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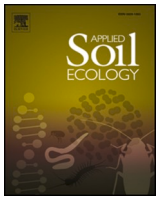

Nematode communities respond more to N enrichment than to plant community changes over decades in tallgrass prairie

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ABSTRACT

Temperate grasslands such as the North American tallgrass prairie are among the most endangered terrestrial ecosystems due to changes in climate and land-use practices. While belowground responses of terrestrial ecosystems to perturbations have received greater attention in recent years, there is a dearth of long-term studies documenting changes over decadal scales. The current study addresses the long-term effects of fire (annual burning or fire exclusion), mowing, and nitrogen (N) and phosphorus (P) fertilization on the structure and composition of a tallgrass prairie nematode community after 32 years of experimental treatments. Fire exclusion resulted in conversion of grassland to woodland, and a general decrease in nematode population densities, while annual prescribed fire maintained a grassland state. Although the change in vegetative state affected overall nematode abundance, vegetative structure was not the major driver of nematode community composition. Rather, changes in nitrogen availability appeared to be the dominant driver of nematode community dynamics. Responses of herbivorous taxa were dominated by interactions among burning, mowing, and N fertilization treatments and varied across taxonomic groups, but a general pattern of increasing relative abundances with N fertilization was observed, particularly in the presence of annual burning or mowing. In contrast, the relative abundance of the fungivorous Tylenchidae, the dominant nematode family in terms of abundance, declined from 44 % to 26 % after 32 years of N enrichment, while fire exclusion favored the opportunistic bacterivorous Rhabditidae. Although higher trophic level responses were generally uninformative, our results confirmed the value of nematode community analysis in soil food web diagnostics, with fungivore to bacterivore ratios and the maturity index (MI) identified as useful community indices.

1. Introduction

Temperate grasslands are one of the biomes with the highest conservation risk (Hoesktstra et al., 2005) and the North American tallgrass prairie, in particular, is one of the most endangered ecosystems on earth, due largely to its conversion to agriculture (Samson and Knopf, 1994). However, it is encroachment of woody vegetation due to more recent changes in land use and environmental conditions that dominates the present threats to the remaining extent of these grasslands. Invasion of shrubs and trees into grasslands and savannas is an issue of growing concern globally (Archer et al., 2017; Stevens et al., 2017), and is known to modify abiotic environments, change the spatial distribution of soil resources, and alter soil biodiversity and ecosystem functions (Wolters et al., 2000).

In tallgrass prairie, fire exclusion is an important proximate driver of woody encroachment (Ratajczak et al., 2014). Frequent spring burning is a common management practice in the Flint Hills of eastern Kansas, where it is used to maximize production of the native warm-season C4 grasses, and also to limit encroachment of woody vegetation. Fire also enhances N limitation due to the N volatilization associated with annual burning (Blair et al., 1998; Seastedt et al., 1991; Turner et al., 1997). Mowing for hay is another common management practice in the Flint Hills with the potential to increase N limitations in tallgrass prairie (Kitchen et al., 2009). Low P availability is characteristic of tallgrass prairie soils in the Flint Hills, but mycorrhizal symbioses compensate for any potential P limitation in the dominant C_4 grasses (Hartnett and Wilson, 1999). Disturbances such as fire and mowing (or grazing), along with associated changes in plant community structure and nutrient

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availability, are primary drivers of belowground processes and feedbacks in tallgrass prairie, including the structure and composition of soil communities (Blair et al., 2000; Rice et al., 1998). Nitrogen loss pathways in burned and unburned prairies, for example, are mediated by pyrovolatilization and microbially-driven processes, respectively, although total soil N losses are similar (Nieland and Zeglin, 2024).

Nematodes dominate soil invertebrate communities in tallgrass prairie in terms of abundance, with maximum population densities exceeding five million m^{-2} (Ransom et al., 1998), and diversity, with 82 genera and 228 species cataloged from a single pasture (Orr and Dickerson, 1967) and 375 species recorded from a single prairie ridge (Mullin et al., 2004). Most species are rare; only ~two dozen species have a specimen frequency higher than 1 % or a sample occurrence >20 %. The most abundant taxa are herbivorous (~40 %), followed by fungivorous (~30 %), omnivorous (~20 %), and bacterivorous (~6 %) species (Todd et al., 2006). In contrast to numerical abundance, the Dorylaimida, which consists predominantly of omnivorous and predaceous species, comprise >40 % of species richness.

Nematodes perform critical functions in the soil food web, and their status as ecological indicators has long been endorsed (Neher, 2010). Numerous indices based on the structure and composition of soil nematode communities have been developed (Bongers, 1990, 1999; Ferris et al., 2001), but linkages between indicator taxa and ecosystem function remain poorly documented in most cases. Notable exceptions include the relative abundance of individual herbivorous (Todd, 1996) and bacterivorous (Yeates, 2003) taxa, and the fungivore to bacterivore ratio, which reflects the successional stage of the decomposer community (Neher, 2010; Todd, 1996; Todd et al., 2006).

The Belowground Plot Experiment (BGPE) was established at Konza Prairie Biological Station in 1986 to investigate the long-term consequences of prairie management practices (burning and mowing) and nutrient (N and P) additions on plants and belowground communities and processes. At the outset, the experimental site was dominated (>95 % of cover) by the C_4 grasses *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum nutans*, but woody species increased to >5 % cover within four years in plots where fire was excluded (Gibson et al., 1993). The final sampling of belowground communities was conducted in 2017, after 32 years of experimental treatments. By this time, plant communities had diverged into conventional grass-dominated prairie in annually burned plots vs. shrub-woodland in unburned, unmowed plots (Supplementary Fig. S1), while mowed plots were dominated by the invasive grass species *Bothriochloa bladhii*. Here we present nematode community responses to the long-term experimental treatments, as well as temporal trends in nematode responses to those treatments throughout the duration of the BGPE. Results from previous nematode-focused sampling in the BGPE are reported in Todd (1996), Jones et al. (2006), and Darby et al. (2013).

2. Materials and methods

2.1. Site description

This study was conducted at the Konza Prairie Biological Station (KPBS), a 3487-ha tallgrass prairie located in the Flint Hills of eastern Kansas. The station is co-owned by The Nature Conservancy and Kansas State University and managed as a Long-Term Ecological Research (LTER) site. The prevailing soil textures at the station are silty clay loams classified as Pachic and Udic Argiustolls (Ransom et al., 1998). Plant communities range from perennial C_4-dominated native (never plowed) grasslands (>90 % of the area) to deciduous riparian forests (Freeman, 1998). Mean annual precipitation is 835 mm, with 75 % falling during the growing season (Hayden, 1998). Mean growing season temperature is 22 °C, peaking at 27 °C in July. Interannual variability in precipitation is high, with growing season precipitation ranging from 55 % to 172 % of mean growing season precipitation during this study.

2.2. Experimental design

The factorial treatment structure of the BGPE consisted of burning (annually burned vs. unburned), mowing (annually mowed vs. unmowed), and fertilization with ammonium nitrate (no N vs. 10 g N m^{-2} annually) or superphosphate (no P vs. 1 g P m^{-2} annually), or both N and P fertilization. The design was a split-strip plot, with burn treatments as whole plots and mow and fertility treatments as subplot treatments arranged in a strip plot design within each whole plot. Whole plots were arranged in a randomized complete block design with four replications. Individual subplots (64 total) were 12.5 m × 12.5 m in size.

2.3. Sampling and extraction procedures

Composite soil samples consisting of either four 5-cm diameter cores (1987, 1989, 1994) or four to twenty 2.5-cm diameter cores (post 1994) were collected to a depth of 20 cm in a systematic pattern from each plot in June or October. Initial samples were collected in October 1987 and 1989, with subsequent sampling events occurring at approximately 5-year intervals. The final sampling occurred in June 2017.

Nematodes were initially extracted from 100 cm^3 subsamples using a modified Christie-Perry technique (Christie and Perry, 1951) consisting of sieving followed by tissue extraction. Due to poor recovery of criconematid nematodes, the centrifugal flotation procedure (Jenkins, 1964) was used after 1994. Extracted nematodes were identified to genus and assigned a feeding habit based on Yeates et al. (1993). A list of nematode genera and species present in the BGPE can be found in Darby et al. (2013).

2.4. Statistical analyses

Data collected in 2017 were subjected to a mixed model analysis of variance using PROC MIXED (SAS OnlineDoc™: Version 8). Fixed effects consisted of experimental treatments (burn, mow, N and P) and their interactions, while random effects consisted of block effects and block × burn, block × burn × mow, and block × burn × N × P interactions. Response variables consisted of total nematode population densities, relative abundances of individual taxa, and nematode community indices, including the maturity index (Bongers, 1990, 1999), and the enrichment and structure indices (Ferris et al., 2001). Post hoc analysis of least squares means was conducted using the LSMEANS/pdiff option in SAS. Patterns in long-term treatment effects on nematode community structure were examined using principal component analysis (PROC PRINCOMP, SAS OnlineDoc™: Version 8).

Linear trends in temporal nematode responses to factorial burning and N fertilization treatments across time (1987–2017), using unpublished data from previous nematode-focused sampling of the BGPE (Todd, 1996; Jones et al., 2006; Darby et al., 2013), were analyzed using a mixed model analysis of covariance (PROC MIXED) with time (in months from January 1987) as the covariate. Regression relationships (slope estimates) were tested against the null hypothesis (H_0) that treatment slopes were equal to zero.

3. Results

3.1. Total nematode abundance

Mean total nematode abundance was 91 % greater ($P = 0.03$) in annual burned plots compared to unburned plots after 32 years of treatment (Fig. 1A, Supplementary Table S1). A four-way interaction (burning × mowing × N × P; $P = 0.04$) was also observed, where burning effects were greatest in the presence of mowing plus N and P enrichment ($P = 0.006$), and in the absence of mowing, but in the presence of N enrichment ($P = 0.012$). Analysis of linear trends across years revealed that the main effect of burning was due to decreasing abundance in plots where fire was excluded (Fig. 1B).

3.2. Herbivore relative abundances

The relative abundance of total herbivorous nematodes was strongly affected by N enrichment ($P = 0.002$), increasing from 31 % in the absence of N enrichment to 46 % in the presence of N enrichment. Individual taxa of herbivorous nematodes, however, varied in their responses (Supplementary Table S1), with the response to N addition largely driven by the Paratylenchidae (*Paratylenchus* and *Gracilacus* spp.), which increased ($P = 0.003$) from a mean of 3 % to a mean of 14 % of total nematode abundance under N enrichment (Fig. 2). Main effects of mowing and burning, mowing, and N interactions were prevalent. The mean relative abundance of the dominant herbivorous genus *Helicotylenchus*, for example, decreased ($P = 0.052$) from 22 % to 13 % in the presence of annual mowing (Fig. 2A), while the mean relative abundance of the Paratylenchidae decreased ($P = 0.004$) from 15 % to 4 % in the combined presence of annual mowing and burning vs. burning alone (Fig. 2B). The greatest relative abundance of the genus *Mesocriconema* (17 %) was observed in the combined presence of burning, mowing, and N enrichment (Fig. 2C). Linear trends across years (Fig. 3) showed increases ($P \leq 0.05$) in relative abundance in burned, N-enriched plots for the Paratylenchidae (Fig. 3B), *Mesocriconema* (Fig. 3C), and *Pratylenchus* (Fig. 3E). *Helicotylenchus* relative abundance responded more quickly (by the 2nd year of treatments) to N enrichment in the presence of burning, but subsequently increased to similar levels in burned, unfertilized plots, as well as unburned plots with or without N enrichment (Fig. 3A). The only decrease in relative abundance was observed for *Tylenchorhynchus* in the absence of burning or fertilization (Fig. 3D).

3.3. Fungivore and bacterivore relative abundances

Among fungivorous taxa, the Tylenchidae (predominantly *Filenchus*, *Basiria*, and *Boledorus* spp.) declined in relative abundance from 44 % to 26 % after 32 years of N enrichment (Fig. 4A, Supplementary Table S1) and displayed a decreasing linear trend across years ($P = 0.05$) in unburned, N-fertilized plots (Fig. 5A). Relative abundance of *Aphelenchus* and *Aphelenchoides* declined ($P \leq 0.05$) through time in the absence of burning and in the presence of burning without N fertilization, respectively (Fig. 5B and C). The final relative abundance of Tylencholaimoidea (*Tylencholaimus* and *Tylencholaimellus*) was similarly reduced ($P = 0.03$) from 2 % to <1 % in the presence of N enrichment, and declined in

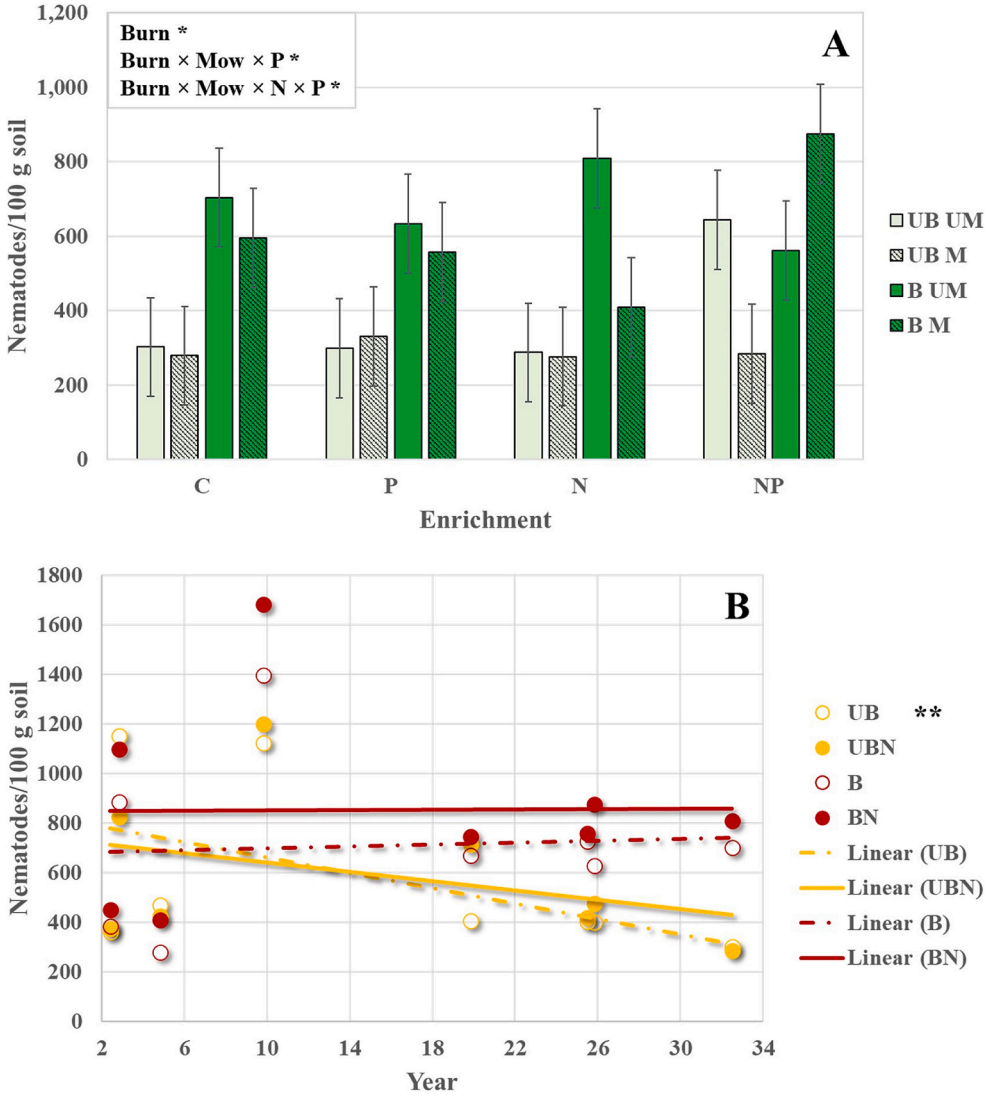

Fig. 1. Effects of burning (B = annually burned vs. UB = unburned), mowing (M = annually mowed vs. UM = unmowed) and nitrogen (N, NP) and phosphorus (P, NP) fertilization treatments vs unfertilized control (C) on total nematode population densities in the Belowground Plot Experiment. (A) Effects after 32 years of experimental treatments; (B) temporal trends in total nematode population densities, with numbers on the x-axis representing years of treatment. Error bars in 2 A represent standard errors of the means ($n = 4$) and *, ** indicate $P \leq 0.05$ and 0.01, respectively, for treatment main effect and interaction means (2 A) and for treatment slopes through time (2B; H_0: slope = 0).

burned and unburned plots through time, regardless of N treatment (data not shown).

Bacterivorous taxa displayed idiosyncratic responses to treatments. The dominant family Cephalobidae (*Acrobeles*, *Acrobeloides*, *Chiloplacus*, and *Eucephalobus* spp.) was relatively unaffected after 32 years of burning, mowing and fertilization treatments (Fig. 4D), but did display steep declines ($P < 0.01$) in relative abundance through time in the presence of annual burning (Fig. 5D). The Plectidae (*Plectus* and *Tylocephalus* spp.) displayed decreased relative abundance in burned plots (Figs. 4E and 5E). The Rhabditidae (*Mesorhabditus* and *Oscheius* spp.) displayed the strongest treatment responses, with maximum relative abundances observed for mowed, P-fertilized plots (8 %) followed by unmowed, unfertilized plots (6 %), both in the absence of burning (Fig. 4F). Relative abundances of the Rhabditidae increased ($P \leq 0.01$) through time in the absence of burning (Fig. 5F).

3.4. Omnivore and predator relative abundances

The Dorylaimoidea (predominantly *Aporcelaimellus*, *Ecumenicus*, *Eudorylaimus*, and *Mesodorylaimus* spp.), which encompasses omnivorous and predaceous taxa, exhibited contradictory responses to experimental treatments. No evidence of burning, mowing, or fertilization effects were observed after 32 years of treatment (Fig. 6A, Supplementary Table S1), but a decreasing trend in relative abundance ($P = 0.03$) was observed for burned plots through time (Fig. 6B). The Belondiroidea (predominately *Axonchium*, *Belondira*, and *Dorylaimellus* spp.), with a mean relative abundance of <1 %, similarly showed no evidence of treatment effects after 32 years, and no trends across time (data not shown). Mean relative abundances of the predaceous genera *Clarkus* and *Mylonchulus* (0.4 %) were negatively impacted ($P < 0.05$) by burning and N fertilization (data not shown).

3.5. Taxa with uncertain feeding habits

Few patterns in treatment responses were discernable for *Prismatolaimus*, a genus (and family) with poorly documented feeding habits (Yeates et al., 1993). The greatest relative abundances (2–3 %) of *Prismatolaimus* after 32 years of treatments were observed for P-fertilized

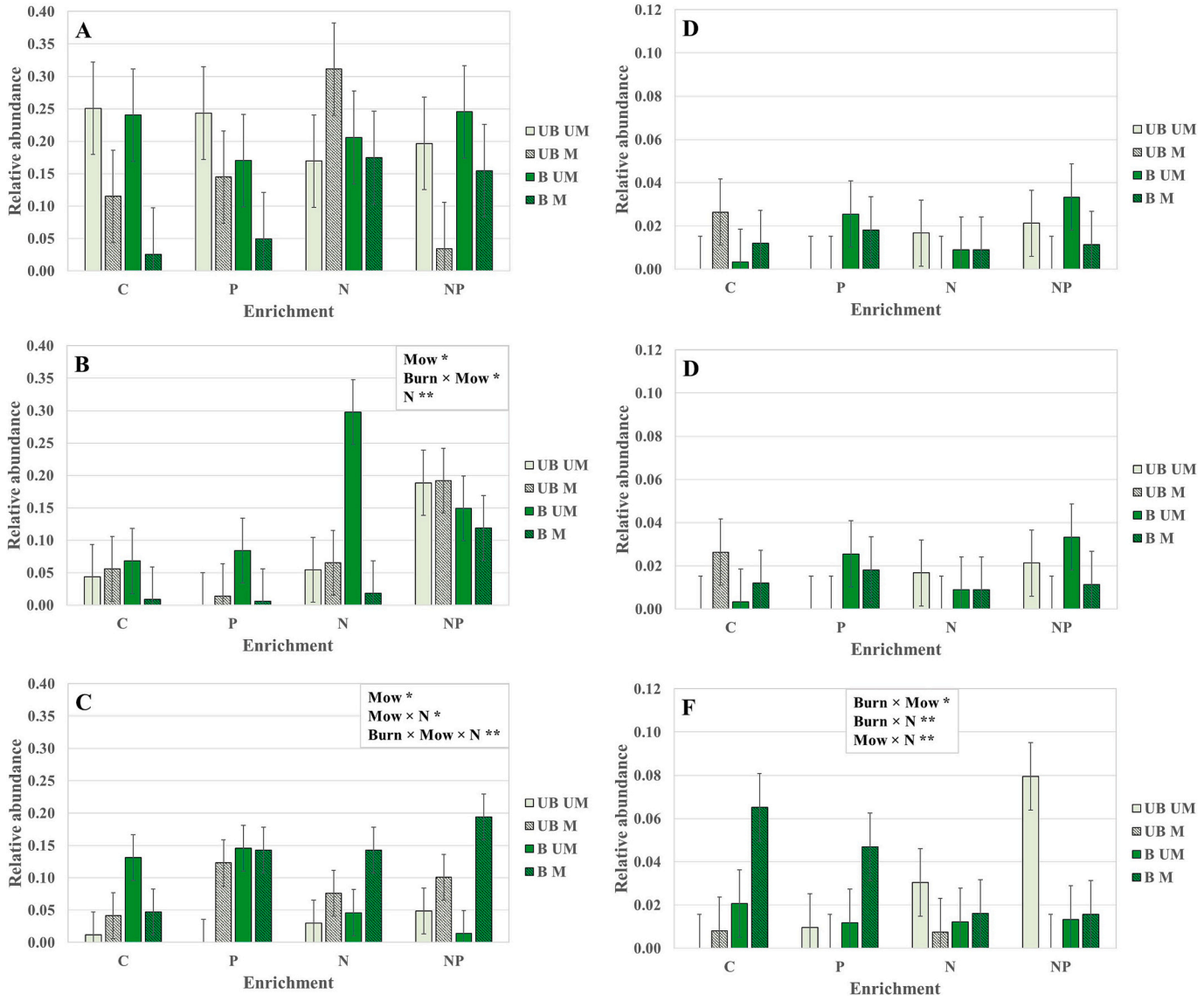

Fig. 2. Effects of burning (B = annually burned vs. UB = unburned), mowing (M = annually mowed vs. UM = unmowed) and nitrogen (N, NP) and phosphorus (P, NP) fertilization treatments vs unfertilized control (C) on herbivorous nematode relative abundances in the Belowground Plot Experiment after 32 years of experimental treatments. (A) *Helicotylenchus*; (B) Paratylenchinae; (C) *Mesocriconema*; (D) *Tylenchorhynchus*; (E) *Pratylenchus*; (F) *Xiphinema*. Error bars represent standard errors of the means ($n = 4$) and *, ** indicate $P \leq 0.05$ and 0.01, respectively, for treatment main effect and interaction means.

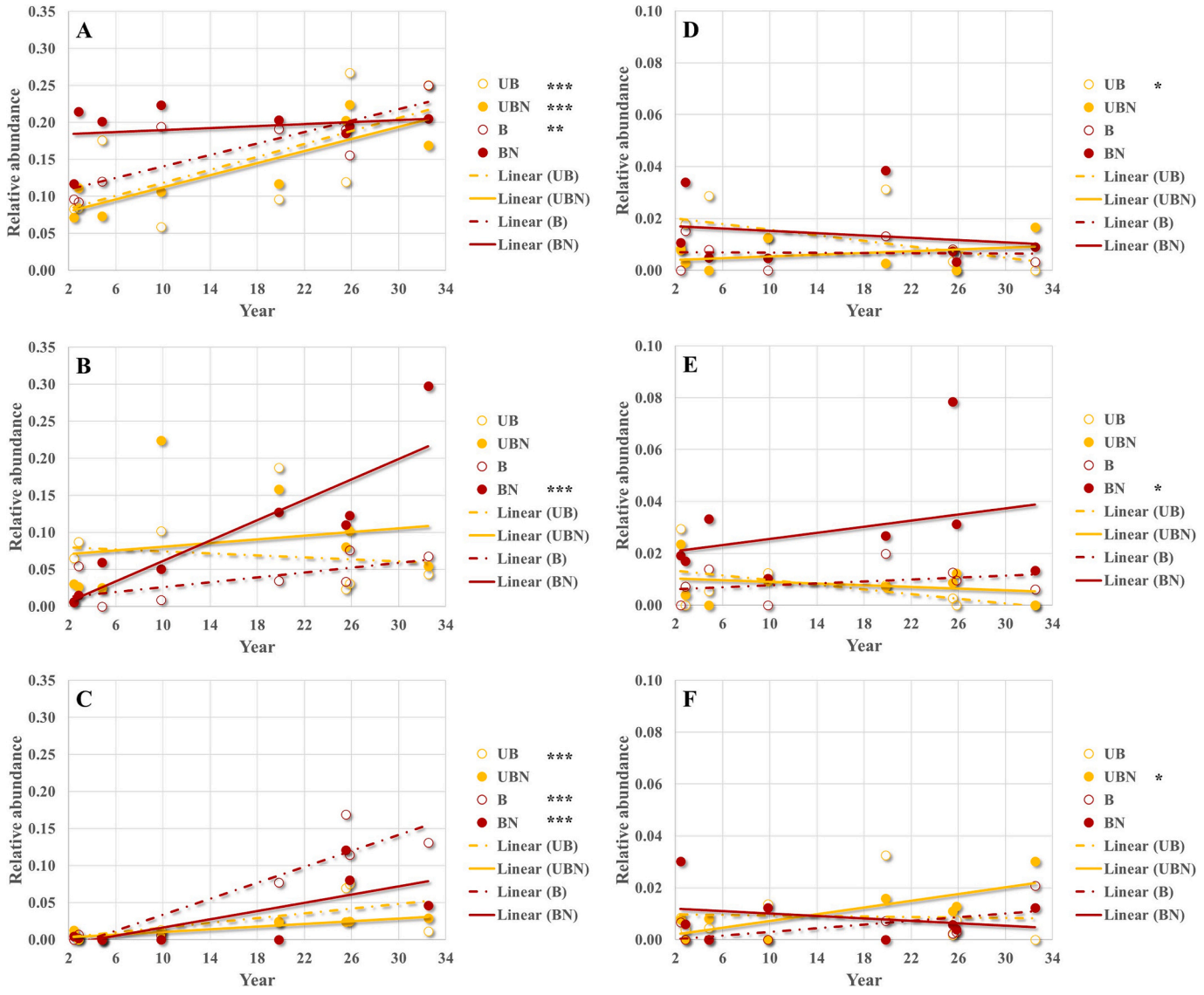

Fig. 3. Effects of burning (B = annually burned vs. UB = unburned) and nitrogen (N) fertilization on temporal trends in herbivorous nematode relative abundances in the Belowground Plot Experiment, with numbers on the x-axis representing years of treatment. (A) *Helicotylenchus*; (B) Paratylenchinae; (C) *Mesocriconema*; (D) *Tylenchorhynchus*; (E) *Pratylenchus*; (F) *Xiphinema*. *, **, *** indicate $P \leq 0.05$, 0.01 and 0.001, respectively, for treatment slopes through time (H_0: slope = 0).

plots regardless of burning or mowing treatments (Fig. 7A). Relative abundances through time declined ($P \leq 0.001$) from a mean of 5 % to <1 % (Fig. 7B). Additional genera (and putative feeding habits sensu Yeates et al., 1993) in this category included *Achromadora* (unicellular eucaryote feeder), *Monhystera* (bacterial feeder, substrate ingestor), *Odontolaimus* (bacterial or unicellular eucaryote feeder), and *Tripyla* (predator), which collectively accounted for 1 % in mean relative abundance, exhibited lower relative abundances in the presence of N or P fertilization (data not shown).

3.6. Principal component analysis and community indices

The first two principal components from the PCA of community structure are presented in Fig. 8. The first principal component accounted for 16 % of the total variation and separated N treatments ($P = 0.001$), as well as burn × mow interaction treatments ($P = 0.04$; Fig. 8A). The second principal component accounted for 13 % of the total variation and further separated N treatments ($P = 0.07$). Taxa with the strongest PC1 eigenvector contributions included the Tylenchidae and *Mesocriconema*, with negative weightings, and the Paratylenchidae, *Aphelenchus*, Plectidae, and Rhabditidae, with positive weightings (Fig. 8B). Taxa with the strongest PC2 eigenvector contributions included Aphelenchus and the Paratylenchidae, with negative weightings, and the Dorylaimida, *Aphelenchoides* and *Prismatolaimus*, with positive weightings.

The fungivore to bacterivore ratio was the most informative community index tested. This ratio was strongly affected ($P \leq 0.001$) by chronic N enrichment, decreasing from 0.84 in unfertilized plots to 0.70 in N-enriched plots. The maturity index (MI) responded to both burning and N effects, with MI increasing ($P = 0.05$) from 2.45 in unburned plots to 2.96 in burned plots, and decreasing ($P = 0.04$) from 2.84 in unfertilized plots to 2.56 in N-enriched plots. The Enrichment Index (EI) and Structure Index (SI) both indicated mow × P interactions ($P < 0.02$), with EI increasing in the combined presence of mowing and P-fertilization, while SI decreased in the presence of mowing alone (data not shown).

4. Discussion

Nematode responses to treatments in this long-term field experiment

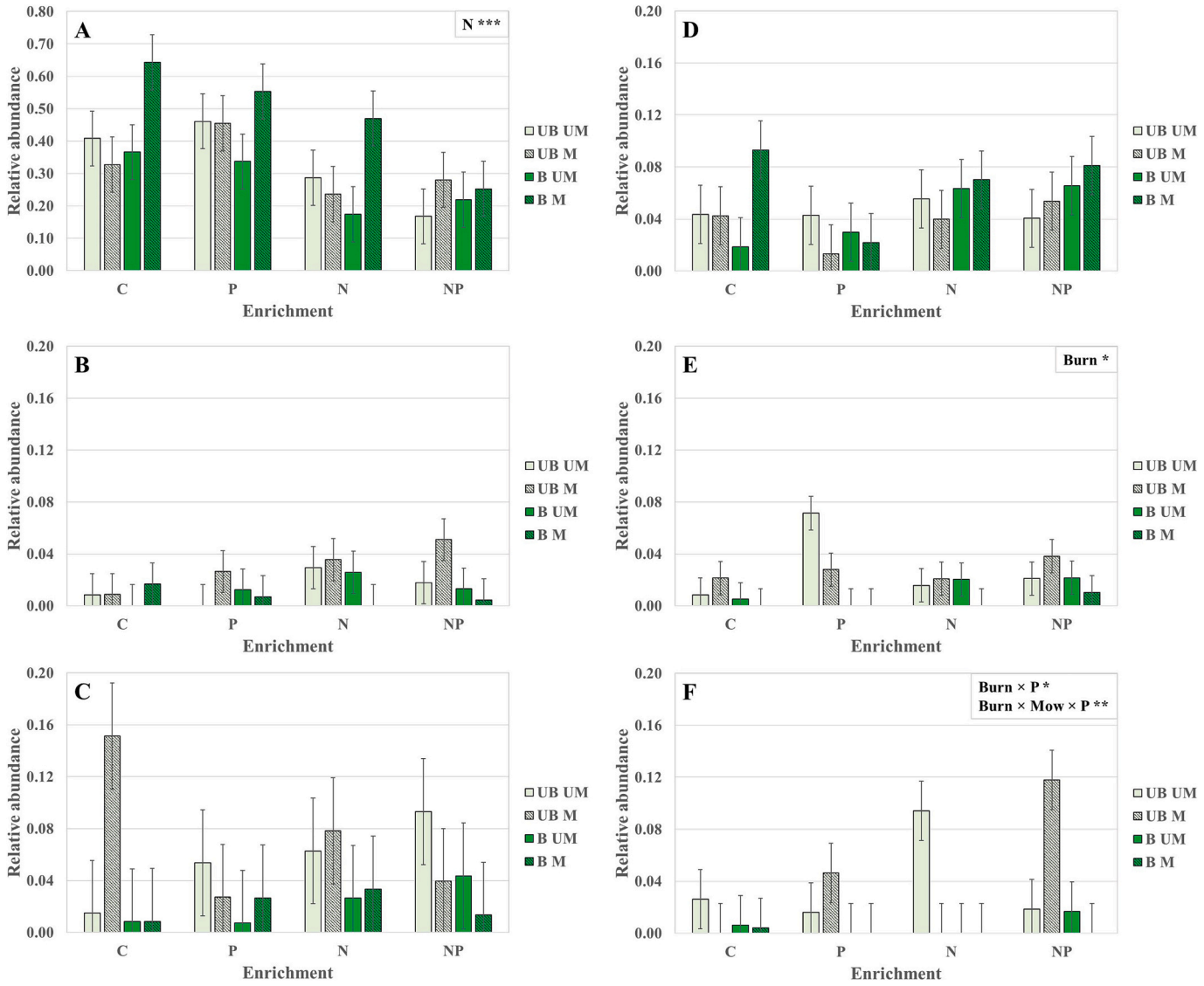

Fig. 4. Effects of burning (B = annually burned vs. UB = unburned), mowing (M = annually mowed vs. UM = unmowed) and nitrogen (N, NP) and phosphorus (P, NP) fertilization treatments vs unfertilized control (C) on fungivorous and bacterivorous nematode relative abundances in the Belowground Plot Experiment after 32 years of experimental treatments. (A) Tylenchidae; (B) *Aphelenchus*; (C) *Aphelenchoides*; (D) Cephalobidae; (E) Plectidae; (F) Rhabditidae. Error bars represent standard errors of the means ($n = 4$) and *, ** indicate $P \leq 0.05$ and 0.01, respectively, for treatment main effect and interaction means.

likely reflected changes in the total soil food web structure. Indeed, the argument for the use of nematodes as ecological indicators of soil food web status is based on this assertion (Neher, 2010). Fortunately, such comprehensive community responses have been monitored at various points throughout the duration of the Belowground Plot Experiment (Benning and Seastedt, 1997; Callaham Jr. et al., 2003; Carson and Zeglin, 2018; Collins et al., 1998; Darby et al., 2013; Garcia and Rice, 1994; Gibson et al., 1993; Kitchen et al., 2009; Todd, 1996). Published reports of responses are summarized in Table 1. Documented patterns include positive effects of both fire and N fertilization on root biomass and root herbivore densities, but these treatments also had negative effects on plant diversity (i.e., favoring dominance of a few species of warm-season grasses). In contrast, divergent effects of fire and N were observed for root and microbial N content, with fire generally decreasing and N fertilization increasing root N concentration and soil microbial biomass N. Effects of annual mowing were largely negative (e.g., reduced root biomass, root N content, microbial biomass C and N, and root herbivore densities), with the exception of plant diversity, which was maintained at higher levels with mowing in the presence of fire and N fertilization. In light of this clear evidence that the BGPE treatments had variable impacts on different components of the total soil food web, in the following sections we provide an interpretation of observed nematode responses in the context of the observed plant and soil changes.

4.1. *Herbivore responses*

The most obvious aboveground effect after 32 years of experimental treatments was the near total conversion of the plant communities from a grassland state at the onset of the experiment to a shrubland or woodland state in the unburned, unmowed plots (Supplementary Fig. S1). Surprisingly, few nematode community variables reflected this conspicuous shift in the plant community. The clearest example of a response to this state change was the herbivorous genus *Mesocriconema*, which displayed a 74 % reduction in relative abundance as plant communities shifted from a grassland state in the absence of burning or mowing, implying a clear preference for grassland habitat. The remaining herbivorous taxa did not follow this pattern even when they exhibited responses to the burning or mowing treatments, suggesting that either these taxa are generalist root herbivores, or they consist of

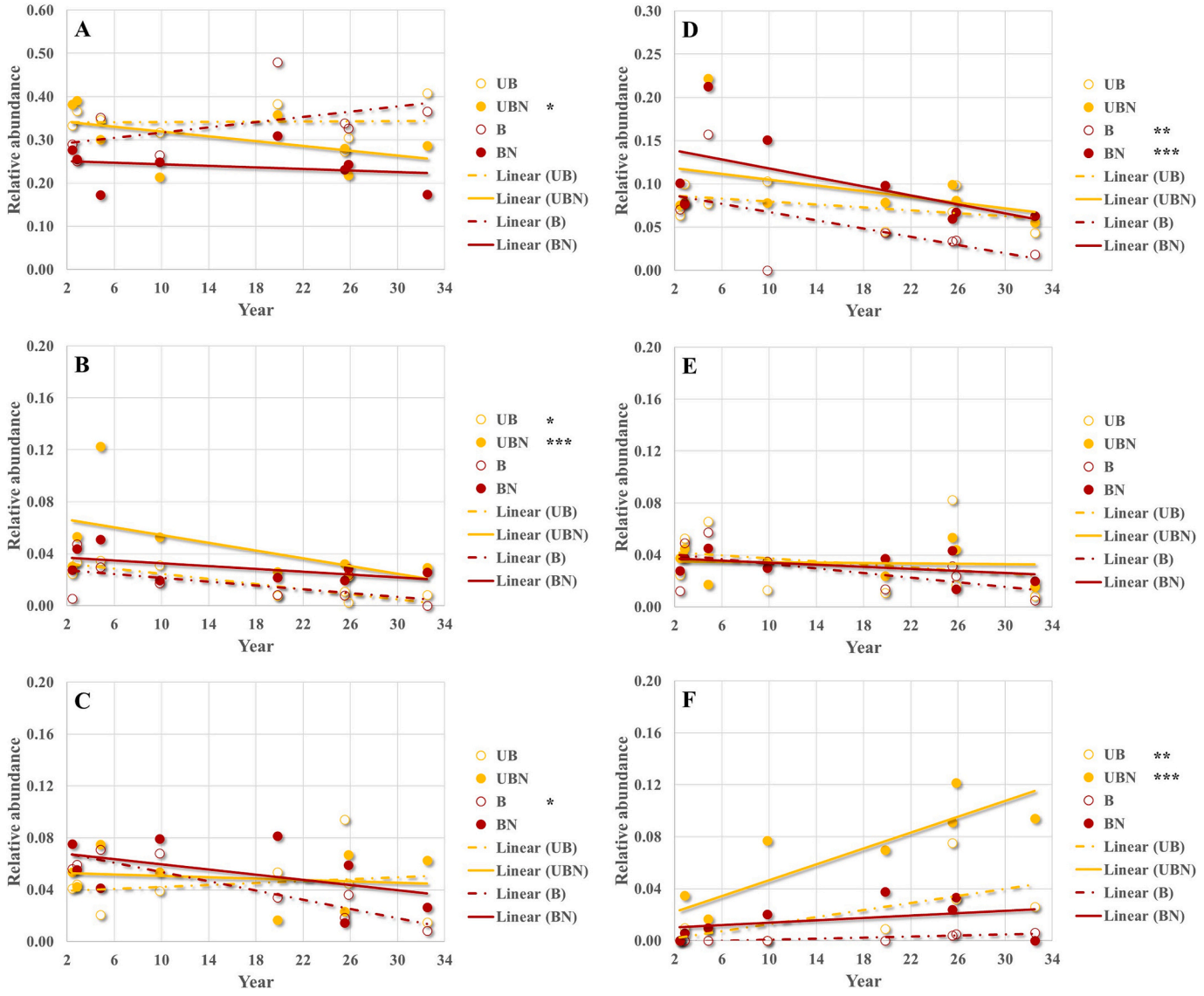

Fig. 5. Effects of burning (B = annually burned vs. UB = unburned) and nitrogen (N) fertilization on temporal trends in frugivorous and bacterivorous nematode relative abundances in the Belowground Plot Experiment, with numbers on the x-axis representing years of treatment. (A) Tylenchidae; (B) *Aphelenchus*; (C) *Aphelenchoides*; (D) Cephalobidae; (E) Plectidae; (F) Rhabditidae. *, **, *** indicate $P \leq 0.05$, 0.01 and 0.001, respectively, for treatment slopes through time (H_0: slope = 0).

mixtures of species with different host preferences that were selectively sorted by changes in vegetation structure. The genus *Helicotylenchus*, for example, consists of at least four species previously identified from the BGPE (Darby et al., 2013). Although this genus is commonly associated with grasses, some species common at Konza Prairie (e.g., *H. platyurus*, *H. pseudorobustus*) have also been reported from soil surrounding the roots of trees and shrubs (Thorne and Malek, 1968).

As observed for other invertebrates (Callaham Jr. et al., 2003), nematode community responses were dominated by interactions among burning, mowing, and fertilizer treatments. This was true for P-, as well as N-fertilization, despite the absence of any P-related main effects. These interactions limit generalizations about nematode responses to specific treatments, but a few consistent patterns can be highlighted. However, unlike macroinvertebrate responses, where treatments resulting in lower quality resources (i.e., depleted nutrient content), such as burning and mowing, generally resulted in lower densities (Callaham Jr. et al., 2003), nematode community responses were more complex, likely reflecting the influence of both resource quantity and quality. For example, total nematode abundance declined through time in the unburned plots and was approximately halved by conclusion of the experiment. This is consistent with well-documented effects of fire on above- and belowground plant productivity in the tallgrass prairie. Specifically, frequent prescribed burning increases both above- and belowground productivity and biomass, while aboveground biomass removal by mowing or grazing reduces belowground productivity and biomass allocation (Todd et al., 1992; Turner et al., 1993; Johnson and Matchett, 2001; Kitchen et al., 2009). In contrast, N fertilization mitigates the N limitation associated with frequent burning and leads to increased belowground productivity and root N content (Blair et al., 1998). These effects are reflected in frequent burning × mowing interactions in herbivore relative abundances, with higher abundances observed only for burned plots in the absence of mowing. This same pattern was observed for root biomass by Kitchen et al. (2009), suggesting that herbivorous nematode abundance may be partly explained by availability of roots. Finally, considering that root biomass, in addition to root N content and turnover, can increase under N fertilization in burned grasslands (Blair et al., 1998), it is perhaps not surprising that we observed increased total herbivore abundance in the presence of N

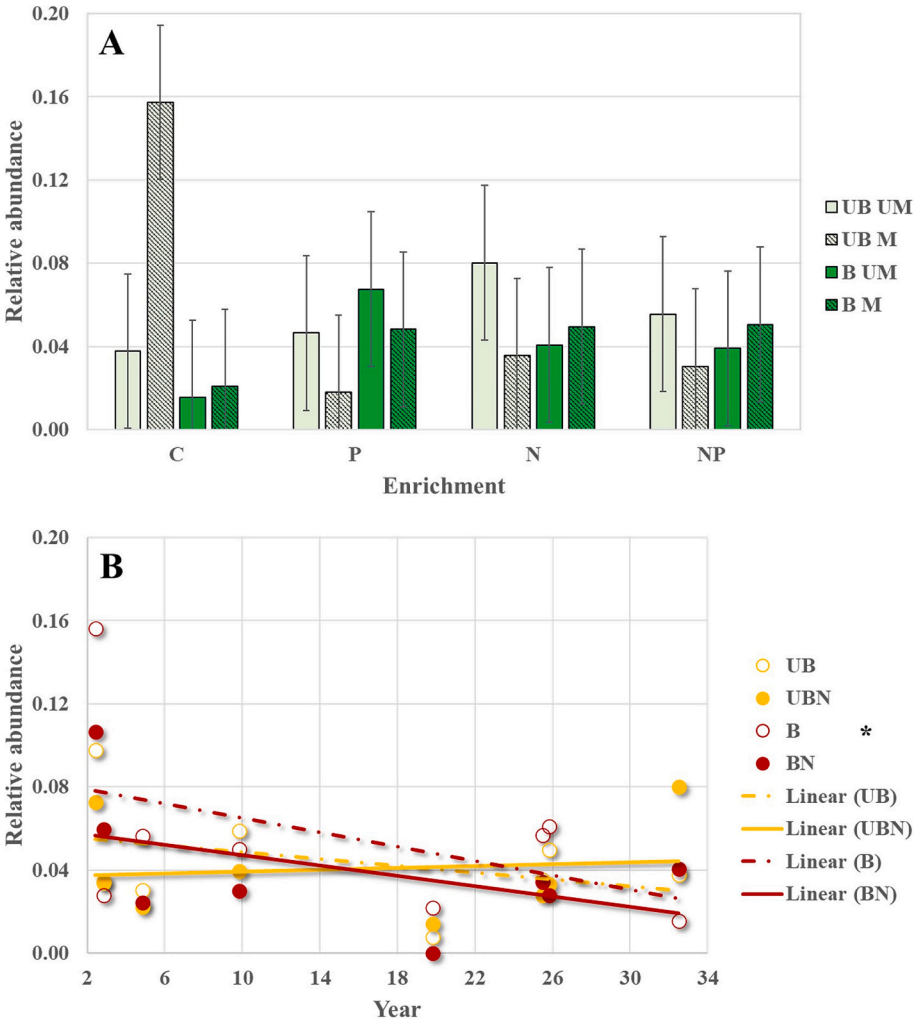

Fig. 6. Effects of burning (B = annually burned vs. UB = unburned), mowing (M = annually mowed vs. UM = unmowed) and nitrogen (N, NP) and phosphorus (P, NP) fertilization treatments vs unfertilized control (C) on relative abundances of omnivorous and predaceous Dorylaimoidea in the Belowground Plot Experiment. (A) Effects after 32 years of experimental treatments; (B) temporal trends in relative abundances, with numbers on the x-axis representing years of treatment. Error bars represent standard errors of the means ($n = 4$) and * indicates $P \leq 0.05$ for treatment main effect and interaction means and for treatment slopes through time (H_0: slope = 0).

fertilization, with the highest abundance observed for burned, N-fertilized plots. The effect of N fertilization on root biomass remains somewhat ambiguous, however, as recent research has shown that belowground plant responses to N addition are context dependent, with both increases and decreases in root biomass possible (Keller et al., 2023).

4.2. *Microbivore responses*

Patterns of fungivorous taxa responses, especially by the Tylenchidae, were opposite those observed for herbivorous taxa, with 34 % higher relative abundance associated with mowing, and 31 % lower relative abundance associated with N fertilization after 32 years of experimental treatments. This group has historically been labelled as root epidermal cell and root hair feeders (Yeates et al., 1993), but our observations do not support this. Early observations from the BGPE suggested that the Tylenchidae (e.g., *Filenchus*) are fungal feeding (Todd, 1996), and more recent evidence confirms this assertion (Okada and Kadota, 2003; Okada et al., 2005). Misassignment of feeding habit in this case would have outsized inferential consequences, as this is the dominant tallgrass prairie nematode family in terms of abundance.

Bacterivore abundances generally responded negatively to burning but positively to N fertilization as expected based on published reports of microbial population responses to changes in resource quality. Burning reduces microbial N (Garcia and Rice, 1994), while N fertilization increases archaeal and bacterial gene abundance, favoring fast-growing microbial taxa (Carson and Zeglin, 2018; Nieland et al., 2021). Nematode responses to burning were driven by the Plectidae and Rhabditidae at the termination of the experiment, while responses to N fertilization primarily reflected a 54 % increase in the relative abundance of the Cephalobidae. Across years, a negative trend in relative abundance was observed for the Cephalobidae in burned plots, while a presumably analogous positive trend in relative abundance was observed for the Rhabditidae in unburned plots (Fig. 5). These two families are important components of the Enrichment Index (EI), which measures the importance of opportunistic bacterivores (e.g., Rhabditidae) in the soil food web and is expected to increase with nutrient enrichment (Ferris et al., 2001). Support for this hypothesis in the present study is weak, however, with an analysis of EI failing to detect either burning or N fertilization effects. Furthermore, while trends in relative abundance of the Cephalobidae and Rhabditidae across time ostensibly reflect burning effects on N availability (e.g., increased relative abundance of opportunistic taxa in unburned plots), other factors such as soil moisture limitations in burned prairie (Briggs and Knapp, 1995) may better explain the results. Since both families increased in the presence of N fertilization and the ratio of their relative abundances remained unchanged, the Rhabditidae

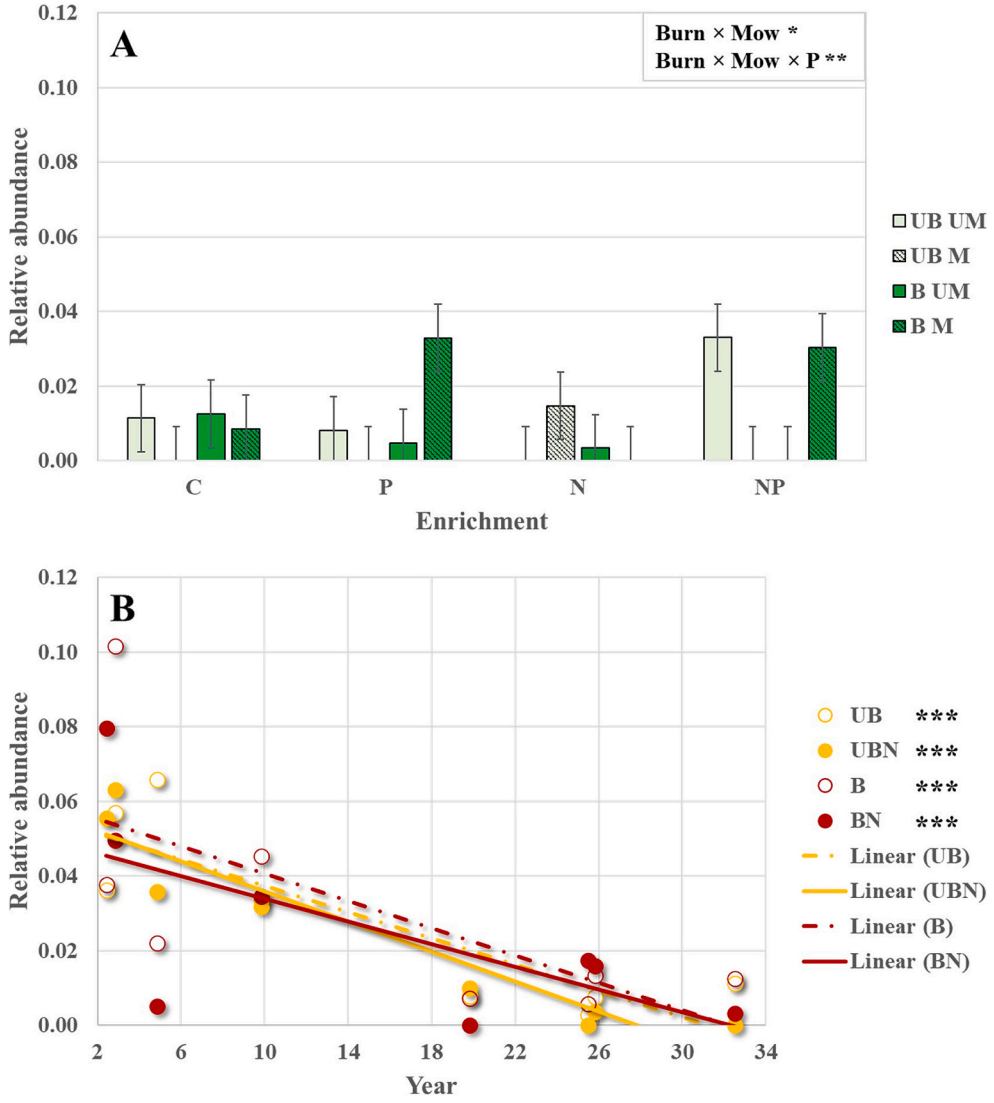

Fig. 7. Effects of burning (B = annually burned vs. UB = unburned), mowing (M = annually mowed vs. UM = unmowed) and nitrogen (N, NP) and phosphorus (P, NP) fertilization treatments vs unfertilized control (C) on *Prismatolaimus* relative abundances in the Belowground Plot Experiment. (A) Effects after 32 years of experimental treatments; (B) temporal trends in relative abundances, with numbers on the x-axis representing years of treatment. Error bars represent standard errors of the means and *, **, *** indicate $P \leq 0.05$, 0.01 and 0.001, respectively, for treatment main effect and interaction means and for treatment slopes through time (H_0: slope = 0).

appear to be no more opportunistic than the Cephalobidae in response to N enrichment. Finally, diversity of responses at higher taxonomic resolution (genus or species) remains an important caveat, as both similar and divergent responses to burning and N enrichment across and within bacterivorous families have been documented (Jones et al., 2006).

4.3. Higher trophic level responses

The order Dorylaimida represents a large, diverse group of nematodes with poorly characterized feeding habits. The feeding strategy most often applied to this group is omnivory, but predatory behavior (on other invertebrates) has been observed for some of the larger taxa, including the common prairie genera *Aporcelaimellus* and *Eudorylaimus* (Yeates et al., 1993). Collectively, the Dorylaimida represents <20 % of total abundance (<10 % in annually burned prairie) but comprises nearly half of the species diversity in the nematode community (Todd et al., 2006). This group is an influential component of the Maturity Index (MI) and the Structure Index (SI) and, as the primary members of the highest trophic level, are reported to be sensitive indicators of ecological disturbance (Bongers, 1990, 1999). Nevertheless, analysis of the relative abundances of the most important dorylaim families in the BGPE, the Aporcelaimellidae and Qudsianematidae (analyzed collectively as the Dorylaimoidea) failed to detect any treatment differences, although abundance did decline across time in annually burned plots. Analysis of SI detected a mowing effect but failed to detect burning or N fertilization effects. Together, these observations raise questions concerning the indicator status of this group. As for the bacterivorous group, conflicting evidence of disturbance sensitivity exists for several taxa (Freckman and Ettema, 1993; Fiscus and Neher, 2002).

4.4. C-N-P stoichiometry and the effects of resource quality vs. quantity

Separation of experimental treatments with PCA was expected to reflect habitat-driven changes in the nematode community and soil food web (Neher et al., 2005). A burning × mowing interaction was observed for the first principal component, but instead of the expected separation of unburned, unmowed plots from treatments with burning or mowing, the combination of burning and mowing was separated from the other treatments. Either the prairie nematode community is resilient to large changes in plant community structure or, more likely, the woodland

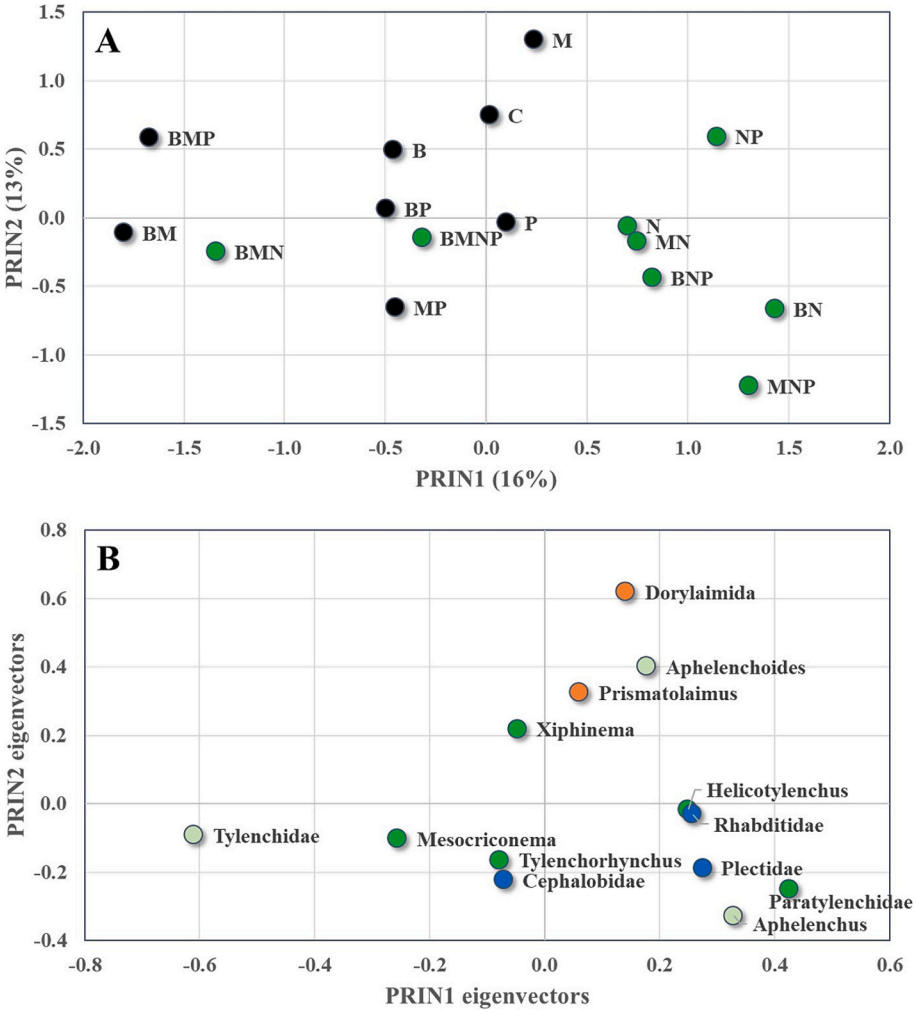

Fig. 8. Principal component analysis of nematode community responses to burning (B), mowing (M), and nitrogen (N) and phosphorus (P) fertilization treatments in the Belowground Plot Experiment. (A) Separation of N treatments (green symbols = fertilized, black symbols = unfertilized) based on the first and second principal components; (B) eigenvectors (taxa weightings) for the first and second principal components.

nematode community still reflects a legacy grassland structure, with insufficient time for nematode dispersal from local gallery forests to isolated woodland patches. A second expectation that differences in the nematode community would reflect N enrichment was strongly supported, with both the first and second principal components showing separation of N treatments. The tallgrass prairie is an N-limited system with high C:N of many resources (e.g., plant roots, microbial biomass), which are known to be associated with fungal-dominated decomposition pathways (Ferris et al., 2001; Rice et al., 1998; Todd, 1996). Predictions of soil food web responses can therefore be made based on C:N stoichiometry. For example, C:N of roots in the tallgrass prairie range from 60 with frequent burning to approximately 30 in the presence of N fertilization (Benning and Seastedt, 1997; Johnson and Matchett, 2001), while C:N of soil fungi and bacteria average values <30 and < 10, respectively (Camenzind et al., 2021; Cleveland and Liptzin, 2007; Garcia and Rice, 1994), and those of soil fauna average ≤ 10 (Osler and Sommerkorn, 2007). The likely explanation is that bacteria and bacterivorous soil fauna should respond more favorably to changes in resource quality under N fertilization than fungi and fungivorous soil fauna, and this is generally supported by the PCA results, as well as the ANOVAs for relative abundances. In this case, nematodes appear to be responding indirectly to the quality (i.e., N content) of root resources via changes in the quantity of food resources (i.e., bacterial densities). C:N stoichiometry suggests that herbivorous taxa should also be strongly N limited, and again, both the PCA and ANOVA results support this, at least for the dominant herbivorous taxa. It is also possible that N fertilization increases plant production (i.e., greater root availability as opposed to greater N availability) but this alternative inference is not supported by observations. Assessment of chronic N fertilization revealed negative effects on root production, while N content of roots remained consistently higher (Rice et al., 1998). Soil and root C:N remained high through the end of the experiment in 2017 (Nieland and Zeglin, 2024). Earlier reports of nematode responses to BGPE treatments further showed that herbivore population densities were correlated with root N content and total root N, but not with live root biomass (Todd, 1996).

No main effects of P fertilization were observed in the current study and no consistent patterns in P fertilization interactions with the other treatments were detectable. Tallgrass prairie soil typically contains low levels of inorganic P but limited availability of this nutrient is mitigated in large part by symbiotic plant associations with arbuscular mycorrhizal fungi (AMF), which are nearly obligate for the dominant plant species (Hetrick et al., 1990, 1992). The only well-documented effect of P fertilization on the prairie soil food web is its inhibitory effect on AMF root colonization (Bentivenga and Hetrick, 1992). Thus, it is likely that P fertilization, offset by reduced mycorrhizal contribution to P availability, resulted in little impact on the soil food web.

Table 1
Published soil environmental and food web responses to experimental treatments in the Belowground Plot Experiment.[a]

Treatment	Positive responses	Negative responses
Annual burning	Grass biomass (Nieland et al., 2021) Root biomass (Benning and Seastedt, 1997; Kitchen et al., 2009) Microbial C (Garcia and Rice, 1994) Bacterial OTU richness (Carson and Zeglin, 2018) Extramatrical mycorrhizal hyphae (Wilson et al., 2009) Cicada (*Cicadettana*) nymphs (Callaham Jr. et al., 2003) and adults (Callaham Jr. et al., 2002) Herbivorous nematode abundance (Todd, 1996) Bacterivorous nematode abundance (Todd, 1996)	Gravimetric water content (Carson and Zeglin, 2018) Plant diversity; woody biomass (Nieland et al., 2021); woody species richness and cover (Collins et al., 1998; Gibson et al., 1993) Root N content (Benning and Seastedt, 1997; Kitchen et al., 2009) Microbial N (Garcia and Rice, 1994) European earthworm density (Callaham Jr. et al., 2003) Cicada (*Neotibicen*) nymphs (Callaham Jr. et al., 2003) and adults (Callaham Jr. et al., 2002) Total invertebrate density and biomass (Callaham Jr. et al., 2003) Predaceous nematode abundance (Todd, 1996)
Annual mowing	Plant diversity (Collins et al., 1998) Native earthworm density & biomass (Callaham Jr. et al., 2003)	Soil C & N (Kitchen et al., 2009) Root biomass (Garcia and Rice, 1994; Kitchen et al., 2009) Root N content (Kitchen et al., 2009) Microbial C & N (Garcia and Rice, 1994) European earthworm density (Callaham Jr. et al., 2003) Cicada (*Neotibicen*) nymphs (Callaham Jr. et al., 2003), and *Cicadettana* adults (Callaham Jr. et al., 2002) Herbivorous beetle larvae density (Callaham Jr. et al., 2003) Herbivorous nematode abundance (Todd, 1996)
N fertilization	Grass aboveground biomass (Nieland et al., 2021) Root N content (Benning and Seastedt, 1997) Microbial N (Garcia and Rice, 1994); soil C:N (Nieland and Zeglin, 2024) Bacterial community composition: species dominance (Coolon et al., 2013); copiotrophic taxa (Carson and Zeglin, 2018; Nieland et al., 2024); archaeal and bacterial 16S rRNA gene abundance (Nieland et al., 2021; Nieland and Zeglin, 2024) Extramatrical mycorrhizal hyphae and root colonization (Wilson et al., 2009) European earthworm density & biomass (Callaham Jr. et al., 2003) Herbivorous beetle larvae density (Callaham Jr. et al., 2003) Adult cicada (*Cicadettana*) emergence density, and individual cicada (*Cicadettana* and *Neotibicen*) female body size (Callaham Jr. et al., 2003) Herbivorous nematode abundance (Todd, 1996) Bacterivorous nematode abundance (Todd, 1996)	Plant diversity (Collins et al., 1998) Microbial biomass (Nieland et al., 2021); bacterial species richness (Coolon et al., 2013); bacterial community composition: oligotrophic taxa (Carson and Zeglin, 2018) Native earthworm density & biomass (Callaham Jr. et al., 2003) Predaceous nematode abundance (Todd, 1996)

[a] Variable responses frequently involved quantitative interactions among treatments (e.g., N fertilization effects were often stronger in the presence of burning than in its absence). P fertilization effects are excluded because they consisted almost exclusively of cryptic treatment interactions.

5. Conclusions

Fire exclusion and N enrichment had cumulative long-term effects on the tallgrass prairie nematode community, while mowing and P fertilization acted as moderators. Although mowing prevented the encroachment of woody vegetation that occurred when fire was suppressed, few nematode responses could be attributed to mowing's effect on vegetative structure. Reductions in herbivorous nematode densities in the presence of mowing are consistent with published reports of reduced root biomass and N content, although the role of invasive grasses (i.e., *Bothriochloa bladhii*) cannot be ruled out. There were also examples of positive responses to mowing by subdominant taxa (e.g., *Mesocriconema*), possibly the result of competitive release.

While fire exclusion had a cumulative negative effect on total nematode population densities, this response similarly appeared not to be directly related to shifts in vegetation structure and was likely driven by complex interactions among biotic and abiotic factors. Fire exclusion has potentially negative impacts on soil communities through reductions in root biomass, as well as potentially positive impacts through increased soil moisture content, although in the latter case, assignment of specific mechanisms is further constrained by the variable responses of nematode taxa to soil water availability (Todd et al., 1999). Direct responses to shifts in vegetation structure were likely limited due to insufficient time or opportunity for nematode dispersal from local gallery forests to isolated woodland patches, thus any observed responses reflect selection rather than succession.

The most consistent nematode responses to N enrichment were observed for selected herbivorous taxa and for taxa involved in decomposition pathways. These responses matched predictions based on well-documented changes in resource quality and quantity observed in the BGP experiment relative to the N-limited conditions that predominate in tallgrass prairie (Table 1). Long-term nematode responses to fire exclusion and N enrichment generally manifested as persistent directional trends that were consistent with the short-term responses reported by Todd (1996), and provide additional qualified support for the use of nematode community structure as an indicator of soil food web status. Higher trophic level responses were generally uninformative and will require greater taxonomic resolution and more reliable information on feeding habits before indices based on these taxa can be recommended. Individual family-level responses provided the greatest diagnostic resolution, but the fungivore to bacterivore ratio and MI were nevertheless informative community indices.

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CRediT authorship contribution statement

T.C. Todd: Resources, Project administration, Methodology, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **J.M. Blair:** Methodology, Writing – review & editing, Writing – original draft. **Mac Callaham, Jr.:** Writing – review & editing, Writing – original draft.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Data availability

The data are available in the Environmental Data Initiative (EDI) Data Portal at https://doi.org/10.6073/pasta/f662e000ec0a0bd72b30e88288712892.

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