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Briny Biology: Nematodes From the Hypersaline Springs of the Central Namib Desert

Amy M. Treonis[1] | Eugene Marais[2] | Gillian Maggs-Kölling[2,3]

[1]Department of Biology, University of Richmond, Richmond, Virginia, USA | [2]Gobabeb Namib Research Institute, Walvis Bay, Namibia | [3]Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa

Correspondence: Amy M. Treonis (atreonis@richmond.edu)

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ABSTRACT

Hypersaline environments approach the physiological limits of metazoan life, yet the distribution, abundance, and community structure of animals in such systems remain poorly resolved. Nematodes, which possess remarkable stress tolerance and cryptobiotic capabilities, provide an ideal model for exploring these limits. We investigated nematode communities in sediments and microbial mats from seven hypersaline desert springs in the central Namib Desert, Namibia, spanning nearly a twenty-fold range in electrical conductivity (EC; 12.3 to > 500 mS cm^{-1}). Using live-extraction methods, we quantified nematode abundance, taxonomic composition, and diversity in relation to spring physicochemical properties. Nematodes were detected in all but four of 84 samples and reached exceptionally high densities (up to 1.6×10^5 individuals 100 g^{-1} dry weight), including in microbial mats in water exceeding 100 mS cm^{-1}. Contrary to expectations, nematode abundance was not correlated with EC, pH, or dissolved oxygen. However, taxonomic richness declined significantly with increasing EC, indicating environmental filtering of diversity. This impacted mainly rare taxa, and EC was not correlated to the Simpson Index of diversity. Community composition differed among springs and between microbial mats and underlying sediments, with mats supporting higher abundances and distinct assemblages. Multivariate analyses showed that site and substrate type explained substantially more variation in nematode communities than measured physicochemical variables. Communities were characterized by low diversity and dominance of a small number of saline-tolerant taxa, particularly *Monhystrella*, which occurred at all sites. Live nematodes were recovered from sediments beneath water with EC > 500 mS cm^{-1}, suggesting that nematodes can persist under extremely high-salinity conditions. Our results demonstrate that hypersaline desert springs can support dense but taxonomically simplified nematode communities and highlight microbial mats as key biological structures that buffer extreme conditions and sustain metazoan life.

1 | Introduction

Establishing the environmental extremes under which life can exist remains an active area of investigation in the life sciences. Because of their extraordinary diversity and broad distribution across aquatic and terrestrial habitats, nematodes are a particularly useful taxon for exploring these limits. Nematodes are microscopic animals (typically < 2 mm) with a remarkable capacity to persist in extreme environments (Hodda and Traunspurger 2021). Although they require water for movement, feeding, and reproduction, nematodes, like rotifers and tardigrades, can survive desiccation, freezing, and high salinity by entering an inactive, cryptobiotic state (Keilin 1959). Cryptobiosis allows nematodes to persist at the edge of habitability, alternating between active and inactive states as environmental conditions fluctuate. Nematodes have been shown to survive extreme temperatures (Borgonie et al. 2011; Shatilovich et al. 2023), total desiccation (Rawson et al. 2024), high arsenic levels (Shih et al. 2019), and tremendous hydrostatic pressures (Kwan et al. 2025). In contrast, the effects of hypersalinity on nematode survival, abundance, and community diversity remain comparatively poorly documented.

One environment in which nematodes may encounter extreme salinity is within the microbial mats and sediments of desert springs. These springs originate from the upwelling of groundwater and become saline through the dissolution of ions from underlying substrates combined with intense evaporative concentration. Hypersaline springs occur in many desert biomes worldwide (Cole 1968; Day and Seely 1988), including the Namib Desert of southern Africa (Figure 1A; Eckardt et al. 2001). The Namib Desert extends in a narrow band more than 2000 km along the Atlantic coast and receives exceptionally low annual rainfall (0–100 mm), with coastal regions additionally influenced by marine fog (Spirig et al. 2019). Across the hyperarid gravel plains of the Namib, small desert springs are scattered and often difficult to detect (Day and Seely 1988; Eckardt et al. 2001). Despite their extreme salinity, these springs represent critical water sources for a wide range of animals, including large mammals, birds, reptiles, and small vertebrates (van Wyk 2023). In spring ecosystems and other extreme freshwater habitats, nematodes frequently dominate metazoan communities (Hodda and Traunspurger 2021), where they function as microbivores and algal grazers and serve as prey for higher trophic levels (Ptatscheck 2021). Although nematodes were reported in high densities from two unnamed Namib Desert springs by Procter (1982), they have not been the focus of subsequent investigation, and their taxonomic composition remains unknown.

Studies of nematodes in the world's most hypersaline aquatic environments remain limited and have produced mixed evidence regarding their habitability. In some of the most extreme systems, nematodes appear to be absent. They have not been detected in the Dead Sea in the Middle East (Al-Daghistani et al. 2024) or in Don Juan Pond, Antarctica (Siegel et al. 1979). Similarly, Heidelberg et al. (2013) did not recover nematode DNA from benthic salt crusts in Lake Tyrrell, Australia, an ephemeral hypersaline lake. In contrast, nematodes have been found in hypersaline systems elsewhere. Nematode DNA was recovered from microbial mats in the Guerrero Negro salt lagoon in Mexico (Feazel et al. 2008), although it is not known if the nematodes were alive. More recently, Jung et al. (2024) extracted living nematodes from microbialites collected from the most hypersaline region of the Great Salt Lake, Utah, USA. All these bodies of water have estimated salinities above 100 mS cm^{-1}. Together, these findings suggest that nematodes can persist, and in some cases remain viable, under extreme saline conditions, but substantial uncertainty remains regarding their abundance, diversity, and community structure across hypersaline environments. More broadly, salinity is well established as a strong environmental filter shaping nematode communities in marine, estuarine, and terrestrial systems (Ocaña and Morales 1992; Poage et al. 2008; Milovankina and Fadeeva 2019; Jung et al. 2024).

We examined nematode communities in sediment and microbial mat samples from seven hypersaline desert springs located in the gravel plains of the central Namib Desert. Our objective was to use the variation in salinity within and among these springs to characterize the abundance and diversity of nematodes in relation to measured spring properties including electrical conductivity (EC, a measure of salinity). We hypothesized that EC is the primary environmental factor structuring nematode abundance and diversity in desert spring habitats. We predicted that mats and sediments associated with the most saline waters would host low abundance and low diversity nematode communities.

2 | Materials and Methods

2.1 | Sampling Sites

Namib Desert springs (Table 1, Figure 1) were sampled between 15 May and 12 June 2023. Spring sites were selected based on Eckardt et al. (2001) and local knowledge of spring locations. The seven springs sampled were located inside Namib Naukluft and Dorob national parks. All were rheocrene, low-flow, cool, hypersaline springs with broadly similar chemistry (Eckardt et al. 2001). Spring length, width, and depth varied, but all were short and shallow (Table 1). The springs also varied in terms of vegetation influence, with some streams hosting plants immediately adjacent to the spring waters (including *Phragmites australis* reeds, *Odyssea paucinervis* grass, and *Tamarix usneoides* shrubs at Swakop, Gungochoab, and WelwitWash only). WelwitWash and WelwitPlain are in areas that host the endemic *Welwitschia mirabilis*, although these plants were not observed near the springs. The landscapes around the other springs were completely barren (Figure 1B). Some springs contained areas of pooled water (Ubib, WelwitWash). All sites had visible salt crusts surrounding the surface waters (Figure 1B). WelwitWash contained surface water in 2023 but was dry in 2024 during a multiyear drought, indicating that the spring is semi-permanent.

2.2 | How Does Water Chemistry Vary Among Springs?

At each of the seven springs, six positions were identified that were spaced evenly from the origin to termination of the surface waters. A surface water sample (1 L) was collected from each position and used to measure dissolved oxygen (DO, mg l^{-1}, Extech DO600, Extech, Nashua, NH). DO was subsequently salinity-corrected (Benson and Krause 1984), and this value was used to estimate oxygen saturation (%, Mortimer 1956). Water samples were frozen (−20°C) after collection and later thawed to room temperature for measurement of electrical conductivity and pH using a calibrated YSI Pro 1030 (YSI Inc., Yellow Springs, OH). Differences in water chemistry among the springs were tested using a one-way ANOVA with site as the sole fixed factor. Normality of variables was assessed using a Shapiro–Wilk test, and EC was log-transformed prior to ANOVA to meet model assumptions. Means were compared using Tukey's Honestly Significant Difference (HSD) multiple comparison procedure. The effect of position along the spring length (six evenly spaced positions) also was assessed using one-way ANOVA.

2.3 | Does Nematode Abundance Differ Among Springs and Between Sediments and Microbial Mats?

At each of the spring positions, a sediment (0–3 cm) and a microbial mat sample were collected using a large spoon, and

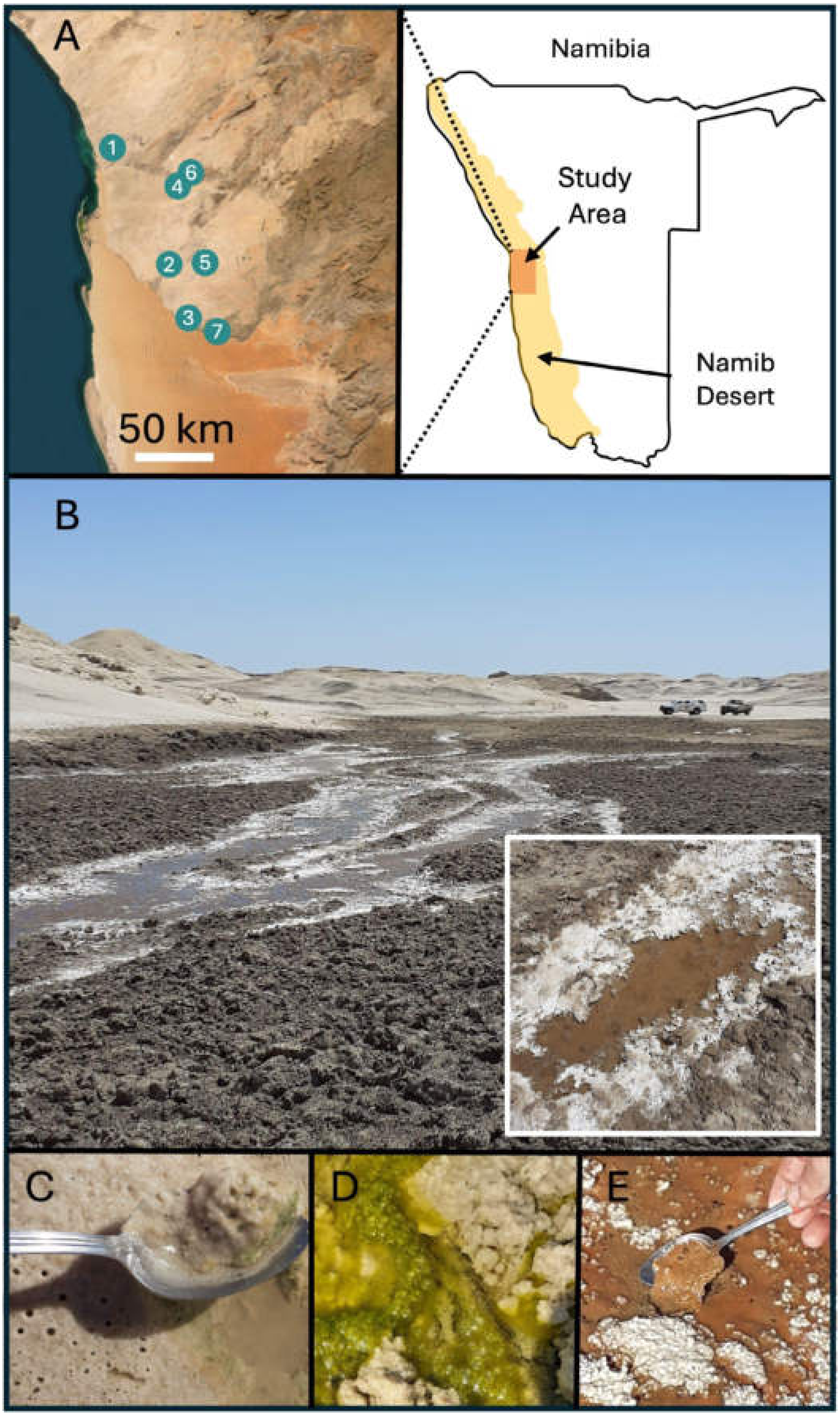


FIGURE 1 | (A) Location of field sites in the Namib Desert, Namibia (Site names corresponding to the numbers are in Table 1), (B) Hosabes spring (inset, salt encrusted water), (C) Microbial mat from Eisfeld spring, (D) Mat from Swakop spring, (E) Mat from Gungochoab spring.

TABLE 1 | Namib Desert spring physical and chemical properties.

Site[a]	GPS (decimal degrees)	Length (m)	Vegetation adjacent to spring	Depth (cm)[b]	Width (cm)[b]	EC (mS cm^{-1})[c]	pH[c]	DO (mg/L)
(1) Eisfeld	−22.48393, 14.57231	245	No	3.0	65.7	104.5 (56.4–173.3)a	7.60 (7.4–7.8) ab	9.21 (1.39–18.13)a
(2) Gungochoab	−23.1858776, 14.9364576	370	Yes	5.5	93	28.6 (16.1–41.1)b	7.50 (6.5–8.1) ab	8.35 (6.44–10.53)a
(3) Hosabes	−23.50707, 15.071623	58	No	1.9	96.7	97.4 (63.1–157.3)a	8.08 (7.5–8.6) ab	8.77 (5.79–14.86)a
(4) Swakop	−22.6940605, 15.0118085	686	Yes	3.3	71.3	67.2 (28.6- > 500) a	7.39 (6.8–7.8)b	7.70 (0–14.34)a
(5) Ubib	−23.167385, 15.190388	183	No	4.0	666.5	28.8 (12.3–58.9)b	8.33 (8.2–8.5)a	14.24 (10.94–18.79)a
(6) WelwitPlain	−22.6494594, 15.0632416	58	Nearby (> 10 m)	6.4	182.8	21.9 (13.5–52.1)b	8.26 (6.9–9.0) ab	14.44 (8.73–19.91)a
(7) WelwitWash	−23.586376, 15.252048	43	No	8.0	84.3	45.9 (22.6–72.4)ab	7.98 (6.8–8.4) ab	7.62 (2.79–12.59)a

[a] Numbers correspond to map locations (Figure 1).
[b] Values are the mean of six locations along the entire length of the spring.
[c] Values are the mean of six water samples with range in parentheses. Values within a column with the same letter are not significantly different (Tukey's HSD, $p > 0.05$).

each was transferred to a 50 mL conical tube. Mats varied in color, depth, and density within and between springs. In some locations, mats were gelatinous, often with discernable layers (Figure 1C–E). In other locations, the mats presented as a scrim of organic material above the sediment that was scraped off. Nematodes were extracted from sediment (60–120 g) and mat samples (20–60 g fresh weight material) over 72 h using a Baermann funnel technique, which relies upon nematodes moving out of the extraction material and therefore only extracts live specimens (Hodda and Abebe 2006). Sample volume was reduced to approximately 500 μL, and nematodes were fixed in 5% hot and cold formalin solutions (Hodda and Abebe 2006). Nematodes were counted using a Zeiss inverted microscope (Carl Zeiss Inc., White Plains, NY).

Differences in nematode abundance among springs and between sample types were tested using a two-way fixed-effects ANOVA with sample type (mat or sediment) nested within spring site. Normality was assessed using a Shapiro–Wilk test, and nematode abundance was log (x+1)-transformed prior to ANOVA to meet model assumptions. Means were compared using Tukey's Honestly Significant Difference (HSD) multiple comparison procedure. Correlations among water parameters and nematode variables were explored using Spearman's Correlation Coefficient.

2.4 | Does Nematode Diversity Differ Among Springs and Between Sediments and Microbial Mats?

During enumeration, nematodes were identified to the lowest taxonomic level possible via microscopy, using Andrássy (2005) and Zullini (2021) as references. Nematode taxa were assigned to trophic groups according to Hodda (2022) and Zullini (2021). After nematode extraction, the sediment or mat material used for extraction was oven-dried for 48 h (105°C). Nematode abundance was calculated based on 100 g dry weight of extracted mat or sediment. Nematode richness (number of taxa present) and the Simpson Index of diversity (Simpson 1949) were calculated. Samples containing no nematodes ($n = 4$) were removed from the dataset. Due to the nonnormal distribution of these variables, which was not correctable by transformation, the Kruskal–Wallis nonparametric test was used to compare sites and sample types, and if the model was significant, Dunn's test was used for pairwise comparisons.

2.5 | How Distinct Are Nematode Communities in Mats and Sediments and Among Sites?

To test whether nematode communities differed among sites and sample types, nematode community composition was analyzed using distance-based redundancy analysis (dbRDA) based on Bray-Curtis dissimilarities calculated from species abundance data. The dataset and R scripts used for this analysis are available at https://github.com/atreonis/NamibSpringNematodes. Environmental variables were z-standardized (centered and scaled to unit variance) prior to analysis. The model included site, sample type, and environmental variables (depth, width, EC, pH, and DO) and was fitted using the *capscale* function in the *vegan* package (Oksanen et al. 2024). Significance of the overall model, individual predictors, and canonical axes was assessed using permutation tests (999 permutations) implemented with *anova.cca*. Model simplification based on these tests retained only site and sample type in the final model, while depth, width, EC, pH, and DO were excluded.

All statistical analyses were performed with R version 4.5 (https://www.r-project.org) (R Core Team 2025).

3 | Results

3.1 | How Does Water Chemistry Vary Among Springs?

Electrical conductivity (EC) averaged 56 mS cm^{-1} across 42 spring water samples. EC exceeded 500 mS cm^{-1} in one sample—the terminus sample at the Swakop River site, which was the longest spring sampled (Table 1). The limit of the instrument was 500 mS cm^{-1} (YSI Inc., Yellow Springs, OH). EC varied among springs (Table 1, ANOVA, site effect $F_{6,35} = 9.131$, $p < 0.00001$). Water samples from Swakop, Eisfeld, and Hosabes springs were significantly more saline than those from Gungochoab, WelwitPlain, and Ubib (Table 1). EC did not vary significantly with position along the length of the springs (ANOVA, position effect, $F_{5,36} = 0.204$, $p = 0.959$).

pH ranged from 6.5–9 and varied among sites, with Ubib water significantly more basic than Swakop (Table 1, ANOVA, site effect $F_{6,35} = 3.584$, $p = 0.00712$). Dissolved oxygen (DO) levels ranged from 0 to 18.8 mg l^{-1}, but Tukey's HSD did not identify differences among the sites (Table 1, one-way ANOVA, site effect $F_{6,35} = 2.973$, $p = 0.0188$). At the time of sampling (mid-day), estimates of oxygen saturation based on DO measurements exceeded 100% at 28 of 42 sampling locations, indicating that robust photosynthetic activity was occurring. Because of the effect of high salinity on oxygen solubility, DO was negatively correlated to EC (Spearman's correlation, $p = 0.0023$). The sample from the Swakop site that had an EC value > 500 mS cm^{-1} measured 0 mg l^{-1} DO. Position in the spring did not influence pH or DO (ANOVA, position effect, $F_{5,36} = 0.204$, $p = 0.375$ and $p = 0.438$, respectively).

3.2 | Does Nematode Abundance Differ Among Springs and Between Sediments and Microbial Mats?

Nematode abundance varied widely in samples, from 0 to 158,014 nematodes 100 g^{-1} dry weight of sediment or mat. Nematodes were found in all but four samples (one each from Hosabes, WelwitPlain, Swakop, and Eisfeld) of the 84 microbial mat and sediment samples collected. Other invertebrates were observed (e.g., insect larvae, mites, copepods, and ostracods) but not enumerated because the extraction method is not appropriate for those groups.

A two-way ANOVA was conducted to examine the effects of site and the nested factor of sample type within site on log-transformed nematode abundance. The site effect was not significant (Figure 2A, $F_{6,70} = 2.017$, $p = 0.0747$), while the nested factor, sample type, had a significant effect on nematode abundance ($F_{7,70} = 4.678$, $p = 0.000241$). Mats contained significantly more nematodes than sediments across the sites (Figure 2A). Nematode abundance was not correlated to EC (Figure 2C), pH, or DO (Spearman's correlation, $p > 0.05$ for each).

3.3 | Does Nematode Diversity Differ Among Springs and Between Sediments and Microbial Mats?

Nine taxa of nematodes were found across the spring samples. Five were common (Figure 3). *Rhabdolaimus* and *Monhystrella* are bacterial-feeders. *Ethmolaimus* and *Paracyatholaimus* feed on bacteria or unicellular eukaryotes (e.g., algae, protists). *Oncholaimus* is a predator that feeds on small animals and/or unicellular eukaryotes. *Monhystrella* was the only taxon found at all sites (Figure 4). Four additional nematode taxa were extremely rare (*Alaimus*, Plectidae, *Prismatolaimus*, and dorylaims) with only 1–7 individuals seen in any sample.

Nematode communities exhibited low diversity overall, with no more than five taxa detected per sample. Richness varied significantly among sites (Figure 2B; Kruskal–Wallis, $df = 6$, $p = 2.72 \times 10^{-6}$) but did not differ between mats and sediments ($df = 1$, $p = 0.378$). Samples from the WelwitWash site contained significantly fewer taxa than most other sites (Dunn's Test, Figure 2B), and *Monhystrella* was the only nematode found there (Figure 4). In contrast, the highest richness was observed at WelwitPlain, Gungochoab, and Swakop, all sites with vegetation near or adjacent to spring water. Patterns in the Simpson's Index mirrored richness, with WelwitPlain having the most diverse communities and WelwitWash the least. Nematode richness was negatively correlated with EC (Figure 2D, Spearman's, $p = 0.0158$), but not with DO ($p = 0.0612$) or pH ($p = 0.1486$), while the Simpson's Index was not correlated with any of those variables ($p > 0.05$ for each).

3.4 | How Distinct Are Nematode Communities in Mats and Sediments and Among Sites?

Nematode community composition differed significantly among sites and sample types, as revealed by a distance-based redundancy analysis (dbRDA) on Bray-Curtis dissimilarities. The best-fit model including site and sample type explained 14.8% of variation in nematode communities (constrained inertia = 6.75, total inertia = 45.65; $F_{7,72} = 1.78$, $p = 0.001$). Permutation tests of individual predictors indicated that both site ($F_{6,72} = 1.74$, $p = 0.001$) and sample type ($F_{1,72} = 2.19$, $p = 0.008$) contributed significantly. Forward tests of the canonical axes revealed that the first two axes (CAP1: $F = 4.77$, $p = 0.001$; CAP2: $F = 3.53$, $p = 0.023$) were significant, together capturing 66% of the constrained variation, whereas the remaining axes were not significant. Overall, site identity accounted for the majority of the constrained variation, with sample type contributing additional independent structure. Taxa associated with sediments included *Prismatolaimus* and Plectidae, while *Monhystrella*, *Ethmolaimus*, *Paracyatholaimus*, and *Oncholaimus* were associated with mats (Figure 5).

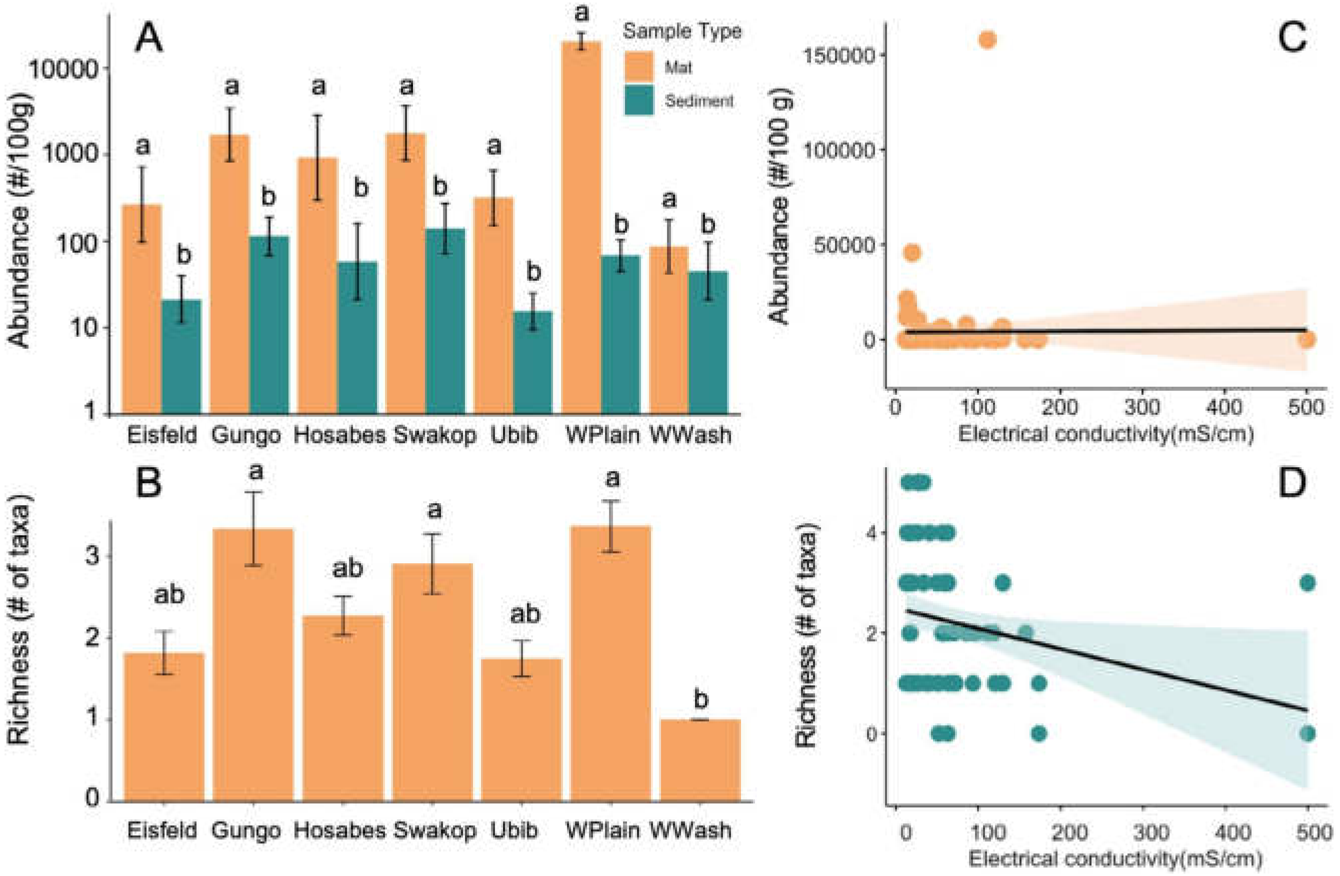


FIGURE 2 | Nematode abundance (A) and taxonomic richness (B) in mat and sediment samples from seven Namib Desert Springs. Values are the mean ± the standard error of the mean ($n = 6$ samples per bar). Bars with the same letter are not significantly different (Tukey's HSD). (C) Correlation between salinity (EC, electrical conductivity) and nematode abundance (C) and nematode richness (D) in spring mat and sediment samples ($n = 84$). The shaded area represents the 95% confidence interval.

Nonsignificant environmental predictors from the initial dbRDA (depth, width, EC, pH, and DO) were excluded during model simplification, indicating that nematode community variation was primarily structured by site and sample type rather than the measured continuous environmental variables. Although electrical conductivity (EC) was initially predicted to be important, it was not retained in the final model, likely due to sample size limitations or collinearity with site. However, even when site and sample type were excluded and only environmental variables were included, EC remained nonsignificant.

3.5 | How Abundant Were Nematodes in Mats and Sediments From the Most Hypersaline Locations?

We measured EC values exceeding 100 mS cm^{-1} in seven water samples (Table 2). Nematodes were found in the sediment samples associated with Swakop water with EC > 500 mS cm^{-1}, but their abundance was low (24.7100 g^{-1} dry weight). Mat samples from that same location did not contain any nematodes (Table 2). The second most saline water sample came from Eisfeld at 173.3 mS cm^{-1}, and mats from there contained a small number of nematodes (15.3100 g^{-1} dry weight), but none were in the sediments (Table 2). A mat sample from a location within Hosabes spring (112 mS cm^{-1}) had the highest nematode density found in any sample across the entire study (1.6×10^5 100 g^{-1} dry weight, Table 2). The taxa found in mats and sediments from these locations consisted of *Monhystrella*, *Alaimus*, and *Rhabdolaimus* only.

4 | Discussion

Hypersaline desert springs of the central Namib Desert support resilient and sometimes dense nematode communities despite extreme osmotic conditions. Contrary to our initial hypothesis, hypersalinity did not limit nematode presence or abundance across the seven springs studied, with the highest density of nematodes found in a mat sample in water at 112 mS cm^{-1}. Instead, salinity constrained taxonomic diversity, with generally only one to two taxa found in samples where EC exceeded 100 mS cm^{-1}. In other samples, community structure was driven primarily by site-specific factors and substrate type. These findings shift the focus from salinity as a dominant abiotic filter to the role of microbial mats as biologically structured habitats that create complex and buffered microenvironments capable of sustaining metazoan life under extreme conditions.

Nematode abundance was remarkably decoupled from electrical conductivity (EC) in these springs, even across a nearly

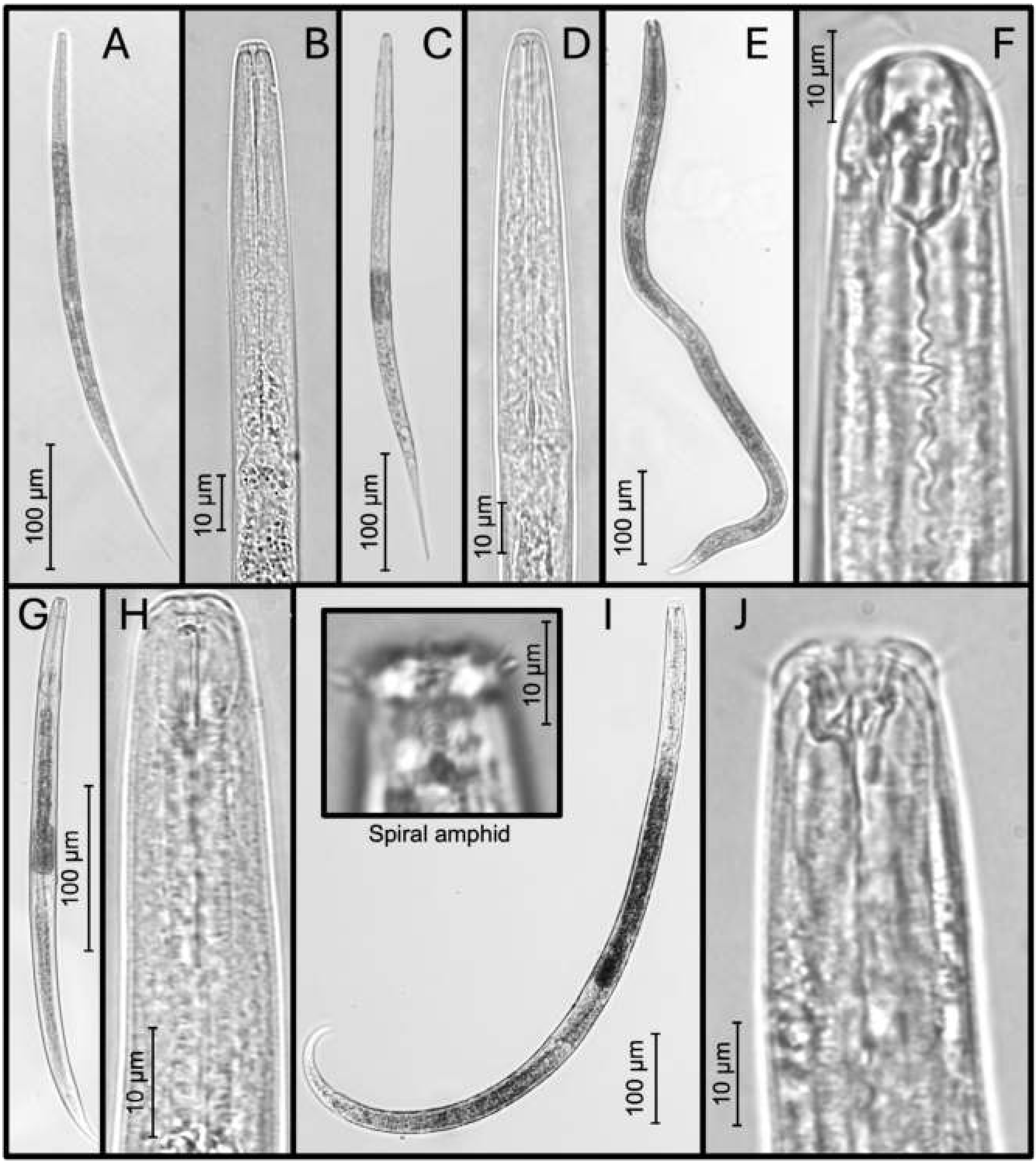
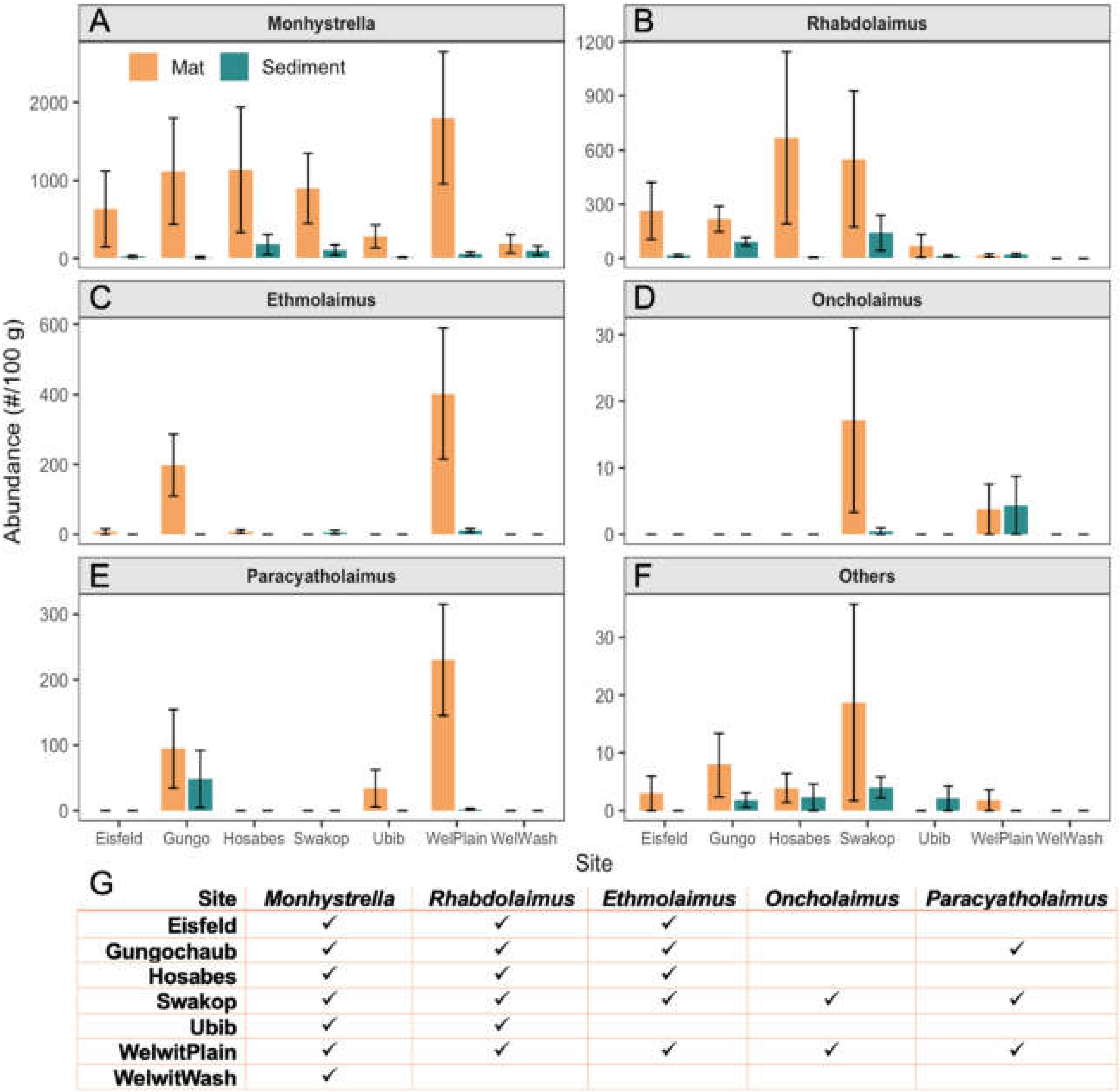


FIGURE 3 | Light micrographs of nematode taxa found in Namib Desert Springs: (A) *Monhystrella*, full body, (B) *Monhystrella*, head region, (C) *Rhabdolaimus*, full body, (D) *Rhabdolaimus*, head region, (E) *Oncholaimus*, full body, (F) *Oncholaimus*, head region, (G) *Ethmolaimus*, full body, (H) *Ethmolaimus*, head region. (I) *Paracyatholaimus*, full body with inset showing spiral amphid on the head, (J) *Paracyatholaimus*, head region.

twenty-fold range in salinity. In contrast, nematode richness declined with increasing salinity, consistent with a filtering effect in which hypersaline conditions exclude less tolerant taxa while permitting high densities of a few specialists. However, this reduction in richness did not translate into substantial shifts in overall community composition: EC was not correlated with the Simpson Index and did not contribute significantly to the dbRDA model, reflecting how assemblages were dominated by the same halotolerant taxa across the salinity gradient. Rare taxa were more likely to be excluded as salinity increased. Overall, community composition was primarily structured by site and substrate type, with microbial mats supporting higher abundances and distinct assemblages relative to underlying sediments. These findings underscore the ecological importance



Site	*Monhystrella*	*Rhabdolaimus*	*Ethmolaimus*	*Oncholaimus*	*Paracyatholaimus*
Eisfeld	✓	✓	✓		
Gungochaub	✓	✓	✓		✓
Hosabes	✓	✓	✓		
Swakop	✓	✓	✓	✓	✓
Ubib	✓	✓			
WelwitPlain	✓	✓	✓	✓	✓
WelwitWash	✓				

FIGURE 4 | Abundance of nematode taxa found in Namib Desert springs. (A) *Monhystrella*, (B) *Rhabdolaimus*, (C) *Ethmolaimus*, (D) *Oncholaimus*, (E) *Paracyatholaimus*, (F) Others (Values are the mean ± the standard error of the mean, $n = 6$ samples per bar). (G) Summary of the distribution of nematodes across the sites (✓ = present at site).

of microbial mats as foundational habitats in extreme aquatic environments.

To date, studies of microbial life in Namib Desert springs have been focused on only one or two springs (Cloete 2015; Johnson et al. 2017; Adriaenssens et al. 2016; Olonade et al. 2021; Martínez-Alvarez et al. 2023), and little is known about how microbial communities might vary across the seven springs included in this study. However, these mats concentrate organic matter, microbial biomass, and primary production, creating resource-rich microhabitats that may outweigh the selective pressure imposed by hypersalinity. Additionally, mats and sediments may contain fine-scale chemical heterogeneity, including gradients in salinity and water activity that are not captured by measurements of overlying spring water. Such microenvironmental buffering likely permits localized biological activity even when bulk conditions approach the limits of habitability.

The dominance of microbial mats in structuring nematode communities suggests strong bottom-up control in these systems. Similar relationships between microbial community composition and nematode assemblages have been documented in estuarine and microbial mat environments (Wu et al. 2019; Allen et al. 2009). In Namib Desert springs, visual heterogeneity among mats was pronounced, and unmeasured variation in microbial productivity, taxonomic composition, or extracellular matrix structure may select for different nematode taxa and

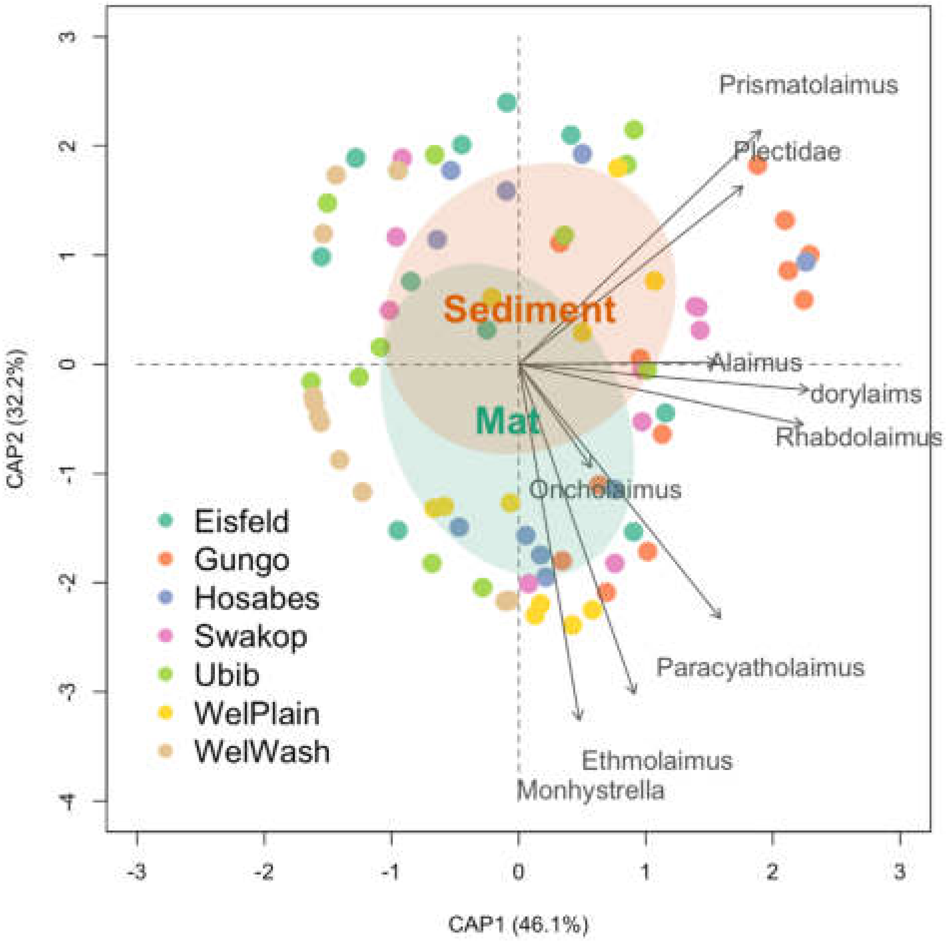


FIGURE 5 | Distance-based redundancy analysis (dbRDA) of nematode community composition across seven springs and two sample types (Sediment and Mat). Points represent individual samples and are colored by site. Transparent ellipses indicate one standard deviation around group centroids for each substrate type. Nematode taxa are represented as vectors (arrows), showing their weighted average positions in the constrained ordination space. The first two canonical axes (CAP1 and CAP2) explained 38.2% and 27.9% of the variation captured by the constrained model, respectively.

TABLE 2 | Nematode density in mats and sediments associated with the highest electrical conductivity values encountered in the Namib Desert springs studied.

Sample	Electrical conductivity (mS cm^{-1})	Mat nematode density (100 g^{-1} dry material)	Sediment nematode density (100 g^{-1} dry material)
Swakop terminus	> 500 mS/cm	0	24.7
Eisfeld terminus	173.3	15.3	0
Hosabes midspring A	157.3	80.9	117.6
Swakop midspring	129.7	6460.3	443.1
Eisfeld midspring	120.5	21.7	2.9
Hosabes terminus	118.6	1760.6	811.2
Hosabes midspring B	112	158014.5	145.7

contribute to the strong site effects observed. Springs are also spatially isolated ecosystems, and despite the potential for wind-mediated dispersal of nematodes (Nkem et al. 2006; Ptatscheck et al. 2018), colonization history and stochastic processes may further reinforce site-specific community structure.

Nematode assemblages in the Namib Desert springs were characterized by low diversity and dominance by a small number of cosmopolitan aquatic taxa. *Monhystrella* was ubiquitous and often numerically dominant, suggesting that members of the family Monhysteridae are exceptionally well adapted to hypersaline environments. Monhysterids are globally distributed in aquatic habitats and are frequently reported from saline and hypersaline systems (Fonseca and Decraemer 2008; Hodda and Traunspurger 2021; Jung et al. 2024). Jung et al. (2025) recently described a new species of Monhysteridae, *Diplolaimelloides woaabi*, from the microbialites of the Great Salt Lake. The prevalence of monhysterids in the Namib Desert springs suggests a combination of physiological tolerance, ecological opportunism, and the ability to exploit microbial-rich habitats with limited competition. Other taxa detected in the springs (*Rhabdolaimus*, *Ethmolaimus*, *Paracyatholaimus*, and *Oncholaimus*) also have documented associations with saline or brackish environments (Feazel et al. 2008; Tsalolikhin 2011; Zullini 2021; Cunha et al. 2022). *Rhabdolaimus* were found in microbial mats associated with stromatolites in hypersaline Shark Bay, Australia (Allen et al. 2009) and in Guerrero Negro, Mexico (Feazel et al. 2008). *Oncholaimus* is a predatory genus occupying the highest trophic level among taxa observed in this study. The restricted distribution of *Oncholaimus* to the vegetated Swakop and WelwitPlain sites suggests that trophic complexity in these springs may depend on localized productivity or detrital inputs.

Cryptobiosis, including osmobiosis induced by osmotic stress, could play a role in nematode persistence in hypersaline desert springs and represents an important topic for future investigation. Cryptobiosis is an extreme response, involving changes in gene expression and cellular biochemistry, the loss of cellular water, and the cessation of metabolism (Hibshman et al. 2020; Rebecchi et al. 2020). Although osmobiosis has received less attention than cryptobiotic responses to freezing or desiccation, physiological overlap among cryptobiotic strategies suggests that nematodes in these environments could rely on conserved molecular mechanisms for survival (Hibshman et al. 2020; Rebecchi et al. 2020). At the same time, dominant taxa must tolerate periods of metabolic activity under saline conditions, likely through osmoregulatory adaptations analogous to those described in the nematode *Caenorhabditis elegans* (Lamitina et al. 2004). Variation in these capacities among taxa may partly explain the measured decline in richness with increasing salinity. The semi-permanent spring at WelwitWash supported communities of *Monhystrella*, but whether these nematodes recolonize from other sites, persist in subsurface refugia, or survive desiccation in cryptobiosis remains uncertain. Overall, these Namib Desert spring nematodes are promising candidates for future experiments to assess their osmotolerance and cryptobiotic capacities, for example through controlled salinity and rehydration assays on *Monhystrella* and co-occurring taxa.

Our study contributes to the emerging body of work exploring nematode occurrence in hypersaline environments. In the Namib Desert springs, we recovered a small number of live nematodes from a sediment sample beneath water with EC exceeding 500 mS cm^{-1}. This may represent one of the highest salinity levels reported for nematode survival, but direct comparisons to other studies are difficult because many do not report EC in mS cm^{-1}. It is unlikely that nematodes can maintain metabolic activity at EC > 200–300 mS cm^{-1}, as even bacterial and archaeal activity is suppressed at such levels (Stevenson et al. 2015). The nematodes we observed were therefore likely reanimated from an inactive, cryptobiotic state, and given their low abundance, they may also have been allochthonous. We also recovered living nematodes in microbial mats at 173 mS cm^{-1}, while the densest communities in our study occurred at Hosabes spring at 112 mS cm^{-1}.

The coexistence of nematodes with dense microbial mats in hypersaline springs has broader implications for understanding ecosystem function under extreme conditions. Such environments may serve as modern analogs of ancient aquatic ecosystems in which microbial mats dominated and macrofaunal disturbance was limited (e.g., stromatolites). While meiofauna have been hypothesized to disrupt laminated microbial structures, our findings, which are consistent with studies from other hypersaline systems (Feazel et al. 2008; Allen et al. 2009), suggest that nematodes can coexist with, and do not inhibit, the development of dense microbial mats. These interactions may resemble those that occurred during early phases of metazoan evolution, when animals first colonized microbial-dominated ecosystems.

Taken together, our results demonstrate that hypersaline desert springs support resilient nematode communities structured more by biological habitat complexity than by bulk physicochemical extremes. Hypersalinity constrains diversity but does not preclude high abundance once tolerant taxa are established. By documenting living nematodes at salinities exceeding previously reported limits and revealing the central role of microbial mats in sustaining metazoan life, this study expands current understanding of the ecological and physiological boundaries of animal life in extreme environments.

Author Contributions

Amy M. Treonis: conceptualization (equal), data curation (lead), formal analysis (lead), funding acquisition (lead), investigation (equal), methodology (lead), resources (equal), writing – original draft (lead), writing – review and editing (lead). **Eugene Marais:** conceptualization (equal), investigation (equal), methodology (supporting), resources (equal), writing – review and editing (supporting). **Gillian Maggs-Kölling:** conceptualization (equal), resources (equal), writing – review and editing (supporting).

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The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data supporting the findings of this study are available from Mendeley Data: https://data.mendeley.com/datasets/nrnht35zfz/1.

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