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Soil organic matter determines the distribution and abundance of nematodes on alluvial fans in Death Valley, California

Amy M. Treonis,† Kelsey A. Sutton, Samantha K. Unangst, Julia E. Wren, Emma S. Dragan, and J. Parr McQueen

Department of Biology, University of Richmond, Richmond, Virginia 23173 USA

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Abstract. Death Valley, located within the Mojave Desert of the United States, is one of the most extreme terrestrial environments on Earth. We studied free-living soil nematode abundance and community structure in soil samples collected from alluvial fans in Death Valley between 2013 and 2018. Our objective was to establish the distribution and abundance of soil nematodes on alluvial fans with respect to soil properties, vegetation, and channels that reflect past and future water flows. The study period spanned an extreme drought for the region but also included a 2016 superbloom of spring annual plants that followed a strong El Niño event. We found that nematode communities were dominated by bacterial-feeding species and had higher densities under shrub canopies than in adjacent interplant soils. Nematode abundance was similar between areas on alluvial fans that were channelized by past water flows and adjacent desert pavement and does not appear to be linked to how water distributes on the fans following rainfall events. Nematode abundance increased during the superbloom in soils around annual plants. Across the study period, soil organic matter content was the only soil variable measured that was significantly and positively correlated to nematode abundance. Overall, nematodes in this extreme environment are adapted to drought, but they are highly dependent on the growth and distribution of both perennial and annual plants to supply the soil organic matter that their microbial food sources rely upon.

Key words: anhydrobiosis; Cephalobidae; climate change; desert shrubs; soil invertebrates; superbloom.

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† **E-mail:** atreonis@richmond.edu

Introduction

Soil nematodes (microscopic roundworms) are globally ubiquitous and widely distributed within desert ecosystems (Treonis et al. 1999, 2012, Pen-Mouratov et al. 2004, 2010, Adams et al. 2007). Death Valley, part of the Mojave Desert of the southwestern United States, experiences a severe rain shadow effect due to its proximity to the east of several other valleys. Subsequently, Death Valley is a true desert and one of the most extreme terrestrial environments on Earth, with annual rainfall totals typically <6 cm (Stachelski 2013). The hottest air temperature officially recorded on Earth was measured in Death Valley in 1913 (56.7°C), and temperatures at the lower elevations typically exceed 37°C daily May–September (Stachelski 2013).

Climate changes that affect the timing or intensity of precipitation and temperature increases that affect evaporation rates may be especially challenging to desert organisms such as nematodes, which already exist at the physiological limits for life (Vale and Brito 2015, Ehleringer and Sandquist 2018). Since 1975, the average yearly temperature in Death Valley has increased by over 2°C (Fig. 1a). Soil temperature (50 cm

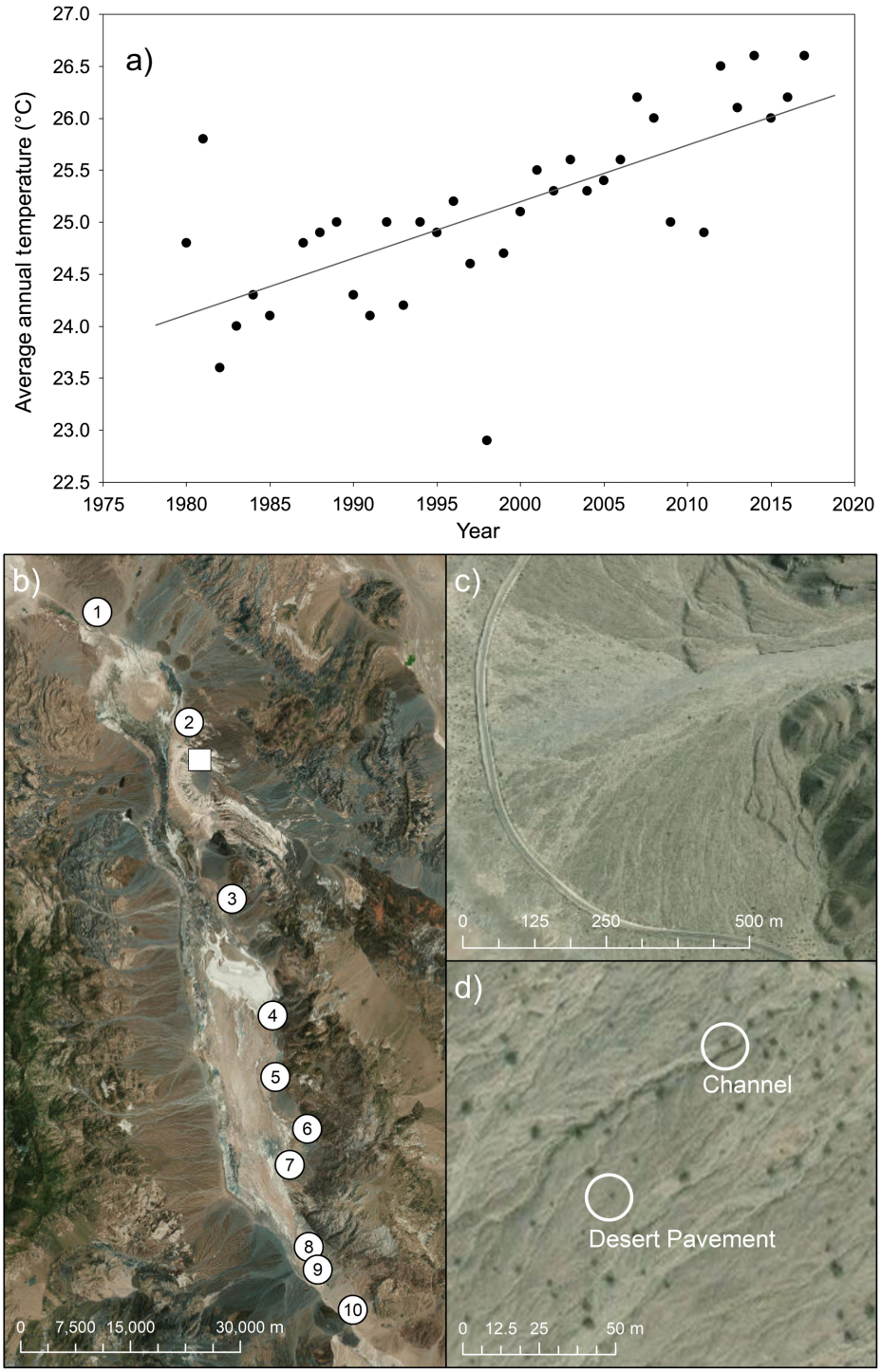

Fig. 1. (a) Average annual temperature in Death Valley, California, as measured at the Furnace Creek meteorological station, (b) satellite image of Death Valley. Circles mark alluvial fan sampling sites (see Table 1 for key). Square denotes National Park Service's Furnace Creek Visitor Center and meteorological station, (c) satellite image of Sidewinder Canyon alluvial fan, (d) examples of channel and desert pavement sites on alluvial fan.

depth) increased 0.79°C per decade on average from 1982 to 2000 in the Mojave Desert (Bai et al. 2014). Precipitation is sporadic and patchy in Death Valley in any year (Stachelski 2013), but the region has experienced increased aridity and drought frequency over the past several decades (Ficklin et al. 2015, Lehner et al. 2018). Furthermore, between 2012 and 2017, southern California, including Inyo Country where Death Valley is located, experienced an extreme drought (Griffin and Anchukaitis 2014, Williams et al. 2015). The region is predicted to become even drier in the coming decades (Cook et al. 2015).

Nematodes require water to move, feed, and reproduce, but they are also capable of using an anhydrobiotic survival strategy that allows them to persist in an ametabolic state when water may not be biologically available (Treonis et al. 2000). Desert soils are hot, sandy, dry, ahumic, alkaline, and saline, all of which are factors that impact the quality and quantity of soil water (Treonis et al. 2016). Landscape features also affect the distribution of water in deserts. In Death Valley, alluvial fans are present on both sides of the valley, forming from sediments deposited by water flowing from higher elevations (Fig. 1c). Visible water is absent on these fans beyond the hours immediately following a rainfall event. Flowing water has eroded shallow (<50 cm) channels into the surfaces of the fans (Fig. 1d), marking where water has flowed in the past and is likely to flow in the future. The adjacent desert pavement only receives precipitation directly from the air and often is overlain by interlocking stones, presenting a smooth surface that can impede water penetration (Dixon 2009).

Plant distribution, diversity, and growth patterns are also critical drivers of nematode abundance and community structure (Freckman and Mankau 1977, Viketoft et al. 2009, Sylvain and Wall 2011). Soil organic matter derived from plants fuels the bacterial and fungal decomposer organisms that microbivorous nematodes graze on (Freckman 1988, Treonis et al. 2010). In Death Valley, perennial plant communities are dominated by xerophyte shrubs with laterally distributed root systems (Hall 2007). Creosote bush (*Larrea tridentata*) is an evergreen shrub and, as a desert specialist, one of the most ubiquitous plants within Death Valley and the Mojave Desert (Hunt 1966). Perennials like creosotebush create resource islands of enhanced soil fertility beneath their canopies (Charley and West 1975, Whitford et al. 1997), which enhance nematode abundance (Freckman and Mankau 1977). Spring-flowering annual plants are also found in Death Valley, but their germination and growth varies from year-to-year due to fluctuations in the timing and quantity of rainfall (Beatley 1974, Bowers 2005). The contribution of these annual plants to supporting nematode communities has not been explored.

Nematodes have not been systematically studied in soils within the low elevation, arid center of Death Valley. The objective of our research was to study the distribution and abundance of free-living soil nematodes on alluvial fans in relation to soil properties, perennial and annual plants, and water channels. We predicted that water, plant, and nematode distribution would be tightly linked in this extreme environment.

Materials and Methods

Site description

Soils (Torrifluvent Entisols) were sampled from alluvial fans in Death Valley on four occasions between 2013 and 2018, as part of several experiments (Fig. 1b, Table 1). Sampling sites on the fans were pre-selected on the basis of shrub presence using satellite imagery (Fig. 1d). Sampled fans are all on the eastern side of Death

Table 1. Death Valley alluvial fan field sites.

Map no.	Site name	Elevation (meters ± sea level)	GPS coordinates
1	Salt Creek	30.6	36.60958° N, 116.99055° W
2	Cow Creek	−57.3	36.50075° N, 116.87817° W
3	Artist's Drive	−41.0	36.32642° N, 116.82536° W
4	Badwater	−76.0	36.21086° N, 116.77528° W
5	Coffin Canyon	−67.6	36.14984° N, 116.77207° W
6	Sheep Canyon	−44.9	36.09841° N, 116.73312° W
7	Sidewinder Canyon	4.0	36.06264° N, 116.75451° W
8	Smith Mountain	−70.0	35.98117° N, 116.73115° W
9	Flat Fan	−44.9	35.95863° N, 116.72028° W
10	Ashford Mill	−19.0	35.91853° N, 116.67722° W

Valley, lie along an 82-km north–south transect, and formed out of sediment deposits from the mountains of the Amargosa Range (maximum elevation = 2663 m). The sampling transect passes through the Badwater region, which is the low elevation center of Death Valley. All sites are located within Death Valley National Park.

Most of the surface area of the alluvial fans is non-vegetated, but perennial shrubs also are present in many areas, distributed evenly and several meters apart (Fig. 1d). These are primarily creosote (*L. tridentata*) and a few desert holly (*Atriplex hymenelytra*). We observed significant shrub mortality on alluvial fans near the center of Death Valley (i.e., Artist's Drive, Badwater, and Coffin Canyon). This shrub mortality predates our study period (2013) but could have been caused by an earlier drought (e.g., 2006–2010). All shrubs observed on these three fans were leafless with bleached stems throughout the study period. The soils sampled at each fan were all rocky sands (>85% sand particles) according to soil texture analysis (Gee and Bauder 1986).

Temperature data were obtained from NOAA (https://www.ncdc.noaa.gov/) that was collected at the Furnace Creek meteorological station near the Visitor Center within Death Valley National Park. Satellite images are from Esri (2018).

Nematode communities in soils around shrubs vs. interplant soils (Experiment 1)

On 18 November 2013, soil samples were collected from seven alluvial fans (Salt Creek, Cow Creek, Artist's Drive, Badwater, Sheep Canyon, Sidewinder Canyon, and Ashford Mill, Table 1). At each site, replicate samples were collected from within the canopy of three mature shrubs (*L. tridentata*) located at least 25 m from each other. Three additional samples were collected from interplant spaces at least 1 m away from shrubs. The soils are extremely rocky and dry, precluding the use a soil corer. Samples were thereby collected using 50-mL plastic beakers as scoops. For each sample, approximately 1 kg of soil was collected from multiple locations surrounding the shrub's main stems. Prior research has shown that nematodes are most abundant in surface soils in the Mojave Desert (Freckman and Mankau 1977). Surface litter was gently scraped away with a spoon, and soil was collected to a depth of 0–5 cm. Neither fine nor coarse roots were encountered. A similar area and depth were sampled for the interplant samples. Soil was sieved on site (2 mm) to remove rocks and large pieces of litter and transferred to a plastic bag (Whirl-Pak, Nasco, Fort Atkinson, Wisconsin, USA). Soil samples were shipped from Las Vegas, Nevada, USA, to the University of Richmond and stored at 4°C until analyzed.

Soil moisture was determined gravimetrically (48 h at 105°C). Soil organic matter was measured as loss on ignition (400°C, 12 h). Suspensions of 10 g of soil in 30 mL of deionized H_2O were mixed and then equilibrated for 30 min. Solution pH was measured with an Orion 3-star pH meter with a silver chloride reference electrode (Thermo Fisher Scientific, Waltham, Massachusetts, USA). Electrical conductivity was measured as an indicator of salinity using a conductivity meter (Traceable, Cole-Parmer, Vernon Hills, Illinois, USA). Nematodes were extracted from 70 g soil using sugar flotation and centrifugation technique (Jenkins 1964) and preserved in 5% formalin. Nematodes were counted using a Zeiss Axiovert 40 CFL inverted microscope (Carl Zeiss MicroImaging, Thornwood, New York, USA).

Nematode abundance associated with annual plants during a superbloom (Experiment 2)

During most springs in Death Valley, some annual wildflowers germinate, grow, and bloom in the inter-shrub areas on alluvial fans. In February 2016, an intense superbloom occurred, and the alluvial fans were carpeted with *Geraea canescens* (Desert Gold) and other ephemeral plants. Soils were sampled on 27–28 February 2016 from three alluvial fans (Artist's Drive, Ashford Mill, and Badwater). For each sample, soil was collected to a depth of 0–5 cm from within a 3-cm radius of the stems of 10 individual *G. canescens* plants growing at least 1 m away from each other. A complementary non-plant sample was similarly collected from 10 non-vegetated soil patches within the same area. Three annual plant samples and three plant-free samples were collected from each of the sites. Soil properties were measured, and nematodes were extracted as described above.

Nematode communities in water channels vs. desert pavement (Experiment 3)

The surfaces of alluvial fans are marked by dry channels through which most water flows

following rainfall events (Fig. 1c, d). In 2016 (27–28 February) and 2018 (6–7 January), soil samples were collected from channels and from desert pavement at four alluvial fans (Artist's Drive, Sidewinder Canyon, Flat Fan, and Ashford Mill). At each fan, three replicate samples were collected as described above from within the canopy of three shrubs growing inside the water channels. Three additional samples were collected from shrubs growing in desert pavement. Soil properties were measured, and nematodes were extracted and evaluated as described above, but a nematode community analysis also was performed. Nematodes from each sample were identified to the family level using morphological features under 50–400 times magnification. Nematodes were not assigned to lower taxonomic levels due to the large number of juveniles present. Nematodes were assigned to trophic groups based on Yeates et al. (1993).

Nematode communities over time (Experiment 4)

Two alluvial fan sites (Artist's Drive and Ashford Mill) were each sampled in 2013, 2014, 2016, and 2018 in the same area in order to monitor nematode abundance over time. At both sites, replicate samples were collected as described above from within the canopy of shrubs growing in desert pavement. Soil properties were measured, and nematodes were extracted and counted.

Nematode communities and soil properties (Experiment 5)

Soil samples (0–5 cm) were collected under shrub canopies on several more alluvial fans in 2014 and 2016 (Cow Creek 2014, $n = 3$; Smith Mountain 2014, $n = 3$; Badwater 2016, $n = 3$; Coffin Canyon 2016, $n = 6$; Table 1). These data were combined with data from Experiments 1–4 (total sample size = 135) and used to (1) test for correlations between nematode abundance and soil properties and (2) to explore variation among all of the alluvial fan sites sampled (Table 1).

Statistical analyses

Statistical analyses were performed with R version 3.5 (R Development Core Team 2018). Multi-factor ANOVA was used to investigate differences in measured variables (Experiments 1–4), including alluvial fan site as one of the main effects and sampling year when applicable. Where effects were significant, means were compared using the Tukey's honestly significant difference multiple comparison procedure. Prior to ANOVA, the Shapiro–Wilk test was used to assess all dependent variables for normality, and data were subsequently $\ln(x + 1)$-transformed (nematode density), ln-transformed (organic matter), or square-root transformed (moisture) as needed. Pearson's r was used to test for correlations among soil properties and nematode abundance (Experiment 5). One outlier point was removed from this analysis due to exceptionally high nematode abundance. A constrained linear canonical ordination (redundancy analysis [RDA], Rao 1964) was performed using the R vegan package (Oksanen et al. 2018) to test the contribution of measured soil properties to the abundance of nematodes from each trophic group, using only samples that contained nematodes. The abundances of each nematode trophic group (bacterial-feeders, fungal-feeders, omnivore-predators) were Hellinger-transformed prior to RDA. A full model incorporating all four measured soil variables was tested. A Bray–Curtis-based nonmetric multidimensional scaling approach was used to explore the degree of similarity among alluvial fan sites with respect to measured soil properties and nematode abundance.

Results

General description of nematode communities in soils from Death Valley alluvial fans

Of the 135 samples collected from Death Valley alluvial fans between 2013 and 2018, 124 contained nematodes. Nematode abundance ranged from 10 to 47,563 kg^{-1} soil, with an average of 2435.4 (median = 782.5). We observed three trophic groups of free-living nematodes: bacterial-feeders, fungal-feeders, and omnivore-predators. No plant-parasitic taxa were found. Nearly all communities were dominated by bacterial-feeding nematodes from the Cephalobidae family, with species from the *Acrobeles*, *Acrobeloides*, *Cephalobus,* and *Zeldia* genera represented. Several different Cephalobidae species usually were found within a single soil sample. Rarely, a species from the Plectidae also was encountered. Fungal-feeders were represented by *Aphelenchus avenae* and *Aphelenchoides* sp. Nematodes from

these genera may also be root-hair feeding (Yeates et al. 1993, Treonis 2017), but given the absence of roots in these soil samples, these nematodes are probably feeding on fungi. The omnivore-predator present was a member of the nematode family Qudsianematidae (*Discolaimium* sp.).

Nematode communities in soils around shrubs vs. interplant soils (Experiment 1)

For all seven alluvial fans sampled in 2013, nematode abundance was higher in soils collected from beneath shrub canopies vs. interplant spaces (ANOVA, plant effect $P = 0.0004$, Fig. 2a). Shrub soils also contained more organic matter ($P = 0.0001$) and were more saline ($P = 0.02$; Fig. 2b). Similar high pH and low moisture levels were measured for all soils regardless of shrub presence ($P > 0.05$, Fig. 2b). These results were similar across the fans; for all measured variables, the interaction effect between soil position (shrub or interplant) and site was not significant ($P > 0.05$).

Nematode abundance associated with annual plants during a superbloom (Experiment 2)

Soils collected from the bases of annual plant stems contained more nematodes than nearby soils that lacked plants (Fig. 3a, ANOVA, plant effect $P = 0.004$). This result was most dramatic at the Badwater fan, where annual plant soils contained a mean of 1800 ± 1015 nematodes/kg vs. 36 ± 32 nematodes/kg for soils lacking plants. By comparison, shrub soils collected at the same site in the same year contained only 26.2 ± 11.3 nematodes/kg ($n = 6$). Salinity, moisture, and pH did not differ between soil with annual plants and soil without (Fig. 3b, ANOVA, plant effect $P > 0.05$) but organic matter was higher (Fig. 4b, ANOVA, $P = 0.019$). These results were similar across the fans; for all measured variables, the interaction effect between soil position (annual plant or interplant) and site was not significant ($P > 0.05$).

Nematode communities in channels vs. desert pavement (Experiment 3)

Nematode abundance was similar in channel and desert pavement soils for all three trophic groups of nematodes (Fig. 4a, ANOVA, soil position effect, $P > 0.05$). Soil moisture, pH, and organic matter content also were similar among channel and desert pavement soils (data not shown, ANOVA, soil position effect $P > 0.05$). Salinity was higher in desert pavement (1.1 ± 0.09 mS/cm) than in channel soils (0.405 ± 0.31 mS/cm; ANOVA, soil position effect $P = 0.043$). For all measured variables, there were no significant interaction effects between soil

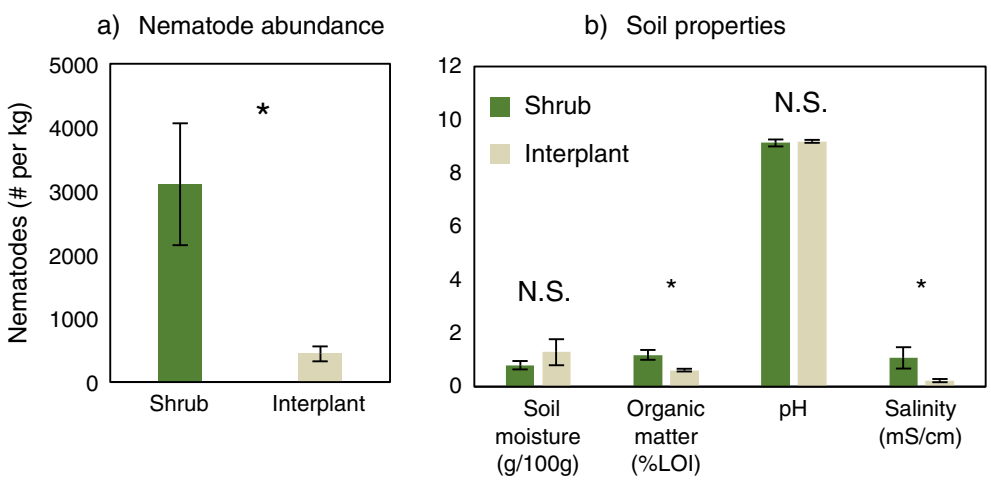

Fig. 2. Nematode abundance (a) and soil properties (b) in soils (0–5 cm) beneath shrub canopies and in interplant spaces in 2013. Soils from seven alluvial fan sites are combined. Values for each bar are means ± the standard error of the mean ($n = 21$). Asterisks indicate significant differences between shrub and interplant means. N.S., not significantly different.

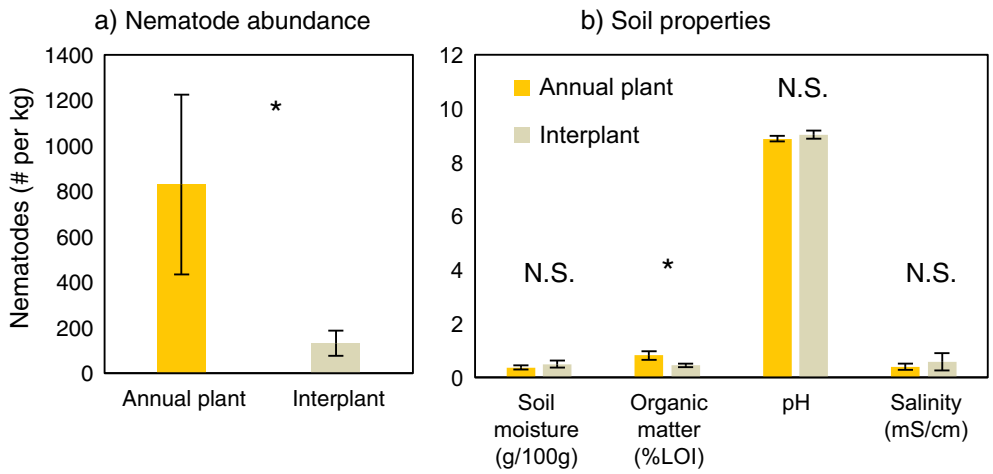

Fig. 3. Nematode abundance (a) and soil properties (b) in soils (0–5 cm) from around the stems of annual plants and from interplant spaces in 2016. Soils from three alluvial fan sites are combined. Values for each bar are means ± the standard error of the mean (n = 9). Asterisks indicate significant differences between plant and interplant means. N.S., not significantly different.

position (channel or desert pavement) and site and/or year ($P > 0.05$).

Nematode abundance over time (Experiment 4)

Nematode abundance declined from 2013 to 2016 at the Artist's Drive and Ashford Mill sites (Fig. 4b, ANOVA, significant year effect, $P < 0.001$). In 2018, however, nematode abundance recovered (Fig. 4b). None of the measured soil properties, including organic matter content, changed significantly over this same time period (data not shown, ANOVA, year effect $P > 0.05$).

Nematode communities and soil properties (Experiment 5)

Across 134 samples collected from alluvial fans from 2013 to 2018, there was a positive correlation between the abundance of nematodes and soil organic matter content (Fig. 5, Pearson's $r = 0.53$, $P < 0.0001$). Salinity, pH, and soil moisture were not correlated to total nematode abundance (data not shown). Very few soils lacked nematodes (11 out of 135). Most of these soils were very saline (mean = 9.3 mS/cm). Moisture content and salinity were positively correlated (Pearson's $r = 0.72$, $P < 0.0001$; data not shown).

RDA found that the first two axes explained 40.1% of the variation in nematode community trophic structure (Fig. 6a). Monte Carlo permutation testing (n = 999) determined the axes explained a significant portion of the variance in the dataset ($P = 0.003$). Bacterial-feeding nematodes, which were the most abundant across the samples, showed correlations to organic matter, moisture, and salinity (Fig. 6a). Fungal-feeders and omnivore-predators did not show correlations to soil variables (Fig. 6a).

Nonmetric multidimensional scaling analysis demonstrates that there were no distinct separations among the 10 alluvial fans sampled with respect to measured variables (nematode abundance, pH, moisture, organic content, salinity, Fig. 6b, Stress value = 0.109), which is consistent with the results from ANOVA for Experiments 1–4 that revealed few significant site interaction effects. Some sites showed more variation across samples than others. In particular, we encountered an unusually broad range of moisture and salinity values in samples collected from the Sidewinder Canyon alluvial fan (Fig. 6b).

Discussion

Annual and perennial plants positively impact soil nematode distribution and abundance in Death Valley

Soil nematodes are widely distributed on the alluvial fans of Death Valley, existing in both

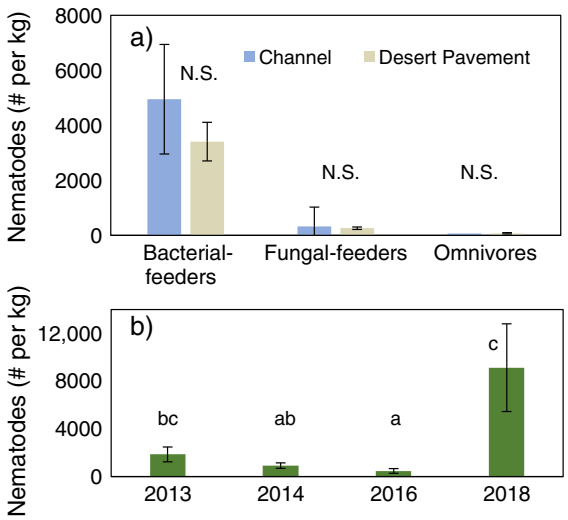

Fig. 4. (a) Nematode abundance by trophic group in channel and desert pavement soils (0–5 cm) under shrubs. Soils from four alluvial fan sites are combined. Values for each bar are means ± the standard error of the mean (n = 24). N.S., not significantly different. (b) Nematode abundance by year at two sites sampled throughout the study period (Artist's Drive and Ashford Mill). Values for each bar are means ± the standard error of the mean (n = 12). Bars with the same letter are not significantly different (Tukey's honestly significant difference, $P > 0.05$).

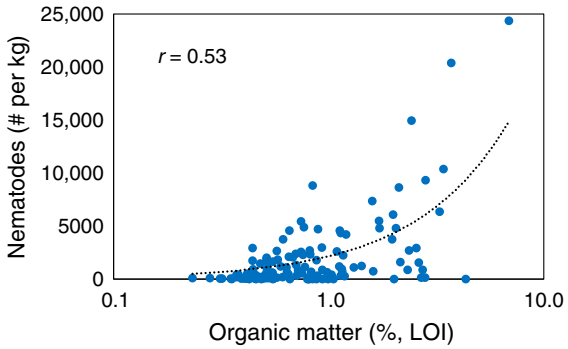

Fig. 5. Correlation between soil organic matter content and nematode abundance in 134 soils collected from alluvial fans in Death Valley.

plant and interplant spaces in one of the most extreme terrestrial environments on Earth. Both perennial and annual plants appear to have significant positive impacts on soil nematodes in Death Valley. First, we found that nematodes are more abundant under the canopy of shrubs than in interplant spaces, even when shrubs are dead. Shrub soils were higher in organic matter content, and nematodes are likely responding to the resource island effect (Charley and West 1975, Whitford et al. 1997). Prior work on Mojave Desert nematode communities outside of Death Valley also demonstrated that the density of nematodes is greatest in soils under shrub canopies (Freckman and Mankau 1977). Studies of nematode communities in the Negev Desert in Israel, including the hyperarid Arava Valley region, also support the influence of shrubs on nematode abundance and the near absence of nematodes in interplant spaces (Pen-Mouratov et al. 2003, 2010).

Second, our study period included the El Niño phase of the Southern Oscillation (2015–2016). This was a particularly strong El Niño event (Kogan and Guo 2016), and strong events are associated with above-average precipitation (Jong et al. 2016). As a result, significant fall and winter rainfall events in Death Valley fueled a February 2016 superbloom of annual wildflowers (Bowers 2005). We documented a rapid, positive effect of these annual plants on nematode abundance and organic matter in soils surrounding the plant stems. Furthermore, the decomposition of these plants may still be sustaining nematode populations. At the Artist's Drive and Ashford Mill sites, shrub soils contained unusually high density of nematodes (>10,000 nematodes/kg) in 2018, comparable to what would be found in an agricultural, grassland, or forest soil. We posit that the increase in nematode abundance at these sites from 2016 to 2018 has two causes. Higher densities of nematodes in 2018 may be due to climactic recovery from the 2012–2017 drought, but it is also likely that nematodes were responding to soil organic matter inputs from the death of the annual plants that grew there during the 2016 superbloom. However, we did not measure a significant increase in soil organic matter content from 2016 to 2018 in interplant soils, and in 2018, we observed that much of the biomass of the annual plants was still standing on the fans as upright, bleached stems. Nonetheless, the rapid response of nematodes to the germination and growth of annual plants in 2016 suggests that the soil food web is generally energy-limited.

Our sampling dates were separated by many months, and therefore, we do not know how

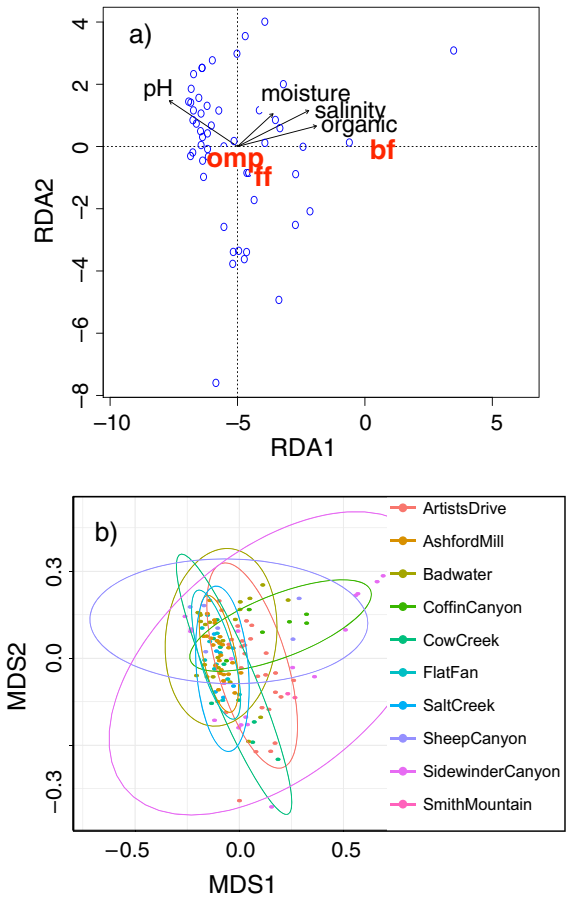

Fig. 6. (a) Ordination biplot for RDA of relationships among soil properties and the abundance of nematode trophic groups (bf, bacterial-feeders; ff, fungal-feeders; omp, omnivore-predators). Circles represent 54 soil samples for which the abundance of each trophic group was determined. Axis 1 explained 38.4% of the variation in the data, and Axis 2 explained 1.6%. (b) Ordination biplot from nonmetric multidimensional scaling (NMDS) analysis of nematode density and soil moisture, organic content, salinity, and pH for soil samples from 10 alluvial fans. Points represent different samples, color coded to distinguish fan sites. Ellipses represent 95% confidence intervals for each alluvial fan.

much variation there might be in Death Valley nematode abundance on smaller time scales (i.e., weekly, monthly). Freckman and Mankau (1986) conducted a monthly survey of nematode communities under *L. tridentata* shrubs in the Mojave Desert, at Rock Valley, Nevada. They found that soil temperature and moisture levels showed seasonal dynamics, and the density of nematodes was tied to these patterns (Freckman and Mankau 1986). Nematodes in surface soils (0–10 cm) showed fluctuation over the year, with their lowest abundance during the hottest and driest months (Freckman and Mankau 1986). Nematodes also declined, counterintuitively, following a July 1974 rainstorm but rebounded within weeks (Freckman and Mankau 1986). In contrast, Liang and Steinberger (2001) found that nematodes increased in abundance under shrubs during seasonal periods of higher soil moisture in the Negev Desert. Prior to our 6–7 January 2018 sampling, there had been no rainfall measured in Death Valley since September 2017 (https://www.ncdc.noaa.gov/), so the extremely high nematode abundances that we measured in January 2018 were not in response to a specific precipitation event.

Nematode distribution is unaffected by water distribution patterns across alluvial fans

Nematodes, like other microscopic invertebrates, use an ametabolic survival strategy known as anhydrobiosis in order to persist during adverse conditions (Treonis and Wall 2005). Given the dryness of Death Valley soils (mean = 0.66 g water/100 g soil across 135 samples), it seems that alluvial fan soil nematodes may spend a significant portion of their life spans in anhydrobiosis, and their growth and reproduction may be confined to the short periods following rainfall events (Treonis et al. 2000). Nematodes that are in an anhydrobiotic state coil their bodies (Freckman et al. 1977). In a preliminary study, we extracted nematodes from soils collected from alluvial fans using a special procedure that employs high molarity sugar solutions instead of water (Freckman et al. 1977). We found coiled nematodes, indicating that they likely were anhydrobiotic, but the temporal dynamics of their use of this strategy remain a topic for further investigation. Overall, our results suggest that nematodes are not as linked to water distribution across fans as we expected, having similar abundance under shrubs in channels where water flows after rainfall and in adjacent desert pavement. Visual assessment of satellite images suggests that shrub distribution is not influenced by the channels either.

Nematode abundance is correlated to soil organic matter content

The ability to use anhydrobiosis allows nematode distribution to be disconnected from moisture availability, and instead, our results suggest that nematode abundance on alluvial fans is primarily correlated to soil organic matter content. Steinberger et al. (1984) also suggested that energy (organic matter) is important for determining the abundance of nematodes in desert soils, as nematodes failed to respond numerically to experimental manipulation of rainfall in a field experiment. Soil organic carbon has also been correlated to nematode abundance within the McMurdo Dry Valleys of Antarctica (Barrett et al. 2004).

Our study period encompassed the 2012–2017 California drought, an event whose severity has been described as without precedent (Robeson 2015). Anthropogenic influences on global climate are believed to have intensified the severity of this drought (Williams et al. 2015). We found that nematode abundance declined significantly from 2014 to 2016. We also observed swathes of dead perennial shrubs at some of our alluvial fan locations, including those where nematode abundance declined during the drought (Artist's Drive and Badwater). The timing of this shrub mortality is unknown, but it predates our study period. The western United States is experiencing increased drought (Ficklin et al. 2015), and the decade before our study also included a drought in the region (2006–2010). Changes in air temperatures (Fig. 1a) and corresponding soil temperatures (Bai et al. 2014) each could have contributed to what appears to be relatively recent shrub mortality. Creosote is an especially long-lived shrub, however, with one plant, located outside of Death Valley in the Mojave Desert, estimated to be almost 12,000 yr old (Vasek 1980). Thus, the death of these shrubs across some alluvial fans in Death Valley is notable. In some areas, desert plants may not be as resistant to climate change as has been suggested (Tielbörger and Salguero-Gómez 2014). Ehleringer and Sandquist (2018) have documented increased mortality of deciduous shrubs in the Death Valley region over the past four decades, complementing our observations for evergreen creosotebush.

While the death of these shrubs does not appear to currently be affecting nematode populations, dead shrubs eventually become tumbleweeds, and the resource island effect will fade. The limited abundance of nematodes that we documented in interplant spaces suggests that nematodes will be lost from fans where shrubs die and blow away or decompose. Although annual plants may germinate and grow at intervals, contributing to nematode persistence, the plants that bloom under superbloom conditions are thought to be holdovers from a wetter Pleistocene (Bowers 2005). Like shrubs, they may be lost in some areas of Death Valley as the climate continues to change.

Cephalobidae nematodes in desert soils

The Mojave Desert has been a rich environment for nematologists studying Cephalobidae, a family of bacterial-feeding nematodes that can have very ornate mouth parts (Nadler et al. 2006). RDA showed that on alluvial fans, these nematodes are associated with soils with higher moisture, salinity, and organic content. *Scottnema lindsayae*, the species of Cephalobidae found in the polar desert soils of Antarctica (Adams et al. 2007), is considered to be a desert specialist, thriving in soils far away from ephemeral meltwater due to the ability to use anhydrobiosis (Treonis et al. 1999). In Death Valley, species of Cephalobidae seem equally capable of flourishing in the extreme environment. The level of diversity of Cephalobidae is high in Mojave Desert soils, and a comprehensive survey of nematode diversity was beyond the scope of this study and is challenging when populations are dominated by juveniles. However, molecular-based characterizations of nematode communities hold considerable promise for future studies of Cephalobidae ecology (Treonis et al. 2018). Future study of Death Valley soil nematode communities focused on characterizing communities at a finer scale (i.e., phylotype-level) may facilitate understanding of the environmental variables favoring co-existence of these assemblages of closely related species.

Conclusions

Death Valley has long been studied as a model for organisms living at the extremes (e.g., the endangered pupfish, *Cyprinodon salinus*, Martin

et al. 2015 and the Badwater snail, *Assiminea infima*, Sada 2001). Free-living soil nematodes, however, are likely to be the animal with the broadest distribution across this unique environment and warrant monitoring for their responses to climate change and other anthropogenic disturbances. In our study, organic matter content was the only measured variable that was correlated to nematode abundance, suggesting that the growth and senescence of perennial and annual plants, from which most organic matter is derived, has a significant impact on soil nematodes. As the climate continues to change, impacts on plant distribution in this extreme environment will also affect soil nematodes.

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