HIGHLIGHTED STUDENT RESEARCH



Soil nematode assemblages respond to interacting environmental changes

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Abstract

Multi-factor experiments suggest that interactions among environmental changes commonly influence biodiversity and community composition. However, most field experiments manipulate only single factors. Soil food webs are critical to ecosystem health and may be particularly sensitive to interactions among environmental changes that include soil warming, eutrophication, and altered precipitation. Here, we asked how environmental changes interacted to alter soil nematode communities in a northern Chihuahuan Desert grassland. Factorial manipulations of nitrogen, winter rainfall, and nighttime warming matched predictions for regional environmental change. Warming reduced nematode diversity by 25% and genus-level richness by 32%, but declines dissipated with additional winter rain, suggesting that warming effects occurred via drying. Interactions between precipitation and nitrogen also altered nematode community composition, but only weakly affected total nematode abundance, indicating that most change involved reordering of species abundances. Specifically, under ambient precipitation, nitrogen fertilizer reduced bacterivores by 68% and herbivores by 73%, but did not affect fungivores. In contrast, under winter rain addition, nitrogen fertilization increased bacterivores by 95%, did not affect herbivores, and doubled fungivore abundance. Rain can reduce soil nitrogen availability and increase turnover in the microbial loop, potentially promoting the recovery of nematode populations overwhelmed by nitrogen eutrophication. Nematode communities were not tightly coupled to plant community composition and may instead track microbes, including biocrusts or decomposers. Our results highlight the importance of interactions among environmental change stressors for shaping the composition and function of soil food webs in drylands.

Keywords Global change · Multi-factor experiment · Nematodes · Soil food web · Semi-arid grassland

Introduction

Recent multi-factor experiments suggest strong potential for interactions among environmental changes to influence biodiversity and community composition (Rillig et al.

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Our results are novel in revealing the importance of interactions among environmental change stressors in affecting the composition and function of soil food webs in a semi-arid grassland.

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2019; Komatsu et al. 2019; Domeignoz-Horta et al. 2020), complicating predictions for our ecological future. Major changes in terrestrial ecosystems include warming, nitrogen deposition, and altered precipitation regimes (Komatsu et al. 2019). However, many experiments focus on single factors (Song et al. 2019), ignoring the potential for interactions among environmental perturbations (Ratajczak et al. 2017; Collins et al. 2020), particularly for soil-dwelling organisms (Rillig et al. 2019; Rudgers et al. 2020). In studies that have examined interactions, multiple factors often interact. For example, in a meta-analysis of plant studies, interactions altered plant community structure more than single factors alone (Komatsu et al. 2019). And, in a multi-factor laboratory experiment involving ten environmental change treatments, soil microbial communities could not be predicted from single treatments alone, and interacting factors caused unexpected responses (Rillig et al. 2019). However, few

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field experiments test for interacting environmental drivers across entire communities or multiple trophic positions. To effectively predict future ecological communities, new approaches must integrate interactions that begin with community reordering via shifts in species relative abundances to wholesale losses (or gains) of species from communities (Smith et al. 2009; Bardgett et al. 2013; Rudgers et al. 2020).

Soil food webs are critical to terrestrial ecosystem health (Bradford et al. 2002) and may be particularly sensitive to interactions among environmental changes. For example, an estimated 0.3 gigaton biomass of nematodes inhabit surface soils globally (van den Hoogen et al. 2019a, b). These consumers affect the soil food web through multi-species interactions that include eating plant roots, bacteria, fungi, and other nematodes (Eisenhauer et al. 2012). Soil invertebrates can reduce microbial and root biomass, the abundance of mycorrhizal fungi, and alter both decomposition rates and plant community composition (Bardgett et al. 1999; Bradford et al. 2002). Among soil invertebrates, nematodes play crucial roles in the ecosystem, serving as both predators and prey (Yeates et al. 1993). Responses of nematode communities to environmental change are important because nematodes influence soil carbon and nitrogen cycles (Guan et al. 2018; Zhu et al. 2018).

Soil invertebrates, such as nematodes, also have high potential exposure to factors such as warming, altered rainfall, and eutrophication caused by fertilizer or atmospheric deposition (Bongers and Bongers 1998; Ferris et al. 2001). At the same time, many soil animals have limited ability to relocate in response to such changes. Nematodes can be excellent bioindicators, because they are sensitive to changes in their environment and can provide valuable information about soil health and quality (Wilschut and Geisen 2021). Because they are so abundant and diverse, nematodes have been used to monitor the impact of pollution, climate change, and other environmental stressors on soil ecosystems (Topalović and Geisen 2023). Past work on soil invertebrate responses to manipulations of environmental change has revealed large community responses but focused largely on mesic ecosystems (see Blankinship et al. 2011). For example, a warming experiment reduced nematode abundance by 50% in a deciduous forest (Stevnbak et al. 2012). In a mesic old field ecosystem, soil moisture content had a larger impact on soil microarthropod community structure than did temperature or elevated atmospheric CO₂ treatments, with effects occurring both directly through manipulated precipitation and indirectly through drying caused by experimental warming (Kardol et al. 2011). A climate change and land use experiment shifted nematode abundance and community structure, suggesting impacts may also be strong for soil invertebrates (Siebert et al. 2020). Given the documented responses of soil food webs to single environmental perturbations, multi-factor experiments can help to resolve how interacting environmental changes alter the diversity and function of soil food webs.

Dryland soil food webs are important to study because drylands cover 45% of terrestrial land surface (Prăvălie 2016), support 40% of the human population (Plaza et al. 2018), and may expand to 56% of global land surface by 2100 as climate warms and dries (Plaza et al. 2018; Maestre et al. 2021). Furthermore, drylands account for one-third of the global soil organic carbon pool, collectively storing ~470 Pg of organic carbon in the top meter of soil (Plaza et al. 2018), and drylands contribute more to temporal variation in global land carbon flux than any other terrestrial ecosystem (Ahlström et al. 2015; Kannenberg et al. 2020). Dryland soil food webs serve ecosystem functions that include cycling of carbon, nitrogen, and water as well as protection against the erosional forces that cause land degradation (Tu et al. 2003; Bardgett et al. 2013; Menta et al. 2018).

Changes to dryland soil food web dynamics will likely affect future carbon sequestration (Fay et al. 2008), given the large role of drylands in C flux. However, the sensitivities of dryland soil invertebrates to environmental changes are understudied, limiting power to predict future biodiversity or shifts in the functional roles of these critical, but often overlooked, animals. A recent cross-site manipulation of precipitation revealed much stronger effects on nematode community structure in mesic than xeric grasslands, including amplification of the ratio of predators to herbivores under wet conditions in mesic sites (Franco et al. 2019). But, more studies on nematode sensitivity to environmental change are needed for dryland ecosystems, which have been understudied relative to mesic conditions.

To fill gaps in knowledge about dryland soil responses to interactions among environmental changes, we evaluated nematode community responses to factorial, long-term manipulations of nitrogen, rainfall variability, and warming in the northern Chihuahuan Desert, the largest hot desert in North America. In the southwestern US, projected environmental changes include warmer nighttime temperatures that arise in part through biophysical feedbacks during shrub encroachment (D'Odorico et al. 2010; He et al. 2015). In addition, atmospheric nitrogen deposition brings nutrients into low nutrient, dryland soils (Fenn et al. 2003; Báez et al. 2007). In our region, some climate projections include increased winter rain during El Niño years (Min et al. 2011; Cai et al. 2015a, b). Therefore, in 2007, we began joint manipulations of nighttime warming, nitrogen (N) inputs, and winter rain in WENNDEx-the Warming El Niño Nitrogen Deposition Experiment in a northern Chihuahuan Desert grassland. We hypothesized that (Hypothesis 1): Environmental changes interact to alter nematode diversity, abundance, community composition, and functional groups more than single factors alone. Because water is the most limited resource in drylands (Noy-Meir 1973), we predicted that El Niño precipitation additions would offset reductions in nematode abundance and diversity caused by warming or nitrogen eutrophication. We also correlated nematode responses with plant community composition to address Hypothesis 2: Nematode community responses to environmental change track the abundance of plant biomass or plant community composition. We expected that nematodes, particularly the plant feeders and microbivores (which eat decomposers of plant litter), would increase with plant biomass. In prior work, forb species richness and biomass increased in warmed, fertilized plots that received additional winter precipitation (Collins et al. 2017). Nematodes can be bacterivores, fungivores, herbivores or omnivores-carnivores, and they occur in every compartment of soil food webs (Yeates et al. 1993). We expected that herbivores nematodes depend most on plant biomass compared to other functional groups because plants constitute their main food source. We focused on soil nematodes to increase general understanding of the interacting consequences of environmental changes on soil food webs in drylands.

Materials and methods

Study site

The nighttime Warming, El Niño, Nitrogen Deposition Experiment (WENNDEx) was established in 2007 in dry grassland just north of the Deep Well meteorological station at the Sevilleta National Wildlife Refuge (SNWR), Socorro, NM, USA (34.359, – 106.688, 1600 m elevation). The vegetation consists of mixed blue grama (*Bouteloua gracilis*) black grama (*B. eriopoda*) grassland. Other grasses include dropseeds (*Sporobolus* spp.) and threeawns (*Aristida* spp.). Herbaceous plants include *Plantago patagonica*, *Hymenopappus filifolius*, and globe mallows (*Sphaeralcea* spp.) (Baur et al. 2021).

Experimental treatments

WENNDEx manipulates three global change factors (nighttime warming, increased winter precipitation, and N addition) in a fully crossed, completely randomized $2 \times 2 \times 2$ 2 design. WENNDEx has 5 replicates of each treatment combination for a total of 40 plots of 3.0×3.5 m each. All replicate plots contain both blue and black grama grass. Nighttime warming was imposed using lightweight aluminum fabric blankets drawn across each warmed plot at night, ~0.5 m from the ground to trap outgoing longwave radiation, which increased winter nighttime air temperature by an average of 1.1 °C and summer nighttime air temperature by 1.5 °C (Collins et al. 2017). Dataloggers controlling shelter movements retracted the blankets when wind speeds exceeded a threshold (to prevent damage) and when rain or snow occurred. Based on long-term climate records, El Niño rains increase average winter precipitation in our area by 50%; more frequent and intense El Niño events are predicted by climate models (Collins et al. 2017; Cai et al. 2015a,b). From 2006 to 2019, we supplemented winter precipitation each year using an irrigation system with reverse osmosis (RO) water because groundwater did not match rain chemistry. Rain was added in six experimental events each winter (January-March) to mimic the total amount (50 mm) and size distribution (four 5 mm events, one 10 mm event, and one 20 mm event each winter) of typical winter-storm events during El Niño years. To augment nitrogen, we used watering cans to add 2 g N m⁻² y⁻¹ as NH₄NO₃ prior to the monsoon season because NH₄-N (57%) and NO₃-N (43%) contribute approximately equally to N deposition at SNWR (Báez et al. 2007). Control plots received the same amount of RO water, the equivalent of a 2 mm rain event. In addition to the imposed treatments, on 4 August 2009, a lightning-initiated fire began on the Sevilleta National Wildlife Refuge. By 5 August 2009, the fire had reached WENNDEx, which was burned extensively though not entirely. Approximately 50% of plots burned, and those plots which did not burn were burned within 3 weeks by the US Fish and Wildlife Service fire crew. Prescribed fire is separately used as a grassland management tool at the Sevilleta National Wildlife Refuge with > 10 year return interval. All plots were burned, so it is unlikely that fire affected our results and would not have affected treatments differentially.

Soil collection and processing

We collected soil nematodes at two time points to capture potential seasonal differences in their sensitivity to environmental changes. On each sampling date, we took 2 soil cores (2.5 cm diameter, 20 cm depth) from each of the 40 WENNDEx plots, near a grass-dominated area toward the center of each plot. We combined the two cores for data collection. Samples were collected during the spring (26 June 2020) and during fall (10 September 2020). Each core was collected in the early morning, coincident with sunrise, and placed into a labeled plastic bag for transportation to the laboratory. Samples were processed within 10 h of collection by placing a subsample from each bag into a modified Baermann funnel (Ingham 1994). Briefly, we placed a thin layer of 50 g of soil on tissue paper that acted as a filter mounted above water in wire-mesh pans (2 mm). We allowed the water to contact the soil via filter paper on the wire mesh. Taking advantage of the hydrophobicity of nematodes, nematodes drilled through the filter paper into the water. After 48 h of incubation at 22 °C, the nematodes in the water were concentrated on a 500-mesh sieve (25 µm aperture). After the total number of nematodes was counted,

100 specimens per sample were randomly selected and identified to genus. If there were fewer than 100 specimens per sample, all specimens were identified to genus (Yeates et al 1993). Morphological identification was completed under a microscope at 400× magnification (eyepiece×objective, 10×40).

Statistical analyses

Hypothesis 1: Environmental changes interact to alter nematode diversity, abundance, community composition, and functional groups more than single factors alone We calculated diversity metrics (genus richness, Shannon diversity index (H'), and the inverse of Simpson's evenness) from the matrix of counts of identified nematode genera from each plot and sampling date using the vegan package in R (Oksanen et al. 2013). We also summed nematode genera in each of the following functional groups representing trophic guilds: bacterivores, fungivores, herbivores, or omnivorecarnivores (Yeates et al 1993). For nematode diversity metrics, total abundance and functional group abundance, we built general linear mixed-effects models with all three treatments, their interactions, the repeated effect of time (2 sampling dates) and the random, repeated effect of plot nested with warming x precipitation x nitrogen. Mixed models were constructed using lmer in the lme4 package in R (Bates et al. 2015) and met assumptions of homogeneity of variances and normality of residuals. We present analysis of deviance results of likelihood ratio tests using the Anova function in the car package (Fox and Weisberg 2018). We decomposed treatment interactions using post hoc Tukey HSD tests among pairs with the emmeans package and provided corresponding P values in the results using pairwise comparisons (Lenth 2021).

Hypothesis 2: Nematode community responses to environmental change track the abundance of plant biomass or plant community composition First, we used a general linear model to correlate total nematode abundance with total estimated plant biomass from Baur et al. (2021), including the fixed factor of sampling date and the date × plant biomass interaction to test for seasonality in the relationship. Second, we examined relationships between the matrix of nematode genus-level composition and the matrix of plant species composition (via estimated biomass) both for the season of collection and for the season prior to nematode collection, to detect lagged effects of plants on nematodes. These analyses used Mantel tests for matrix correlations, implemented in Primer (Clarke and Gorley 2006). Black grama grass (Bouteloua eriopoda) is the foundational plant species in this ecosystem, we used DIST-LM to associate genus-level nematode composition with black grama biomass and linear models to associate the abundance of each nematode functional group with black grama biomass, including biomass during the season of collection and also during the prior season to detect potential lag effects, using Primer for DIST-LM and lm in R for regression analysis (Clarke and Gorley 2006). We also conducted similar DIST-LM for summed biomass of annual forbs, perennial forbs, and all grasses. In prior results, the largest plant responders to interactive treatments were the annual forbs (Collins et al. 2017).

Results

Across 40 samples collected over 2 time points, we estimated on average 31.9 ± 2.71 nematodes per 50 g of dry soil, with nearly double the abundance of nematodes in September (40.1 ± 4.2) than in June (23.8 ± 3.0) (Time, P < 0.0001, Table 1). Of the total nematodes identified across all samples, 50% were bacterivores, 26% were herbivores, 18% were omnivores/carnivores, and 6% were fungivores. We detected 16 genera, of which *Acrobeles* was most abundant (23% of total nematodes), followed by *Acrobeloides* at 22% and *Helicotylenchus* at 15%. June samples had a mean richness of 5.7 ± 0.4 nematode genera per sample, whereas September samples were more diverse with 6.9 ± 0.4 genera per sample (Time, P = 0.0129, Table 1). September samples had 40% fewer fungivores than June, but 50% more herbivores, 100% more bacterivores, and 200% more omnivores/carnivores.

Hypothesis 1: Environmental changes interact to alter nematode diversity, abundance, community composition, and trophic functional groups Nematode diversity: Additions of El Niño winter rains buffered declines in nematode diversity caused by nighttime warming (Fig. 1A-C, Table 1, Warming \times Precipitation, Diversity P = 0.0506, Richness and evenness P < 0.05). First, in plots with no rain additions, nematode Shannon diversity declined 25% with nighttime warming (Fig. 1A, P = 0.0037). However, in plots with winter rain added, there was no significant decline in nematode diversity under warming (P = 0.57). The interactive effects of warming and precipitation on nematode diversity occurred through both changes in genus-level richness (Warming \times Precipitation, P = 0.0460; Table 1) and evenness (Warming \times Precipitation, P = 0.0412, Table 1). Under ambient precipitation, warming reduced genus-level richness by 32% (Fig. 1B, P = 0.0058) and evenness by 28% (Fig. 1C, P = 0.0059), but had no significant influence when rain was added (richness, P = 0.72, evenness P = 0.77). Due to the declines with warming under ambient precipitation, the main effect of warming was also negative (Table 1), with, on average, a 19% decline in richness (P = 0.0121), a 16% decline in evenness (P = 0.0121), and a 15% decline in diversity (P = 0.0042).

 Table 1
 Results from statistical analysis of interacting environmental change factors on nematode communities: composition and diversity indices

Effect	Composition		Shannon H'		Richness		Evenness		Abundance	
	Pseudo-F	Р	ChiSq	Р	ChiSq	Р	ChiSq	Р	ChiSq	Р
Warming	0.90	0.4891	8.22	0.0042	6.58	0.0103	6.29	0.0121	0.79	0.3726
Precipitation	0.81	0.5614	0.01	0.9028	0.14	0.7039	0.01	0.9813	0.21	0.6458
Nitrogen	0.89	0.4896	1.92	0.1657	1.53	0.2168	0.48	0.4899	0.58	0.4455
Time	18.44	0.0001	4.33	0.0374	6.19	0.0129	0.50	0.4777	17.91	< 0.0001
Warming × Precipitation	1.50	0.1699	3.82	<u>0.0506</u>	3.98	0.0460	4.17	0.0412	3.21	0.0731
Warming × Nitrogen	0.61	0.7432	0.43	0.5119	0.00	1.0000	0.42	0.5179	0.11	0.7407
Warming×Time	1.14	0.3375	6.22	0.0126	2.03	0.1542	0.36	0.5511	0.14	0.7063
Precipitation × Nitrogen	1.34	0.2236	0.37	0.5409	1.43	0.2325	6.62	0.0101	0.90	0.3433
Precipitation×Time	1.04	0.4148	2.93	0.0871	2.23	0.1356	1.62	0.2025	1.08	0.2990
Nitrogen×Time	1.33	0.2360	1.40	0.2361	1.43	0.2325	1.72	0.1891	0.09	0.7653
Warming × Precipitation × Nitrogen	0.80	0.5754	0.43	0.5117	0.58	0.4473	0.33	0.5662	0.04	0.8398
Warming × Precipitation × Time	2.10	0.0369	0.34	0.5598	0.16	0.6906	0.13	0.7143	1.52	0.2175
Warming × Nitrogen × Time	1.01	0.4351	3.39	0.0656	5.24	0.0221	3.92	0.0477	0.00	0.9586
Precipitation × Nitrogen × Time	3.04	0.0031	2.05	0.1517	2.53	0.1114	2.56	0.1098	5.52	0.0189
Warming × Precipitation × Nitrogen × Time	1.39	0.2075	0.04	0.8406	0.01	0.9207	0.19	0.6612	0.01	0.9379

P values < 0.05 are shown in bold, and those < 0.07 are underlined

In contrast to the buffering effect of precipitation, nitrogen instead amplified the negative impacts of warming on nematode diversity (Table 1, Fig. S1A–C), but only during spring (Warming×Nitrogen×Time, Table 1: Richness and evenness, P < 0.05). In spring, genus-level richness and evenness were unaffected by warming (richness P = 0.49, evenness P = 0.27) unless nitrogen was added. Under nitrogen addition in spring, warming reduced both richness and evenness by ~47% (richness P = 0.0083, evenness P = 0.0008, Fig. S1A–C), indicating synergistic impacts of warming and fertilization. Despite interactive effects of both precipitation and nitrogen with warming, there were no significant three-way interactions among environmental change treatments (Table 1).

Nematode abundance: We uncovered no strong interactive influences of environmental change treatments on total nematode abundance, although abundance was significantly greater in September than June (Time, P < 0.0001, Fig S1D), demonstrating sufficient statistical power to detect treatment effects. While the interaction among Precipitation×Nitrogen×Time was statistically significant (P = 0.0189, Table 1), contrasts within each sampling period revealed no significant interactions among treatments within a time period (all P > 0.12), likely because total abundance was highly variable, ranging from 2 to 147 nematodes per 50 g soil. The patterns, however, suggested nitrogen effects depend upon precipitation. Under ambient precipitation, June nematode abundance declined by 53% when fertilizer was added (control abundance mean = 31.2 ± 90.1 s.e., + nitrogen = 14.8 ± 90.1 s.e., P = 0.12), but the nitrogen-caused decline disappeared with precipitation addition (P = 0.58).

Nematode community composition: In contrast to diversity and total abundance, nematode community composition responded most strongly to the interacting factors of precipitation and nitrogen additions rather than to nighttime warming (Fig. 2, Precipitation × Nitrogen × Time, P = 0.0031, Table 1). However, precipitation also interacted with warming to influence composition (Warming × Precipitation \times Time, P = 0.0369, Table 1). During the spring, nematode composition significantly diverged with the addition of nitrogen when precipitation was added (P = 0.0168, Fig. 2), but was unaffected by nitrogen under ambient precipitation (P=0.16). However, this interactive effect did not occur following the monsoon season (September collection date, P = 0.39). When we decomposed the interaction between warming and precipitation for each collection date, neither time point was significant (P > 0.13), indicating that warming effects on composition were minor relative to nitrogen effects.

Nematode functional groups: All nematode functional groups responded to the interactive effects of precipitation and nitrogen (Table S1). The general pattern was that nitrogen had no effect on either bacterivore or fungivore abundance under ambient precipitation, but increased these decomposer functional groups when El Niño precipitation was added, and thus water was less limiting. In contrast, nitrogen addition strongly reduced herbivore abundance



Fig. 1 Interactive effects of winter El Niño precipitation additions and nighttime warming on nematode community diversity metrics; A Shannon diversity index, B genus-level evenness, C genus-level richness, and total nematode abundance per 50 g soil (D). Bars show means with s.e. averaged over the nitrogen fertilization treatment and two sample collection dates because these did not significantly

interact (Table 1). Asterisks indicate significant pairwise contrasts (*P < 0.05) between ambient temperature and nighttime warming within each nematode community response metric following Tukey HSD tests (gray: no nighttime warming; firebrick: nighttime warming treatment)

under ambient precipitation, but precipitation mitigated that reduction.

Bacterivores. Bacterivorous nematodes (Acrobeles, Acrobeloides, Protorhabditis, Mesorhabditis, Cephalobus) were jointly sensitive to nitrogen fertilizer and precipitation (Table S1; Precipitation × Nitrogen × Time, P=0.0170). Under ambient precipitation, fertilizer marginally reduced bacterivores by 68% (Fig. 3A, contrast P=0.0563), although only during June, not in September (P=0.81). In contrast, under precipitation addition, nitrogen instead increased bacterivore abundance by 95%, although the pairwise contrast was not significant because of high plot-to-plot variability (June, P=0.16; September, P=0.72).

Fungivores (Aphelenchoides). Precipitation and nitrogen addition also jointly affected fungivore abundance (Table S1; Precipitation × Nitrogen × Time, P = 0.0030). During June, in plots with added winter rain, nitrogen fertilizer doubled the number of fungivores (Fig. 3B, P = 0.0366). However, in plots with ambient precipitation, fungivores did not respond

to nitrogen (P = 0.15), and during September, treatments had no influence (P > 0.3).

Herbivores (Tylenchorhynchus, Mesorhabditis, Helicotylenchus). Herbivorous nematodes responded to interactions between precipitation and fertilizer during June, but differently than bacterivores and fungivores (Table S1; Precipitation × Nitrogen × Time, P = 0.0128). Under ambient precipitation, nitrogen reduced herbivores by 73% in spring (Fig. 3C, P = 0.0490), but not in September (P = 0.23). Under increased precipitation, nitrogen did not significantly affect herbivores during either season (P = 0.82).

Omnivores/Carnivores (Aporcelaimus). Omnivorous and carnivorous nematodes were grouped together as the least abundant functional group, and like other groups, responded to the interaction of fertilizer and precipitation (Fig. 3D, Table S1; Precipitation × Nitrogen × Time, P = 0.0307). However, no pairwise contrasts were significant due to high variance and low abundance.



Fig. 2 NMDS plot of the interactive effects of nitrogen fertilizer and winter El Niño precipitation addition on nematode community composition during June 2020. Small points represent each plot. Large

points are treatment centroids with s.e. Nighttime warming did not significantly interact with precipitation or nitrogen to affect community composition (Table 1)

Hypothesis 2: Nematode community responses to environmental change track the abundance of plant biomass or plant community composition Nematode abundance was uncorrelated with total plant biomass, regardless of season of collection (Fig. 4). Although nematode abundance differed significantly by season in the linear model (P < 0.01), it was uncorrelated with plant biomass matched by season of collection (P=0.45), and there was also no interaction between sampling date and plant biomass (P=0.68). June nematode community composition had no relationship with plant community composition in either the prior fall [Mantel test (Spearman *rho*): 0.007, P=0.49], or the concurrent spring (*rho*: 0.09, P=0.09). September nematode communities were also uncorrelated with plant community composition during the concurrent fall (*rho*: -0.086, P = 0.89) or the prior spring (*rho*: -0.09, P = 0.92). June nematode composition was not correlated with the biomass of the most common grass, black grama (*Bouteloua eriopoda*), during the prior fall (DIST-LM, pseudo-F = 1.12, P = 0.33) or the concurrent spring (pseudo-F = 1.38, P = 0.20). September nematode communities also did not correlate with black grama grass in either season (fall pseudo-F = 1.26, P = 0.28; spring pseudo-F = 0.79, P = 0.45). However, September nematode composition was significantly correlated with total grass biomass in the concurrent fall (DIST-LM, pseudo-F = 3.40, P = 0.04). Herbivores (*rho*: 0.41, P < 0.001), bacterivores (*rho*: 0.53, P < 0.001), and omnivores–carnivores (*rho*: 0.33, P = 0.0027) were significantly positively correlated with







Fig. 3 Nematode functional groups under additions of winter El Niño precipitation and nitrogen fertilizer including A bacterivores, B fungivores, C herbivores, and D omnivores and carnivores. Bars show means with s.e. for spring/June sampling when treatment interactions occurred, averaged over nighttime warming which did not interact

with precipitation or nitrogen (Table S1). Asterisks indicate a significant pairwise contrast (*P<0.05) between control and nitrogen addition within each level of the winter El Niño precipitation treatment (Tukey HSD tests) (gray: no nighttime warming; dark goldenrod: nighttime warming treatment)



Fig.4 Linear regression of total nematode abundance versus total estimated live aboveground plant biomass (g/m^2) at WENNDEx where grey circles are spring (June nematodes) and brown diamonds are fall (September nematodes)

total grass biomass (Fig. 5A, B, D). No other significant correlations between nematode trophic groups and plant functional groups were detected, except for a significant positive correlation between omnivores–carnivores and perennial forb biomass (*rho*: 0.048, P = 0.05) (Fig. S2).

Discussion

Our long-term global change experiment revealed that soil nematode communities were particularly sensitive to interactions involving precipitation addition together with other environmental change factors, either nighttime warming or nitrogen fertilizer addition. On average across other environmental change factors, warming and nitrogen addition reduced nematode diversity, genus-level richness, and evenness. Increased winter precipitation generally reversed the negative effects of warming or nitrogen on nematode communities. **Fig. 5** Linear regression of nematode trophic group (herbivores, bacterivores, fungivores and omnivores–carnivores) abundance versus total estimated live grass biomass (g/m²)



Precipitation mitigated declines in nematode diversity caused by nighttime warming

Soil nematodes generally live in the water film around soil particles, and their activities, such as predation and reproduction, depend on soil water (Yeates 1979), root production, and carbon availability (Franco et al. 2022). In our experiment, winter water additions increased winter soil moisture by ~15% with some carryover into spring (Collins et al. 2017). This increase in soil water content should promote nematode movement and predation, potentially buffering against declines in rare taxa under warmer nighttime temperatures, and explaining the increased diversity (Fig. 1). Thus, we suggest that warming significantly reduced soil water content, which is the most limiting factor in drylands (Collins et al. 2014), and the addition of precipitation alleviated the negative effect of warming on soil drying. Such increases under water additions were similar to findings of Andriuzzi et al. (2020), who showed that increased precipitation led to larger nematode populations. However, a different study reported that increased annual precipitation reduced nematode diversity in arid and semi-arid sites by reducing rare drought-adapted taxa (Franco et al. 2019). In the latter study, Acrobeles was reported to be the most common drought-tolerant taxon, consistent with our finding that bacteria-eating nematodes were the most abundant nematodes in our dryland experiment. *Acrobeles* may be drought tolerant because they tend to become smaller in dry areas than in wet ones (Franco et al. 2022). *Acrobeles* can also quickly synthesize the sugars needed to survive and shorten their reproductive cycle under stress (Wu et al. 2022).

Precipitation addition reversed declines in functional groups caused by nitrogen fertilization, but warming exacerbated the negative effects of nitrogen

Prior studies have documented that nitrogen addition reduces the number, complexity, and functional diversity of nematode communities (Liang et al. 2009; Liu et al. 2016), similar to our results. Long-term inputs of concentrated nitrogen can cause soil acidification (Ye et al. 2018), and soil pH is an important environmental factor that determines the number and distribution of soil microorganisms and nematodes (Hoogen et al. 2019a, b). For example, ammonium toxicity can directly affect the growth and reproduction of soil nematodes (Wei et al. 2012), which could reduce nematode diversity and abundance. However, the soils at our site have high buffering capacity due to high calcium carbonate availability, with pH values ranging from 8.2 to 8.5 (Kieft et al. 1998). Therefore, impacts due to reduced soil pH are an unlikely mechanism in our system, especially under the low nitrogen addition rates in our experiment (2 g m⁻² yr⁻¹).

We detected declines in the abundance of herbivorous nematodes under nitrogen addition, but only in control plots that did not receive additional winter rain (Fig. 3), suggesting that ongoing increases in atmospheric nitrogen deposition (Fenn et al. 2003; Lamarque et al. 2013) could negatively affect this nematode consumer group. However, the addition of winter rain buffered herbivorous nematodes against declines with nitrogen fertilization. Large rain events, similar to those we added in WENNDEx, reduced soil nitrogen availability in a nearby Chihuahuan Desert grassland dominated only by black grama (Brown et al. 2022). Large rain events may increase turnover in the soil microbial loop (Bonkowski 2004), leading to recovery of herbivorous nematode populations.

Importantly, we uncovered the novel finding that additions of winter rain could reverse declines in the abundances of functional groups caused by nitrogen fertilization and boost the abundances of bacterivores and fungivores. These reversals of nitrogen impacts may occur because water is the primary limiting factor in arid ecosystems. Reversals were stronger for bacterivores and fungivores than for herbivores or carnivores (Fig. 3), perhaps indicating high sensitivity of nematodes connected to soil microbes rather than to plants. The differential effects on nematode functional groups were consistent with other results in which increased precipitation had minimal effects on the herbivorous nematodes that live outside of plant roots (ectoparasites of plants), which is the location in the soil that our sampling targeted (Ankrom et al. 2020). Greater soil moisture can also increase nutrient turnover and nutrient availability, and our results suggest that prior reports of benefits from low doses of nitrogen to nematode abundance (Berg and Verhoef 1998; Sjursen et al. 2005) likely depend on water availability.

Our results also indicated antagonistic synergy between warming and fertilization: the lowest values of nematode diversity, richness, evenness, and abundance occurred in plots that were both warmed and fertilized (Fig. S1, Table 1). These synergies occurred only in spring, likely because May and June are both hot and dry, whereas during the later summer months and early fall, heat and fertilizer can be buffered by monsoon rains. Therefore, the dually negative impacts of warming and nitrogen addition may be strongest during the most stressful part of the growing season. Reductions in nematode diversity under nitrogen line up with the common result of reduced plant diversity with fertilization (e.g., Bobbink et al. 2010), and changes in the plant community could underlie declines in nematode diversity. However, nematode responses were not closely coupled to plant community composition, total plant biomass, or biomass of the dominant plant species in our study in either spring or fall (Fig. 4), suggesting that plant-nematode dynamics in drylands may be more decoupled than in mesic ecosystems (see also Ankrom et al. 2020). We did find temporal correspondence in that nematode abundance declined when plant biomass was lower in spring relative to fall when plant biomass booms following summer monsoon rain. Correspondingly, fall samples had 40% fewer fungivores than June, but 50% more herbivores, 100% more bacterivores, and 200% more omnivores/carnivores. The nematode community may commonly be decoupled from the plant community in drylands due to restrictions on soil carbon and nitrogen cycling caused by water limitation (Nielsen and Ball 2015; Ma et al. 2018). Instead, the impacts of nitrogen addition on nematode populations in our experiment were more likely to be mediated through changes in the amount and composition of soil microbes. Ongoing work has detected declines in the dominant Cyanobacteria in biological soil crusts under nitrogen additions in WENNDEx (Patton, M. T., unpublished data). High soil resource availability could also reduce plant allocation of carbon to roots (Meng et al. 2022), with a potential cascade to rhizospheric or soil surface microbes that feed bacterivorous and fungivorous nematodes (Eisenhauer et al. 2012).

Nematode taxa and functional groups differed in sensitivities to environmental change

Differentiated responses of functional groups or species to interacting environmental changes may cause corresponding changes in ecological functions by restructuring the soil food web. For example, the ratio of bacterivores to fungivores can define the energy flow path through the soil ecosystem by influencing whether organic matter decomposition is dominated by fast, bacterial decomposition channels or slow, fungal decomposition channels (Ruess et al. 2000; Eisenhauer et al. 2012). In our study, bacterivorous nematodes (Acrobeles, Acrobeloides, Protorhabditis, Mesorhabditis, *Cephalobus*) (Table 2) were the most sensitive to fertilizer under additions of winter rains (Fig. 3). They declined by 68% with fertilizer under ambient precipitation, but conversely increased by 95% with fertilization under precipitation addition. Interestingly, there was no correlation between soil moisture and the abundances of either Acrobeloides or Acrobeles nematodes in another study (Bakonyi and Nagy 2000), although the genus Acrobeles dominated dry environments in another system (Griffin et al. 1996). Bacterivores can strongly reduce bacterial biomass, change bacterial community composition (Griffiths et al. 1999; Postma-Blaauw et al. 2005; Blanc et al. 2006), and increase plant nutrient uptake and growth (Ingham et al. 1985; Djigal et al. 2004). By preying on bacteria, these microbivores can also enhance

Table 2Results of SIMPERanalysis comparing the twotreatments that significantlydiffered in nematode genus-level composition in June2020: + Precipitation + Nitrogenversus + Precipitation Control

Genus	Functional group	+ Precipita- tion + Nitrogen	+ Precipitation control	Cum. %	
Acrobeles	Bacterivore	1.1	4.6	17.8	
Acrobeloides	Bacterivore	2.4	4.7	32.5	
Helicotylenchus	Herbivore	0.9	2.9	44.0	
Aphelenchoides	Fungivore	0.9	2.78	54.6	
Aporcelaimus	Carnivore/Omnivore	1.4	2.1	64.3	
Protorhabditis	Bacterivore	0.9	2.0	73.8	
Pratylenchus	Herbivore	2.3	2.2	82.0	
Tylenchorhynchus	Herbivore	1.4	0.8	87.8	
Mesorhabditis	Bacterivore	1.0	0.4	92.1	

Average abundance for each taxon is shown, and taxa are ranked from the most to least important contributors to the differences between these two treatments. Cumulative percentage contribution to the dissimilarity in community composition between nitrogen addition and control in the precipitation addition treatment is also included

rhizospheric deposits in the form of readily available carbon compounds (Sundin et al. 1990). Therefore, it would be interesting to follow up with assays on soil bacterial composition and microbial biomass. Nematodes, together with bacterivorous protists, can additionally increase root branching, thereby improving plant nitrogen uptake and plant production (Trap et al. 2016). Up to 20% of bacterial nitrogen and 75% of phosphorus ingested by nematodes can be released for plant absorption (Trap et al. 2016). This nutrient increase mechanism appears to be particularly important in soils with low nutrient availability (Bjørnlund et al. 2012), and may, therefore, have a large influence on plant growth in nutrient-poor grasslands, such as ours. Thus, it could be informative to assess foliar C:N ratios or other aspects of plant nutritional status.

The combined effects of nitrogen addition and increased rainfall doubled the number of fungal-eating nematodes (Fig. 3). The abundance of fungivorous nematodes in soils is usually an order of magnitude lower than the number of bacterivorous nematodes, despite the fact that these fungivores serve as the major consumers of fungi in soil food webs (de Ruiter et al. 1995). Our results were consistent with this general pattern. In addition, fungivores selectively consume taxa of fungal prey, thereby altering the composition of the fungal community (Ruess et al. 2000). In turn, this effect can promote plant growth by stimulating plant symbiotic mycorrhizal fungi and increasing their nutrient transfers to host plants (Hua et al. 2014). The increase in fungivores under fertilized, wet conditions may, thus, affect the composition and abundance of fungi in soils and plant roots. Our results predict that if nitrogen deposition continues to increase, and winters remain dry, our ecosystem will experience declines in both bacterivores and fungivores (Fig. 3).

Nematodes at top trophic positions (omnivores and predators) are central to the food web because they prey on nearly all smaller organisms, including root-feeding nematodes (de Ruiter et al. 1995; Khan and Kim 2007) and can indirectly benefit plant growth (Khan and Kim 2007; Dietrich et al. 2020). However, omnivore and predator abundances also depend on prey abundance. In our study, predators were the least abundant functional group (Fig. 3), possibly indicating that omnivores and predators in this soil food web are primarily regulated by bottom-up processes.

Nematode communities did not closely track plant communities

Plant community composition and functional group biomass were not strong drivers of nematode abundance or community composition in our focal semi-arid grassland. Among the plant variables we assessed, total grass biomass was the only correlate of nematode trophic group abundances, and plant community composition was relatively similar across treatments in our experiment (Collins et al. 2017). Therefore, we conclude that the direct effects of our environmental change treatments on nematode communities were larger than any indirect effects via plant responses. Many functional groups of nematodes may not directly interact with plants, but instead have indirect interactions via other organisms in the rhizosphere. Although root feeders can reduce plant growth, our methods did not include internal rootfeeding taxa, and some root feeders (at low densities) can instead stimulate plant growth by inducing root exudates that increase microbial activity and thereby increase soil nutrient availability (Bardgett et al. 1999; Tu et al. 2003; Gebremikael et al. 2016). Plant communities typically respond strongly to multiple global change factors (Blankinship et al. 2011; Komatsu et al. 2019; Avolio et al. 2021), but in the WENNDEx experiment, we detected much larger changes in nematode communities than in plant communities (Collins et al. 2017). This disconnection of nematodes from the plant response to environmental change may be common for dryland soil nematodes if the infrequency of rains decouples plant responses, which require large rain pulses, from responses in the soil food web.

Caveats

Nematodes are water-membrane organisms (Blake 1961). Drought causes nematodes to move deeper into the soil to avoid desiccation (Schimel 2018). But, nematodes are not as migratory as earthworms, and cannot move to very deep soils (Blume et al. 2016). Because we collected soil to 20 cm depth (the depth of most plant roots and above the petrocalcic layer), we estimate that we sampled deeply enough to capture most nematode diversity in the soils of our system. However, deeper sampling and homogenizing a larger number of soil samples per plot may have increased the detection of rare taxa and could possibly alter conclusions about the responsiveness of nematode diversity to our treatments. In addition, separately extracting nematodes from particular soil depths could have refined insights into which groups respond at particular soil depths, providing greater understanding of the biology of nematodes in dryland food webs. Subsequent work could further consider the relationship between soil structure and nematodes.

Conclusion

Our long-term, multi-factor experiment in a Chihuahuan Desert grassland highlighted the overriding importance of interactions among environmental change stressors-particularly those involving precipitation-for altering nematode abundance, diversity, and community composition and restructuring the relative abundances of nematode functional groups. Our results predict that future climate warming and increasing rates of atmospheric nitrogen addition could reduce grassland nematode biodiversity and alter the relative abundances of genera and functional groups, but that these negative effects may be reversed in years with wet winters. Bacterivorous and fungivorous nematodes were the most abundant and most sensitive to environmental manipulations, and declines in these taxa under warming or fertilization could be a slow turnover of soil nutrient cycling and cause deterioration of ecosystem biogeochemical processes.

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Author contribution statement SLC conceived and designed the field experiment. LM, SW, MP, PO, and LEB collected the data. LM, JAR, SW, MP, and LEB analyzed the data. LM, SW, and JAR wrote the manuscript; other authors provided editorial advice.

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Data availability All data and scripts will be available on the Environmental Data Initiative at the time of publication.

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Declarations

Conflict of interest The authors declare no competing financial interests.

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