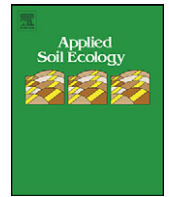




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Spatial variation in biodiversity and trophic structure of soil nematode communities in a subtropical savanna parkland: Responses to woody plant encroachment

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ABSTRACT

Woody plant encroachment into grasslands generally increases spatial heterogeneity of soil properties and processes and creates “islands of fertility” beneath woody canopies. However, little is known regarding the potential for these changes to influence spatial variation in soil fauna. We quantified population sizes, biodiversity, and trophic structure of soil nematode communities in a savanna parkland where woody plant clusters developed in grassland during the past century. Total nematode density was constant across transects from centers of woody clusters into grasslands. Family richness and Simpson's Dominance Index indicated nematode communities in grasslands and grassland/cluster edges were significantly more diverse than positions within the woody clusters. Relative densities of all nematode trophic groups changed significantly along the transect. Bacterivores nearly doubled in relative density from grassland (35%) to cluster centers (60%), apparently in response to higher concentrations of soil microbial biomass in wooded areas. Relative densities of plant parasitic nematodes decreased along transects from grasslands (35%) to centers of woody clusters (10%), implying decreased nematode herbivory in woody clusters despite much higher root biomass there. The structure index indicated nematode communities within woody clusters were more simplified than those in grassland and edge communities due to reductions in densities of omnivores and predators. Although nematode densities were lower at 10–20 than 0–10 cm, nematode community characteristics were generally similar between soil depths. Changes in nematode community and trophic structure described here could influence biogeochemical processes, species interactions, and successional processes in regions where woody plants are encroaching into grasslands.

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1. Introduction

The encroachment of woody vegetation into grasslands around the world is a major land cover change that has consequences for biodiversity and ecosystem function (Scholes and Archer, 1997; Asner et al., 2004; Boutton et al., 2009; Van Auken, 2009). This change in physiognomy alters both the distribution of resources and the magnitude of ecosystem processes under and around the woody plants, generally resulting in resource enrichment and higher rates of biological activity in soils beneath their canopies relative to the original grassland (Schlesinger et al., 1990; McCulley et al., 2004; Maestre et al., 2009). These “fertile islands” associated with tree/shrub canopies generate spatial heterogeneity and create gradients of soil resources and biological processes

(e.g. above- and belowground litter inputs, soil organic matter and nutrient content, soil microbial biomass and activity) that change from the tree/shrub bole into the surrounding herbaceous vegetation (Schlesinger and Pilmanis, 1998; Breshears, 2006). These “fertile islands” generally increase in size, both horizontally and vertically, with time following woody plant establishment (Throop and Archer, 2008).

The structure and function of belowground communities are likely to interact strongly with the spatial heterogeneity of soil resources induced by woody plant encroachment into grass-dominated ecosystems (Freckman and Virginia, 1989; Freckman and Mankau, 1986; Partel and Helm, 2007; Pen-Mouratov et al., 2008). However, despite the role of soil organisms in controlling key ecosystem processes (e.g. belowground herbivory, nutrient mineralization, etc.), little is known regarding the impact of woody encroachment on soil communities. Responses of nematodes are of particular interest because they are the most numerous soil mesofauna, they occupy all consumer trophic levels within the soil food web, and their activities are known to influence mineralization rates of limiting nutrients and plant community dynamics (Ferris

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et al., 1998; Bardgett et al., 1999; De Deyn et al., 2003; Bonkowski, 2004). Therefore, their biodiversity, community composition, and trophic structure can provide important insights regarding many aspects of ecosystem function (De Ruiter et al., 2005).

In the Rio Grande Plains of southern Texas, subtropical trees and shrubs have encroached into areas that were once grassland, resulting in a savanna parkland landscape consisting of discrete clusters of woody plants embedded in a grassland matrix (Whittaker et al., 1979; Archer et al., 1988). Compared to the original grassland, these woody clusters have increased above- and belowground primary productivity (Archer et al., 2001), biomass and density of roots (Watts, 1993; Hibbard et al., 2001; Millard et al., 2008), storage of C and N in soil organic matter (Liao et al., 2006a,b; Boutton et al., 2009), and soil microbial biomass (McCulley et al., 2004; Liao and Boutton, 2008). Thus, these woody clusters are effectively “fertile islands” in the grassland matrix of this parkland landscape. We recently showed that these changes in the distribution and abundance of key energy resources (roots and microbial biomass) resulting from woody encroachment are associated with significant changes in the structure of nematode communities in this savanna parkland (Biederman and Boutton, 2009). More specifically, nematode communities in the centers of woody clusters are strongly dominated by bacterivores, while those in the original grasslands are comprised of nearly equal proportions of plant parasites, fungivores, and bacterivores. Furthermore, these differences in nematode community structure became more pronounced with time following woody encroachment.

Although we know that nematode communities are significantly different between centers of woody clusters and the adjacent grasslands (Biederman and Boutton, 2009; Freckman and Mankau, 1986), there may be other important horizontal and/or vertical spatial patterns in nematode community structure in savanna landscapes. For example, soil community diversity corresponds to increases in substrate multiplicity created by increasing plant species richness (De Deyn et al., 2004; Viketoft, 2007), such as those found at the tree grass boundary. Furthermore, declining food resources and pore space with soil depth generally correlate with reduced nematode density and diversity in lower soil depths (Sohlenius and Sandor, 1987; Yeates et al., 2008). This decay in diversity with depth may be more pronounced in the grass communities, which have shallower root distributions (Archer et al., 1988).

Therefore, the purpose of this study was to examine spatial variation in population sizes, biodiversity, and trophic structure of soil nematode communities in relation to vegetation and soil properties that have strong potential to influence these soil organisms (Ettema and Wardle, 2002). We characterized this spatial variability at two soil depths (0–10 and 10–20 cm) along transects extending from the centers of woody clusters out into adjacent open grasslands in a savanna parkland. We hypothesized that: (1) differences in nematode communities would be greatest between the centers of woody clusters and open grasslands; (2) changes in nematode communities would occur continuously along the entire transect rather than abruptly at the grassland-woody cluster edge; (3) biodiversity of nematodes would be greatest at the grassland-cluster edge where both woody and herbaceous species are present; and (4) biodiversity and population densities of nematodes will decrease with increasing depth in the soil profile.

2. Methods

2.1. Site description

Research was conducted at the Texas AgriLife La Copita Research Area located 65 km west of Corpus Christi, Texas on the eastern

edge of the Central Rio Grand Valley Plains (27°40'N; 98°12'W). The climate is subtropical, with a mean annual temperature of 22 °C. The mean annual precipitation is 715 mm, with peaks in May–June and September. Topography consists of nearly level uplands that grade (1–3% slopes) into lower-lying drainage woodlands. Soil pH ranges from 6.3 to 6.5 and is not significantly affected by vegetation type (Liao and Boutton, 2008). Elevations range from 75 to 90 m. Upland soils are Typic Argiustolls (Runge Series) with sandy loam texture (80% sand, 10% silt, and 10% clay) (Boutton et al., 2009). Domestic livestock have grazed La Copita over the past century.

Evidence from sequential aerial photography, the isotopic composition of soils, tree ring analyses, and vegetation dynamics modeling indicates that this region was once open grassland and that woody plant encroachment into grasslands has occurred over the past 150 years (Archer et al., 1988; Boutton et al., 1998, 1999; Archer et al., 2001, 2004). This pattern of encroachment appears to have been driven largely by its unpalatability to grazing livestock and reduced fire frequency (Archer et al., 2001; Van Aiken, 2009).

The uplands are dominated by C₄ grasslands, which are interspersed with small, discrete clusters of woody plants. Dominant C₄ grasses in uplands include species of *Paspalum*, *Bouteloua*, *Chloris*, and *Eragrostis*. *Prosopis glandulosa* is the dominant plant species in all wooded landscape elements. *P. glandulosa* is the first woody plant to colonize in grasslands and subsequently facilitates recruitment of other woody plant species beneath its canopy, either through the provision of soil moisture through hydraulic lift (Teague et al., 2001), or as perching structures for seed-dispersing birds (Archer et al., 1988). Common understory woody species include *Condalia hookeri* (M.C. Johnst.), *Celtis pallida* (Torr.), *Zanthoxylum fagara* (L.), *Diospyros texana* (Scheele.), *Zizyphus obtusifolia* (T.&G.), and *Berberis trifoliolata* (Moric.). Plant nomenclature follows Correll and Johnston (1970). Additional details on plant communities, successional dynamics, and changes in belowground ecosystem processes have been presented elsewhere (Archer et al., 1988, 2001; Boutton et al., 1998; McCulley et al., 2004; Liao et al., 2006a,b; Liao and Boutton, 2008).

2.2. Study design

Six woody clusters, each comprised of a single *P. glandulosa* tree and associated understory shrubs, were identified in an upland area of approximately 2 ha located within a grazing exclosure established in 1985. Because these woody clusters are established only after *P. glandulosa* colonizes the grassland (Archer et al., 1988), the age of each cluster is the same as that of its *P. glandulosa* tree. Regression equations were used to predict the age of *P. glandulosa* trees from their basal diameter (Stoker, 1997). These six clusters were chosen to encompass the age distribution of most woody clusters on the landscape. These clusters were aged 34, 41, 56, 64, 78, and 86 years and were between 21 and 134 m apart. Herbaceous vegetation is largely absent from woody clusters within this age range.

In each woody cluster, four transects were established (one in each cardinal direction) running from the center of each cluster out into the adjacent grassland. All of these elements are within the long-term grazing exclosure. Along each transect, soils were collected in four locations: (1) at the base of the bole of the founding *P. glandulosa* tree (bole); (2) halfway between the *P. glandulosa* bole and the cluster/grassland edge (mid); (3) at the cluster/grassland edge (edge); and (4) in the adjacent grassland at least 5 m from any woody plants (grass). Transects were approximately 10 m in length, but varied slightly as a function of the diameter of each woody cluster.

2.3. Soil collection and analyses

For every transect, one soil core (20 cm deep \times 2.5 cm diameter) was taken at each position defined above (bole, mid, edge, grassland), and separated into two depth increments (0–10 and 10–20 cm). Soil samples from identical transect positions within each cluster were composited by depth, mixed thoroughly and placed in a cooler for transport. Sampling was confined to the upper 20 cm of the soil profile as this interval encompasses nearly all of the A-horizon, and contains the highest concentrations of potential resources for soil nematodes (plant roots and microbial biomass) at this site (Boutton et al., 1999; Liao and Boutton, 2008).

Gravimetric water content of each soil sample was determined by weighing an aliquot of soil before and after drying at 105 °C for 48 h in order to express nematode densities by soil dry weight (per kg of soil). An additional aliquot of soil was passed through a 2 mm screen to remove large organic fragments, dried at 60 °C, ground with a centrifugal mill and analyzed for soil organic carbon (SOC) and soil total nitrogen (STN) concentrations using a Carlo Erba EA-1108 elemental analyzer (ThermoElectron, Woburn, MA).

2.4. Nematode extraction, identification, and community characterization

Nematodes were extracted within 24 h of soil collection from approximately 100 g of soil using sugar centrifugation (Coleman et al., 1999) and preserved in 5% formalin. All nematodes within a sample were identified to family and enumerated using an inverted microscope at 40 \times magnification. Feeding habits were assigned to nematode families according to Yeates et al. (1993), with the exception of root-hair feeders, which were placed in the fungal feeders group as recommended by Forge et al. (2003).

Nematode communities were characterized using several different indices that quantified their structure and function. Nematode diversity was evaluated as family richness (total number of families in a sample) and the Simpson index of dominance ($D = 1/\sum p_i^2$) (Simpson, 1949). Other indices used included the ratio of fungivores to microbivores [(fungivores/root-hair feeding nematodes)/(fungivores/root-hair feeding + bacterivores nematodes)] (Neher and Campbell, 1994); the maturity index ($MI = \sum v(i)^* f(i)$ for non-plant parasitic nematode families), this provides an assessment of the successional status of the nematode community based on life history characteristics of the species that comprise the community, with values ranging from 1 (dominated by opportunistic rapid colonizers, analogous to r-strategists) to 5 (dominated by later successional persister species, analogous to K-strategists); the plant parasite index ($PPI = \sum v(i)^* f(i)$ for plant parasitic nematode families) and (Bongers, 1990; Yeates, 1994), the plant parasite index (PPI) is identical in concept to MI, but is based only on the life history characteristics of the plant parasitic nematodes; the enrichment index ($EI = 100(\sum k_e n_e / (\sum k_e n_e + \sum k_b n_b))$), which is based on the potential responsiveness of opportunistic nematode guilds to food resource enrichment, with values ranging from 0 to 100 with higher EI values indicating a greater proportion of opportunistic microbivores capable of responding rapidly to resource enrichment; and the structure index ($SI = 100(\sum k_s n_s / (\sum k_s n_s + \sum k_b n_b))$) with values ranging from 0 to 100 and higher values indicating greater connectedness of the nematode food web due to higher proportions of omnivorous and predatory nematodes (Ferris et al., 2001). The variables used include p_i , the proportion of nematode family to total density; v_i , c-p value of the i th taxa; f_i , frequency of the i th taxa; k , the weight assigned to each nematode guild; n , the density of nematodes within each guild; b , basal guild; e , enrichment guild; s , structure guild.

Table 1

ANOVA results (F -values) evaluating the effects of transect position, soil depth, and their interaction on soil properties and nematode community characteristics.

| Variable | Transect position | Soil depth | Position \times depth |
|---|-------------------|------------|-------------------------|
| <i>Soil characteristics</i> | | | |
| Gravimetric water content | 0.44 | 4.46 | 8.0** |
| Soil organic carbon (g C kg ⁻¹ soil) | 18.6*** | 113.5*** | 16.35*** |
| Soil total nitrogen (g N kg ⁻¹ soil) | 17.7*** | 99.03*** | 17.73*** |
| Soil C/N ratio | 3.4* | 1.4 | 2.3 |
| <i>Nematode density and diversity</i> | | | |
| Total nematodes (kg ⁻¹ soil) | 2.9 | 10.14* | 2.2 |
| Family richness | 2 | 9.76* | 0.79 |
| Simpson's index of dominance | 23.1*** | 0.5 | 0.9 |
| <i>Nematode trophic structure</i> | | | |
| Fungi vore/microbivore ratio | 6.7* | 0.5 | 0.7 |
| % Bacterivores | 12.36*** | 4.2 | 1.6 |
| % Fungivores/root-hair feeders | 3.0 | 0.02 | 1.4 |
| % Plant parasites | 3.5* | 5.5 | 2.2 |
| % Omnivores | 7.4** | 1.1 | 4.8* |
| <i>Nematode community indices</i> | | | |
| Maturity index | 10.9*** | 11.5* | 2.2 |
| Plant parasite index | 0.5 | 0.2 | 1.0 |
| Enrichment index | 0.7 | 31.7** | 0.8 |
| Structure index | 14.0*** | 1.9 | 4.8* |

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

2.5. Statistical analysis

These observational data were analyzed using a strip-plot design with transect position, soil depth, and their interaction as main effects and cluster, cluster by position, and cluster by depth as random effects in a PROC MIXED model (SAS Version 9.2; SAS Institute Inc., Cary, NC, USA). This model was determined to be the most parsimonious based on REML AIC statistic. Least square difference post-hoc tests were used to determine differences within response variables. Correlations between nematode community descriptors and soil physical characteristics in each soil depth were performed with SPSS (SPSS Version 13.0.1; SPSS Inc., Chicago, IL, USA). When evaluating the effects of transect position and soil depth on densities of individual nematode families, only those families with an average density higher than 10.0 individuals kg⁻¹ soil were analyzed statistically (Bakonyi et al., 2007). Significance was declared at 0.05 for all analyses.

3. Results

3.1. Soil properties

Soil moisture content of the soil depended on the position with in the transect (Table 1). In the grassland, soil moisture was greater in 10–20 cm soils and at the canopy's edge both soil layers had similar soil moisture (Fig. 1a). At the mid-canopy and bole, soil moisture was greater in the surface soils.

The concentrations of both SOC and STN were affected by the interaction between transect position and soil depth (Table 1). In the 0–10 cm depth increment, both SOC and STN increased by approximately 200% along the transects from open grassland to the mesquite bole (Fig. 1b and c). However, in the 10–20 cm depth increment, SOC increased by 75% and STN increased by 50% from grassland to bole. Soil C:N ratios increased with proximity to the bole, but the different soil layers were not significantly different (Table 1 and Fig. 1d).

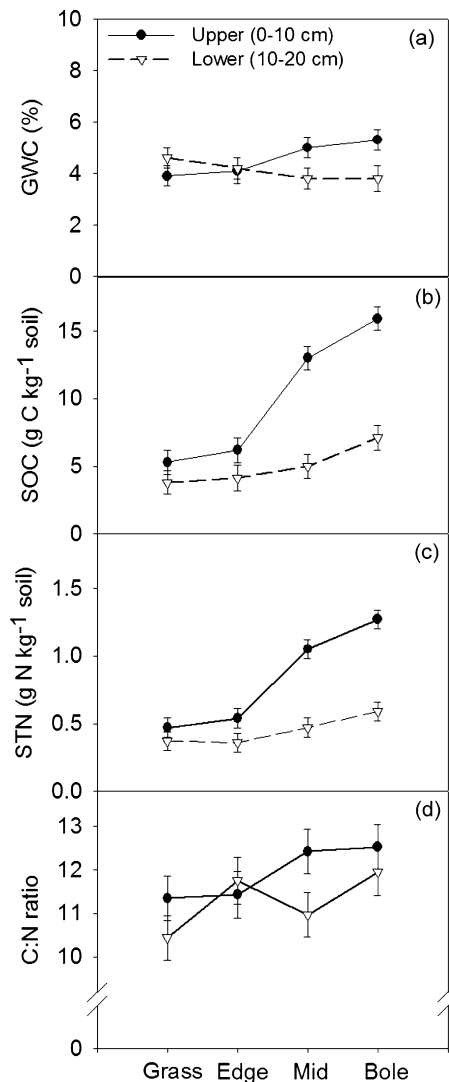


Fig. 1. Gravimetric water content (GWC) (a), soil organic carbon (SOC) concentration (g C kg^{-1} soil) (b), total soil nitrogen (STN) concentration (g N kg^{-1} soil) (c) and the ratio of soil C:N (d) with respect to transect position and soil depth at La Copita Research Area, spring 2007. Each point represents mean \pm se ($n=6$).

3.2. Population densities and biodiversity of soil nematodes

Total nematode density (individuals kg^{-1} soil) was significantly greater in the 0–10 cm soil depth (range 10,000–20,000 kg^{-1} soil) than at 10–20 cm (range 7500–11,000 kg^{-1} soil), but transect position had no effect on this variable (Table 1 and Fig. 2a). The total family richness was 27.

Thirteen nematode families were represented by at least 10 individuals kg^{-1} soil in every soil sample (Table 2). Of this group, the densities of six families were significantly affected by position along the transects (Table 3). Densities of nematodes belonging to families classified as bacterivores (e.g. the Cephalobidae and Plectidae) generally increased along the transects from the grasslands towards the bole of the mesquite tree. In contrast, densities of nematodes in families classified as plant parasites (e.g. Criconematidae, Dolichodoridae and Hoplolaimidae) decreased significantly from the grasslands towards the centers of the woody clusters (Tables 2 and 3). Densities of nematodes in families characterized as omnivorous or predatory were too low to be analyzed statistically, and approached 0 individuals kg^{-1} soil in bole, mid, and edge transect positions (data not shown).

Soil depth affected the densities of several common nematode families. The Cephalobidae, Plectidae, Aphelenchidae, Aphelenchoididae and Leptonchidae all had greater densities at 0–10 cm than at 10–20 cm (Tables 2 and 3). However, the density of individuals in the Anguinidae family was significantly greater at 10–20 cm compared to the 0–10 cm soil depth (Tables 2 and 3).

Nematode family richness varied significantly in response to soil depth. The 0–10 cm increment had 1–2 more families than the 10–20 cm depth (Table 1 and Fig. 2b). Simpson's index of dominance was significantly higher in grassland and edge soils (6–8) than in mid-canopy or bole positions (3–5), but was not significantly different between soil depths (Table 1 and Fig. 2c).

3.3. Trophic structure of nematode communities

The relative density of most trophic groups was significantly affected by transect position (Table 1). In the surface soil, bacterivores comprised a significantly greater proportion of the nematode population in soils from the mid-canopy and bole transect positions ($\approx 60\%$) (Fig. 3a) compared to edge and grassland ($\approx 35\%$) (Fig. 3a). In contrast, plant parasites represented a significantly smaller proportion of the nematode population in soils from bole (10%) and mid-canopy (13%) transect positions compared to edge (25%) and grassland (35%) positions (Fig. 3c). The relative densities of omnivores were affected by the interaction of position and layer, with greater densities in the surface soils at the grass and edge positions and similar densities between the layers at mid-canopy and bole positions (Table 1 and Fig. 3d). Predatory nematodes were rare in grassland and edge positions, and were almost completely absent from mid-canopy and bole transect positions (data not shown).

The ratio of fungivores to microbivores (Fig. 2d) was similar for both soil depth increments, but was significantly lower in the mid-canopy and bole positions (≈ 0.3) compared to grassland and edge positions (≈ 0.5). MI values were all < 2.5 in this study (Fig. 2e). Transect position affected MI, with somewhat higher values at the grassland and edge. MI values were also significantly higher at 0–10 cm than at 10–20 cm (Table 1). PPI was not affected by transect position nor depth (Fig. 2f and Table 1). EI values ranged from 40 to 75, but were not affected by position along the transect; however, EI was significantly lower in the 0–10 cm soil depth than in the 10–20 cm depth (Fig. 4 and Table 1). Nematode communities in soils from the bole and mid-canopy transect positions had significantly lower SI values than those from the grassland and edge communities (Table 1 and Fig. 4).

3.4. Correlations with soil characteristics

Correlations between soil characteristics and the nematode community in the 0–10 cm soil depth are provided in Table 4. The only significant correlation in the 10–20 cm soil depth was nematode family dominance and SOC, which were negatively correlated (-0.499 ; $p=0.018$).

4. Discussion

4.1. Spatial variation in soil characteristics

Spatial variation in SOC and STN was distinct, with both parameters decreasing continuously from the centers of woody clusters into the grasslands. This pattern has been documented previously at this site, and develops as a consequence of higher rates of above- and belowground primary production in woody clusters (Archer et al., 2001; Boutton et al., 2009). Although not quantified in our study, patterns of SOC and STN have been shown to have strong positive correlations with root biomass, soil microbial biomass, soil respiration, and nitrogen mineralization at this site (Hibbard et al.,

Table 2
Nematode family density (mean number of individuals kg⁻¹ soil \pm s.e., $n = 6$) of the most abundant families (with mean density > 10.0 individuals kg⁻¹ soil) from each transect position and soil depth.

| | Surface (0–10 cm) soils | | | | Sub-surface (10–20 cm) soils | | | |
|------------------|-------------------------|-----------------|-----------------|----------------|------------------------------|-----------------|-----------------|----------------|
| | Grass | Edge | Mid | Bole | Grass | Edge | Mid | Bole |
| Anguinidae | 105 \pm 189 | 128 \pm 207 | 0 \pm 21 | 31 \pm 189 | 527 \pm 189 | 871 \pm 207 | 350 \pm 189 | 145 \pm 207 |
| Aphelenchidae | 579 \pm 85 | 418 \pm 93 | 293 \pm 93 | 316 \pm 85 | 173 \pm 85 | 297 \pm 93 | 144 \pm 85 | 101 \pm 93 |
| Aphelenchoididae | 579 \pm 140 | 870 \pm 146 | 467 \pm 146 | 676 \pm 140 | 85 \pm 140 | 196 \pm 146 | 83 \pm 140 | 79 \pm 146 |
| Cephalobidae | 3931 \pm 75 | 2581 \pm 811 | 7684 \pm 811 | 5838 \pm 746 | 1355 \pm 746 | 1357 \pm 810 | 2069 \pm 746 | 1778 \pm 811 |
| Cricematidae | 175 \pm 66 | 104 \pm 68 | 41 \pm 68 | 19 \pm 66 | 97 \pm 66 | 498 \pm 68 | 22 \pm 66 | 17 \pm 68 |
| Dolichodoridae | 741 \pm 135 | 69 \pm 147 | 54 \pm 147 | 79 \pm 135 | 452 \pm 135 | 257 \pm 147 | 100 \pm 135 | 12 \pm 147 |
| Heteroderidae | 156 \pm 53 | 144 \pm 58 | 113 \pm 58 | 87 \pm 53 | 252 \pm 53 | 144 \pm 58 | 71 \pm 53 | 229 \pm 58 |
| Hoplolaimidae | 4591 \pm 1100 | 1130 \pm 1201 | 147 \pm 1201 | 62 \pm 1100 | 855 \pm 1100 | 1050 \pm 1201 | 867 \pm 1100 | 81 \pm 120.1 |
| Leptonchidae | 1430 \pm 114 | 1051 \pm 123 | 952 \pm 123 | 398 \pm 114 | 490 \pm 114 | 521 \pm 123 | 302 \pm 114 | 210 \pm 122 |
| Monhysteridae | 1111 \pm 385 | 1002 \pm 408 | 2557 \pm 408 | 1021 \pm 385 | 1484 \pm 385 | 1715 \pm 408 | 1991 \pm 385 | 1211 \pm 408 |
| Paratylenchidae | 978 \pm 1043 | 853 \pm 1078 | 2783 \pm 1077 | 506 \pm 1043 | 1533 \pm 1044 | 457 \pm 1078 | 4156 \pm 1044 | 824 \pm 1077 |
| Plectidae | 221 \pm 90 | 323 \pm 97 | 910 \pm 97 | 454 \pm 89 | 83 \pm 90 | 194 \pm 97 | 276 \pm 89 | 124 \pm 97 |
| Tylenchidae | 1594 \pm 408 | 1169 \pm 446 | 2144 \pm 444 | 1242 \pm 408 | 936 \pm 407 | 1162 \pm 444 | 1174 \pm 408 | 1895 \pm 444 |

Table 3
ANOVA results (F -values) evaluating the effects of transect position, soil depth, and their interaction on the densities of the most abundant nematode families (with mean density > 10.0 individuals kg⁻¹ soil).

| Nematode family | Trophic group | Position | Depth | Position \times depth |
|------------------|-----------------------------|----------|--------|-------------------------|
| Anguinidae | Fungivore/root-hair feeding | 1.50 | 9.4* | 0.9 |
| Aphelenchidae | Fungivore/root-hair feeding | 1.7 | 13.6* | 1.4 |
| Aphelenchoididae | Fungivore/root-hair feeding | 2.6 | 11.5* | 1.2 |
| Cephalobidae | Bacterivore | 5.0* | 32.0** | 4.1* |
| Cricematidae | Plant parasite | 4.4* | 10.6* | 28.3* |
| Dolichodoridae | Plant parasite | 7.8** | 0.1 | 1.2 |
| Heteroderidae | Plant parasite | 1.4 | 1.9 | 1.1 |
| Hoplolaimidae | Plant parasite | 1.8 | 1.1 | 2.0 |
| Leptonchidae | Fungivore/root-hair feeding | 14.0*** | 26.1** | 6.5** |
| Monhysteridae | Bacterivore | 6.6* | 0.2 | 1.7 |
| Paratylenchidae | Plant parasite | 1.80 | 1.9 | 1.1 |
| Plectidae | Bacterivore | 6.4** | 30.3** | 4.7* |
| Tylenchidae | Fungivore/root-hair feeding | 0.6 | 0.5 | 1.9 |

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

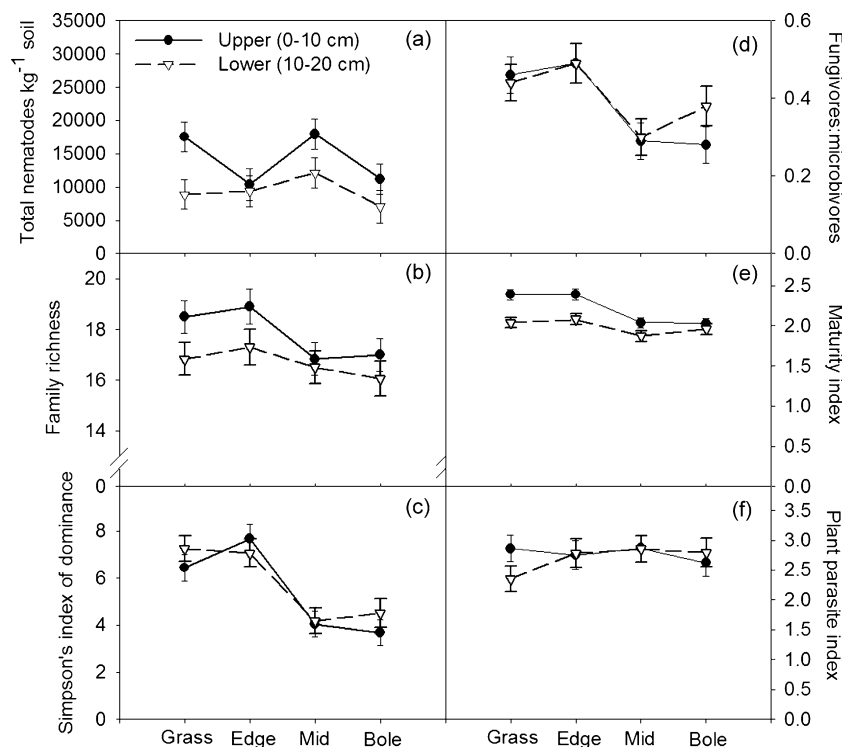


Fig. 2. Total nematode density (kg⁻¹ soil) (a), nematode family richness (b), Simpson's index of dominance (c), the ratio of fungivores/root-hair feeders to microbivores (fungivores/root-hair feeders + bacterivores) nematodes (d), maturity index (e) and plant parasite index (f) with respect to transect position and soil depth at La Copita Research Area, spring 2007. Each point represents mean \pm s.e. ($n = 6$).

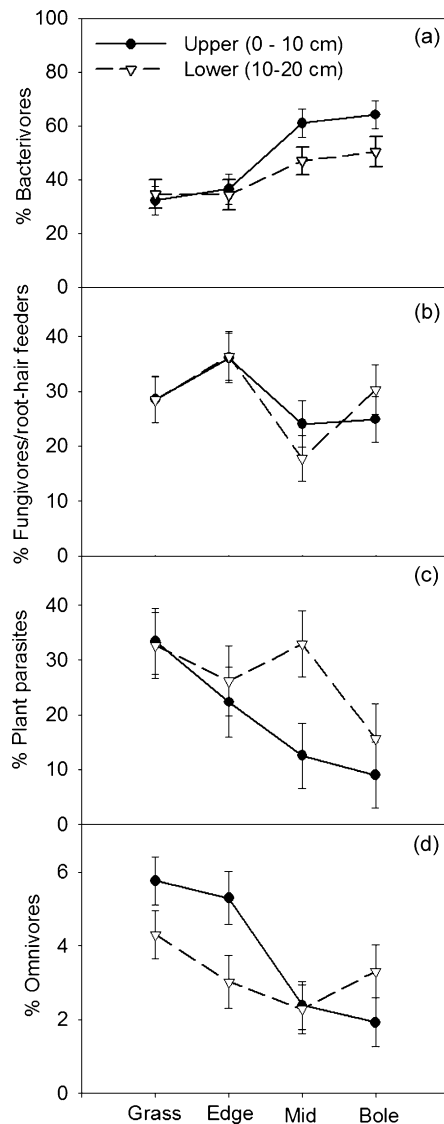


Fig. 3. The relative density of bacterivores (a), fungivores/root-hair feeders (b), plant parasites (c) and omnivores (d) nematodes with respect to transect position and soil depth at La Copita Research Area, spring 2007. Each point represents mean \pm se ($n=6$).

2001; McCulley et al., 2004; Liao and Boutton, 2008; Millard et al., 2008). At the time of sampling, soil moisture patterns were also affected by the interaction of transect and depth, possibly driven by plant species differences in rooting depth, evapotranspiration, and/or hydraulic lift. Thus, the development of woody clusters in this ecosystem increases the spatial heterogeneity of soil resources that are likely to have significant effects on the biodiversity and trophic structure of nematode communities in this ecosystem.

4.2. Spatial variation in population densities and biodiversity of soil nematodes

Nematode communities at the *P. glandulosa* bole change with age, however, earlier studies suggest that rate of changes, such as increasing bacterivory and decreasing root herbivory and omnivory, slows in clusters older than 30 years (Biederman and Boutton, 2009). Although total nematode population density did not change across transects from the centers of woody clusters out into open grasslands (Fig. 2a), the biodiversity and trophic structure of nematode communities showed significant spatial variability. Family

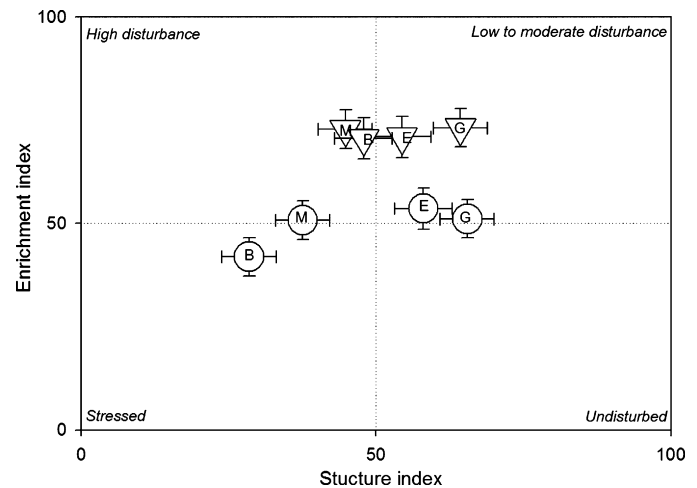


Fig. 4. Mean nematode weighted faunal profiles of each transect position along axes of structure (SI) and enrichment (EI) (mean \pm se, $n=6$) at La Copita Research Area, spring 2007. Circles indicate means from upper soil depth (0–10 cm) and triangles indicate means from lower soil depth (10–20). The letters B, M, E and G represent samples from the bole, mid-canopy, edge and grass positions, respectively.

diversity and Simpson's index of dominance were highest at the grassland/woody cluster edge, and lowest in the interior of woody clusters (Fig. 2b and c). This may reflect relatively high plant species diversity at the ecotone where both herbaceous and woody species are present, which may provide a diversity of plant and microbial energy sources capable of being utilized by the nematode community (Ettema, 1998). Decreases in overall diversity within the woody clusters reflect increased dominance of bacterivore families (especially Cephalobidae and Plectidae), and concomitant decreases and/or losses of nematodes in plant parasite, omnivore, and predator families (Table 3). Thus, following woody plant encroachment, nematode communities in woody clusters become less diverse and increasingly dominated by fewer families.

4.3. Spatial variation in nematode trophic structure

The relative density of plant parasitic nematodes decreased continuously along the transects from 33% of the nematode community in grasslands to 13% of the community at the bole of the central mesquite tree (Fig. 4c). This is directly opposite the spatial pattern for root biomass, which increases continuously from $1.5 \pm 0.2 \text{ kg m}^{-2}$ in the grassland areas to $4.8 \pm 1.0 \text{ kg m}^{-2}$ at the bole of the mesquite tree (Millard et al., 2008). This suggests that the root tissue near the bole is generally not available to this group of organisms (Yeates, 1999; Porazinska et al., 2003; Engelkes et al., 2008), perhaps due to mechanical properties or antiherbivore chemical

Table 4

Correlations between soil physical characteristics and the nematode community in the 0–10 cm soil depth.

| | STN | SOC | Soil C/N ratio |
|--|---------|---------|----------------|
| Total nematodes (kg^{-1} soil) | −0.03 | −0.05 | −0.04 |
| Family richness | −0.54** | −0.55** | −0.4 |
| Simpson's index of dominance | −0.73** | −0.73** | +0.42* |
| Fungivore/microbivore ratio | −0.66** | −0.66** | −0.36 |
| % Bacterivores | +0.76** | +0.77** | 0.49* |
| % Fungivores/root-hair feeders | −0.28 | −0.28 | −0.11 |
| % Plant parasites | −0.62** | −0.62** | +0.41* |
| % Omnivores | −0.64** | −0.66** | −0.57** |
| Maturity index | −0.63** | −0.64** | −0.43* |
| Plant parasite index | 0.54 | 0.01 | 0.3 |
| Enrichment index | −0.37 | −0.34 | −0.05 |
| Structure index | −0.75** | −0.74** | −0.38 |

* $P < 0.05$.

** $P < 0.01$.

defense mechanisms associated with roots in the woody plant communities at this site (Van Dam, 2009). For example, the dominant sub-canopy tree, *Z. fagara*, belongs to a genus in the Rutaceae family known to produce antibiotic chemicals, including compounds with demonstrated antinematode activity (Joymati et al., 2003). Furthermore, root tissues from woody clusters at La Copita Research Area have concentrations of suberin-derived substituted fatty acids that are approximately 50% higher than those in roots from remnant grasslands (Filley et al., 2008), which may represent a mechanical and/or biochemical deterrent to root-feeding nematodes (Galeano et al., 2003; Bernards and Bastrup-Spohr, 2008). An alternative hypothesis would be that lower relative densities of plant parasitic nematodes in the woody clusters may be due to top-down effects, such as increased levels of predation on that functional group by soil fauna not quantified in this study, such as mites or amoebae.

Regardless of the cause, the lower densities of plant parasites under bole and mid-canopy transect positions strongly suggest that nematode herbivory is reduced in woody clusters. Nematodes are generally considered to be among the most abundant and significant belowground herbivores, and the potential for plant parasitic nematodes to alter competitive relationships between plant species and to influence the direction of plant succession is well-documented (De Deyn et al., 2003; Van der Putten et al., 2005; Porazinska et al., 2007). Therefore, we speculate that these apparently reduced levels of herbivory may favor expansion of woody clusters at the expense of grasslands.

The detritivore portion of the nematode community also demonstrated significant changes in population size, community composition, and trophic structure along the transects from grasslands into woody clusters. The change in relative densities of bacterivores was particularly large, ranging from 35% in the grasslands and edge transect positions to 60% in mid-canopy and bole positions. Hence, bacterivorous nematodes were likely responding to the larger pool sizes of soil microbial biomass in the woody clusters (400–700 mg C kg⁻¹ soil) compared to the grasslands (300–400 mg C kg⁻¹ soil) (McCulley et al., 2004; Liao and Boutton, 2008). Interestingly, there was a sharp decrease in the ratio of fungivores to microbivores within the boundaries of the woody clusters. This may signal that the fungal proportion of the soil microbial biomass in clusters is less abundant than the bacterial component (Ettema and Bongers, 1993). However, it could also be hypothesized that the fungal species found within the woody clusters may be better defended (chemically and mechanically) against fungivorous nematodes.

This shift towards bacterivory could contribute to changes in ecosystem function following woody encroachment at this site, as rapid nutrient dynamics are a hallmark of bacterial-based energy channels (Coleman et al., 1983; Wardle, 2002; Osler and Sommerkorn, 2007). In fact, soils under woody clusters have significantly higher C and N mineralization rates than grassland soils (Hibbard et al., 2001; McCulley et al., 2004), and these accelerated nutrient turnover rates may be partially attributable to the increased importance of bacterivorous nematodes in those clusters (Bongers et al., 1997). These changes in nutrient turnover rates could affect the long-term accrual and storage of nutrients following woody encroachment. In addition, accelerated nutrient turnover may influence the short-term availability of limiting nutrients such as N and P (Anderson et al., 1981), thereby altering plant-microbe and/or plant-plant interactions and successional processes in this savanna parkland ecosystem.

Although omnivores represent a small proportion of the total nematode population, their relative densities declined from 6% in grassland and edge transect positions to 2% in mid-canopy and bole positions. And, although predators are rare in grassland and edge positions, they are extinct in woody clusters older than 16 years (Biederman and Boutton, 2009). Apparently for these reasons,

the SI for both the grassland and edge transect positions is significantly greater than that for the mid-canopy and bole positions inside the woody clusters. Thus, nematode food webs in woody clusters are relatively simplified, with strong dependence on bacterivory and few interactions involving higher trophic levels such as omnivores and predators. In contrast, energy flow through nematode food webs in grasslands appears to be more diversified (with nearly equal proportions of bacterivores, fungivores, and plant parasites) and more connected due to larger populations of nematodes at higher trophic levels.

The manner in which the relative densities of bacterivores and omnivores change across the transects appears to be different than that for the plant parasites. While plant parasites change in a more-or-less continuous fashion along the length of the transects, the other nematode trophic groups appear to change somewhat more abruptly in the region between the grassland/cluster edge and the mid-canopy region of the cluster (Fig. 3). We hypothesize that the root resources that support the plant parasites vary continuously across the transect, while the microbial resources that sustain the bacterivores, fungivores, and omnivores have a more discontinuous spatial distribution that changes rapidly near the grassland/cluster edge.

4.4. Spatial variation with soil depth

Total nematode density and family richness were significantly lower at 10–20 cm compared to the 0–10 cm depth increment. This probably reflects the fact that important soil resources (such as SOC, STN, microbial biomass, and root biomass) all decline rapidly with increasing soil depth in both grasslands and woody clusters at this site (Liao and Boutton, 2008; Boutton et al., 2009). Although some of the other characteristics of nematode communities increased or decreased with soil depth, the general absence of interactions between transect position and soil depth (Table 1) indicates that spatial variation in nematode community characteristics observed at 0–10 cm was similar to the spatial variation observed at 10–20 cm depth. However, it is important to note that the root systems of these grasslands extend to approximately 1 m and those of the woody clusters extend to depths >4 m (Boutton et al., 1999), and that nematodes can be found as deep as 6.8 m in some savanna ecosystems in Texas (Jackson et al., 2002). Therefore, the patterns that we describe here for the upper 20 cm of the soil profile may not reflect spatial characteristics of nematode communities in these deeper regions of the soil profile.

4.5. Potential role of abiotic factors

It is possible that gradients of abiotic environmental factors exist along these transects from open grasslands to the centers of the woody clusters that might influence soil nematode population densities, biodiversity, and trophic structure. However, we know that all of our transects were located on the same soil series, and that soil particle size distributions are identical between grasslands and woody clusters (Liao and Boutton, 2008; Boutton et al., 2009). Thus, hydrologic and soil gas exchange characteristics influenced by soil texture should be generally similar. For example, mean annual volumetric soil moisture was shown to be comparable (0.06 cm³ cm⁻³) between grasslands and woody clusters at both the 0–10 and 10–20 cm depth increments (McCulley et al., 2004). However, hydraulic redistribution may alter diurnal patterns of soil moisture availability between the clusters and grasslands (Potts et al., 2010). Furthermore, mean annual soil temperature at the 5 cm soil depth was significantly lower in woody clusters (25.7° C) than in grasslands (26.7° C); and, soil temperatures in woody clusters tended to be slightly lower during the day, and slightly warmer at night compared to grasslands (McCulley et al., 2004). Although the

role of abiotic factors warrants further attention in this context, known differences appear to be minor, and we suggest that differences in nematode communities documented in this study are primarily a function of woody plant encroachment into grassland which results in concomitant changes in basal resources (i.e. roots and microbial biomass) for the nematode food web.

5. Conclusions

The encroachment of woody plant clusters increased the spatial heterogeneity of soil resources in this subtropical savanna parkland, as evidenced by higher concentrations of SOC and STN beneath woody canopies relative to the grassland matrix. These changes in resource availability influence spatial variation in biodiversity and trophic structure of soil nematode communities along transects from the center of woody clusters into open grasslands. Although the bole and grasslands represent the end-points in defining nematode communities (H1), the rate of change along the transect varied with trophic group (H2): plant parasites decreased gradually from grassland to bole and bacterivores and omnivores had more disjointed changes with the greatest separation between mid-canopy and edge. Nematode family diversity had a similar disjointed pattern (H3). Family diversity and Simpson's index of dominance are highest at the grassland/woody cluster edge, and lowest in the interior of woody clusters. This likely reflects the high plant species diversity in this ecotonal position where both herbaceous and woody species are present, and may indicate a higher diversity of potential energy resources for nematodes at the grassland/cluster edge. Energy flow through nematode food webs in grasslands and at the grassland/cluster edge appeared to be relatively diversified (with nearly equal proportions of bacterivores, fungivores, and plant parasitic nematodes) and more connected due to larger populations of nematodes at higher trophic levels. In contrast, nematode food webs in the interior of woody clusters are relatively simplified, with strong dependence on bacterivory, a greatly reduced plant parasite load, and few interactions involving higher trophic levels such as omnivores and predators. Finally, total nematode density and family richness were reduced with depth (H4), however the response of individual families to soil depth varied. As nematodes are significant regulators of ecosystem function, the spatial distribution of their trophic groups in grasslands vs. woody clusters has potential consequences for the bioavailability of limiting nutrients, plant-microbe and plant-plant interactions, and the future trajectory of successional processes in this subtropical savanna parkland ecosystem.

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