

RESEARCH ARTICLE

Precipitation effects on nematode diversity and carbon footprint across grasslands

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Abstract

Free-living nematodes are one of the most diverse metazoan taxa in terrestrial ecosystems and are critical to the global soil carbon (C) cycling through their role in organic matter decomposition. They are highly dependent on water availability for movement, feeding, and reproduction. Projected changes in precipitation across temporal and spatial scales will affect free-living nematodes and their contribution to C cycling with unforeseen consequences. We experimentally reduced and increased growing season precipitation for 2 years in 120 field plots at arid, semiarid, and mesic grasslands and assessed precipitation controls on nematode genus diversity, community structure, and C footprint. Increasing annual precipitation reduced nematode diversity and evenness over time at all sites, but the mechanism behind these temporal responses differed for dry and moist grasslands. In arid and semiarid sites, there was a loss of drought-adapted rare taxa with increasing precipitation, whereas in mesic conditions increases in the population of predaceous taxa with increasing precipitation may have caused the observed reductions in dominant colonizer taxa and yielded the negative precipitation–diversity relationship. The effects of temporal changes in precipitation on all aspects of the nematode C footprint (respiration, production, and biomass C) were all dependent on the site (significant spatial × temporal precipitation interaction) and consistent with diversity responses at mesic, but not at arid and semiarid, grasslands. These results suggest that free-living nematode biodiversity and their C footprint will respond to climate change-driven shifts in water availability and that more frequent extreme wet years may accelerate decomposition and C turnover in semiarid and arid grasslands.

KEYWORDS

carbon cycling, climate change, drought, soil fauna, spatiotemporal scales

1 | INTRODUCTION

Soil biodiversity and their ecosystem functions are threatened by climate change (Bardgett & Van Der Putten, 2014; Orgiazzi et al., 2016). At the same time, soil biodiversity plays a prominent control on the rate of climate change by governing the pace of organic matter processing and soil carbon (C) cycling (Crowther et al., 2019). Among the multitude of climate change factors affecting soil biodiversity, changing precipitation is likely to be a dominant driver of shifts in community composition and functioning of soil fauna that dwell in soil-water films such as nematodes (Blankinship et al., 2011; Franco et al., 2019). Nematodes are important organisms affecting the global soil C cycle primarily through their effects on primary production and organic matter decomposition (Filser et al., 2016; Gebremikael et al., 2016; Ingham et al., 1985; Vestergård et al., 2019). However, limited empirical evidence exists of how nematode diversity and the C utilization for production and respiration by nematode assemblages (i.e., C footprint; Ferris, 2010) respond to increasing precipitation extremes and how such responses may vary from dry to humid ecosystems. Free-living nematodes, contrary to their plant-parasitic counterparts which complete the entirety or part of their life cycles associated with plant tissues, have limited shelter against the effects of environmental changes (Eisenback, 1993). Therefore, this group of invertebrates occupying multiple trophic categories (bacterivores, fungivores, omnivores, and predators) may be highly vulnerable to extreme drought and deluge events.

Spatially, nematode family composition strongly relates to long-term mean annual precipitation (MAP) globally (Nielsen et al., 2014). This pattern reflects the influence that climate has on local soil properties and vegetation composition (Chen et al., 2015). There is evidence showing that species richness of soil biota is driven by spatial heterogeneity (Curd et al., 2018; Ettema & Wardle, 2002; Nielsen et al., 2010), which is increased by moisture in the soil habitat and thus tends to be higher in moist than in dry environments (Treonis et al., 1999). Temporally, responses of soil nematodes to changes in water availability in a given site could be within minutes to hours (Vandegheuchte et al., 2015), and an added complexity is that effects of extreme dry and wet events on nematode community composition and trophic structure can vary across ecosystem types (Franco et al., 2019). In mesic grasslands, water pulses may increase predation that, in turn, decreases total nematode abundance (Franco et al., 2019) and may increase taxonomic diversity by suppressing dominant species and hence reducing competition among nematode taxa (Song et al., 2016). In arid grasslands, however, nematode communities can be highly resistant to temporal changes in precipitation (Darby et al., 2011; Franco et al., 2019; Freckman et al., 1987; Vandegheuchte et al., 2015). Therefore, the effects of temporal changes in precipitation on nematode diversity may be dependent on the long-term local climate and ecosystem type.

The differences in size, behavior, and activity that is provided by greater species diversity, besides their total metabolic, is related to the magnitudes of ecosystem services of nematodes and other

organisms (Ferris & Tuomisto, 2015). Therefore, consistent patterns may be expected among responses of nematode diversity and functioning to environmental drivers such as precipitation. Nematodes feeding on bacteria, fungi, and soil algae are also prey of other nematodes and microfauna (Hunt et al., 1987; Yeates et al., 1993), thereby functioning as key links of the C transfer from primary producers to higher trophic levels (Ferris, 2010; Freckman, 1988). The C footprint, which encompasses nematode C biomass, production, and respiration, provides important estimates of the contribution of these organisms to C cycling (Freckman & Mankau, 1986). The nematode C footprint conveys additional information on the biomass, metabolic activity, and magnitude of C flow in soil food webs and provides an effective method for monitoring resource availability and estimating the contribution of nematodes to ecosystem functioning (Ferris, 2010; Ferris et al., 1997). Here, we used respired, production, and biomass C for nematode communities, obtained by combining nematode abundance and mean biomass estimates of each nematode genus, to assess the effects of changes in precipitation on nematode C footprint.

The objective of this study was to investigate the responses of free-living nematodes to temporal and regional changes in precipitation. We assessed nematode biodiversity and functioning responses through genus diversity and C footprint across three US grassland sites. We manipulated incoming precipitation for 2 years along a regional gradient from arid to semiarid and mesic ecosystems to answer the question of how free-living nematode diversity, community structure, and C footprint respond to spatial and temporal changes in precipitation.

2 | MATERIAL AND METHODS

2.1 | Study site

This study was conducted along a large-scale precipitation gradient including three grassland ecosystems in the United States. The arid site is located in the Jornada Basin Long Term Ecological Research Site (32°30'N, 106°47'W) and is classified as Northern Chihuahuan Desert. MAP is 245 mm, and approximately 60% of rainfall occurs between June and October. The dominant vegetation is *Bouteloua eriopoda* (Havstad & Schlesinger, 2006). The semiarid site in the shortgrass steppe grassland is located at the Semiarid Grassland Research Center (40°40'N, 104°45'W) in the northeast of Nunn, Colorado. MAP is 321 mm, with majority of rainfall occurring from April to September. This site is dominated by *Bouteloua gracilis*, contributing more than 60% of land cover (Lauenroth & Burke, 2008). The mesic grassland is a tallgrass prairie located in the Konza Prairie Biological Station (39°05'N, 96°35'W) in Northeastern Kansas. MAP is 835 mm, with main rainfall occurring from April to September. The dominant vegetation is *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum nutans* (Knapp, 1998). Soils are of fine clay loam texture in both the arid and semiarid sites, and silty clay loam at the mesic grassland (Franco et al., 2019).

2.2 | Experimental design and soil sampling

The experimental design in each of the three grassland sites consisted of five levels of growing season precipitation manipulation: large and small water reduction, large and small water addition, and an ambient control. Treatments were replicated eight times and randomly allocated to plots, which were at least 5 m apart and 5×2.5 m in size. These treatments corresponded to the first and 10th percentile of long-term precipitation for the rainfall reduction treatments and to the 90th and 99th percentile of long-term precipitation for the rainfall addition treatments at each site. In this way, treatments across sites had drought/deluges that were similarly relative to their historic record. We manipulated rainfall by using an Automated Rainfall Manipulation System that consists of coupled rainout shelters and irrigation plots as described by Gherardi and Sala (2013). The experiment was in place for the 2016 and 2017 growing seasons.

At the end of the 2016 and 2017 growing seasons, soil was sampled using 2.5 cm diameter corers to 10 cm depth. Four subsamples per plot were collected under the dominant plants in each site. Subsamples were pooled together to form one sample per plot. There were 120 samples in total (5 treatment \times 8 replicates \times 3 sites). Large roots and other debris were manually removed. Samples were placed into individual plastic bags in the field and stored at 4°C until laboratory analyses. Further details on the experimental setting and sampling events can be found in Franco et al. (2019).

2.3 | Nematode extraction and identification

Nematodes were extracted from 100 g of fresh soil using Baremann funnels (Hooper, 1970) and fixed with formalin (5%) for further identification (Southey, 1986). Total nematode numbers were counted for the whole sample, and the first 150 free-living nematodes encountered in the counting dish were identified to genus for each sample using an inverted light microscope (Olympus CKX41, 100 \times magnification). The free-living nematodes were assigned to the following functional groups: Ba_x, Fu_x, Op_x, and Pr_x (where $x = 1-5$), that represent the functional groups of bacterivores, fungivores, omnivores, and predators, respectively, on the colonizer-persister (c-p) scale (1-5) (Bongers & Bongers, 1998). Gravimetric soil moisture was calculated by oven-drying 50 g of fresh soil at 105°C for 48 h. Standardized nematode population abundances were calculated as number of individuals per kg of soil (corrected to oven-dry weight equivalent).

2.4 | Numerical analysis

We calculated Shannon diversity index and Evenness index (Ferris et al., 2001; Yeates, 2003; Yeates & Bongers, 1999). Nematode dry weight was calculated as 20% of fresh weight, and nematode biomass C was calculated as 52% of dry weight (Ferris, 2010). Nematode respiration and production calculations are based on C

utilization of components of the nematode assemblages calculated from published dimensions of each species and averaged across genera (Ferris, 2010). The production component is the lifetime amount of C partitioned into growth and egg production, and the respiration component assesses C utilization in metabolic activity (Ferris, 2010). We retrieved estimates for fresh body biomass of the nematode genera occurring in our samples from the "Nemaplex" database (developed and maintained by Howard Ferris, University of California, <http://nemaplex.ucdavis.edu/Ecology>). To produce the final values, we multiplied the mean values per genus with the observed number of individuals per genus and per sample.

Changes in precipitation through time within sites (growing-season received precipitation) resulted from a combination of variability between years and received precipitation in each plot calculated by multiplying incoming precipitation by the percent reduction or addition associated with each treatment. The effects of site and received precipitation (with interaction term) on nematode parameters (diversity and evenness indices, relative abundance of functional groups, C footprints) were tested in mixed-effect models with the two variables as fixed effects, and plot identity as the random effect. For all models, p -values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question, and the conditional r^2 (that of the whole model, including the random effect) was calculated following Nakagawa and Schielzeth (2013). We accounted for a large number of zero counts for two of the functional groups (Ba₃ and Pr₅) by fitting a zero-inflated model with negative binomial error (Long, 1997). Responses of the functional groups Ba₄, Fu₃, Pr₃, and Pr₄ could not be tested due to extremely high-frequent zero values.

The nonmetric multidimensional scaling (NMDS) on Bray-Curtis dissimilarity matrix was used to performed ordination on site and received precipitation based on nematode genera composition, followed by nonparametric multivariate analysis of variance (np-MANOVA) to test the effect of site and received precipitation. Significance was based on permutation test using 999 permutations (Oksanen et al., 2016). The mixed-effect models and npMANOVA were performed in nlme (Pinheiro et al., 2014) and vegan (Oksanen et al., 2016) packages in R 3.3.2 (R Core Team, 2014). Differences at the $p < .05$ levels were considered to be statistically significant.

3 | RESULTS

3.1 | Nematode diversity along spatial and temporal precipitation gradients

Our results showed that nematode genus diversity and evenness responded to spatial (site) and temporal (received precipitation) changes in precipitation in different ways (Figure 1). Increasing received precipitation had negative effects on diversity across all three sites, but with a steeper slope for the arid compared to the mesic site ($-9 \times 10^{-4} \pm 3 \times 10^{-4}$, $p = .0097$; whole model $p_{\text{interaction}} = .0022$, $r^2 = .27$; Figure 1a). Increasing received precipitation also had a

FIGURE 1 Alpha diversity, Shannon index (a) and evenness index (b, c) of nematode community, as a function of received water in precipitation manipulation plots and sites. Asterisks indicate the p -value for each independent variable (** $<.001$, ** $<.01$, * $<.05$, ns = non-significant) [Colour figure can be viewed at wileyonlinelibrary.com]

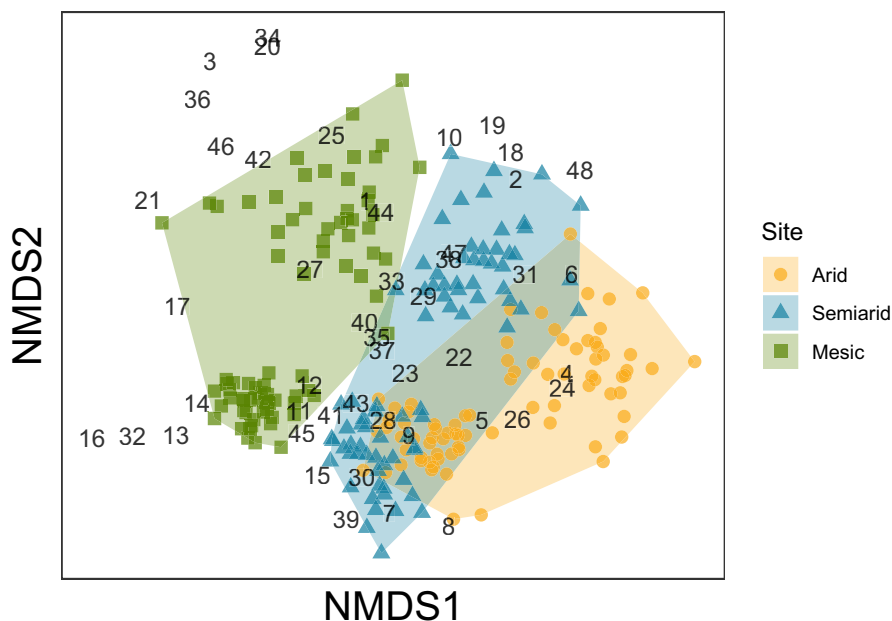
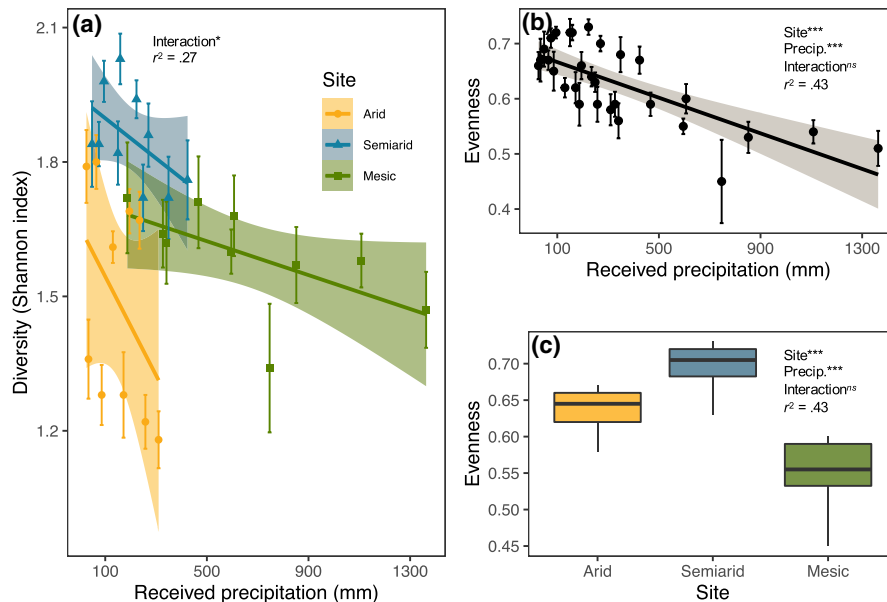


FIGURE 2 Nonmetric multidimensional scaling (NMDS) plot of nematode genera composition as a function of site (Bray-Curtis). Numbers indicate nematode genera: 1 = *Rhabditis*, 2 = *Panagrolaimus*, 3 = *Panagrellus*, 4 = *Acrobelus*, 5 = *Chiloplacus*, 6 = *Acrobeloides*, 7 = *Cervidellus*, 8 = *Acrolobus*, 9 = *Cephalobus*, 10 = *Anaplectus*, 11 = *Plectus*, 12 = *Eucephalobus*, 13 = *Eumonhystera*, 14 = *Wilsonema*, 15 = *Rhabdolaimus*, 16 = *Achromadora*, 17 = *Prismatolaimus*, 18 = *Metataterocephalus*, 19 = *Teratocephalus*, 20 = *Cylindrolaimus*, 21 = *Alaimus*, 22 = *Aphelenchoides*, 23 = *Paraphelenchus*, 24 = *Aphelenchus*, 25 = *Diphtherophora*, 26 = *Tylencholaimus*, 27 = *Tripyla*, 28 = *Thonus*, 29 = *Microdorylaimus*, 30 = *Dorydorella*, 31 = *Eudorylaimus*, 32 = *Epidorylaimus*, 33 = *Pungentus*, 34 = *Enchodelus*, 35 = *Prionchulus*, 36 = *Mylonchulus*, 37 = *Aporcelaimellus*, 38 = *Paraxonchium*, 39 = *Torumanawa*, 40 = *Discolaimium*, 41 = *Discolaimus*, 42 = *Ecumenicus*, 43 = *Mesodorylaimus*, 44 = *Prodorylaimus*, 45 = *Dorylaimellus*, 46 = *Axonchium*, 47 = *Carcharolaimus*, 48 = *Chrysonemoides* [Colour figure can be viewed at wileyonlinelibrary.com]

negative effect on genus evenness, but in this case the effect was independent from site ($p_{\text{site}} < .0001$, $p_{\text{precip}} < .0001$, $p_{\text{interaction}} = .1301$, $r^2 = .43$; Figure 1b). Across sites, the mesic site showed lower evenness compared to the arid site (-0.07 ± 0.02 , $p = .0104$; Figure 1c).

Across all sites and treatment plots, 48 nematode genera were identified, with 36 in the arid site, 37 in the semi-arid site and 46 in the mesic site (Tables S1–S3). The most abundant genera in the drier

sites were both bacterial feeders from the family Cephalobidae; *Acrobelus* in the arid site; and *Acrobelus* and *Cephalobus* in the semi-arid site. The most abundant genus in the mesic site was the fungal feeder *Aphelenchoides*. The cosmopolitan and dominant taxa at all these sites were *Acrobelus*, *Cervidellus*, *Cephalobus*, *Aphelenchoides*, and *Thonus*. The mesic site had endemic taxa such as *Panagrellus*, *Achromadora*, *Cylindrolaimus*, *Alaimus* and *Enchodelus*.

3.2 | Nematode taxonomic and functional community structure along spatial and temporal precipitation gradients

An NMDS ordination based on the distribution of site and received precipitation following by npMANOVA test showed strong associations in nematode community structure among sites ($df = 2$, $f = 63.35$, $r^2 = .33$, $p = .001$; Figure 2). Received precipitation explained only a marginal portion of the variance on the taxonomic structure of nematode communities ($df = 1$, $f = 8.89$, $r^2 = .02$, $p = .001$). The semiarid site was associated with a larger number of nematode genera compared to the arid and mesic sites (Figure 2). The arid site was more related to bacterivore and fungivore taxa (1–2 c-p groups), whereas the mesic site was related to omnivore and predator taxa.

The effects of received precipitation on the relative abundance of all c-p groups 1 and 2 were dependent on site (significant received precipitation \times site interactions; Figure 3). For fungivore and omnivore 2–4 c-p groups, there were null to negative effects in the drier sites that became positive at the mesic site. The opposite pattern (positive effects at the drier sites that became negative at the mesic site) occurred with Ba_1 and Ba_2 . The relative abundance of all groups was highest at the mesic site, except for Ba_2 (Figure 3) which comprised over 60% of the nematode community at the arid and semiarid sites (Tables S1 and S2). In the mesic site, Ba_2 , Ba_3 , Fu_2 , and Op_5 all contributed over 10% of individuals.

3.3 | Precipitation effects on nematode C footprint

Carbon footprints for the life course of free-living nematodes suggest that more C is used in respiration than in growth (Figure 4). The effects of temporal changes in precipitation on nematode respired, produced, and biomass C were all dependent on site (significant received precipitation \times site interaction; $p_{\text{respired}} = .0493$, $r^2_{\text{respired}} = .82$, $p_{\text{production}} = .0001$, $r^2_{\text{production}} = .92$, $p_{\text{biomass}} = .0174$, and $r^2_{\text{biomass}} = .85$; Figure 4). At the mesic site, nematode respired, production, and biomass C decreased at a rate of -1.90 , -0.56 , and $-0.71 \mu\text{g C}$, respectively, for each 1-mm increase in received precipitation. Conversely, all C variables increased or remained relatively stable with increasing received precipitation at the semiarid and arid sites (Figure 4).

4 | DISCUSSION

4.1 | Free-living nematode communities across the spatial precipitation gradient

In our study, nematode genus evenness was lower in the mesic compared to the drier sites (Figure 1), indicating that spatial changes in precipitation and other covarying ecosystem properties alter proportional diversity (i.e., taxa evenness) likely by shaping ecological drivers such as competition, predation, and succession, each of

which can impact evenness without any change in species composition (Wilsey & Potvin, 2000). This result suggests that long-term mesic conditions alleviate multiple resource stresses, acting to disadvantage less abundant nematode species adapted to low resource conditions in favor of dominant species. Species of the drought-tolerant Cephalobidae family (Landesman et al., 2011) from the Ba_2 functional group comprised the majority of individuals in both the arid and semiarid ecosystems, whereas more fungivorous and omnivorous genera occurred in the mesic site. This change in dominance across the regional precipitation gradient is illustrated by the sharp decrease in relative abundance of Ba_2 from over 70% in arid to under 30% in mesic precipitation regimes (Figure 3). Regional differences in community structure were confirmed when performing environmental fitting of MAP onto the ordination plot (Figure 2). Taken together, these results provide further support to the idea that changes in nematode communities across the regional precipitation gradient involved shifts in proportional genus diversity without necessarily affecting genus richness. Differences in plant production and species composition could also have played a role, for example through effects on resource availability and different root exudates (Sikder & Vestergård, 2020).

4.2 | Free-living nematode communities across temporal precipitation gradients

Increasing growing season precipitation had negative effects on both genus diversity and evenness (Figure 1a,b). At arid and semiarid sites, these negative temporal relationships were driven by the loss of rare taxa, as indicated by the negative relationships between received growing season precipitation and the relative abundance of nematodes in nondominant “persister” functional groups (guilds “4” and “5” in the colonizer-persister scale; Figure 3). These groups comprise mainly omnivore and predaceous dorylaimid nematodes with long generation time, low reproduction rates, and slow movement that are indicators of high ecological maturity of nematode communities, but are also highly sensitive to disturbance (Bongers, 1999). Our results suggested that changes in water availability in dry ecosystems had disturbed drought-adapted nematode communities mainly through its impacts on rare species, thus decreasing diversity and increasing dominance by colonizer taxa.

At the mesic grassland, the negative precipitation–diversity and precipitation–evenness relationships resulted from negative responses of the highly abundant Ba_1 and Ba_2 groups that were not compensated by positive responses of persister taxa (fungivorous and omnivorous groups; Figure 3). These results suggest that at moist grasslands, a different mechanism yields the negative temporal precipitation–diversity relationships other than the decline in sensitive rare taxa found at the drier sites. We argue that the increased abundance of omnivorous taxa that possibly feed on other nematodes with increasing precipitation strengthened the top-down regulation of microbivorous nematodes. This effect of drought on

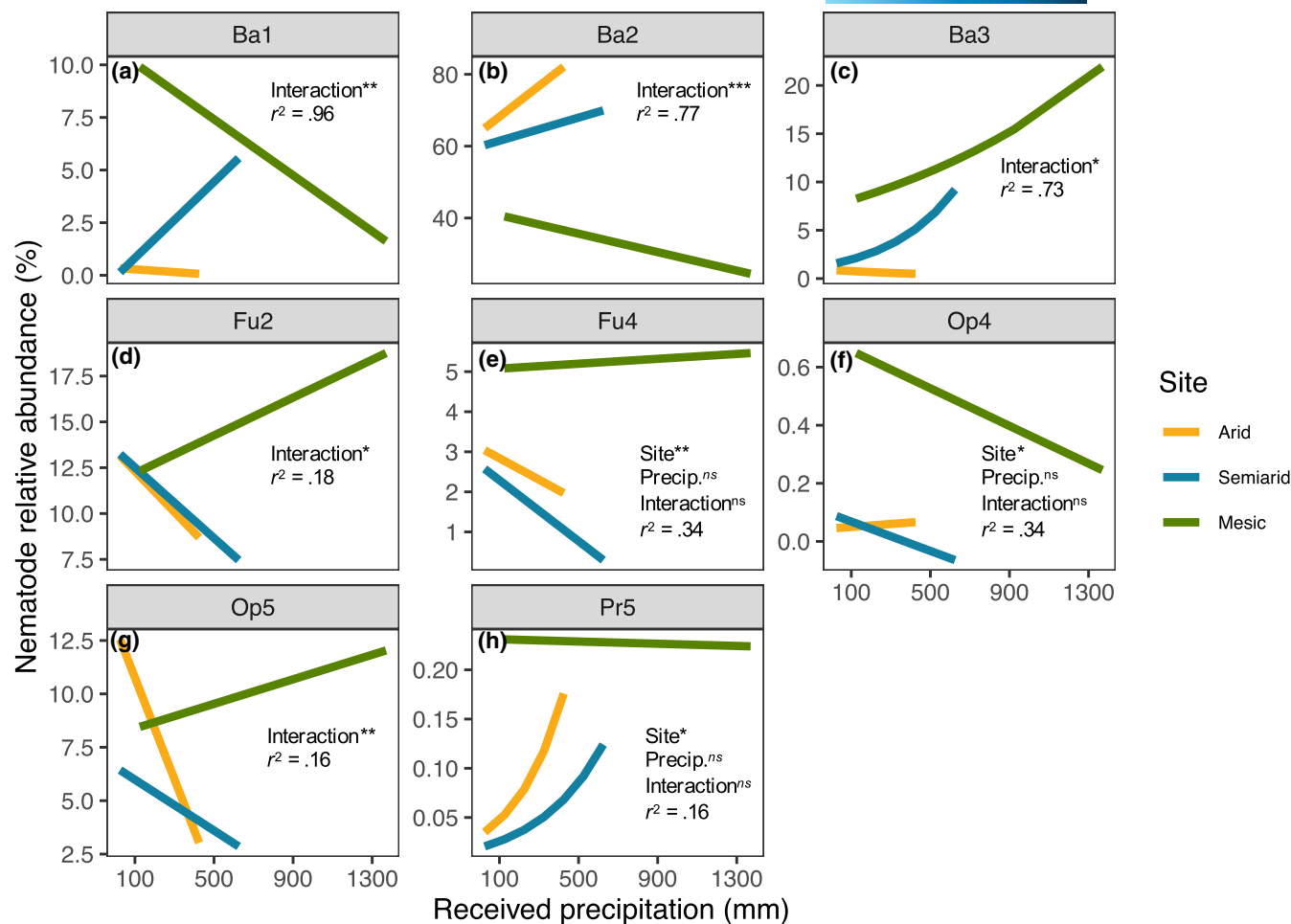


FIGURE 3 Relative abundance of nematode functional groups as a function of received water in precipitation manipulation plots and site. Ba, bacterivores (a–c); Fu, fungivores (d, e); Op, omnivores (f, g); Pr, predators (h); numbers following the functional groups indicated the c-p values. Ba3 and Pr5 were modeled in negative binomial models given the moderate frequency of zero values. No model could be fit for Ba₄, Fu₃, Pr₃, and Pr₄ due to highly frequent zero values. Asterisks indicate the *p*-value for each independent variable (**<.001, *<.01, <.05, ns = non-significant) [Colour figure can be viewed at wileyonlinelibrary.com]

nematode trophic interactions has been previously reported (Franco et al., 2019), but its negative impacts on taxonomic diversity and evenness were opposite to what we predicted based on previous shorter studies (Landesman et al., 2011; Song et al., 2016; Yan et al., 2018). Our results suggest that increased predation caused by the higher abundance of omnivores in wet years affect not only dominant taxa as presumed, but it may also cause the loss of less abundant taxa such as *Panagrolaimus* and *Acrolobus* (Table S3).

4.3 | Precipitation effects on free-living nematode carbon footprint

Our results showed that contrary to diversity responses, effects on nematode contributions to C cycling as measured by respiration, production, and biomass C varied among sites across the regional gradient, with negative effects at the mesic site that became positive to null at semiarid and arid grasslands (Figure 4). Thus, consistent responses of nematode diversity and C metabolism occurred at mesic

conditions, but not at drier environments. This distinguished response in semiarid and arid conditions may be related to the increased abundance of colonizer bacterivorous taxa with increasing received precipitation (Figure 3; Ba₁, Ba₂, Ba₃ c-p groups), which points to a greater flow of resources into the soil food web through the bacterial rather than fungal decomposition pathway. Bacterial-based decomposition channels indicate a fast turnover of the available organic matter by the soil food web, possibly resulting in high rates of C and nutrients mineralization (Porazinska et al., 1999). Therefore, an increase in the frequency of extreme wet years may accelerate decomposition and C turnover in semiarid and arid grasslands but not in mesic ecosystems. These changes in nematode C are likely to affect global C cycling given that (1) arid and dryland regions make of three fifths of all terrestrial ecosystems on the earth, and (2) that the amount of C respired by soil nematodes globally is equivalent to roughly 15% of C emissions from fossil fuel use (van den Hoogen et al., 2019).

Taken together, our findings indicate that spatial changes in precipitation from dry to moist grasslands affect the proportional taxonomic diversity and dominance in free-living nematode

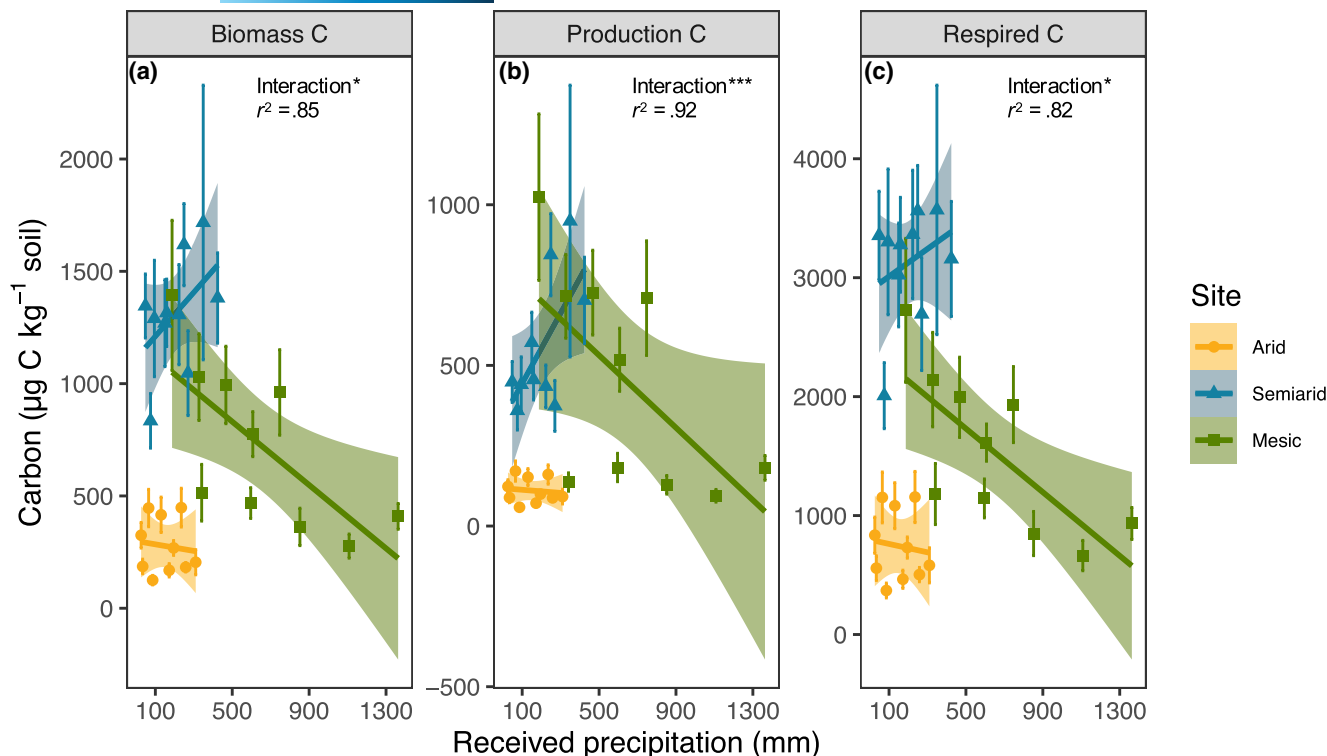


FIGURE 4 Biomass (a), produced (b), and respired carbon (c) during the life course of nematodes as a function of received water in precipitation manipulation plots site. Asterisks indicate the p -value for each independent variable (**<.001, *<.01, *<.05, ns = non-significant) [Colour figure can be viewed at wileyonlinelibrary.com]

communities. Whereas annual changes in precipitation in one location affect both species diversity and evenness, different mechanisms drive these temporal responses at arid and mesic grasslands. In arid and semiarid conditions, there was a loss of drought-adapted rare taxa with increasing precipitation, whereas in mesic conditions presumed increases in predation of colonizer dominant taxa with increasing precipitation yielded the negative precipitation–diversity relationship. Nematode C footprint responses to temporal changes in precipitation were consistent with diversity responses at mesic, but not at semiarid and arid, grasslands, indicating that more frequent extreme wet years may increase the number of bacterial-feeding nematodes and accelerate decomposition and C turnover in semiarid and arid grasslands through the bacterial decomposition pathway. By providing the first quantification of spatial and temporal precipitation–nematode diversity and precipitation–nematode function relationships, this study contributes to the fundamental understanding of the functioning of arid, semiarid, and mesic grassland ecosystems and to better predictions of soil biodiversity responses to a changing climate.

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CONFLICT OF INTEREST

There is no conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

Nematode diversity and abundance data: All data presented in this study are archived in the figshare Data Repository (Franco et al., 2021).

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REFERENCES

- Bardgett, R. D., & Van Der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, 515, 505–511. <https://doi.org/10.1038/nature13855>
- Blankinship, J. C., Niklaus, P. A., & Hungate, B. A. (2011). A meta-analysis of responses of soil biota to global change. *Oecologia*, 165, 553–565. <https://doi.org/10.1007/s00442-011-1909-0>
- Bongers, T. (1999). The Maturity Index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. *Plant and Soil*, 212(1), 13–22.

- Bongers, T., & Bongers, M. (1998). Functional diversity of nematodes. *Applied Soil Ecology*, 10(3), 239–251. [https://doi.org/10.1016/S0929-1393\(98\)00123-1](https://doi.org/10.1016/S0929-1393(98)00123-1)
- Chen, D., Cheng, J., Chu, P., Hu, S., Xie, Y., Tuvshintogtokh, I., & Bai, Y. (2015). Regional-scale patterns of soil microbes and nematodes across grasslands on the Mongolian plateau: Relationships with climate, soil, and plants. *Ecography*, 38, 622–631. <https://doi.org/10.1111/ecog.01226>
- Crowther, T. W., van den Hoogen, J., Wan, J., Mayes, M. A., Keiser, A. D., Mo, L., Averill, C., & Maynard, D. S. (2019). The global soil community and its influence on biogeochemistry. *Science*, 365, eaav0550. <https://doi.org/10.1126/SCIENCE.AAV0550>
- Curd, E. E., Martiny, J. B. H., Li, H., & Smith, T. B. (2018). Bacterial diversity is positively correlated with soil heterogeneity. *Ecosphere*, 9, e02079. <https://doi.org/10.1002/ecs2.2079>
- Darby, B. J., Neher, D. A., Housman, D. C., & Belnap, J. (2011). Few apparent short-term effects of elevated soil temperature and increased frequency of summer precipitation on the abundance and taxonomic diversity of desert soil micro- and meso-fauna. *Soil Biology and Biochemistry*, 43(7), 1474–1481. <https://doi.org/10.1016/j.soilbio.2011.03.020>
- Eisenback, J. (1993). Interactions between nematodes in cohabitation. In M. W. Khan (Ed.), *Nematode interactions* (pp. 134–174). Springer.
- Ettema, C., & Wardle, D. A. (2002). Spatial soil ecology. *Trends in Ecology & Evolution*, 17, 177–183. [https://doi.org/10.1016/S0169-5347\(02\)02496-5](https://doi.org/10.1016/S0169-5347(02)02496-5)
- Ferris, H. (2010). Form and function: Metabolic footprints of nematodes in the soil food web. *European Journal of Soil Biology*, 46, 97–104. <https://doi.org/10.1016/j.ejsobi.2010.01.003>
- Ferris, H., Bongers, T., & de Goede, R. G. M. (2001). A framework for soil food web diagnostics: Extension of the nematode faunal analysis concept. *Applied Soil Ecology*, 18, 13–29. [https://doi.org/10.1016/S0929-1393\(01\)00152-4](https://doi.org/10.1016/S0929-1393(01)00152-4)
- Ferris, H., & Tuomisto, H. (2015). Unearthing the role of biological diversity in soil health. *Soil Biology and Biochemistry*, 85, 101–109. <https://doi.org/10.1016/j.soilbio.2015.02.037>
- Ferris, H., Venette, R. C., & Lau, S. S. (1997). Population energetics of bacterial-feeding nematodes: Carbon and nitrogen budgets. *Soil Biology and Biochemistry*, 29, 1183–1194. [https://doi.org/10.1016/S0038-0717\(97\)00035-7](https://doi.org/10.1016/S0038-0717(97)00035-7)
- Filser, J., Faber, J. H., Tiunov, A. V., Brussaard, L., Frouz, J., De Deyn, G., Uvarov, A. V., Berg, M. P., Lavelle, P., Loreau, M., Wall, D. H., Querner, P., Eijsackers, H., & Jiménez, J. J. (2016). Soil fauna: Key to new carbon models. *SOIL*, 2, 565–582. <https://doi.org/10.5194/soil-2-565-2016>
- Franco, A. L. C., Gherardi, L. A., De Tomasel, C. M., Andriuzzi, W. S., Ankrom, K. E., Shaw, E. A., Bach, E. M., Sala, O. E., & Wall, D. H. (2019). Drought suppresses soil predators and promotes root herbivores in mesic, but not in xeric grasslands. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 12883–12888. <https://doi.org/10.1073/pnas.1900572116>
- Franco, A. L. C., Guan, P., Cui, S., Tomasel, C., Gherardi, L. A., Sala, O. E., & Wall, D. H. (2021). Soil nematode genera diversity and precipitation changes in grasslands. Dataset. <https://doi.org/10.6084/m9.figshare.17225453>
- Freckman, D. W. (1988). Bacterivorous nematodes and organic-matter decomposition. *Agriculture, Ecosystems & Environment*, 24, 195–217. [https://doi.org/10.1016/0167-8809\(88\)90066-7](https://doi.org/10.1016/0167-8809(88)90066-7)
- Freckman, D. W., & Mankau, R. (1986). Abundance, distribution, biomass and energetics of soil nematodes in a Northern Mojave Desert ecosystem. *Pedobiologia*, 29(129), 142.
- Freckman, D. W., Whitford, W. G., & Steinberger, Y. (1987). Effect of irrigation on nematode population dynamics and activity in desert soils. *Biology and Fertility of Soils*, 3, 3–10. <https://doi.org/10.1007/BF00260571>
- Gebremikael, M. T., Steel, H., Buchan, D., Bert, W., & De Neve, S. (2016). Nematodes enhance plant growth and nutrient uptake under C and N-rich conditions. *Scientific Reports*, 6, 32862. <https://doi.org/10.1038/srep32862>
- Gherardi, L. A., & Sala, O. E. (2013). Automated rainfall manipulation system: A reliable and inexpensive tool for ecologists. *Ecosphere*, 4, art18. <https://doi.org/10.1890/ES12-00371.1>
- Havstad, K. M., & Schlesinger, W. H. (2006). Introduction. In K. M. Havstad, W. H. Schlesinger, & L. F. Huenneke (Eds.), *Structure and function of a Chihuahuan desert ecosystem* (pp. 3–15). Oxford Univ Press.
- Hooper, D. J. (1970). Extraction of free-living stages from soil. In J. F. Southey (Ed.), *Laboratory methods for work with plant and soil nematodes* (pp. 5–30). Ministry of Agriculture, Fisheries and Food.
- Hunt, H. W., Coleman, D. C., Ingham, E. R., Ingham, R. E., Elliott, E. T., Moore, J. C., Rose, S. L., Reid, C. P. P., & Morley, C. R. (1987). The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils*, 3(1–2), <https://doi.org/10.1007/BF00260580>
- Ingham, R. E., Trofymow, J. A., Ingham, E. R., & Coleman, D. C. (1985). Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecological Monographs*, 55, 119–140. <https://doi.org/10.2307/1942528>
- Knapp, A. K. (1998). *Grassland dynamics: Long-term ecological research in tallgrass prairie*. Oxford University Press.
- Landesman, W. J., Treonis, A. M., & Dighton, J. (2011). Effects of a one-year rainfall manipulation on soil nematode abundances and community composition. *Pedobiologia*, 54, 87–91. <https://doi.org/10.1016/j.pedobi.2010.10.002>
- Lauenroth, W., & Burke, I. (2008). *Ecology of the shortgrass steppe: A long-term perspective (Long-term Ecological Research Network)*. Oxford University Press.
- Long, J. S. (1997). Regression models for categorical and limited dependent variables. In B. S. Everitt & T. Hothorn (Eds.), *A handbook of statistical analyses using R*. Sage Publications.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Nielsen, U. N., Ayres, E., Wall, D. H., Li, G., Bardgett, R. D., Wu, T., & Garey, J. R. (2014). Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. *Global Ecology and Biogeography*, 23, 968–978. <https://doi.org/10.1111/geb.12177>
- Nielsen, U. N., Osler, G. H. R., Campbell, C. D., Neilson, R., Burslem, D. F. R. P., & Van Der Wal, R. (2010). The enigma of soil animal species diversity revisited: The role of small-scale heterogeneity. *PLoS One*, 5, e11567. <https://doi.org/10.1371/journal.pone.0011567>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2016). *Vegan: Community ecology package*. R package version 2.3-4. <http://CRAN.R-project.org/package=vegan>
- Orgiazzi, A., Panagos, P., Yigini, Y., Dunbar, M. B., Gardi, C., Montanarella, L., & Ballabio, C. (2016). A knowledge-based approach to estimating the magnitude and spatial patterns of potential threats to soil biodiversity. *Science of the Total Environment*, 545–546, 11–20. <https://doi.org/10.1016/j.scitotenv.2015.12.092>
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2014). nlme: Linear and nonlinear mixed effects models. *R Package Version*, 3, 1–117.
- Porazinska, D., Duncan, L., McSorley, R., & Graham, J. (1999). Nematode communities as indicators of status and processes of a soil ecosystem influenced by agricultural management practices. *Applied Soil Ecology*, 13, 69–86. [https://doi.org/10.1016/S0929-1393\(99\)00018-9](https://doi.org/10.1016/S0929-1393(99)00018-9)
- R Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Sikder, M. M., & Vestergård, M. (2020). Impacts of root metabolites on soil nematodes. *Frontiers in Plant Science*, 10, 1792. <https://doi.org/10.3389/FPLS.2019.01792>

- Song, M., Li, X., Jing, S., Lei, L., Wang, J., & Wan, S. (2016). Responses of soil nematodes to water and nitrogen additions in an old-field grassland. *Applied Soil Ecology*, 102, 53–60. <https://doi.org/10.1016/J.APSOIL.2016.02.011>
- Southey, J. F. (1986). *Laboratory methods for work with plant and soil nematodes*. Technical bulletin 2. Ministry of Agriculture and Fisheries.
- Treonis, A. M., Wall, D. H., & Virginia, R. A. (1999). Invertebrate biodiversity in Antarctic Dry Valley soils and sediments. *Ecosystems*, 2, 482–492. <https://doi.org/10.1007/s100219900096>
- van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., de Goede, R. G. M., Adams, B. J., Ahmad, W., Andriuzzi, W. S., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Cares, J. E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., ... Crowther, T. W. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature*, 572, 194–198. <https://doi.org/10.1038/s41586-019-1418-6>
- Vandegheuchte, M. L., Sylvain, Z. A., Reichmann, L. G., de Tomasel, C. M., Nielsen, U. N., Wall, D. H., & Sala, O. E. (2015). Responses of a desert nematode community to changes in water availability. *Ecosphere*, 6, art44. <https://doi.org/10.1890/ES14-00319.1>
- Vestergård, M., Dam, M., Mortensen, L. H., Dyckmans, J., & Christensen, B. T. (2019). Natural ¹³C abundance reveals age of dietary carbon sources in nematode trophic groups. *Soil Biology and Biochemistry*, 130, 1–7. <https://doi.org/10.1016/J.SOILBIO.2018.11.024>
- Wilsey, B. J., & Potvin, C. (2000). Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology*, 81(4), 887–892. [https://doi.org/10.1890/0012-9658\(2000\)081\[0887:BAEFIO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0887:BAEFIO]2.0.CO;2)
- Yan, D., Yan, D., Song, X., Yu, Z., Peng, D., Ting, X., & Weng, B. (2018). Community structure of soil nematodes under different drought conditions. *Geoderma*, 325, 110–116. <https://doi.org/10.1016/J.GEODERMA.2018.03.028>
- Yeates, G. W. (2003). Nematodes as soil indicators: Functional and biodiversity aspects. *Biology and Fertility of Soils*, 37(4), 199–210. <https://doi.org/10.1007/s00374-003-0586-5>
- Yeates, G. W., & Bongers, T. (1999). Nematode diversity in agroecosystems. *Agriculture, Ecosystems & Environment*, 74(1–3), 113–135. [https://doi.org/10.1016/S0167-8809\(99\)00033-X](https://doi.org/10.1016/S0167-8809(99)00033-X)
- Yeates, G. W., Bongers, T., De Goede, R. G. M., Freckman, D. W., & Georgieva, A. S. S. (1993). Feeding habits in soil nematode families and genera – An outline for soil ecologists. *Journal of Nematology*, 25, 315–331.

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