

# Cattle grazing increases microbial biomass and alters soil nematode communities in subtropical pastures

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## Abstract

This study focused on examining the impacts of cattle grazing on belowground communities and soil processes in humid grasslands. Multiple components in the soil communities were examined in heavily grazed and ungrazed areas of unimproved and improved bahiagrass (*Paspalum notatum* Flugge) pastures in south-central Florida. By using small (1-m × 1-m) sampling plots, we were able to detect critical differences in nematode communities, microbial biomass, and mineralized C and N, resulting from the patchy grazing pattern of cattle. Soil samples were collected on three occasions between June 2002 and June 2003. Microbial C and N were greater ( $P \leq 0.01$ ) in grazed than in ungrazed plots on all sampling dates. Effects of grazing varied among nematode genera. Most genera of colonizer bacterivores were decreased ( $P \leq 0.10$ ) by grazing, but more persistent bacterivores such as *Euteratocephalus* and *Prismatolaimus* were increased, as were omnivores and predators. Higher numbers of persisters indicated that grazing resulted in a more structured nematode community. Some herbivores, particularly Criconeematidae, were decreased by grazing. Abundance of omnivores, predators, and especially fungivores were strongly associated with C mineralization potential. Strong correlation of microbial C and N with nematode canonical variables composed of five trophic groups illustrates important links between nematode community structure and soil microbial resources. Including the analysis of nematode trophic groups with soil microbial responses reveals detection of grazing impact deeper into the hierarchy of the decomposition process in soil, and illustrates the complexity of responses to grazing in the soil foodweb. Although highly sensitive to grazing impacts, small-scale sampling could not be used to generalize the overall impact of cattle grazing in large-scale pastures, which might be determined by the intensity and grazing patterns of various stocking densities at the whole pasture level.

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**Keywords:** Microbial C; Microbial N; Mineralization; Nematode community structure; Soil food web; Small-scale sampling

## 1. Introduction

Grazing of grassland by large herbivores can have substantial indirect effects on soil organisms, and might have significant impact on plant productivity and community structure (Bardgett et al., 1998). Sustained productivity in grazing systems, including efficient recycling of nutrients and minimizing nutrient loss, depend upon soil biological processes and the interaction between grazing, nutrient mineralization, and soil biological communities

(Yeates et al., 1997). Studies of the influence of domestic livestock on soil biological processes and communities in managed grasslands have produced contradictory results, indicating that more studies need to be done under a range of environmental and climatic conditions so that reasons for discrepancies among current studies may be resolved.

Results from research examining the impact of grazing on nematode communities have been mixed. Bardgett et al. (1997) observed declines in nematode abundance following cessation of grazing in upland pasture, which they attributed to declines in microbial abundance as a food source for many microbivorous nematodes. They also observed that grazing more than doubled nematode abundance at some locations but not others, which they

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attributed partly to differences in soil type and vegetation. Similarly, Freckman et al. (1979) observed a greater abundance of nematodes in a grazed than in an ungrazed grassland. However, Stanton et al. (1984) detected no differences in nematode communities between long-term grazed and ungrazed treatments, and heavy grazing by cattle had no effect on nematode biomass or seasonal densities (Smolik and Dodd, 1983). On the other hand, Wall-Freckman and Huang (1998) found that even though grazing treatments had no effect on nematode absolute abundances, they influenced the percent contribution of fungal-feeding nematodes, which were higher in long-term grazed than in an ungrazed treatment. In other studies, heavy grazing by sheep (30/ha) reduced nematode abundance (King and Hutchinson, 1976, 1983), as did mowing to simulate grazing (Todd, 1996), but grazing by prairie dogs increased abundance of plant-parasitic nematodes (Ingham and Detling, 1984). Yeates and King (1997a) reported that percentage of bacterivorous nematodes was greater in an ungrazed grassland than in a grazed grassland. In a similar study (Yeates and King, 1997b), no differences were observed in nematode diversity between ungrazed native and improved grassland (changes in vegetation and fertilization), but a loss of plant-feeding species coupled with a marked increase in microbial-feeding species resulted in a lower total nematode maturity index ( $\Sigma$ MI) in the improved grassland. The variable results obtained in previous studies make it difficult to predict impacts of grazing on soil nematode communities.

Soil microbial biomass does not respond in a uniform way to herbivory by livestock or other large grazers in grazed ecosystems and has been observed to increase or decrease in response to grazing of the plant community (Bardgett and Wardle, 2003). Grazing livestock increase incorporation of surface litter into the soil, which can increase total soil organic matter. Furthermore, herbivory can increase root exudation of labile C compounds, which can stimulate growth of the rhizosphere microbial community (Bardgett et al., 1998; Holland et al., 1996; Yeates et al., 1997; Hamilton and Frank, 2001). Bardgett et al. (1997) showed that microbial biomass increased with increasing intensity of sheep grazing and declined following cessation of grazing. In other studies grazers either reduced microbial biomass or had no effects on microbial biomass (Harrison and Bardgett, 2004; Sakaran and Augustine, 2004; Tracy and Frank, 1998). Bardgett and Wardle (2003) proposed that positive, negative, or neutral effects from grazing on soil biota and ecosystem function are possible depending upon the balance of these effects. They suggested that positive effects are most common in ecosystems of high soil fertility, whereas negative effects are most common in unproductive ecosystems. However, mammalian grazing for two years in semiarid grassland in Kenya decreased soil microbial biomass in sites of both high and low fertility, despite the fact that grazing stimulated aboveground production in nutrient-rich sites and depressed it in nutrient-poor sites (Sakaran and

Augustine, 2004). Therefore, there is a need to examine the response of the soil microbial biomass to grazing under different climatic and soil conditions.

Previously, studies of the impact of cattle grazing densities on nematode communities in subtropical rangelands in south-central Florida showed that nematode communities were influenced more by rainfall (McSorley, 1996), season, and pasture types (McSorley and Frederick, 2000) than by cattle stocking densities. The lack of effect from stocking densities was surprising, since it is expected that any disturbance that influences the food source or environment of nematodes will be reflected in the abundance and composition of the nematode communities (Wasilewska, 1989). It is anticipated that cattle grazing should increase the input of organic matter into the soil, increase microbial activities, and thus enhance microbial feeding nematodes. However, cattle often graze discontinuously and create small-scale patchiness in vegetation that may influence the spatial distribution of belowground communities and processes. Under these conditions, it is possible that the common soil sampling practice of collecting and compositing systematic soil cores from a given area may not be adequate for assessing the impact of grazing because soil from intensively grazed and less intensively grazed grass patches are mixed together. Similar concern about the heterogeneity within ecosystems has been raised by Augustine and Frank (2001) and by Bardgett and Wardle (2003). Therefore, in the current project, the impact of cattle grazing on nematode communities and labile C and N pools was investigated in small-scale plots ( $1 \times 1 \text{ m}^2$ ) in heavily grazed and completely ungrazed pasture areas to pinpoint grazing effects in a heterogeneous environment. Soil samples were taken following three grazing seasons to examine the consistency of grazing impact. The specific objective of this study was to determine the effect of cattle grazing on nematode communities, microbial biomass, and readily mineralizable pools of C and N. In addition, we examined whether grazing had predictable effects on different groups of nematodes and whether these effects could be linked to changes in soil organic matter and, in particular, to microbial biomass and rapidly cycling pools of C and N.

## 2. Materials and methods

### 2.1. Site description

The study was conducted at the MacArthur Agro-Ecology Research Center at Buck Island Ranch located in Highlands County, Florida ( $27^{\circ}09'N$ ,  $81^{\circ}11'W$ ). Soil samples were collected from heavily grazed and ungrazed sites on three sampling dates at termination of three successive grazing seasons. Two sets of samples (6 June 2002, 3 June 2003) were collected from the semi-native pasture that has never been fertilized, was dominated by a mixture of bahiagrass (*Paspalum notatum* Flugge) and native grasses, mainly blue stem (*Andropogon* spp.),

Table 1  
Seasonal changes in some soil physical and microbiological properties and grass height as affected by grazing in improved and semi-native pastures at Buck Island Ranch, south Florida

Soil variable <sup>a</sup>	Grazing treatment					
	Semi-native pasture 6 June 2002		Improved pasture 19 November 2002		Semi-native pasture 3 June 2003	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Bulk density (g cm <sup>-3</sup> )	1.07 <sup>b</sup>	1.03	0.99	0.84**	1.01	1.00
Water content (%)	0.14	0.14	0.38	0.35 <sup>@</sup>	0.35	0.33 <sup>@</sup>
Organic matter (%)	12.27	10.82	15.22	10.47**	12.24	10.84
Grass height (cm)	6.32	23.75*** <sup>c</sup>	10.72	33.52***	22.38	40.12***
Inorganic N (μg g <sup>-1</sup> )	2.56	3.04	1.67	2.21	1.79	1.91
Microbial N (μg g <sup>-1</sup> )	64.47	37.04*	135.64	63.14***	104.70	51.80**
N <sub>min</sub> (μg g <sup>-1</sup> )	4.89	4.75	8.85	12.65	0.93	6.10 <sup>@</sup>
Microbial C (μg g <sup>-1</sup> )	292.14	209.62*	781.15	355.60***	697.91	331.73**
C <sub>min</sub> (μg g <sup>-1</sup> )	102.75	69.38 <sup>@</sup>	236.80	165.15*	285.86	253.66

<sup>a</sup>N<sub>min</sub> and C<sub>min</sub> are N and C mineralization potential determined as N and C mineralized in 10-day aerobic laboratory incubations.

<sup>b</sup>Values represent means of the measured grass and soil variables (N = 10).

<sup>c</sup>Values followed by <sup>@</sup>, \*, \*\* or \*\*\* indicate significant differences between grazed and ungrazed treatments within a date at P ≤ 0.10, 0.05, 0.01 and 0.001, respectively according to analysis of variance.

*Panicum* spp., carpet grass (*Axonopus* spp.), and grazed primarily during the winter months (November–April). One set of samples (19 November 2002) was collected from an improved pasture that was historically (since 1996) fertilized, planted primarily with bahiagrass, and grazed mainly during the summer months (May–October). The dominant soil type in the improved pastures was a siliceous, hyperthermic Arenic Endoaqualfs, while that in the semi-native pastures was a loamy, siliceous, hyperthermic Arenic Glossaqualfs (United States Department of Agriculture, 1989). These soils have an A horizon consisting of loose friable fine sand ranging in depth from 10 to 30 cm with a pH of 4–6.5, and a light gray acidic E horizon consisting of single-grained fine sand and ranging in depth from 10 to 45 cm. A detailed account of the general site characteristics and pedon descriptions is provided by Gathumbi et al. (2005). As typical of grazing practices in south-central Florida, cattle were rotated from semi-native pasture in the winter to improved pasture in the summer, due to the extreme wet condition in the semi-native pasture during the summer. The sampling times selected were at the end of grazing cycles in improved (November) and semi-native (June) pastures.

Soils from grazing treatments were collected from pastures with 35 cow–calf pairs per pasture (or 1.73 and 1.08 cow–calf units per ha for improved and semi-native pastures, respectively), while those from the control treatment (no grazing) were collected from pastures that had not been grazed since 1996. Ten individual samples from 1 m × 1 m quadrats (plot) were collected for each grazing treatment at the end of a grazing cycle. These individual sampling plots were spaced along a transect, with each plot spaced 5 m from the center of the previous plot. Sampled plots consisted entirely of bahiagrass and samples were taken at least 1 m away from any visible

manure deposition. In grazed plots, all of the grass within the 1-m × 1-m plots had been grazed, which was clearly observed from the clipped leaf blades remaining after browsing by cattle. There was no evidence of any grazing (even by wildlife) in ungrazed plots. Soil and moisture conditions were relatively constant among plots as well (Table 1). Sites were carefully chosen so that the botanical composition (bahagrass) was not different between grazed and ungrazed plots. The sampling was conducted three times, following termination of grazing cycles (19 November 2002 in improved pasture, 6 June 2002 and 3 June 2003 in semi-native pasture). At the time of sampling, the height of grass was measured at four locations within each quadrat to obtain an average height per plot. A composite soil sample consisting of 12 cores (2.5 cm diameter × 20 cm deep) was collected from each plot. Each composite soil sample was placed into a plastic bag, mixed thoroughly, and divided into two portions. Approximately one-half of each sample was retained at the MacArthur Agro-Ecology Research Center for analysis of soil inorganic N fractions, microbial biomass C and N, soil organic matter, and bulk density. The remainder of each sample was transported in an insulated cooler to the University of Florida in Gainesville, FL, for extraction of nematodes.

## 2.2. C and N assays

Soil inorganic N (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N) was determined in field moist soil for all samples. Approximately 10 g of soil was extracted using 2 M KCl (4:1 extractant:soil), shaken for 1 h, and then filtered. The filtrate was analyzed for NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N on an air-segmented continuous flow autoanalyzer (Alpkem Corp., Clackamas, OR). Microbial biomass C and N were measured in field moist soils using a chloroform fumigation incubation method

(Brookes et al., 1985; Vance et al., 1987; Horwarth et al., 1996; Harris et al., 1998). The microbial biomass C (MBC) was calculated using the method of Horwarth et al. (1996), and microbial biomass N as described by Harris et al. (1998). The chloroform fumigation incubation method also provides a measure of C and N mineralization potential, which here refers to the amount of C and N mineralized during the 10-day incubation of control (unfumigated) samples in the laboratory. Soil organic matter was determined by the loss-on-ignition method (450 °C for 16 h).

### 2.3. Nematode assay

For nematode extraction, a 100-cm<sup>3</sup> subsample was removed from each sample, suspended in 1.7 L water, and passed through a sieve with 38- $\mu$ m openings. Nematodes and debris remaining on the sieve were then separated by centrifugation (Jenkins, 1964). Extracted nematodes were identified to genus in most cases (exceptions were Rhabditidae and some Tylenchidae and Neotylenchidae) and counted under an inverted microscope. Nematodes were assigned to five trophic groups (bacterivores, fungivores, herbivores, omnivores, predators) based on Yeates et al. (1993), except that *Filenchus*, *Tylenchus*, and related Tylenchidae were classified as fungivores based on more recent literature (McSorley and Frederick, 1999; Okada and Ferris, 2001). Several indices of nematode community structure were also calculated, including richness, determined as the total number of different taxa reported per sample; dominance, computed as Simpson's (1949) index ( $\lambda$ ), across the range of genera present; and diversity, computed as  $1/\lambda$ . Ratios of fungivores ( $F$ ) to bacterivores ( $B$ ) were calculated, both as  $F/B$  (Freckman and Ettema, 1993) and as  $F/(F+B)$  (Neher, 1999). The maturity index (MI) as refined by Yeates and Bird (1994) was calculated as the weighted average of colonizer–persister ( $c-p$ ) values for each taxon according to the 1 to 5  $c-p$  scale defined by Bongers and Bongers (1998). Nematodes were assigned to guilds according to trophic groups and  $c-p$  values (Bongers and Bongers, 1998) for calculation of three additional indices defined by Ferris et al. (2001). These include the enrichment index (EI), emphasizing the importance of nematode guilds that quickly respond to nutrient enrichment of the soil food web; structure index (SI), emphasizing the more persistent members of the nematode community; and channel index (CI), emphasizing the relative roles of fungivores and bacterivores in decomposition (Ferris et al., 2001).

All data were analyzed by one-way analysis of variance (ANOVA) using SAS software (SAS Institute Inc., Cary, NC) to compare differences between grazed and ungrazed plots at each sampling date. Data were transformed if necessary according to Steel and Torrie (1980), but untransformed means are presented. Data on nematode abundance were log-transformed by  $\log_{10}(x+1)$ , whereas the percentages that were consistently less than 20%

(% fungivore in 2001, and % omnivores and predators in both years) were square-root transformed by  $\sqrt{(x+0.5)}$  prior to ANOVA. Analyses for most of the community indices were based on their true means except for the  $F/B$  and  $F/(F+B)$  in 2001 which were arcsine transformed by arcsine ( $\sqrt{x}$ ) since very small values were involved. However, in all cases untransformed means are presented in tables.

### 2.4. Relationship between nematode community and soil C and N

To further investigate relationships between nematodes and soil C and N forms, canonical correlation analyses (Ludwig and Reynolds, 1988) were performed on the entire data set, using the CANCECORR procedure of SAS (SAS Institute Inc., Cary, NC). The canonical correlation analysis examined associations between C and N (C–N) forms and nematode trophic groups. The C–N forms investigated included total inorganic N, microbial biomass N and C, and mineralization potential of N and C in 10-day laboratory incubations. Nematode trophic groups consisted of the abundance of bacterivores, fungivores, herbivores, omnivores, and predators.

## 3. Results

### 3.1. Impact of grazing on soil C and N

Grass was much taller ( $P \leq 0.001$ ) in ungrazed plots than in grazed plots on all sampling dates, providing a good indication of grazing intensity in the sampling plots (Table 1). For the semi-native pastures, the lower grass heights in 2002 than in 2003 were likely due to the fact that the pastures were burned in February 2002 and thus the grass height measurement represents only 4 months of growth during the late winter/spring dry season. Grass productivity was not determined at the sampling locations, but larger scale sampling across the pastures examined in this study showed that cattle in the grazed pastures utilized about 30–35% of the available forage in improved and seminative pastures in 2002 (Arthington et al., unpublished data). Averaged over 3 production cycles, forage availability at the end of the grazing cycle in the improved pastures was 2.6 and 3.8 Mg ha<sup>-1</sup> for highly grazed and ungrazed pastures respectively, while the corresponding values for semi-native pasture were 2.3 and 3.1 Mg ha<sup>-1</sup> (Arthington et al., unpublished data).

Microbial biomass C and N were, in most sampling dates, nearly two times greater in heavily grazed than in ungrazed pastures in both improved and semi-native pastures areas (Table 1). Carbon mineralization potential also tended to be greater in grazed than ungrazed pastures in 2002, although the differences were not as great as for microbial biomass C. Nitrogen mineralization potential in lab incubations was usually not affected by grazing, although it tended to be higher ( $P \leq 0.10$ ) in ungrazed than

grazed semi-native pastures in June 2003 (Table 1). Soil organic matter was greater in grazed than ungrazed improved pastures in November 2002, but did not differ between grazed and ungrazed semi-native pastures. Bulk density was only different between grazed and ungrazed plots on 19 November 2002.

### 3.2. Impact of grazing on nematode communities

Many nematode genera were affected by grazing, although results were often inconsistent across sampling dates, although some trends were apparent (Table 2). When they were affected by grazing ( $P \leq 0.10$ ), omnivore and predator genera were always more abundant in grazed plots. On the other hand, some herbivores, such as *Helicotylenchus* and members of the Criconematidae (*Criconema*, *Hemicycliophora*, *Hemicriconemoides*, *Mesocriconema*) tended to be more abundant in ungrazed plots (Table 2), but *Tylenchorhynchus* was more abundant in the grazed plot on one occasion. When affected by grazing, many of the bacterivores in guilds Ba<sub>1</sub> and Ba<sub>2</sub> (bacterivores with *c-p* values of 1 and 2, respectively) except for *Acroboloides*, *Chronogaster*, and *Turbatrix*, were more abundant in ungrazed than grazed plots, but usually on only one sampling date (Table 2). *Cervidellus* showed the most consistency in greater abundance in ungrazed plots. Bacterivores in guild Ba<sub>3</sub> (*Euteratocephalus* and *Prismatolaimus*) were more abundant in grazed plots on two different sampling dates, once in improved and once in semi-native pastures. *Chronogaster* (guild Ba<sub>2</sub>) showed a trend similar to bacterivores in guild Ba<sub>3</sub>.

Among the indices of nematode community structure, maturity index, enrichment index, and structure index were most consistently affected ( $P \leq 0.10$ ) by grazing (Table 3). Enrichment index was lower in grazed than in ungrazed plots on two sampling dates and structure index was increased ( $P \leq 0.10$ ) by grazing on all three sampling dates. Maturity index was increased by grazing, except on 6 June 2002 when the opposite trend occurred (Table 3).

### 3.3. Relationship between nematode community and C and N forms

When data were pooled across grazing treatments and sampling dates, the first canonical correlation between nematode trophic groups and C–N forms was highly significant ( $P \leq 0.001$ , Table 4), indicating a strong association between nematodes and soil C or N forms. The high value of the standardized coefficient for fungivores in the canonical variable for nematode trophic groups (0.620) indicates the importance of the fungivore trophic group in the association between nematodes and C–N forms. While coefficient for canonical variable and the correlation coefficient are independent of each other, the high correlation ( $r = 0.748$ ) between fungivores and the first canonical variable for C–N forms further supports this trend (Table 4). Bacterivores, omnivores, and predators

also showed significant correlation with the canonical variable of C–N forms (Table 4). Trends within the first canonical variable for C–N forms were much stronger for C mineralization potential than for other C–N forms, and the canonical variable of nematode groups were strongly correlated ( $r = 0.829$ ) with C mineralization potential (Table 4). Data from the canonical correlation between C and N forms and soil organic matter content showed that Microbial C and N were significantly correlated with organic matter content ( $r > 0.500$ , data not shown). However, no nematode trophic group was correlated with the soil organic matter content ( $r < 0.500$ , data not shown).

## 4. Discussion

### 4.1. Impacts of grazing on soil C and N pools

Microbial biomass C and N were strongly enhanced by grazing at this subtropical grassland in south-central Florida. Since grazing habits of cattle involve mostly grazing in patches rather than browsing over wide areas, heterogeneity of resources entering the soil is likely to create variability in grazing effects. In this experiment, the grazing impact was restricted to a small-scale sampling plot with a defined sample representing grazing at a high cattle-stocking density without any visible effect from current fecal deposits. In contrast, the ungrazed plots were taken from a fenced pasture that had not been grazed since 1996. The clear effect of grazing on increasing microbial biomass C and N on all sampling dates was expected for pastures in nutrient-rich soils. Grazing cattle incorporate organic matter as they trample plots, add labile inputs through urine and feces, and usually stimulate new root biomass, resulting in higher root/shoot as well as leaf: stem ratios, and possible greater exudation of labile C from roots (Milchunas and Lauenroth, 1993; Bardgett et al., 1998; Bardgett and Wardle, 2003; Sakaran and Augustine, 2004), all of which should result in an enhanced resource environment for microbial growth.

The consistent strong response of microbial biomass nutrients to grazing in this subtropical grassland is consistent with observations in temperate grasslands. Sheep grazing significantly increased microbial biomass in hill pasture in England, purportedly due to changes in the quality and quantity of detrital inputs to soil (Bardgett et al., 1997). Other workers have suggested that moderate grazing increases root exudation that may enhance microbial biomass activity in the field (Holland et al., 1996; Mawdsley and Bardgett, 1997). Hamilton and Frank (2001) demonstrated that clipping of grazing-tolerant grass promoted root exudation of C, which was quickly assimilated to the microbial population in the rhizosphere. Although we did not measure root production, exudation, or detrital quality in our plots, the large increases in microbial biomass nutrients in grazed plots indicate that grazing increased C availability to the soil microbial community either directly through increased inputs of

Table 2  
Effects of cattle grazing on numbers of nematode taxa in Buck Island Ranch, south Florida

Nematode taxa	<i>c-p</i> <sup>a</sup>	Nematodes/100 cm <sup>3</sup> soil					
		6 June 2002		19 November 2002		3 June 2003	
		Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
<b>Bacterivores</b>							
Diplogasteridae	1	2	0 <sup>@</sup>	34	30	2	6*
<i>Panagrolaimus</i>	1	0	4	1	8***	1	1
Rhabditidae	1	14	5	9	40**	34	68
<i>Turbatrix</i>	1	0	0	4	0**	0	2*
<i>Acrobeloides</i>	2	79 <sup>b</sup>	34* <sup>c</sup>	34	50 <sup>@c</sup>	65	113
<i>Acrobeles</i>	2	0	0	2	12 <sup>@</sup>	0	0
<i>Cephalobus</i>	2	4	1	0	1 <sup>@</sup>	0	0
<i>Cervidellus</i>	2	1	1	2	16**	1	10***
<i>Chronogaster</i>	2	1	0	22	5***	43	15**
<i>Eucephalobus</i>	2	6	3	34	30	41	24
<i>Monhystera</i>	2	0	0	1	1	5	2
<i>Plectus</i>	2	0	0	2	9*	9	9
<i>Tylocephalus</i>	2	0	0	0	0	0	4*
<i>Wilsonema</i>	2	0	0	14	5	0	0
<i>Zeldia</i>	2	3	0**	0	9**	0	6***
<i>Euteratocephalus</i>	3	0	0	10	0*	3	0 <sup>@</sup>
<i>Prismatolaimus</i>	3	2	1	13	5*	72	34**
<i>Rhabdolaimus</i>	3	0	0	0	0	8	2**
<i>Alaimus</i>	4	2	0**	0	0	0	0
Total		122	64**	150	206	307	326
<b>Fungivores</b>							
<i>Aphelenchoides</i>	2	2	3	13	24*	0	1
<i>Aphelenchus</i>	2	0	0	2	0	0	0
<i>Echphydophora</i>	2	8	3	1	1	18	67***
<i>Filenchus</i>	2	116	59*	57	49	213	282
Neotylenchidae	2	0	0	2	6*	48	28*
<i>Nothotylenchus</i>	2	0	0	0	2**	0	0
Tylenchidae	2	0	0	0	0	4	1 <sup>@</sup>
<i>Tylencholaimus</i>	2	0	0	0	0	4	5
<i>Tylenchus</i>	2	5	2	3	5*	14	10
<i>Diphtherophora</i>	3	0	0	0	0	2	0 <sup>@</sup>
Total		131	68*	79	89	306	396
<b>Herbivores</b>							
<i>Criconema</i>	3	0	0	5	13*	21	18
<i>Helicotylenchus</i>	3	11	41 <sup>@</sup>	8	11*	8	24
<i>Hemicycliophora</i>	3	0	0	3	20	0	5**
<i>Hemicriconemoides</i>	3	16	22	22	121***	41	47
<i>Meloidogyne</i>	3	0	0	2	3	12	4
<i>Mesocriconema</i>	3	4	9	24	33	0	24**
<i>Tylenchorhynchus</i>	3	126	114	96	12***	62	104
Tylenchulus	3	0	0	0	0	152	43
<i>Paratrichodorus</i>	4	0	0	7	5	0	0
Total		187	157	166	219	298	271
<b>Omnivores</b>							
<i>Eudorylaimus</i>	4	0	0	2	0***	3	2 <sup>@</sup>
Total		0	0	3	0**	4	3
<b>Predators</b>							
<i>Tobrilus</i>	5	0	0	0	0	6	2**
Total		1	0*	1	1	8	3**
Total nematodes <sup>d</sup>		420	313 <sup>@</sup>	402	523	930	1009

<sup>a</sup>Ranking of nematodes on a 1 (colonizer) to 5 (persister) scale according to Bongers and Bongers (1998).

<sup>b</sup>Values are means of 10 replications.

<sup>c</sup>Values followed by @, \*, \*\* or \*\*\* indicate significant differences between grazed and ungrazed treatments within a date at  $P \leq 0.10, 0.05, 0.01$  and  $0.001$ , respectively, according to analysis of variance on  $\log_{10}(x+1)$  transformed values.

<sup>d</sup>Total nematodes include unidentifiable nematodes as well as rare ( $< 2/100 \text{ cm}^3$  soil) taxa that were not affected by grazing.

Table 3  
Effects of cattle grazing on nematode community indices in Buck Island Ranch, south Florida

Nematode index <sup>c</sup>	6 June 2002		19 November 2002		3 June 2003	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
% Bacterivores	28.92 <sup>a</sup>	18.95 <sup>*b</sup>	39.06	39.19	33.58	32.28
% Fungivores	28.74	24.31	18.71	16.50	35.05	39.39
% Herbivores	35.60	48.61 <sup>*</sup>	40.21	42.49	29.03	26.76
% Omnivores	0.04	0.04	0.67	0.03 <sup>**</sup>	0.45	0.28
% Predators	0.10	0.02 <sup>*</sup>	0.30	0.14	1.05	0.26 <sup>**</sup>
<i>F/B</i>	1.05	0.89	0.54	0.50	1.17	1.40
<i>F/(F+B)</i>	0.50	0.50	0.32	0.31	0.50	0.55
Richness	17.00	13.00 <sup>**</sup>	21.00	23.00	28.00	30.00
Dominance	0.26	0.25	0.14	0.14	0.16	0.16
Diversity	4.09	4.26	8.19	8.85	6.91	6.78
MI	2.30	2.46 <sup>*</sup>	2.44	2.27 <sup>*</sup>	2.35	2.22 <sup>*</sup>
EI	48.04	49.78	39.75	55.36 <sup>**</sup>	45.00	51.57 <sup>@</sup>
SI	7.16	3.40 <sup>*</sup>	26.44	6.44 <sup>**</sup>	34.29	17.38 <sup>***</sup>
CI	66.10	67.78	53.72	35.88 <sup>*</sup>	76.82	63.13

<sup>a</sup>Values are means of 10 replications.

<sup>b</sup>Values followed by @, \*, \*\* or\*\*\* indicate significant differences between grazed and ungrazed treatments within a date at  $P \leq 0.10$ , 0.05, 0.01 and 0.001, respectively according to analysis of variance.

<sup>c</sup>*F* = fungivore, *B* = bacterivore, MI = maturity index, EI = enrichment index, SI = structure index, CI = channel index.

Table 4  
Canonical correlation between nematode trophic groups and carbon (C) or nitrogen (N) forms

Nematode trophic group	Coefficient for first canonical variable for nematode trophic group	Correlation coefficient between trophic group and canonical variable of C–N form
Bacterivores	0.055	0.635
Fungivores	0.620	0.748
Herbivores	0.074	0.386
Omnivores	0.335	0.648
Predators	0.193	0.474
C–N form	Coefficient for first canonical variable for C–N form	Correlation coefficient between C–N form and canonical variable of nematode group
Total inorganic N	–0.099	–0.203
Microbial N	–0.040	0.076
Mineralized N	0.018	–0.324
Microbial C	0.094	0.158
Potential C mineralization	0.976	0.829

First canonical correlation between nematode trophic groups and C–N forms = 0.835 ( $P \leq 0.001$ ).

waste products and litter or indirectly through altering C allocation or flows in the rhizosphere.

#### 4.2. Impact of grazing on nematode communities

In a previous study in the same pastures, relatively few effects of cattle density on nematode population levels were observed when relatively large (10 m × 10 m) plots were used (McSorley and Frederick, 2000). In the current study, which utilized small (1 m × 1 m) plots, differences ( $P \leq 0.10$ ) in population levels between grazed and ungrazed plots were observed for many different nematode genera. The contrasting results of the current study and previous work

with larger plots (McSorley and Frederick, 2000) suggest that impact of grazing on nematode communities occurs often within pastures but on a small local scale. Grazing is heterogenous in these highly productive subtropical pastures, with patches of intensively grazed areas interspersed with ungrazed patches. Random sampling across larger areas may include grazed, partially grazed, and ungrazed patches, providing overall average values that underestimate the influence of grazing on soil biological communities. The small plot size without the presence of cow dung for this grazing study also avoided confounding effects from organic input from cow dung, thus focusing on grazing impact alone.

If soil microbial C and N increased with grazing, one would expect to observe increased abundance of nematodes, if bottom up effects on the soil foodweb were significant. Results from other studies have been mixed but increases in microbial productivity do not always result in increases in the standing crop of microbial feeding nematodes (Mikola, 1999; Yeates et al., 1999a). In our study total nematodes numbers were not influenced by grazing but nematode with different  $c-p$  value were affected differently by grazing. Nematode persisters or  $k$ -strategists with  $c-p$  value  $\geq 3$  (which typically put maximum investment into survival), including omnivores, predators, and bacterivores in guild Ba<sub>3</sub>, were often more abundant in grazed plots. Possibly grazing assured a stable supply of nutrients and food sources for maintenance of these groups. In contrast, nematode  $r$ -strategists (which put maximum investment into fecundity) in guilds Ba<sub>1</sub> and Ba<sub>2</sub> tended to be more abundant in ungrazed plots. These trends are reflected in the enrichment index, which is driven by enrichment guilds including Ba<sub>1</sub>, and the structure index, which indicates a more structured nematode community with more persisters ( $k$ -strategists).

Mulder et al. (2003) did not find a pattern of differential grazing effects on nematodes with different  $c-p$  values. They reported that most omnivorous and predatory genera are highly sensitive to livestock densities, and that heavy grazing reduced the abundance of most nematodes in the Dutch Soil Quality Network sampling program, except for *Chiloplacus* (Ba<sub>2</sub>) and *Thonus* (P<sub>5</sub>). However, in that study low livestock density treatment was associated with an organic farming system, whereas the high-density treatment was associated with a conventional farming system using biocides and chemical fertilizers. Furthermore, landscape-scale constraints on soil organic matter content and plant production can have a greater effects than grazers on microbial abundance (Sakaran and Augustine, 2004), so it is possible that organic inputs confounded the influence of grazing in the Dutch grazing systems. It is possible that differences between our results and those from Mulder et al. (2003) were due to differences in sampling time, as well as to clear definition of grazed vs ungrazed plots. We took samples at the end of the seasonal cattle grazing cycles, when the cattle had just been transferred to other pastures. At this time, the grass height in grazed plots was significantly much shorter than in ungrazed plots, resulting in significant differences in niche conditions between the treatments. Lower EI and higher MI and SI in grazed plots than ungrazed plots suggested a nematode community in the grazed plots composed more abundant nematodes with higher  $c-p$  values, thus a more structured community than ungrazed plots.

The response of predatory nematode groups in our study did not necessarily coincide with population patterns of potential prey under our conditions. Abundance of the cephalobids (Ba<sub>2</sub>) which appear to be the “preferred prey” in some situations for predatory nematodes (Yeates and Wardle, 1996) was lower in grazed plots, but abundance of

omnivorous and predatory nematodes was higher in grazed plots. It is possible that populations of nematode predators and prey were out of sync due to successional processes or time lags in population dynamics. Wardle et al. (1995) reported that abundance of omnivores and predators was increased when their bacterivore prey had increased three months earlier. Alternatively, predator-prey interactions in nematode communities can result in top-down control of prey populations by top predators (Allen-Morley and Coleman, 1989; Mikola and Setälä, 1998), and increased predator abundance in grazed plots may have down-regulated populations of some microbial feeding groups. However, discrete sampling of populations in one point in time, such as in our study, does not necessarily provide adequate information for inferring predator-prey interactions in soil foodwebs.

Our observation that herbivores were lower in grazed plots whenever significant differences between treatments occurred, was consistent with results reported in several other studies (King and Hutchinson, 1976, 1983; Todd, 1996; Mulder et al., 2003) suggesting that heavy grazing was detrimental to herbivorous nematodes. In the current study this grazing effect is especially true for nematodes in the Criconematidae. An opposite trend was observed for *Tylenchorhynchus*, suggesting that possibly the sedentary behavior of Criconematidae contributed to their inability to search for new feeding roots after plants and roots were impacted from grazing.

#### 4.3. Relationships between nematodes and soil C and N

In general, the multivariate statistical analyses from this small-scale sampling project demonstrated that nematodes showed much stronger associations with mineralized C than with N. Associations between fungivores or bacterivores and the microbial C of their food sources may be expected, but trends with N were less evident, and historically, it has been difficult to relate population fluctuations of nematode consumers and their microbial food sources (Mikola, 1999; Neher, 1999; Yeates et al., 1999a). Bardgett et al. (1996) showed bacterially-dominated pathways occurred in more intensively grazed sites and slower-cycling, more fungal-dominated pathways occurred in the absence of grazing (Bardgett et al., 1996). Ferris and Matute (2003) found that the cumulative amounts of N mineralized were directly related to the EI, and inversely related to the slope of CI (i.e. the rate at which decomposition changed from bacterial to fungal).

Although Yeates et al. (1999b) found a strong correlation between nematode abundance and soil microbial C, we found much stronger relationships with potentially mineralized C than microbial C, illustrating a stronger link between nematode communities and rates of C turnover than with standing stocks of microbial biomass. Calculated canonical variables were strongly weighted toward potential mineralized C, and if simple correlation coefficients ( $r$ ) are calculated individually between abundance of each

nematode trophic group and mineralized C, strong correlations ( $P \leq 0.01$ ) are evident ( $r = 0.746$  for fungivores,  $r = 0.635$  for omnivores,  $r = 0.618$  for bacterivores, and  $r = 0.475$  for predators with mineralized C). Since mineralization is an important and common result of soil nematode activities during decomposition of organic substrates (Ingham et al., 1985), it is not surprising that strong relationships between mineralized C and nematode fungivores or bacterivores would be apparent. The relationships between mineralized C and omnivores or predators are additional support for the theory of Yeates and Wardle (1996) that these nematode groups accelerate mineralization by their feeding on the nematode fungivores and bacterivores that might otherwise immobilize nutrients. Although we did not analyze fungal and bacterial contributions to microbial biomass, our nematode community data does not indicate that grazing shifted the community from a slow-cycling, fungally dominated system to a fast-cycling, bacterially dominated system as was observed with heavy sheep grazing in Great Britain (Bardgett et al., 1996). Possible reasons for this inconsistency could be the strong climate and soil differences between the two studies.

## 5. Conclusions

The current study demonstrated the importance of examining grazing effects on soil biological communities under a variety of climatic conditions, and revealed the importance of small-scale patchiness in grazing effects on soil biological communities. Grazing resulted in a clear increase in soil microbial biomass C and N forms, and also significantly influenced soil nematode communities. However, the impacts of grazing on nematodes depended upon nematode life strategy (as indicated by *c-p* group). Nematode community indices suggest that cattle grazing shifted the nematode community to a community with a higher maturity index and more structure, as evidenced by decreases in some bacterivores in guilds Ba<sub>1</sub> and Ba<sub>2</sub> in grazed plots, accompanied by increases in more persistent groups (Ba<sub>3</sub> bacterivores, omnivores, and predators). Some herbivores, particularly Criconematidae, were negatively impacted by grazing. Omnivores, predators, bacterivores, and especially fungivores were strongly associated with short-term C mineralization rates, reinforcing the important association of these groups with decomposition and mineralization. The overall impact of cattle grazing on nematode community dynamics might be determined by the intensity of stocking densities and grazing patterns. Strong correlation between the nematode canonical variables with microbial C and N suggested that the impact of grazing on nematode communities is expected to be as variable as that on microbial biomass (Bardgett and Wardle, 2003), for which soil fertility, plant species, and herbivore types could play a greater role. Including nematode communities as indicators for grazing impact provides insight and detection of effects deeper into the

hierarchy of the decomposition process in soils and indicates the complexity of responses to grazing in the soil foodweb.

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