring. Observed effects on soil microbivores seemed to reflect the 'immediate' above-ground primary production potential and to follow micro-organism dynamics. On the other hand, observed effects on root-feeding nematodes seemed to reflect the integral effect of past and current grazing regimes on plant community root biomass and quality.

Keywords – defoliation, ecological indices, functional guilds, grassland, grazing, (de)-intensification, urea.

Ecological connections between above-ground and below-ground biota are believed to play a critical role in the structuring and functioning of terrestrial ecosystems (van der Putten *et al*., 2001; Wardle *et al*., 2004). The ability of herbivores to initiate changes in plant communities and above- and below-ground food webs is an area of current ecological interest (Masters *et al*., 1993; Bardgett *et al*., 1998). In natural or semi-natural grassland ecosystems, herbivores can influence plant community structure, primary production, growth and turnover of plant roots (Frank & McNaughton, 1993; Chase *et al*., 2000; Johnson & Matchett, 2001). Grazing affects, directly and indirectly, the soil biota involved in dead organic matter decomposition (Holt, 1997; Bardgett *et al*., 2001; Sankaran & Augustine, 2004; Patra *et al*., 2005) and nutrient cycling (Hassink, 1992; Frank *et al*., 2000; Le Roux *et al*., 2008). Yet these effects often appear context-dependent and confusing (Milchunas & Lauenroth, 1993; Bardgett & Wardle, 2003; Mikola *et al*., 2009).

There are major reasons why understanding and predicting grazing-induced effects in soil biota, and especially microfauna, have been rarely successful in ecological studies. First, grassland composition and productivity is known to influence soil biota properties (Vitekoft *et al*., 2009; Sohlenius *et al*., 2011). Next, grazing is a combination of numerous factors that simultaneously affect plants and their environment. Indeed, defoliation affects plant growth and carbon (C) allocation (Ferraro & Oesterheld, 2002; Klumpp *et al*., 2009), which can in turn influence root C exudation patterns (Paterson & Sim, 1999)

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DOI:10.1163/138855411X574558

and the rhizosphere organisms that rely on this C (Hamilton & Frank, 2001; Saj *et al*., 2008). Concomitantly, defoliation decreases the amount of coarse organic matter (*i.e.*, above-ground litter) that enters the soil (Burke *et al*., 1999) whilst animal excreta (dung and urine) create nitrogen (N)-rich and organic matter (OM)-rich patches in the upper layers of soil (Afzal & Adams, 1992; Bogaert *et al*., 2000). The animal excreta provide resources for soil microbiota (Bittman *et al*., 2005; Forge *et al*., 2005; Le Roux *et al*., 2008) and often support vigorous plant production (Day & Detling, 1990; Steinauer & Collins, 2001). Consequently, because so many different factors are likely to influence soil functioning in grazed grasslands, these factors are often tested separately and the variables studied chosen accordingly.

Even when the relative importance of defoliation and urine/dung inputs to the soil are tested together, only a handful of authors consider soil microfauna (*i.e.*, protista and nematodes; Wang *et al*., 2006; Mikola *et al*., 2009; Schon *et al*., 2010, 2011). Yet, microphageous nematodes and protista constitute the two main microfaunal groups that influence micro-organism activity and they are long recognised as important regulators of soil OM decomposition and nutrient release processes (*e.g*., Ingham *et al*., 1985; Djigal *et al*., 2004; Ekelund *et al*., 2009; Yeates, 2010). We believe that the study of pasture effects on soil functioning should more regularly include these biotic groups. When information is available on nematodes, defoliation intensity (without addition of urea or animal manure) is generally positively associated with the abundance of free-living soil nematodes (Bardgett *et al*., 1997; Mikola *et al*., 2001a; Schon *et al*., 2010). Moreover, Wang *et al*. (2006) reported that effects of grazing varied among nematode genera: grazing decreased abundance of coloniser bacterivores, whereas more persistent bacterivores, omnivores and predators were increased. Yet, it has also been reported that the relative frequencies of nematode trophic groups did not differ among pasture management practices (Mills & Adl, 2006; Schon *et al*., 2011).

The world-wide socio-economic instability induces pasture management regimes to change regularly from intensification to de-intensification, and *vice versa*. To investigate the response of the soil nematofauna community structure and composition during the transition phase from intensive to extensive grazing regimes, and inversely, we performed a 2-year mesocosm experiment with pasture monoliths. These monoliths, obtained from a long-term sheep grazing experiment (details in Louault *et al*., 2005), had been subjected to reciprocal shifts of grazing regimes. In this study we aimed at: *i*) evaluating whether the free-living nematofauna community patterns were mainly determined by the present, past or both grazing regimes during the 2-year period of monitoring; and *ii*) testing the hypothesis that application of a high grazing regime on a previously ungrazed system would lead to a faster response than termination of grazing on a previously intensively grazed one.

Materials and methods

Experimental design

The study was carried out with grassland monoliths from a permanent semi-natural mesic pasture that had experienced a moderate grazing from approximately 34 years before being subjected to high- or low-grazing intensity levels by sheep without fertilisation in 1989 and for 14 years (Louault *et al*., 2005). Field plots under high grazing intensity (H) were cut once and sheep-grazed four times per year, whereas field plots under low grazing intensity (L) were grazed only once a year. The grass composition under high grazing was dominated by *Holcus lanatus*, *Lolium perenne*, *Agrostis capillaris*, *Festuca arundinacea*, *Taraxacum officinale* and *Trifolium repens*, whereas that under low grazing was dominated by *Elytrigia repens*, *Agrostis capillaris*, *Arrhenatherum elatius*, *Festuca rubra* and *Vicia cracca* (Loiseau *et al*., 2005).

The studied grassland was located at Theix, France (3°1′E, 45°43′N at 870 m a.s.l.), on a fertile brown and slightly acidic sandy soil (53% sand, 22% loam, 25% clay, pH 5.6) with total C content of 4.1% and total N content of 0.42% (Le Roux *et al*., 2003). Procedures to select and extract grassland monoliths are described by Klumpp *et al.* (2007a). Briefly, in June 2002, 28 monoliths (L 0.5 × W 0.5 × H 0.4 m) were sampled from H and L grassland plots (56 in total). Following extraction, 24 monoliths of each pre-experimental treatment were placed in eight mesocosms closed by transparent canopy enclosures (L 1.5 × W 0.5 × H 0.75 m), each containing three monoliths of the same grazing treatment (H or L). The remaining four monoliths from both grassland types (4 × L and 4 × H) were grown outdoors as controls. Mesocosms were placed under natural light; air humidity and temperature were adjusted to outdoor conditions. Monoliths were watered one to three times a week to target a soil water potential of *ca* −30 kPa. At the start of the experiment, in May 2003, half of the mesocosms

of pre-experimental treatments were switched to the opposite grazing treatment, resulting in four replicate mesocosms designated as follows: constant low grazing (LL), constant high grazing (HH), shift to high grazing (LH) and shift to no grazing (HL). During the experiment, 'high grazing' was simulated by cutting at 5 cm height and applying artificial urine five times per year (5 g N m^{-2} per application and 250 kg N ha^{-1} $year^{-1}$, see Klumpp *et al*., 2007a). Monoliths that were neither cut nor fertilised during the experiment were labelled as 'low grazing' to be consistent with that of Klumpp *et al*. (2007a).

Soil sampling

To characterise the initial soil nematode community patterns, the eight control monoliths (4 × L; 4 × H) were destructively sampled before the change of management (April 2003). During the experiment, at each soil harvest (1.5, 5, 12, 17, 24 and 27 months after application of the treatment), half a monolith per mesocosm was sampled giving four replicate samples for each treatment (HH, LL, HL, LH). The two halves of the mesocosm were separated by a stainless steel plate and the empty space was filled with sand. A vertical soil slice (L 0.4 × l 0.06 × H 0.1 m) of the upper horizontal layer (0-10) was sampled and a 250 g subsample of fresh soil was used for nematode extraction.

Nematode extraction, counts and determination

Nematodes were extracted using a slightly modified Cobb method (s'Jacob & van Bezooijen, 1986), from 250 g of moist soil. The extraction technique consists of successive sieving using 500 μm, 250 μm, 200 μm, 100 μm and 50 μm (three times for this last size) meshes, keeping each fraction remaining on the sieves, followed by cotton wool extraction for 48 h. All individuals within two clean 5 ml water suspensions over 50 ml were screened and counted with a stereomicroscope and fixed in hot (65°C) 4% formaldehyde. Next, nematodes were transferred into solutions of increasingly concentrated glycerol until finishing in pure glycerol, in order to improve their morphological observation on mass slides. Per sample, an average of 163 individuals was identified at least at genus level by light microscopy (400-600× magnification). In addition, predominant morphotypes were fixed and individually mounted on slides to be identified at the species level, at higher magnification (1000×). For some morphotypes, it was impossible to find adults, allowing only identification at genus level.

Nematode taxa were then assigned to trophic groups modified from Yeates *et al*. (1993): bacterial feeders (Ba), fungal feeders (Fu), facultative root feeders (Frf), obligate root feeders (Orf), omnivores (Om) and predators (Pr). In addition, nematodes were allocated to coloniser-persister (c-p) classes following Bongers (1990). The coloniser-persister scale ranged from 1 to 5, and could vary within a trophic group; thus, bacterial feeders with a c-p class of 1 were placed in feeding guild Ba_1 and fungal feeders with a c-p class of 4 were placed in feeding guild Fu_4.

Three nematode ecological indices were calculated after Ferris *et al*. (2001):

$$\text{Enrichment index (EI} = 100 \times (e/(e+b))),$$
$$\text{Structure index (SI} = 100 \times (s/(b+s))) \text{ and}$$
$$\text{Channel index (CI} = 100(0.8Fu_2)/(3.2Ba_1 + 0.8Fu_2))$$

where e is the abundance of nematodes in the basal component weighted by their k_e values; b is the abundance of nematodes in the basal component weighted by their k_b values; s is the abundance of nematodes in the structural component weighted by their k_s values; k_e is the weighting assigned to guilds Ba_1 and Fu_2 (enrichment component); k_b is the weighting assigned to guilds Ba_2 and Fu_2 (basal component); and k_s is the weighting assigned to guilds $Ba_{3\text{-}5}$, $Fu_{3\text{-}5}$, $Om_{4\text{-}5}$ and $Pr_{2\text{-}5}$ (structural component). EI is meant to assess food web response to availability of resources (Ferris *et al*., 2001). SI indicates whether the soil community is basal (typical for example of disturbed systems) or structured (typical of more stable systems) (Ferris *et al*., 2001). Finally, CI indicates the putative predominant decomposition pathways, *i.e.*, it is meant to quantify the relative importance of the fungal-fed and the bacterial-fed trophic channels of the soil decomposer food-web (Ferris *et al*., 2001). Finally, the Nematode Channel Ratio (NCR) was calculated after Yeates (2003): NCR $= B/(B+F)$, where B and F are, respectively, the relative contributions of bacterial- and fungal-feeding nematodes to total nematode abundance.

Statistical analyses

Multivariate patterns in nematode communities were investigated on transformed species abundances (57 taxa from all replicates). A permutational multivariate ANOVA (PERMANOVA) was performed to determine the statistical significance of the effects of treatments and sampling time on the nematode community structure.

PERMANOVA tests were based on 9999 restricted permutations of the data. Pair-wise comparisons were performed within treatments and sampling times to discriminate significant ($P < 0.05$) nematode community patterns. To quantify the kinetics of the nematode community structure after the grazing regime switch, we surveyed community composition dissimilarity percentages (SIMPER) of: *i*) plots that experienced a grazing regime switch; and *ii*) constant low and constant high grazing regimes (*i.e.*, LH *vs* LL and HL *vs* HH). PERMANOVA and SIMPER are routines of PRIMER v6 added with PERMANOVA+ (Anderson *et al*., 2008).

The predictor variables (*i.e.*, grazing treatments) were related to overall patterns in the data using an overlay in principal-component analysis (PCA) graph. PCA calculations were performed using XLSTAT (Addinsoft XLSTAT, version 2009) and were based on correlation matrices in order to standardise variables of varying scales and magnitudes. Sampling time was used as a supplementary variable and therefore did not weight the axes combinations.

Absolute abundance of each taxon, relative abundance of nematode trophic groups and ecological indices were analysed by multifactorial ANOVA (4×6) with independent factors being: grazing regimes (LL, HH, LH, HL), and time after the change in above-ground grazing regime (1.5, 5, 12, 17, 24, 27 months). The relative abundance of nematode trophic groups was also compared between treatments at each sampling time by ANOVA (initial stage included). Homogeneity of variances was tested using Levene's test and, when needed, the data were log-transformed to meet the homogeneity assumption of ANOVA. Following ANOVA, Tukey test was used to find the statistically significant differences between treatment level means. If the homogeneity of variance was not met even after transformation, the data were analysed using non-parametric Kruskal–Wallis test. Statistical significance was set at $P < 0.05$ and the analyses were performed using SPSS 17.0 (SPSS, 2008).

Results

Above-ground grazing regime significantly influenced nematode community structure (pseudo-$F = 2.55$; $P = 0.001$). All the treatments differed in their nematofaunal community structure (characterised by the absolute abundance of the 57 nematode taxa recorded during the experiment) from each other except HH and HL (data unpubl.). Sampling time significantly affected nematode community structures as well (pseudo-$F = 5.14$; $P = 0.001$) and pair-wise tests showed that the latter were significantly different between each date (data unpubl.). Total nematode abundance varied significantly with time ($F = 10.823$, $P < 0.01$) but not between treatments (Table 1). No interaction between sampling time and treatments was detected. Total nematode abundance was greatest at 1.5 months (13.0 nematodes (g dry soil)$^{-1}$) and least at 12, 17, 24 and 29 months (6.1, 6.9, 6.3 and 6.5 nematodes (g dry soil)$^{-1}$, respectively). At 0 and 5 months intermediate abundances were measured (9.2 and 10.4 nematodes (g dry soil)$^{-1}$). Bacterial-feeding nematodes were on average the more numerous (48%), followed by obligate root feeders (19%) and facultative root feeders (14%). Fungal feeders (8%) and predators (8%) were more abundant than omnivores (2%; Table 1).

Characterisation of soil nematofauna at the beginning of the experiment

The soil nematode community differed before the start of the experiment between high grazing (H) and low grazing (L). Significant differences were as follows: the Channel index (CI) was significantly lower and bacterial-feeding Rhabditidae more abundant in samples coming from the high-grazing intensity grassland (respectively, $F = 8.34$, $P = 0.028$ and $F = 6.73$, $P = 0.041$). The structural component of some trophic groups also differed significantly: carnivorous – especially Ca_4 *Tripyla filicaudata* ($F = 6.15$, $P = 0.048$) – and obligate root-feeding nematode Orf_4 *Pungentus* sp. ($F = 8.32$, $P = 0.028$) were more abundant in low-grazing intensity samples.

Effect of grazing regime switching on relative abundances of trophic groups

No interaction between sampling time and grazing treatment was detected for any of the nematode trophic groups (Table 1). Except for facultative root feeders, the proportions of all trophic groups were significantly affected by sampling time (Table 1; Fig. 1). The grazing treatment significantly affected bacterivores, fungivores and facultative root feeders (Table 1). The proportion of facultative root feeders was higher in monoliths that had been submitted to pre-experimental low- (LL and LH) than to high-grazing (HH and HL). It was higher as well in plots that had been submitted to a grazing switch in comparison with constant-low or constant-high grazing treatments (*i.e.*, LH > LL and HL > HH, respectively). The proportion of bacterial feeders was lower in constant-

Table 1. *Relative abundances (%) of nematode trophic groups, and nematode ecological indices. Density of four nematode taxa out of 38 that presented significant differences between the four pasture treatments averaged over six sampling dates.*

	Treatment				Treatment	Date	Treatment × Date
	LL[1]	LH	HL	HH			
Facultative root feeders (%)	16.6 b[2]	17.9 a	12.2 c	11.0 d	****[3]	ns	ns
Obligate root feeders (%)	17.4	19.6	20.8	18.8	ns	****	ns
Bacterial feeders (%)	42.1 b	44.9 ab	51.2 ab	54.9 a	***	****	ns
Fungal feeders (%)	14.3 a	6.4 b	6.3 b	6.6 b	****	***	ns
Omnivores (%)	2.2	1.8	1.2	1.2	ns	****	ns
Predators (%)	7.4	9.4	8.2	7.5	ns	****	ns
Enrichment index (EI)	46.6 b	32.8 c	50.9 a	45.8 b	**	***	ns
Structure index (SI)	55.3	58.3	55.2	47.4	ns	****	ns
Channel index (CI)	34.9 a	35.5 a	18.6 b	26.7 b	***	ns	ns
Nematode channel ratio (NCR)	0.75 b	0.88 a	0.89 a	0.89 a	****	ns	ns
Aglenchus agricola (Frf_2)	37.7 b	51.6 a	18.2 c	23.5 c	****	****	ns
Pratylenchus crenatus (Orf_3)	9.6 ab	6.3 b	20.4 a	16.8 ab	*	ns	ns
Plectus pusillus (Ba_2)	30.7 a	95.3 b	88.0 b	125.3 b	****	****	ns
Rhabditidae (*Bursilla monohystera* and *Protorhabditis oxyuroides*) (Ba_1)	40.9 ab	21.6 b	79.4 a	49.1 ab	*	****	ns

[1] LL, constant low grazing; LH, shift to high grazing; HH, constant high grazing; HL, shift to low grazing.
[2] Average of the six dates (1.5, 5, 12, 17, 24 and 29 months after the change in the above-ground grazing regime), n = 24.
[3] $*P < 0.10$; $**P < 0.05$; $***P < 0.01$; $****P < 0.001$; ns, not significant.

low grazing than in constant-high grazing treatments (Table 1). By contrast, the proportion of fungal feeders was higher in constant-low grazing than in the other treatments (Table 1).

The proportion of facultative plant feeders was higher in plots that had been submitted to pre-experimental low-grazing than high grazing treatments 1.5 months after the start of the experiment (Fig. 1). At 5 months, the proportion of fungal feeders was higher in constant-low than constant-high grazing plots (Fig. 1). At 12 months, the proportion of fungal feeders was higher in constant-low plots than in those that experienced high-grazing (Fig. 1). At 17 months, the proportion of bacterial feeders was significantly higher in HH than in LH plots (Fig. 1). Finally, at 27 months, the proportion of carnivores was higher in plots that experienced low-grazing (Fig. 1).

Nematode taxa

Fifty seven nematode taxa were recorded during the experiment. The mean abundance of the 38 main taxa per treatment (LL, LH, LH, HH) is presented in Appendix A. Two-way ANOVAs were performed on these 38 taxa, which represented more than 98% of total nematode abundance. A significant effect of the sampling time was measured for many taxa, yet only four taxa showed significant treatments effects (Appendix A; Table 1). Facultative root feeder, *Aglenchus agricola*, was significantly more abundant in monoliths that had been submitted to pre-experimental low than high grazing regime (Table 1). The obligate root feeder, *Pratylenchus crenatus*, was marginally more abundant when grazing intensity was decreased (HL) than when it was increased (LH) (Table 1). The bacterial feeder, *Plectus pusillus*, was significantly more abundant in monoliths that experienced high grazing than in the constant low-grazing treatment. Finally, Rhabditidae abundances were marginally higher in HL than in LH treatments (Table 1).

Nematode ecological indices and community structure

Enrichment index (EI), Channel index (CI) and Nematode Channel Ratio (NCR) varied significantly with grazing treatment, while EI and Structure index (SI) varied with sampling time. The four indices tested showed no interaction between sampling time and grazing treatment (Table 1). EI was respectively the lowest in LH, intermediate in LL and HH and highest in HL treatments. CI

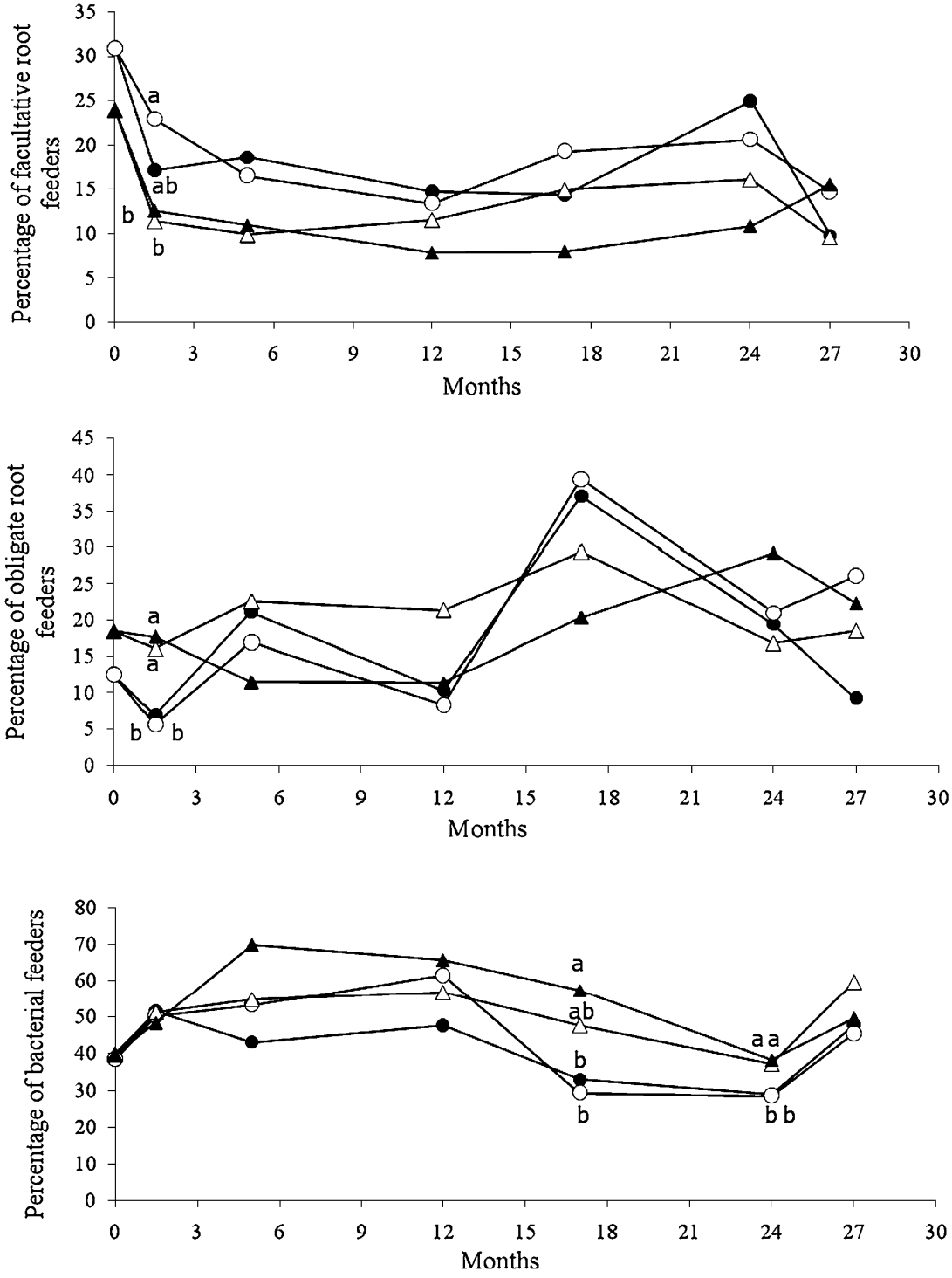

Fig. 1. *Temporal changes in the percentage of the different nematode feeding groups for the four pasture treatments (%). (▲) HH: constant high grazing; (●) LL: constant low grazing; (△) HL: shift to low grazing; (○) LH: shift to high grazing. At each date, points followed by different letters are significantly different.*

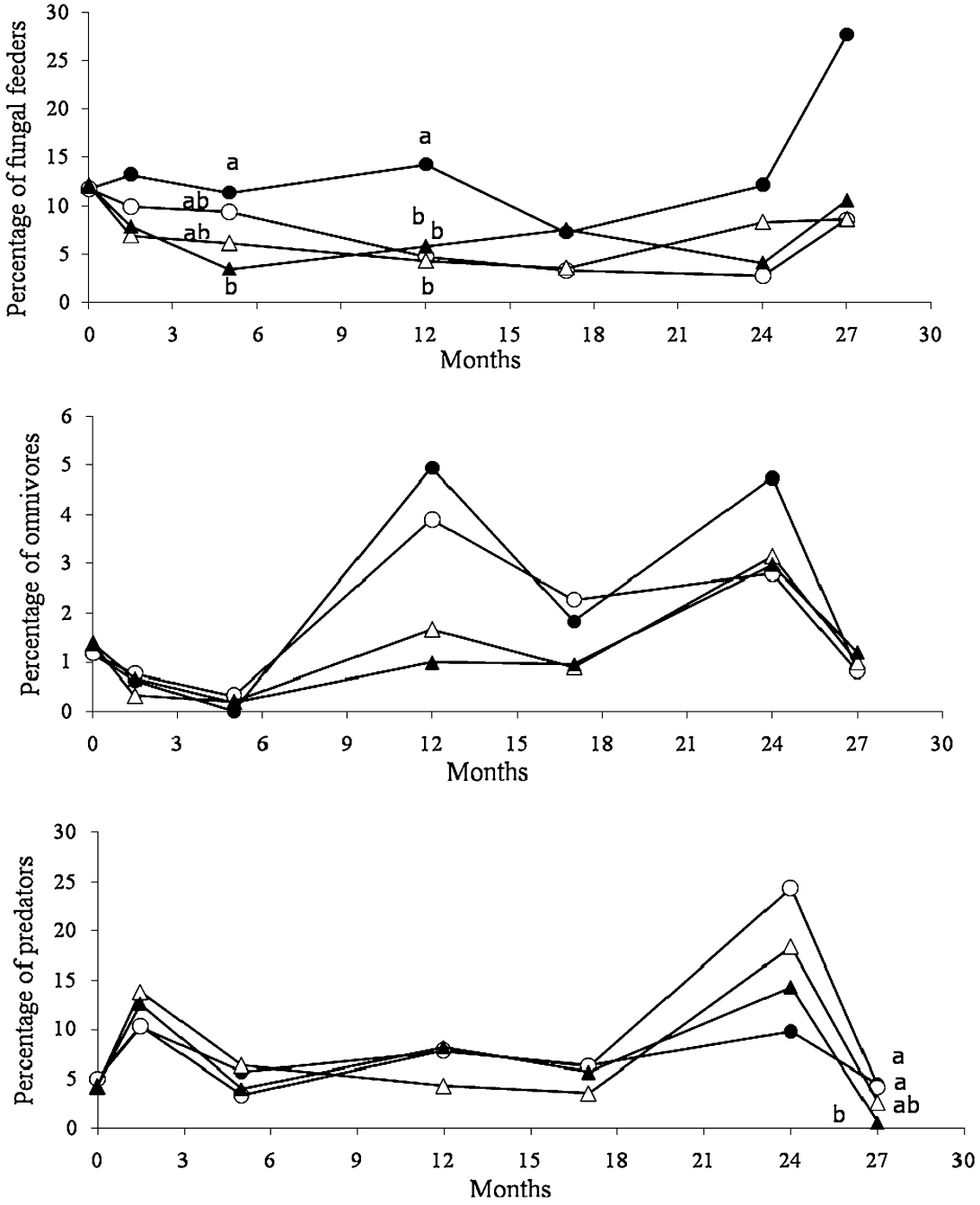

Fig. 1. *(Continued.)*

was significantly higher in monoliths submitted to pre-experimental low (LL and LH) than high (HH and HL) grazing regimes (Table 1). Finally, NCR was significantly higher in monoliths that experienced high grazing (Table 1).

The first two axes of the principal component analysis explained 55.1% of the total variance of the nematode community structure characterised by the relative abundance of nematode trophic groups (Fig. 2). Obligate root feeders, facultative root feeders, omnivores and predators

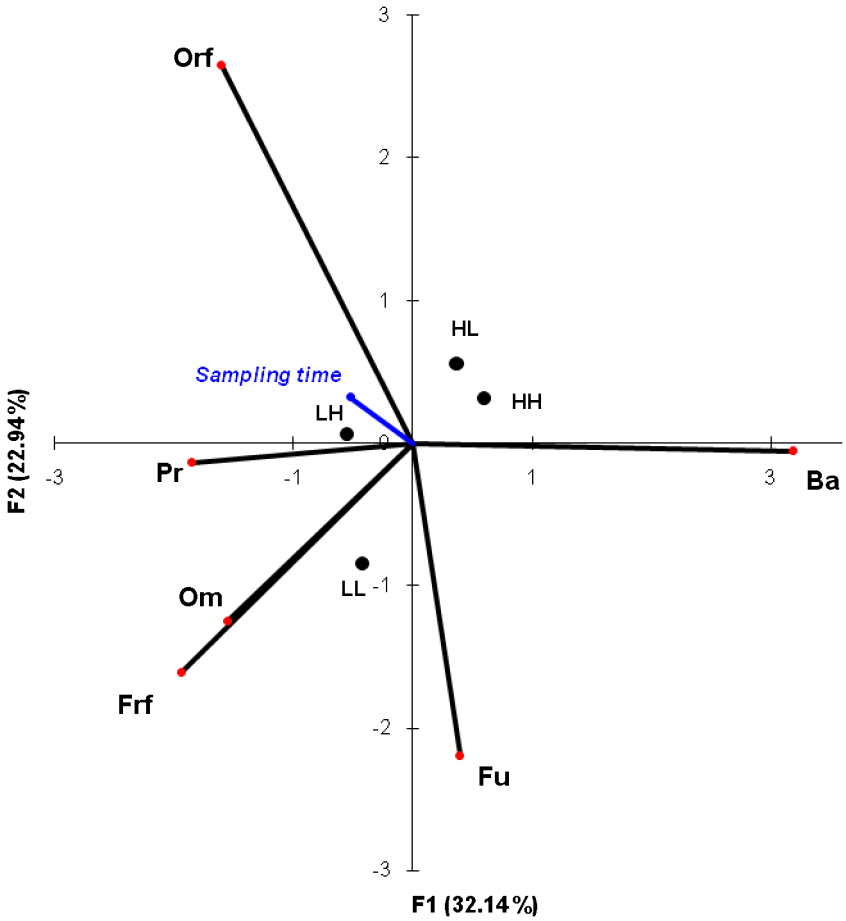

Fig. 2. *Principal component analysis (PCA) of nematofauna composition in feeding groups (%) (Orf: obligate root feeders; Frf: facultative root feeders; Ba: bacterial feeders; Fu: fungal feeders; Om: omnivores; Pr: predators) with sampling time as supplementary variable and PCA scores on trophic group relative abundance for the four pasture treatments; HH: constant high grazing; LL: constant low grazing; HL: shift to low grazing; LH: shift to high grazing. This figure is published in colour in the online edition of this journal, which can be accessed* via *http://www.brill.nl/nemy*

contributed negatively to the first axis whereas bacterial feeders contributed positively. Pre-experimental grazing regimes were clearly discriminated on the first axis: pre-experimental highly grazed systems (HH, HL) showed positive values whilst extensively grazed ones (LL, LH) showed negative values. Fungal feeders contributed negatively to the second axis and discriminated constant-low grazing treatment (LL) from treatments that included high grazing (HH, HL, LH) (Fig. 2).

The highest dissimilarity percentages were found between nematode composition of the two constant grazing regimes, HH and LL. Throughout the experiment, dissimilarity percentages between LH and LL and between HL and HH were lower than between control treatments (HH *vs* LL; Fig. 3, top panel). Five months after switching the grazing regime, dissimilarity percentages between LH and LL increased more than between HL and HH. Two years after switching the grazing regime, the nematode composition of plots submitted to a switch, LH and HL treatments were dissimilar from that of HH and LL plots, respectively (Fig. 3, bottom panel).

Discussion

In this study we investigated the role of past and current grazing regimes on grassland soil nematofauna. We found that: *i*) the free-living nematofauna community patterns were determined by both present and past grazing regimes

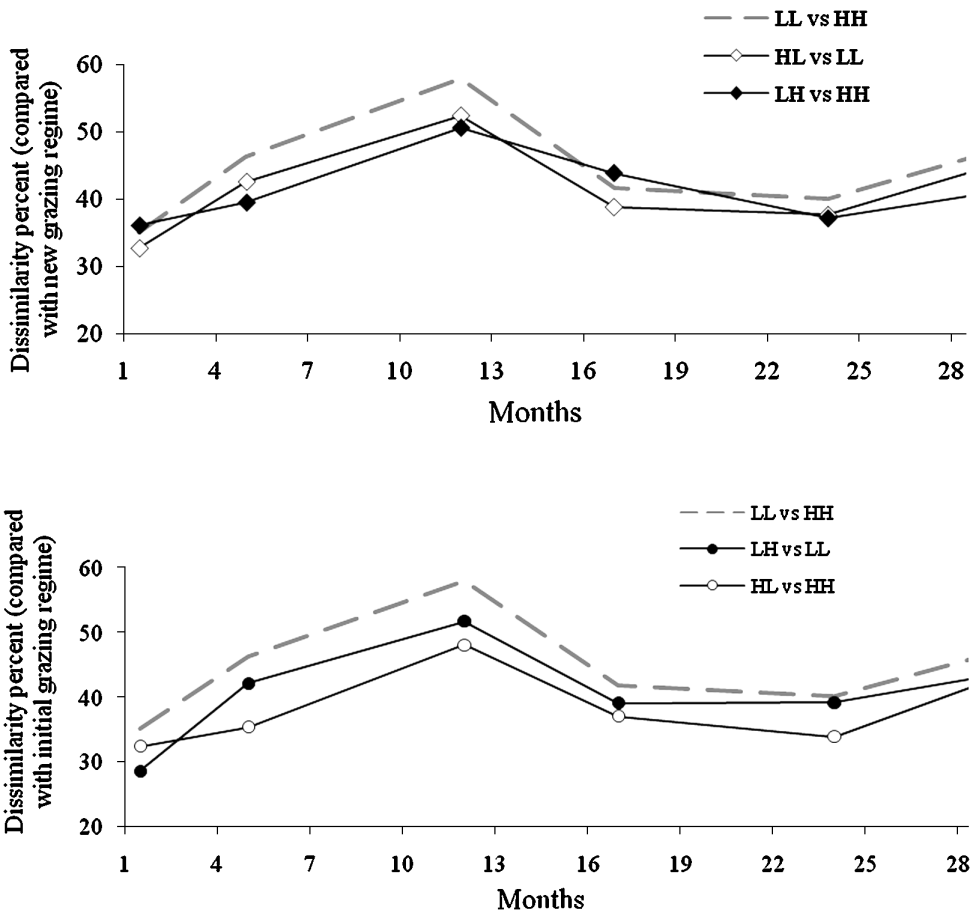

Fig. 3. *Temporal changes in the dissimilarity percentage between the nematode community structure for: top) mesocosms submitted to a change in above-ground grazing regime and control ones submitted to the past grazing regimes (●: LH* vs *LL treatments; and ○: HL* vs *HH treatment), and bottom) mesocosms submitted to a change in grazing regime* vs *control ones submitted to the new grazing regime (◆: LH* vs *HH treatments; and ◇: HL* vs *LL treatments). The dissimilarity percentages between the two controls (LL* vs *HH) are presented for comparison.*

during the two-year period after switching the grazing regime; and *ii*) the application of a high grazing regime on a previously less grazed system led to a faster response of the nematofauna than termination of grazing on a previously highly grazed system.

Effect of the past grazing regime

The two pre-experimental grazing regimes, whilst characterised by comparable total nematode abundance, led to significantly different nematode community structures. In several experiments, free-living nematode abundances have been found to be unrelated to the grazing regimes (Smolik & Dodd, 1983; Wall-Freckman & Huang, 1998; Wang *et al*., 2006) but sometimes grazing also increased the nematode abundance (Bardgett *et al*., 1997; Schon *et al*., 2010). In our case, relative abundances provided a better insight of nematode community response to above-ground grazing. The fungal-fed decomposition pathway appeared more important in the low-grazing pre-experimental intensity grassland than in that subjected to high-grazing intensity. This is in accordance with observations that disturbed grassland soils tend to develop a faster decomposition pathway by promoting opportunist/competitive plant species that fuel a regular/faster return of nutrient-rich dead organic matter to the soil (Lavorel *et al*., 2004; Loiseau *et al*., 2005). Since the CI difference was mainly due to a difference in abundance of bacterivorous Rhabditidae, we would hypothesise that

Rhabditidae may indicate the faster nutrient dynamic that occurred in the pre-experimental high grazing grassland. Concordantly, the constant-low grazing treatment (LL) was characterised by higher relative abundance of fungal-feeding nematodes, lower relative abundance of bacterial-feeding nematodes, lower NCR and higher CI than soils that experienced high grazing (HH, HL, LH). When comparing with Klumpp *et al*. (2007a), who worked with the same samples, CI seems to follow net ecosystem productivity.

Finally, when looking at herbivorous nematodes, facultative root feeders were more abundant in plots characterised by past low grazing. Accordingly to other findings (Mikola *et al*., 2001a; Klumpp *et al*., 2009) it appears that, in the mid-term at least, past low grazing can affect root-feeding populations by decreasing the quantity of live roots available.

Effect of the current grazing regime

The two current grazing regimes, whilst characterised by comparable total nematode abundance, also influenced the switched plots as showed by the PERMANOVA, the PCA and the percentage of dissimilarity between the communities. In our case, significant effects on nematode community structure were only noticed when intensive grazing was applied to a previously extensively grazed system. The percentage of dissimilarity between plots that experienced previous high grazing (HH *vs* HL) remained lower than between plots that experienced low grazing (LL *vs* LH). Accordingly, cessation of grazing on a previously grazed system (HL *vs* HH) led to fewer modifications of nematode taxa abundances and no significant effects at the community scale.

The key change due to grazing intensification (LL *vs* LH) within the nematode community was the decrease of the relative abundance of fungal-feeding nematodes which consequently promoted NCR. Of note is the fact that the relative abundance of bacterial-feeding nematodes did not increase significantly, yet the abundance of the dominant bacterial-feeding nematode *Plectus pusillus* increased significantly after application of grazing of previously ungrazed mesocosms. Since the abundance of *Plectus* sp. had been previously correlated with higher soil C and N (Liang *et al*., 2005) and because it is significantly higher in plots that experienced high-grazing (HH, HL and LH), *P. pusillus* could indicate past or present intensive management (both in term of quantity of resource that enters the soil and turnover). This hypothesis, however, contrasts with the EI results. Since the EI of the two shifted treatments are different from those of constant-low and constant-high grazing, this clearly illustrate a change of resource availability. Yet, the EI of the putatively 'enriched' plots (LH) were the lowest and that of HL plots the highest – which was unforeseen. The higher abundance of opportunistic Rhabditidae (*Bursilla monohystera* and *Protorhabditis oxyuroides*) in HL plots explains the significant effects observed. We would have expected a high abundance of Rhabditidae in grazed treatments (*e.g*., LH) since such enrichment opportunist nematodes usually respond positively to such enrichment (Ferris *et al*., 2001; Mikola *et al*., 2001b). Rhabditidae have already been found more numerous under non-grazed grassland (Wang *et al*., 2006); hence, it appears that an interaction occurred between the past and the present effects of grazing management, leading to an unpredictable EI and forecast of enrichment opportunist guilds. In our case, even though NCR does not account for c-p classes, it seemed clearly able to discriminate the enrichment of the environment when switching from low to high grazing.

Nematode community, plant cover characteristics, soil organic carbon content and microbial community patterns

Working with the same samples, Klumpp *et al*. (2007a) found that after 12 months LH plots lost on average 43% root biomass in comparison with LL, whilst HL plots gained on average 28% root biomass in comparison with HH. This result shows differential root biomass dynamics according to the direction of the grazing regime switch but also points out potential alteration of root quality that could occur. Indeed, root feeders are influenced by species composition and development stages of plants (see, for example, Verschoor, 2001). Besides, when studying defoliation intensity effects on soil food web, Mikola *et al*. (2001a) found that decreased root biomass induced by increasing intensity of defoliation was probably compensated by improved root quality which, in turn, supported root-feeding nematodes. In our case, since root biomass of plots that were submitted to a grazing shift were statistically similar, the significant difference observed between LH and HL treatments for root-feeding nematodes could reflect past plant species composition effect on the quality of roots that were produced after a switch of grazing regime.

Furthermore, free-living nematode community patterns depend both directly and indirectly on the microbial compartment (Wardle, 2002; Villenave *et al*., 2004). Working with the same samples, Attard *et al*. (2008) found that the

application of high grazing to pre-experimental low grazing plots (LH) induced a change in the structure of the whole soil bacterial community within 5 months, whereas changes were observed only at 12 months when the grazing shift had been operated in the other direction (HL). These results appear compatible with the nematode community structure changes we observed. However, during the 2 years of the experiment, it was not possible to measure significant changes in the nematode taxa or trophic group abundance between dates. The number of replicates (four) seemed too low (according to the variability of the composition of the initial nematofauna in each plot) to allow the measurement of significant changes in a few months. It seems that the main changes in nematode community structure occurred very rapidly after application of the grazing regime (1-6 months). After application of high grazing to pre-experimental low grazing (LH) plots, induced bacterial community structure changes occurred prior to changes in plant species composition and soil organic carbon content.

Two important plant parameters were determined by past grazing regimes during the two-year period after changes in grazing regime: net ecosystem productivity and net below-ground carbon storage were significantly higher for ecosystems previously submitted to a low (LL and LH) rather than a high (HH and HL) grazing regime, irrespective of the grazing level during the experiment (Klumpp *et al*., 2007b). By contrast, above-ground net primary productivity was significantly affected by the present grazing regime and was enhanced in grazed monoliths during the experiment. Moreover, it showed faster response to increasing than to decreasing grazing level during the experiment (Klumpp *et al*., 2007b). Since, nematofaunal community structure was found to follow the same trend its measured and/or calculated changes would be able to reflect the 'immediate' above-ground primary production potential.

Conclusion

This study shows that grassland soil nematofauna responded faster and more markedly to the application of intensive grazing regime on a previously extensively exploited system than the other way round. In addition, nematofauna community structure was determined by both the past and current grazing regimes, and this occurred during the two years of monitoring. Observed effects on soil microbivores seemed able to reflect the 'immediate' above-ground primary production potential and to follow microflora dynamics. By contrast, observed effects on root-feeding nematodes seemed to reflect the 'balance' effects of past and current grazing regimes on plant community root biomass and quality.

Acknowledgements

This work was supported by the French Programme ECCO-PNBC "Géotraits" and by the Agence de l'Environnement et de la Maîtrise de l'Energie (ADEME, France) by the programme "Nemageco-Icones". We thank all contributors who carried out data acquisition, especially Cyril Blanc.

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Appendix A. *Mean nematode taxa densities (ind. (100 g dry soil)$^{-1}$) and standard errors (SE) of trophic groups (type) and their coloniser-persister scale (c-p) in the different treatments after the change in the above-ground grazing regime.*

	Type[1]	c-p	Treatment							
			LL[2]		LH		HL		HH	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Filenchus (*vulgaris* and *baloghi*)	Frf	2	76.6	10.9	65.9	8.9	58.8	8.6	58.4	9.4
Aglenchus agricola	Frf	2	37.7	8.0	51.6	8.2	18.2	3.9	23.5	5.8
Boleodorus (*thylactus* and *volutus*)	Frf	2	23.6	5.6	26.4	7.2	18.6	4.6	16.5	3.8
Tylodoridae	Frf	2	3.8	1.2	4.8	1.5	4.8	1.3	2.8	1.1
Helicotylenchus (*digonicus* and *pseudorobustus*)	Orf	3	60	13.5	105.5	25.6	131.8	24.4	118.8	23.7
Paratylenchus (*nanus* and *macrodorus*)	Orf	2	14.4	4.3	14.7	3.8	11.2	2.9	13	3.0
Pratylenchus crenatus	Orf	3	9.6	2.5	6.3	1.8	20.4	4.7	16.8	5.3
Pungentus sp.	Orf	4	10.6	2.5	9.1	2.4	4.5	1.9	0.8	0.5
Amplimerlinius sp.	Orf	3	5.2	2.2	8.5	2.6	6.8	2.6	4.6	1.6
Axonchium sp.	Orf	5	4.1	1.3	4.6	2.0	3.6	1.2	2.8	1.1
Xiphinema sp.	Orf	5	5.6	3.4	4.4	1.7	0.0	0.0	0.6	0.5
Longidorus sp.	Orf	5	4.1	1.3	3.2	1.6	0.3	0.2	1.8	0.7
Plectus pusillus	Ba	2	30.7	12.5	95.3	34.5	88	28.0	125.3	38.8
Acrobeloides nanus	Ba	2	105.1	19.5	102	19.1	65.2	11.7	60.9	9.6
Rhabditidae (*Bursilla monohystera* and *Protorhabditis oxyuroides*)	Ba	1	40.9	12.9	21.6	5.7	79.4	32.5	49.1	10.6
Eucephalobus and *Heterocephalobus*	Ba	2	39.2	6.6	53.3	13.3	42.9	9.2	43.3	8.2
Dauerlarvae	Ba	1	25.7	7.8	11.0	2.9	45.7	11.8	48.8	13.0
Anaplectus porosus	Ba	2	23.4	4.2	21.4	3.5	30.8	7.0	37.4	11.2
Plectus tenuis	Ba	2	17.5	5.3	20.2	4.4	18.3	3.6	22.9	5.7
Rhabdolaimus sp.	Ba	3	13.5	4.1	20.7	6.5	29.0	9.1	13.2	4.5
Odontolaimus chlorus	Ba	3	10.0	3.5	18.5	5.2	9.0	4.4	7.1	2.4
Prismatolaimus dolichorus	Ba	3	8.5	2.6	7.6	3.3	9.9	4.5	10.1	5.8
Acrobeles mariannae	Ba	2	0.2	0.2	0.2	0.2	13.7	4.6	16.8	6.2
Aphanolaimus sp.	Ba	3	3.6	1.4	7.9	1.8	10.0	2.9	7.7	3.0
Cervidellus sp.	Ba	2	11.7	4.8	7.7	3.4	6.0	4.3	2.2	0.8
Tylocephalus auriculatus	Ba	2	3.3	1.5	3.7	1.8	5.2	1.4	1.0	0.5
Monhystera sp.	Ba	2	2.8	1.1	0.6	0.3	4.7	1.4	4.4	1.7
Aphelenchus avenae	Fu	2	40.8	7.2	22.7	4.8	20.0	5.1	23.9	5.3
Aphelenchoides sp.	Fu	2	23.1	4.1	20.3	4.5	15.2	5.2	16.4	3.2
Ditylenchus sp.	Fu	2	15.8	4.8	7.6	2.0	9.3	4.5	6.6	1.9
Diphtherophora communis	Fu	3	12.1	2.8	5.1	1.2	9.0	3.2	10.3	2.9
Thornematidae	Om	5	4.1	1.3	5.0	1.4	3.8	1.5	4.0	1.5
Enchodelus sp.	Om	4	5.7	2.3	3.5	1.5	1.1	0.5	4.3	1.8
Aporcellaimellus sp.	Pr	5	25.2	6.0	30.5	5.4	33.0	7.6	27.6	6.8
Mylonchulus stigmaturellus	Pr	4	6.5	2.2	13.6	4.3	19.7	8.7	14.0	5.2
Tripyla filicaudata	Pr	3	13.5	4.0	9.6	3.1	10.7	4.3	12.3	4.9
Mylonchulus stigmaturus	Pr	4	4.5	1.7	13.4	4.2	6.4	2.1	8.3	2.2
Anatonchus tridentatus	Pr	4	1.8	0.9	4.4	2.2	1.0	0.5	0.3	0.2
Others[3]			12.6	2.6	14.9	4.7	15.3	2.8	8.6	2.2

[1] Type (trophic group): Ba, bacterial feeders; Fu, fungal feeders; Frf, facultative root feeders; Orf, obligate root feeders; Om, omnivores; Pr, predators.

[2] LL, constant low grazing; LH, shift to high grazing; HH, constant high grazing; HL, shift to low grazing.

[3] Others include the taxa *Alaimus*, Brevibuccidae, Bunonematidae, Chromadoridae, Criconematidae, *Diploscapter*, *Dorylaimoides*, *Epidorylaimus*, *Eudorylaimus*, *Hoplotylus*, *Lelenchus*, *Nygolaimus*, Onchulidae, *Paravulvus*, *Rotylenchulus*, *Seinura*, *Thonus*, *Trichodorus* and *Wilsonema.*