

Responses of a desert nematode community to changes in water availability

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Abstract. The most recent climate models unequivocally predict a strong drying trend for the southwestern USA within the next century. Soil nematodes are a highly important component of desert ecosystem functioning, but rely on water films for movement. However, it is currently poorly understood how different trophic groups of nematodes respond to chronic presses as well as short-lived pulses of altered water availability, especially in arid systems where such changes are expected to have the greatest impact. The aim of this study was to assess the effects of both instantaneous and long-term variation in water availability on desert soil nematode trophic groups. We hypothesized that nematode abundance would respond positively to both short- and long-term increases in moisture. Based on the ecology of the different trophic groups we further made predictions about their relative rates of response. We increased or decreased precipitation from ambient levels in the Chihuahuan Desert for four consecutive years and sampled soil nematodes after two, three and four years. We tested the effects of altered precipitation treatments through time as well as gravimetric soil moisture at the time of sampling on the abundance of the different nematode trophic groups. In contrast to our hypotheses, the abundances of most nematode trophic groups were unaffected by the amount of precipitation, even after four years of altered precipitation. Plant-parasitic nematodes from low moisture soils were the only group that reacted positively to increased precipitation from the third year onwards. Trophic groups responded differently to soil moisture, with bacterivores decreasing with increasing moisture and omnivores showing a positive relationship that diminished over time. We show that in general, these desert nematodes were not limited by precipitation, and were highly resilient to decreases therein. However, when also considering the effects of soil moisture, some more complex patterns and differences among trophic groups emerged. We discuss potential mechanisms explaining these observations and contrast our findings with those from other ecosystems around the world. We conclude that deserts harbor nematode communities that seem more resilient to altered water availability than other ecosystems.

Key words: drought; precipitation; resilience; soil ecology; soil moisture; trophic groups.

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INTRODUCTION

An unprecedented combination of global change drivers and their associated disturbances is likely to push many ecosystems beyond the limits of their resilience within the current century (IPCC 2007). Globally, both the area affected by drought as well as the frequency of heavy precipitation events are predicted to increase (IPCC 2007). Although climate models predict an increase in precipitation in many regions of the United States (IPCC 2007), the southwestern states are predicted to become drier within the next century (Seager et al. 2007), with an increase in the duration and intensity of droughts and number of dry days and a decrease in the occurrence of wet extremes (Cayan et al. 2010, Singh et al. 2013). A recent meta-analysis (Blankinship et al. 2011) has shown that soil biota are in general more sensitive to changes in precipitation than to CO₂ or temperature (see also Ayres et al. 2008), suggesting that altered precipitation regimes may have significant impacts belowground. Nematodes are the most abundant multicellular animals on the planet (Lambshhead 2004), are found at all trophic positions in the soil food web, and are involved in various ecological processes such as decomposition, nutrient cycling, and plant productivity (Ingham et al. 1985, Yeates et al. 1993, Bardgett et al. 1999). It is therefore necessary to understand how this functionally important component of the ecosystem will react to the future reduction in water availability and to assess whether the system is resilient to the effects of increased drought.

Soil nematodes are aquatic animals that depend on water films around soil particles for their movement (Freckman et al. 1987). Changes in the thickness of the water film may moderate nematode movement and consequently community structure. In general, species of larger body size, such as the longer living, K-selected predaceous nematodes that are somewhat slower moving would require a larger water film around soil particles to maintain their activity compared to nematodes in other trophic groups such as smaller sized, faster moving bacterial feeders with r-selected life strategies (Demeure et al. 1979, Freckman 1988, Yeates et al. 2002). Plant-parasitic nematodes are active in the moist

rhizosphere and dependent on water around the plant root, although they can move some distances in soil water films towards plant roots (Prot and van Gundy 1981). Decreasing water availability reduces activity and reproduction until nematodes die or enter a reversible ametabolic survival state called anhydrobiosis (Crowe et al. 1977, Treonis and Wall 2005, Perry and Wharton 2011).

Individual-level responses of nematodes to increases in water availability are expected to occur within minutes to hours, such as reactivating from the anhydrobiotic state and an increased rate of feeding and metabolism, respectively (Fig. 1). If a higher moisture level persists for days to weeks, population-level responses can be expected through increased hatching from eggs or dispersal into the newly wetted soil from pockets of moisture that acted as refugia. It is, however, unlikely that such a relatively short-lived change in water availability (pulse) will offset changes in nematode populations caused by a chronic alteration in water availability (press). Such changes are thought to be more indirect and mediated by the resources these nematodes depend upon, such as bacteria, fungi and plant roots. Bacterial communities are quite sensitive to drought but also quite resilient, bouncing back when soil is rewetted (Barnard et al. 2013). Fungi, on the other hand, can reach pockets of water through air-filled soil pores, and are therefore more resistant to drought. This resistance notwithstanding, because of their slower growth rates, fungi are less resilient to drought than bacteria, i.e., less able to recover quickly once their abundance has declined (Barnard et al. 2013). Plants, especially in arid ecosystems, have strategies that conserve moisture, which enable them to withstand periods of drought longer than bacteria or fungi. When altered levels of water availability persist over longer timescales, changes in plant growth and resource allocation lead to changes in litter quantity, and changes in plant species composition result in altered litter quality (Murphy et al. 2002, Cleland et al. 2013). These litter changes in turn are expected to affect the structure of nematode communities through changes in abiotic factors and microbial communities (San-aulah et al. 2011).

The “hierarchical-response framework (HRF)”

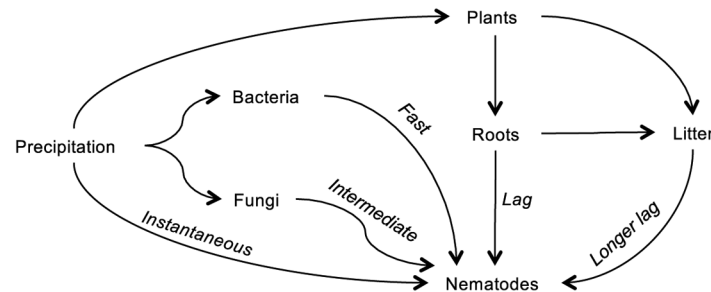


Fig. 1. Conceptual diagram of different time lags on the effects of precipitation on nematodes. Instantaneous effects occur for example through activation of anhydrobiotic nematodes. Fast and intermediate responses include increases in microbial populations upon which bacterivorous and fungivorous nematodes feed, as well as dispersal of nematodes from moist soil pockets (refugia) into the surrounding soil. Lag effects are mediated by changes in plant biomass/populations. Increases in root-derived resources are expected to occur after a relatively short lag period, while changes in litter quantity and composition are expected to take a longer time. Note that nematodes can in turn affect many of the components of this graph, but as this is not the scope of this paper, these arrows were omitted for clarity.

(Schwinning and Sala 2004, Smith et al. 2009) provides a theoretical basis for predicting how ecosystems will react to chronic resource alterations under global change. The HRF proposes a temporal hierarchy of mechanisms with fast responses at the organismal level (physiology, metabolism), followed by population-level changes, species reordering and finally community alterations caused by immigration and extinction. Our study system is limited by water, the availability of which is predicted to decrease as the ecosystem becomes chronically drier. According to the HRF, these attributes make our system prone to fast changes with altered water availability, allowing individual- and population-level responses to take place in the time span of days to years. In addition, the HRF predicts that different trophic groups will react at different rates to altered resource availability, depending on the particulars of their ecology. The HRF is not incompatible with theory about ecosystem responses to natural disturbances in resource availability, which usually have the characteristics of a pulse rather than a press (Noy-Meir 1973). Such pulse events also have the potential, but are not prerequisite, for large ecosystem changes, and their effects can depend on co-occurring chronic resource alterations (Scheffer et al. 2001). In the light of this existing theoretical work, we propose a number of hypotheses about the responses of a desert nematode community to alterations in water

availability.

We hypothesize that nematodes increase in abundance with water availability, because nematodes are dependent on water for their activity (H1). We further hypothesize that nematode numbers react both to long-term changes in water availability (H1a) and short-term pulses of water (H1b). A second hypothesis is that different trophic groups of nematodes show different degrees of sensitivity towards changes in water availability (H2). Plant-parasitic nematodes live in close association with plant roots, and thus permanently have access to plant cell contents. Furthermore, they only need to leave roots and move within water films around soil particles to disperse. They are therefore expected to be least sensitive to short-term changes in water availability (Stevnbak et al. 2012). Plants in a desert ecosystem quickly extract any moisture that enters the soil, creating a moisture gradient in the root zone. When soil moisture levels increase sufficiently, the drier soil close to the roots will become wetter, enabling bacterivorous nematodes in the rhizosphere to increase in abundance as they reactivate from anhydrobiosis, migrate from areas with lower moisture or multiply in response to increasing bacterial populations. Fungivorous nematodes are able to draw water from a larger volume of soil through the hyphal network of the fungi they feed on, and are hypothesized to be less responsive to changes in soil water availability than bacter-

ivores, but more so than plant parasites. Predatory and omnivorous nematodes on the other hand are expected to be most sensitive to both short- and long-term changes in water availability, as they are large-bodied, requiring thicker water films to move around and actively hunt their prey. We expect bacterivorous nematodes to respond slower to chronic changes in water availability than omnivores and predators, but faster than fungal feeders, because fungi are generally more resistant to drying than bacteria (Barnard et al. 2013). Plant-parasitic nematodes are expected to respond numerically to chronic changes in water availability through changes in root biomass, and therefore are hypothesized to show the slowest reaction of all trophic groups. Finally, we hypothesize that long-term effects of changes in water availability on nematode densities increase with time (H3). These effects can occur through changes in plant litter quality and quantity, which provide positive feedback mechanisms reinforcing the initial changes.

To test the above hypotheses, we investigated the abundance of different trophic groups of nematodes collected during three consecutive years from experimental plots at the Jornada Long Term Ecological Research site (LTER) that had experienced reduced, ambient or increased amounts of incoming precipitation. We studied short-term responses in nematode numbers by looking at the relationship between gravimetric soil moisture measured at the time of sampling and the abundance of the different nematode groups (H1b). To study long-term responses in nematode numbers, we investigated the relationship between the abundance of the different nematode groups and growing season precipitation received in the altered precipitation regimes during the three years (H1a, H2 and H3).

METHODS

Site description and experimental design

The experiment was conducted in the Jornada Basin, site of the Jornada LTER in New Mexico, USA, and the largest desert in North America, the Chihuahuan Desert, where a long-term experiment to manipulate annual precipitation (PPT) was underway (Reichmann et al. 2013). The Jornada desert has three distinct seasons; the hot and wet summer from July to October; the

cold and variable winter from November to February; and the hot and dry spring from March to June (Freckman et al. 1987, Virginia et al. 1992). Vegetation was dominated by black grama (*Bouteloua eriopoda* (Torr.) Torr.) and mesquite (*Prosopis glandulosa* Torr.). Mean annual precipitation from 1915 to 1995 was 245 mm, of which most occurs during the growing season period of 1 July to 1 October. The experimental design consists of 132 6.25-m² plots arranged in three blocks. Within each block, 44 plots were subjected to five levels of water input: –80% reduced, –50% reduced, ambient, +50% increased, or +80% increased PPT. Reductions in precipitation were obtained by using rainout shelters similar to the ones used by Yahdjian and Sala (2002), which were installed in November 2006. These were permanent rainout shelters that remained in place for the duration of the experiment. For the irrigated treatments, an irrigation system was installed to water the plots with sprinklers. Plots were watered from July to October on the days after PPT events that were greater than 2 mm, using rainfall collected off-site. Due to a drier than average growing season during 2009, wet treatments received five additional irrigation events of 20 mm each in September.

Sampling, extraction and identification

Soil samples for nematode extraction and identification were taken at the end of each of three consecutive growing seasons (mid-September 2008, early October 2009 and late October 2010). We chose the end of the hot and wet season for sampling because this corresponds with a peak in the abundance of soil biota in this system (Freckman et al. 1987, Virginia et al. 1992). Furthermore, in a year-long study of nematode responses to short moisture pulses in this desert, nematodes were most responsive at this time of year (Freckman et al. 1987). In 2009, treatments were changed for several plots in the context of another experiment. For this study, only 2009 and 2010 data from plots that received the same precipitation manipulation treatment throughout the three years of sampling were included in analyses, along with all data from 2008.

A soil core (10 cm deep and 2.5 cm in diameter) was collected from each plot from under black

grama and placed into Whirl-Pak sampling bags (Nasco, Fort Atkinson, WI, USA) and then deposited into coolers to minimize animal activity until returned to Colorado State University. In the laboratory, samples were gently homogenized, opened under a laminar flow hood (to reduce contamination) and subsampled for soil and invertebrate analyses within three days of collection.

Soil moisture was determined gravimetrically: a subsample was taken from each soil core and placed into a 105°C drying oven for 48 hours (50 g in 2008 and 2010, 15 g in 2009). Gravimetric soil moisture was calculated as the moisture mass (fresh minus dry soil mass) divided by dry soil mass. Nematodes were extracted from another subsample (100 g in 2008 and 2010, 50 g in 2009) using a sugar centrifugation flotation method (Freckman and Virginia 1993) and animals were counted and sorted to trophic groups while live (Yeates et al. 1993), within days of extraction. Nematodes were counted at 100–400× using an Olympus CKX41 inverted microscope. When necessary, samples were diluted before enumeration of nematodes and the dilution factor was recorded. The condition of some nematodes was not good enough to determine the trophic group. These nematodes were not included in the total count for the analyses. The nematode samples were ultimately preserved in 5% formalin solution. The 2009 and 2010 nematode and moisture data from the control, +80% and –80% treatments have been used together with data from natural gradients in an earlier wider assessment of soil fauna responses to soil moisture availability at different sites and across time (Sylvain et al. 2014).

Statistical analyses

To investigate the long-term relationships between precipitation and nematode density, a generalized linear mixed model was applied for each trophic group and the total number of nematodes with growing season precipitation (in mm, continuous variable), year (categorical) and their interaction as fixed effects. Block, block by precipitation and block by year by precipitation interactions were included as random effects. To assess whether any effect of precipitation on nematode densities was mediated through changes in soil moisture, the above models were

repeated with soil moisture at the time of sampling as a covariate. These models enabled us to disentangle the contributions of both long-term alterations of precipitation and short-term available soil moisture to the nematode densities we measured. An initial significant effect of precipitation disappearing after including a significant soil moisture term in the model would imply that the precipitation effect was mediated by changes in soil moisture. If precipitation did not significantly relate to nematodes in either model but soil moisture did, this would mean that responses to short-term moisture pulses were overriding any effects of long-term alterations in precipitation. No relationship with soil moisture but a significant influence of precipitation would indicate that nematodes reacted mostly to the long-term manipulations of available moisture and were not sensitive to short-term pulses. No significant effect of either precipitation or soil moisture, would suggest that nematode densities in this system are mostly determined by factors unrelated to moisture availability. Finally, a significant effect of both precipitation and soil moisture would demonstrate that after taking into account the effects of the long-term precipitation manipulations, remaining variation could additionally be explained by short-term moisture availability.

All models used a negative binomial distribution and a log link function. Tests were based on the Kenward-Roger approximation of the denominator degrees of freedom and type III sums of squares. Dilution factor and soil dry weight were combined into an offset variable that was included to model nematode numbers per kg dry soil. Because no predatory nematodes were found in 2008, only data from the two other years were analyzed for this group. Likewise, only two samples from 2010 contained fungivorous nematodes, yielding a poorly fitted model and some extreme parameter values when including soil moisture. Therefore, the 2010 data for fungivorous nematodes were omitted from this analysis. All analyses were performed in SAS 9.3 (SAS Institute, Cary, NC, USA).

RESULTS

Nematode density varied greatly between individual soil samples. The average nematode

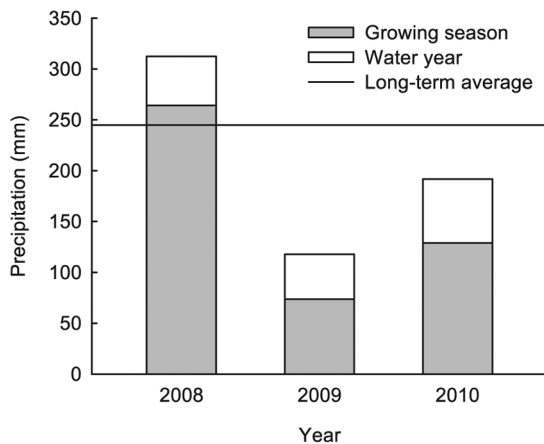


Fig. 2. Ambient growing season precipitation amounts, as part of ambient water year precipitation, during the three years of sampling compared to the long-term average from 1915 to 1995.

numbers per kg dry soil and their standard deviations across treatments and years were as follows: 8844 (SD: 13394) bacterivores, 45 (SD: 111) fungivores, 55 (SD: 180) predators, 1585 (SD: 1830) omnivores and 1425 (SD: 2335) plant parasites. The frequency distribution of the groups was positively skewed, i.e., a high proportion of low counts and a few high values, which is not uncommon for count data of spatially clustered organisms. About 5% of all nematodes could not be identified to trophic group. Of the others, 73.98% were bacterivores, 0.38% fungivores, 13.26% omnivores, 0.46% predators and 11.92% plant parasites.

Effect of growing season precipitation on nematode trophic group densities

During our study period, the precipitation pattern was characterized by a slightly wetter than average year (2008), followed by two dry years (2009 and 2010) (Fig. 2). Growing season and water year precipitation were highly correlated, with the majority of the precipitation falling during the growing season in all three years. Precipitation amounts over the entire growing season did not correlate with gravimetric soil moisture at the time of sampling, except in 2009, confirming the idea that instantaneous water availability and long-term water availability are decoupled.

We did not find any significant main rela-

tionship between changes in growing season PPT and the density of any of the nematode trophic groups nor for total nematode density (Table 1, Figs. 3G–L, 4). Bacterivore, omnivore and plant parasite densities—and therefore total nematode density—varied significantly between sampling years. While the density of predatory nematodes did not change between 2009 and 2010, no predatory nematodes were recovered in 2008. Moreover, the interaction between year and growing season PPT was not significant for any of the nematode trophic groups, suggesting that the lack of response to altered precipitation persisted over the three years of sampling.

Effect of gravimetric soil moisture on trophic group densities

A significant negative relationship between gravimetric soil moisture and bacterivorous nematode numbers was observed (Table 1, Fig. 3A). Indeed, within years, bacterivores preferred lower soil moisture (Fig. 3A). For any given year, bacterivore numbers were higher at a low than at a high level of soil moisture, except in 2008, for high levels of precipitation (Fig. 4A). However, the precipitation by soil moisture and precipitation by soil moisture by year interactions were not significant (Table 1). No significant relationships involving gravimetric soil moisture could be detected for fungivorous nematodes (Table 1, Figs. 3B, 4B). Omnivorous nematodes reacted according to a significant interaction between soil moisture and year (Table 1). There was a positive relationship between soil moisture and omnivore density in 2008, which disappeared in 2009 and switched to a negative relationship in 2010 (Figs. 3C, 4C). The slopes of the relationship between precipitation and plant parasite density differed among years, but differently so for different amounts of soil moisture ($P = 0.06$; Table 1). In 2009 and 2010 there was a positive effect of precipitation at low soil moisture levels, but a negative one at high soil moisture levels, cancelling each other out across all soil moisture values, while in 2008 the slope for both low and high levels of soil moisture was shallow and similar (Figs. 3D, J, 4D). At low moisture levels, the effect of precipitation became more positive over time, whereas at high moisture levels the effect became more negative over time. Note that

Table 1. Results of the generalized linear mixed models of the effects of year and precipitation (models without soil moisture) and of soil moisture, year and precipitation (models with soil moisture) on nematode trophic group and total nematode density.

Effect	Models without soil moisture			Models with soil moisture		
	df	F	P	df	F	P
Bacterivorous nematodes						
Yr	2, 59.86	27.41	<0.0001	2, 54.14	2.47	0.0940
PPT	1, 57.03	0.19	0.6671	1, 50.34	1.98	0.1651
Yr × PPT	2, 57.51	0.92	0.4053	2, 47.14	0.91	0.4102
Sm	1, 51.81	5.48	0.0231
Yr × Sm	2, 54.35	0.89	0.4163
Sm × PPT	1, 50.97	3.04	0.0870
Yr × Sm × PPT	2, 48.51	0.55	0.5823
Fungivorous nematodes						
Yr	2, 62	2.48	0.0916	1, 41.78	0.03	0.8549
PPT	1, 62	1.08	0.3025	1, 42	0.43	0.5165
Yr × PPT	2, 62	1.39	0.2570	1, 42	0.16	0.6899
Sm	1, 42	0.07	0.7895
Yr × Sm	1, 42	0.04	0.8359
Sm × PPT	1, 42	0.10	0.7548
Yr × Sm × PPT	1, 42	0.01	0.9362
Omnivorous nematodes						
Yr	2, 57.42	25.04	<0.0001	2, 56	12.09	<0.0001
PPT	1, 47.29	0.63	0.4323	1, 45.77	0.75	0.3904
Yr × PPT	2, 49.07	1.14	0.3289	2, 47.7	1.92	0.1585
Sm	1, 51.09	0.00	0.9528
Yr × Sm	2, 55.87	5.16	0.0088
Sm × PPT	1, 46.82	0.43	0.5139
Yr × Sm × PPT	2, 48.32	2.08	0.1364
Plant-parasitic nematodes						
Yr	2, 57.53	5.3	0.0077	2, 49.76	0.19	0.8255
PPT	1, 54.82	0.12	0.7316	1, 46.9	3.68	0.0610
Yr × PPT	2, 55.73	1.67	0.1970	2, 52.49	3.85	0.0276
Sm	1, 46.18	0.55	0.4638
Yr × Sm	2, 49.18	0.40	0.6704
Sm × PPT	1, 49.4	4.98	0.0302
Yr × Sm × PPT	2, 53.25	2.90	0.0637
Predatory nematodes						
Yr	1, 28.69	1.24	0.2747	1, 28	1.93	0.1754
PPT	1, 32	0.70	0.4084	1, 28	0.18	0.6709
Yr × PPT	1, 32	2.35	0.1350	1, 28	0.00	0.9745
Sm	1, 28	0.57	0.4561
Yr × Sm	1, 28	1.94	0.1749
Sm × PPT	1, 28	0.38	0.5436
Yr × Sm × PPT	1, 28	0.00	0.9749
Total nematodes						
Yr	2, 58.71	27.01	<0.0001	2, 53.11	3.24	0.0471
PPT	1, 56.82	0.01	0.9087	1, 50.86	1.43	0.2376
Yr × PPT	2, 57.19	0.47	0.6245	2, 51.29	1.13	0.3325
Sm	1, 50.95	4.50	0.0387
Yr × Sm	2, 53.08	1.19	0.3113
Sm × PPT	1, 50.84	1.89	0.1748
Yr × Sm × PPT	2, 51.62	0.78	0.4631

Notes: Yr: year, PPT: growing season precipitation, Sm: gravimetric soil moisture.

the effect of precipitation became increasingly stronger from 2008 over 2009 to 2010 at low soil moisture, but as the low moisture values in 2010 were much higher than in 2009 (Fig. 3), the slope for low moisture for 2010 is still less steep than for 2009 (Fig. 4D). Predatory nematodes, similarly to fungivores, did not react to gravimetric soil

moisture in any measurable way (Figs. 3E, 4E, Table 1). The density of all nematodes combined was negatively related to gravimetric soil moisture (Table 1). The pattern of total nematode density was very similar to that of the bacterivorous nematodes (Figs. 3E, 4F), which made up 74% of this total.

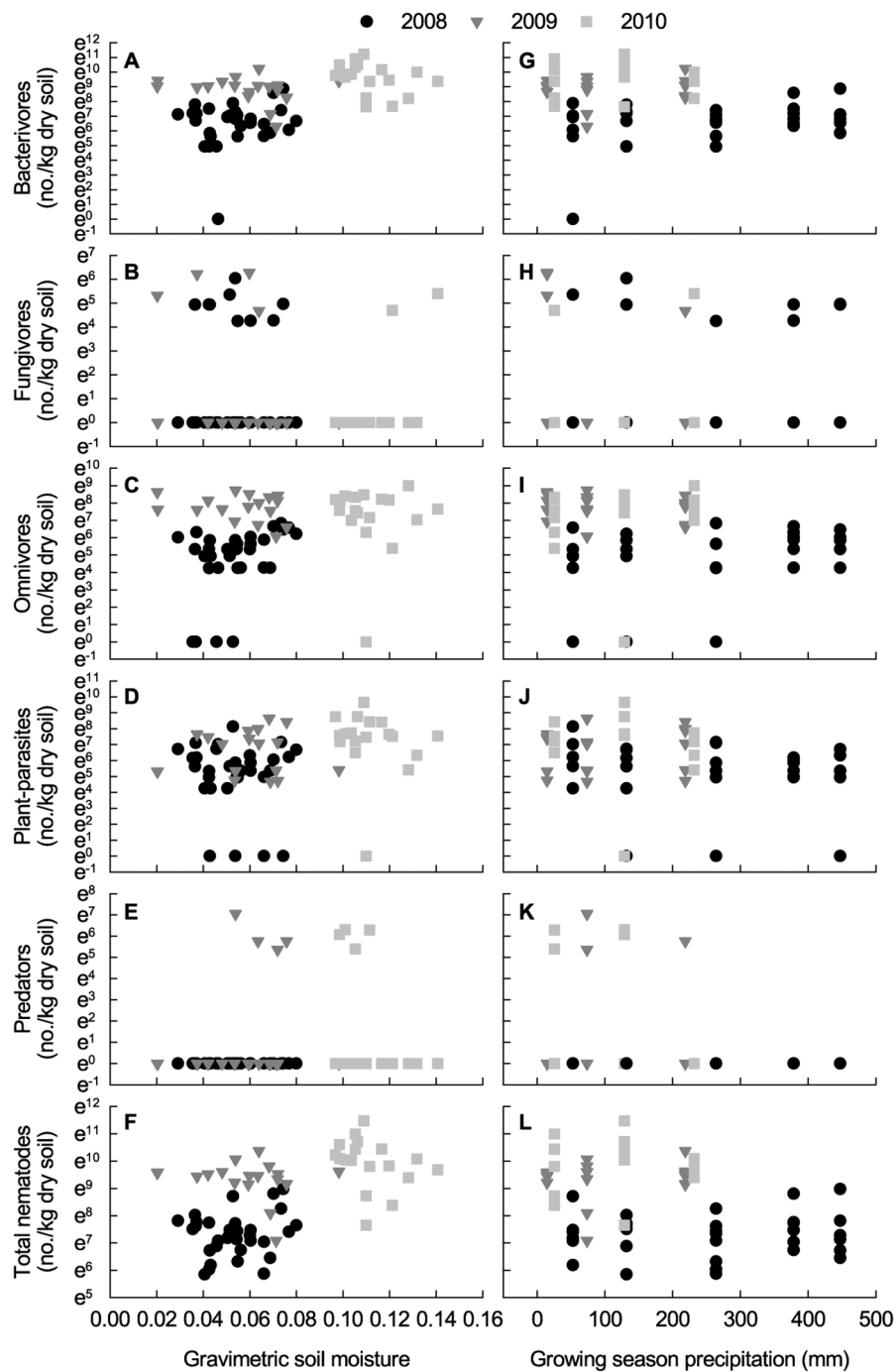


Fig. 3. Numbers per kg dry soil of the different nematode trophic groups and the sum total of the trophic groups in relation to gravimetric soil moisture (panels A–F) and growing season precipitation (panels G–L) for three years of sampling. (A, G) Bacterivores; (B, H) fungivores; (C, I) omnivores; (D, J) plant parasites; (E, K) predators; (F, L) total nematodes. A constant of 1 was added to nematode numbers to visualize zeroes on a log scale.

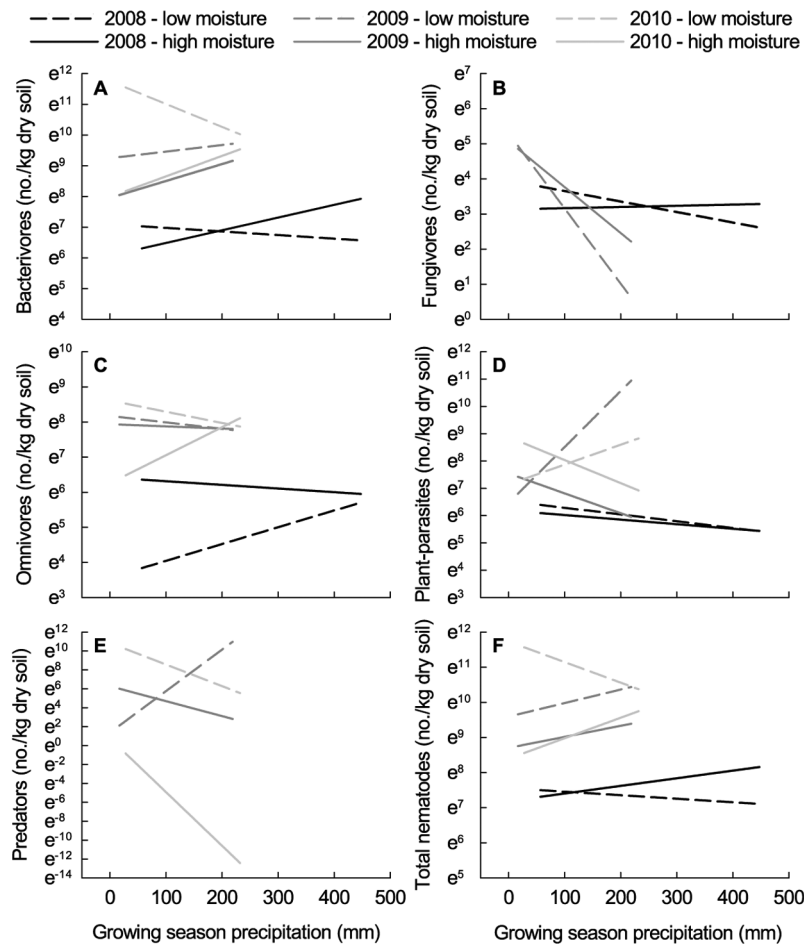


Fig. 4. Predicted numbers per kg dry soil of the different nematode trophic groups and the sum total of the trophic groups from models including growing season precipitation, gravimetric soil moisture and year of sampling as predictors. The relationship between growing season precipitation and predicted nematode numbers is displayed at two discrete levels of the continuous soil moisture variable for each of the three years, in order to enable a two-dimensional representation of the three surfaces fitted in three-dimensional space. We selected the average soil moisture minus 1.5 standard deviations for each year as representative low soil moisture value and the average soil moisture plus 1.5 standard deviations for each year as representative high soil moisture value. (A) Bacterivores; (B) fungivores; (C) omnivores; (D) plant parasites; (E) predators; (F) total nematodes.

DISCUSSION

Contrary to our expectations, we did not observe an overall increase in nematodes with increased precipitation, nor a decrease with decreased precipitation. Similarly, we found no general positive response to soil moisture across the trophic groups. Our data, therefore, did not support the hypothesis that nematodes generally increase in abundance with water availability (H1). Plant parasites were the only trophic group

to respond to altered precipitation in accordance with H1a, but only in soils with low moisture content. In contrast to H1b, bacterivorous nematodes reacted negatively to soil moisture. Omnivores shifted from responding positively to soil moisture in 2008 to a lack of response in 2009 and a negative reaction in 2010. The positive response in 2008 is in line with our hypothesis H1b, however (and in contradiction to H3) this correlation weakened over time instead of becoming stronger.

Nematode responses to long-term alterations in water availability

In other ecosystems nematode densities decreased with drought (Landesman et al. 2011, Stevnbak et al. 2012) or increased with water addition (Smolik and Dodd 1983, Landesman et al. 2011). Two earlier studies in deserts, however, found that water additions affected the abundance of none of the nematode trophic groups (Darby et al. 2011) or only that of plant parasites (Freckman et al. 1987). From semiarid systems, more idiosyncratic patterns emerge, with some nematode genera increasing and others decreasing under drying conditions, also depending on the soil temperature (Bakonyi and Nagy 2000, Bakonyi et al. 2007). A study conducted across mesic, xeric and arid grasslands and a polar desert found that soil nematode numbers decreased with increased moisture availability in each ecosystem except for the arid site, where no relationship was found (Sylvain et al. 2014). In a recent meta-analysis Blankinship et al. (2011) demonstrated that the effect of precipitation on soil biota abundance was independent of taxon, body size or trophic group, but did depend on ecosystem type; while this effect was positive in boreal forests, coniferous forests and deciduous forests, no effect was observed in grassland, heathland or tundra. In addition, effects of altered precipitation were independent of mean annual precipitation, but decreased with mean annual temperature and increased with duration of the experimental treatment. It is noteworthy that our results do not contradict these findings of fewer responses in non-forest ecosystems and a decrease in effect of precipitation alteration in warmer regions. The limited existing literature on longer-term precipitation effects on desert soil nematodes seems to confirm the idea that desert ecosystems could merely represent a so far understudied end member of this spectrum (Freckman et al. 1987, Darby et al. 2011). However, these two studies only included increased, not decreased amounts of precipitation, and had a shorter duration than our study. One study in a cold Antarctic desert found no effect of 8 years of yearly water additions on nematode populations, and thus further strengthens this idea (Simmons et al. 2009). As our precipitation additions were percentages of the ambient level, during the dry years 2009 and

2010 the increased precipitation plots only received a similar amount of precipitation as the control plots in 2008 (see Fig. 3). The nematodes may have shown a greater response if a similarly large water addition as in 2008 would have been sustained throughout the three years. However, as such dry years are likely to increase in frequency, our observed sequence of one average and two dry years seems more relevant for drawing conclusions for the future.

Nematode responses to short-term alterations in water availability and instantaneous soil moisture

In other desert studies, discrete irrigation events did not result in altered soil nematode numbers in the short term, i.e., when comparing numbers before and after an irrigation event (Whitford et al. 1981, Freckman et al. 1987). In the Chihuahuan Desert, Freckman and Virginia (1989) found a negative correlation between plant-parasitic nematode abundance and soil moisture, but only within some sites. However, irrigation events can induce a fast switch from anhydrobiotic to active forms (Whitford et al. 1981). Our centrifugation method was not suitable for extracting nematodes in their anhydrobiotic state and would have resulted in their reactivation to metabolic activity. As our counts thus reflect active plus anhydrobiotic and dead nematodes, we may not have detected such a switch in activity. Yet, soil moisture is often a good predictor of soil nematode abundance at short timescales (Freckman and Virginia 1989, Bouwman and Zwart 1994). Short irrigation pulses over a time span of 30 days in the New Mexican desert did not affect soil nematode abundance, while the addition of a litter layer did (Steinberger et al. 1984). Together, these results suggest that desert nematodes are highly adapted to low water availability by mechanisms such as anhydrobiosis, do not suffer numerically from short to rather long periods of drought and are limited by factors other than water availability, possibly resource quantity and quality (Steinberger et al. 1984). A negative relationship between soil moisture and nematode abundance, like we found in the case of bacterivorous and total nematodes, has been reported elsewhere (Freckman and Virginia 1989, Ruan et al. 2012, Sylvain et al. 2014). Interestingly, Sylvain et al.

(2014) observed such a negative relationship for all nematode trophic groups in all studied ecosystems, except the Jornada desert, where none of the groups responded to soil moisture. This discrepancy with our findings from the same location may be due to the different time period of our study. In addition, Sylvain et al. (2014) analyzed data pooled across different years. Our analysis enabled us to detect the negative relationship between soil moisture and bacterivorous and total nematode abundance, once the overall year-to-year variation in nematode abundance was accounted for. The pattern for omnivores, whose response to soil moisture changed from positive to negative over time, is a further example of how an explicit consideration of time can yield additional insights. The complex responses of plant parasites to soil moisture and precipitation over time in our study are not necessarily at odds with the negative correlation between soil moisture and plant-parasitic nematode abundance observed by Freckman and Virginia (1989). At higher precipitation values in 2009 and 2010, a similar pattern may have been found in our study, as precipitation affected plant parasites positively in low but negatively in high moisture sites in these years.

Responses of different nematode trophic groups to changes in water availability

Even though the trophic groups differed in their responses to water availability, as put forward in H2, the order of sensitivities did not match our expectations. The initial positive response of omnivores to soil moisture is in line with our hypothesis that this group has a higher sensitivity to altered water availability. The fact that the positive relationship of 2008 disappeared in 2009, even though the soil moisture gradient was similar in both years, suggests that these omnivores were somehow able to adapt to the differences in soil moisture. Soil moisture values were higher at the time of sampling in 2010 than in both 2008 and 2009, and may just have been beyond the optimum for these nematodes, explaining the negative effect of soil moisture during this year. We hypothesized that plant parasites would be least sensitive to altered water availability, but this turned out to be the only group showing a response to precipitation, albeit after a time lag, and only in moisture-limited

soils. Fine root growth may have increased under the influence of increased precipitation in these low moisture soils, enabling a proliferation of plant-parasitic nematodes. The consistently negative response of bacterivores to soil moisture seems counterintuitive. However, a simulation model of the effects of soil moisture on desert populations of *Acrobeloides*, a general bacterivore (Moorhead et al. 1987), suggested that total populations can be larger under low soil moisture as anhydrobiosis protects nematodes from mortality. This group furthermore comprises many smaller-bodied taxa, which may not immediately suffer from a reduction in water film thickness. As these nematodes actively filter bacteria within these water films, thinner films could mean a concentration and consequently higher capture rate of their prey. It is noteworthy that although the usually large-bodied omnivores and predators tend to be K-strategists and often smaller bodied bacterivores tend to be r-strategists, both categorizations do not coincide completely. Furthermore, juveniles of larger-bodied groups are small, and could thus be less restricted by thinner water films, just like the adults of smaller-bodied nematode groups such as bacterivores. Juvenile omnivores might be feeding exclusively on bacteria and act as functional bacterivores during this life stage. Future studies combining morphometric, age and functional data about nematodes could provide more insight into the detailed mechanisms of nematode responses to water availability in soils.

Some studies have reported a lack of response to water availability across trophic levels in nematode communities (Whitford et al. 1981, Steinberger et al. 1984, Darby et al. 2011). Others have shown different (Bouwman and Zwart 1994, Landesman et al. 2011) or consistent responses among trophic groups (Smolik and Dodd 1983, Schnürer et al. 1986, Stevnbak et al. 2012), or genus-specific responses within trophic groups (Bakonyi et al. 2007). It thus seems difficult to identify a general hierarchy in the responses of the different nematode trophic groups as proposed by H2. However, it is noteworthy that in desert ecosystems often none of the trophic groups reacted to altered water availability while the studies that reported consistent responses were conducted in more

mesic systems. Freckman et al. (1987) found that annual plant parasite density increased with irrigation, while the density of other trophic groups was unchanged. This is similar to our result for plant parasites under low soil moisture, even though Freckman et al. (1987) did not observe the lag in response we did. Our samples, however, were collected from underneath black grama, while their work was conducted underneath litter of creosote (*Larrea tridentata*). The authors attributed the response of the plant parasites to an increase in activity and growth of the lateral surface root system of creosote. We know that in our system black grama root production decreases with drought and increases with irrigation (O. E. Sala and L. G. Reichmann, *unpublished data*), so a similar mechanism may be operating under black grama. The soil moisture values reported in Freckman et al. (1987) were comparable to our 2008 and 2009 values. So this does not seem to explain why we only observed this response in the low moisture soils, also in 2009. Perhaps creosote takes advantage of increased precipitation across the moisture gradient, while black grama only does so in the drier soils and is limited by other factors than water availability in moister soils. An alternative explanation for the lower numbers of plant parasites in the plots with lower amounts of precipitation and soil moisture and for the decrease in omnivore numbers with decreasing soil moisture in 2008, is that these nematodes migrated into the deeper soil layers as the surface layer dried out. However, this would not explain why the pattern for omnivores was only found in the first year of sampling. Moreover, plant parasites only started responding after three years of precipitation manipulations. This is more indicative of a slow numerical response caused by altered reproduction and mortality than of migration, which is expected to occur faster. Virginia et al. (1992) found no difference in nematode abundance between the 0–10 and 10–20 cm layer in this desert, so this does not support the idea that the deeper, moister layers harbor more nematodes. Furthermore, Whitford et al. (1981) did not observe migration of nematodes between the litter layer and underlying soil in response to wetting and drying. They established that these nematodes rather activate from or go into anhydrobiosis as moisture

increases or decreases, respectively.

Evolution of nematode responses to water availability through time

According to H3, we expected the relationship between nematode numbers and precipitation to become stronger over time. The pattern for plant-parasitic nematodes was in line with H3, with the effect of precipitation becoming more positive, but only so at low levels of soil moisture. This implies that plant-parasitic nematodes were only limited by precipitation in the drier soils of this desert environment. Few studies have addressed nematode responses to altered water availability throughout a time period longer than one growing season. Darby et al. (2011) sampled nematodes throughout the duration of the experiment and found no effects of increased precipitation frequency at any of the sampling times. Freckman et al. (1987) sampled soil nematodes over the course of a year, both before and after each simulated rainfall event of either 6 mm per week or 25 mm monthly, and from control plots. None of the trophic group densities differed before and after irrigation, and except for plant parasites, none of the trophic group densities reacted to irrigation when averaged over the year. However, in the warm wet season, total nematode and omni-carnivore densities were lower in the 25-mm treatment, while plant parasites reached higher densities in the irrigated treatments compared to the control. In the cold variable season, both omni-carnivores and plant parasites had higher densities in the irrigated plots. We sampled in the warm wet season, in which Freckman et al. (1987) found nematodes to be most responsive to moisture pulses, to optimize detectability of responses. However, we cannot rule out that certain nematode groups would have showed a different response in another season, as Freckman et al. (1987) found in the case of omni-carnivores. Note, though, that in their study, responses to moisture additions did not generally become larger as time progressed, as proposed by H3.

The chance of observing effects of altered water availability on nematodes does not seem to increase strongly with time as a lack of responses as well as significant changes in nematode abundance have been found both in studies of a month or less (Whitford et al. 1981,

Steinberger et al. 1984, Schnürer et al. 1986, Bouwman and Zwart 1994) and of at least two years (Darby et al. 2011, Stevnbak et al. 2012). Again, none of the ecosystems in which consistent responses were found were deserts, while all studies that found no response in any of the trophic groups were conducted in deserts.

In summary, we demonstrate that a desert nematode community did not react numerically to reductions or increases in precipitation, across a range of soil moisture values. Only in the driest soils did plant-parasitic nematodes increase with precipitation after some years. Our study is the first to assess how both increased and decreased precipitation interact with instantaneous moisture availability to affect nematode communities in a desert ecosystem, and how these effects evolve over time. Our results are in line with earlier, shorter-term studies showing that desert nematode populations as a whole do not seem to respond to increased water availability. In addition to this lack of water limitation, our study reveals that desert nematodes seem to be quite resistant to drought, even at a timescale of multiple years. Our results thus suggest that in the face of the drying trend predicted for certain desert regions, there may well be some leeway for desert nematodes communities and their roles in ecosystem functioning, with the exception of plant-parasitic nematodes under prolonged drought.

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