Hierarchical Patterns of Soil Nematode Biodiversity in the Atacama Desert: Insights Across Biological Scales

Laura Villegas[a,1], Laura Pettrich[b], Esteban Acevedo-Trejos[c], Arunee Suwanngam[d], Nadim Wassey[e], Miguel L Allende[f], Alexandra Stoll[g], Oleksandr Holovachov[h], Ann-Marie Waldvogel[i,2], and Philipp H. Schiffer[j,2]

[a]**Department of Biology, University of Cologne, Zülpicher Str. 47b, 50674 Cologne, Germany.ORCID ID: 0000-0002-0906-8373. Corresponding author.**
[b]**Department of Biology, University of Cologne, Zülpicher Str. 47b, 50674 Cologne, Germany.ORCID ID: 0000-0003-4587-0563**
[c]**Helmhotlz Center Postdam, GFZ German Research Center for Geosciences, Wissenschaftpark "Albert Einstein", Telegrafenberg, 14473 Potsdam, Germany.ORCID ID: 0000-0003-4222-7062**
[d]**Faculty of Agriculture, Kasetsart University, 50 Lat Yao, Chatuchak, 10900 Bangkok, Thailand. ORCID ID: 0000-0002-3524-0915**
[e]**Department of Biology, University of Cologne, Zülpicher Str. 47b, 50674 Cologne, Germany.**
[f]**Center for Genome Regulation, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, 78ORCID ID: 00003 Santiago, Chile.ORCID ID: 0000-0002-2783-2152**
[g]**Centro de Estudios Avanzados en Zonas Aridas, Universidad La Serena, Raúl Bitrán 1305, 1720256 La Serena, Chile.ORCID ID: 0000-0001-6115-1628**
[h]**Department of Zoology, Swedish Museum of Natural History, Frescativägen 40, 114 18 Stockholm, Sweden.ORCID ID: 0000-0002-4285-0754**
[i]**Department of Biology, University of Cologne, Zülpicher Str. 47b, 50674 Cologne, Germany. ORCID ID: 0000-0003-2637-0766**
[j]**Department of Biology, University of Cologne, Zülpicher Str. 47b, 50674 Cologne, Germany. ORCID ID: 0000-0001-6776-0934**
[1]**Corresponding author**
[2]**Both authors contributed equally and are the senior authors**

ABSTRACT

Species diversity and distribution, in relation to how they interact with their environment is a major focus of ecological research. Particularly for soil ecosystems, information about geographical patterns of biota is scarce despite the pivotal role of soils as ecosystem service providers. The Atacama is the driest non-polar desert on earth: water is scarce, high salinity patches are frequent and water bodies have high concentrations of metals. It is believed that only specialized taxa can survive in this Desert. Accordingly, only some microbial life-forms and few plants, and vertebrates are present. Above ground invertebrates have been reported in the desert but its soils have not been comprehensively analyzed. By studying different areas in the Atacama, we aim to better understand resilience of soil organisms in times of global aridification. Nematodes are one of the most important groups of soil organisms in abundance and biodiversity. Here, we investigated diversity of soil nematodes at the genetic, taxonomic, community and life-cycle levels. We find distinct patterns and assemblages along the different habitats in the desert: dune systems, high altitude mountains, saline lakes, river valleys and fog oases. We also find that distribution of asexual taxa is more likely to occur at higher altitudes, and that the distribution of genera richness in the Atacama follows a latitudinal diversity gradient, as well as an increase with increasing precipitation. Our work shows that even under extreme environmental conditions stable, healthy soil communities can persist, but we see indicators of poor soil food webs.

Keywords: Biogeography | Nematodes | Environment | Latitude | Atacama

1 INTRODUCTION

Understanding which factors shape the diversity and distribution of species has been a major focus of ecological research. Studies examining the interaction of organisms with their immediate environment have focused on analyzing the influence of various factors, including ecological, geological, and geographical parameters in diverse systems (e.g aquatic and soil) (Nisa et al., 2021; Döge et al., 2015; Gaston, 2000; Alvial et al., 2012; Marshall et al., 2012). From cycling of nutrients, mineralization, and control of pest species (Zhang et al., 2017), to carbon sequestration and storage, soils and processes therein play a key role in food security, water supply and quality, as well as in shaping biodiversity (Lal et al., 2015). Globally, at least 58% of species inhabit soils (Anthony et al., 2023), including microorganisms and different size classes of fauna (Wall et al., 2012). Accordingly, soils have received extensive attention in research, in particular in arable areas. Generally however, geographical patterns of biota in soils in relation to environmental parameters remain poorly understood. This is mainly due to limited data available on the true diversity and distribution of many soil organisms (Bardgett and van der Putten, 2014; Anthony et al., 2023).

Even less data is available for soil systems in regions with extreme environmental conditions, such as deserts. Abiotic factors such as strong temperature fluctuations, minimal annual precipitation, and high evaporation rates contribute to the aridity of deserts as systems (Ward, 2016) and pose significant challenges for life to exist and persist. However, despite these harsh conditions, deserts and their soil systems also feature a variety of spatially distributed micro-habitats and niches, including limestone areas, dune systems, saline patches, among others, that can support diverse life forms (Ward, 2016). Given the current global trend of aridification (Ma et al., 2024; Chai et al., 2021; Burrell et al., 2020), the study of biodiversity in desert soils appears imperative to better understand and predict distribution of organisms in times of global change.

The Atacama Desert, the driest non-polar desert on Earth, receives less than 200 mm of rainfall annually. Despite the long term stability of the general geological system, regional environmental patterns can be seen (Hartley et al., 2005; Jordan et al., 2014). For example, the long-term aridity is reflected in the distribution of sulfates, chlorides, and nitrates in soils of the Atacama, which affect community composition across various taxa (Voigt et al., 2020; Zhang et al., 2019; Xi et al., 2016; Pereira et al., 2015). Diverse micro-habitats present throughout the Atacama Desert are, for example, areas with alkaline soils, dune systems, fog oases, soils with high salinity and arsenic content. These areas support different specialized taxa including microbial life forms, plants and a limited number of vertebrate animals (Knief et al., 2020b; Morales, 2013; de Bienes Nacionales, 2022; Maza et al., 2019; Arndt et al., 2020; Gómez-Silva and Batista-García, 2022; Eshel et al., 2021; Eduardo Palma et al., 2005; Marín et al., 2021; Knief et al., 2020a; Acosta et al., 2023; Hakobyan et al., 2023).

Invertebrate biodiversity remains understudied in the Atacama, with research primarily focused on above-ground fauna (Zúñiga-Reinoso and Predel, 2019; Pizarro-Araya et al., 2021; Nitsche et al., 2023), leaving soil invertebrates poorly sampled and their distribution patterns unclear (Marín et al., 2021; Anthony et al., 2023; Gadea, 1963; Edgington et al., 2010; Jimenez Roco, 1972). One important component of soil biota are nematodes, with estimates of their global diversity ranging from 5×10^5 to 1×10^8 species (Anthony et al., 2023). Their diverse assemblages and contributions to soil nutrient turnover, carbon sequestration, and regulation of bacterial populations, among other roles in soil ecosystems worldwide, make them important indicators of soil condition(Yeates, 2003; Satjarak et al., 2021; Edgington et al., 2010; Wood et al., 2019). This significance is further supported by their use as functional indicators, which is based on their life cycle characteristics, such as diverse feeding types and reproductive strategies (Yeates, 2003; Sieriebriennikov et al., 2014). Members of Nematoda have adapted to life in extreme conditions: they can survive low oxygen conditions in deep sea environments (Zeppilli et al., 2017), daily freezing cycles in Antarctica (Yeates, 1970; Maslen and Convey, 2006), and potentially kilometer deep mines (Borgonie et al., 2011). Particular families are prevalent and diverse in arid and desert areas, surviving low water regimes, including the Mojave (De Ley, 2014), the Chihuahuan (Whitford and Steinberger, 2021), Monte (Boström and Holovachov, 2013) and Namib deserts (Treonis et al., 2022). Additionally, many nematode genera have evolved parthenogenetic lineages (Schiffer et al., 2019), which are hypothesised to have a founder advantage in extreme environments ('geographical-parthenogenesis')(Hörandl, 2006). It could thus be assumed that in an extreme environment, such as the Atacama, parthenogenesis is more frequent than sexual (female + male) reproduction. Published records of nematodes from the Atacama Desert are usually based on very few or single individuals (Gadea,

1963). Consequently, it is uncertain whether patterns of soil invertebrate biodiversity correlate with the regional and local ecology, adaptive strategies such as feeding type or reproductive mode, or if broader global trends, such as environmental gradients in species richness (Gaston, 2000), apply in the extreme environment of the Atacama Desert.

In this study we analyzed which factors shape invertebrate biodiversity in soils of the Atacama Desert using nematodes as a model system. We sampled six localities spaced from north to south of the desert including sand dunes, saline lake-shore sediments, and high altitude mountain regions, in order to obtain a comprehensive understanding of biogeographic patterns in terms of genetic diversity, life-history (reproductive strategy and reproductive mode) and community composition. Despite extreme and persistent aridity being a primary limiting factor in the Atacama Desert, we found strong local patterning throughout different niches (e.g. sand dunes, saline lakes, fog oases, river valleys). Using both, a genera richness modeling approach and a reproductive mode probabilistic modeling approach, we found broader scale patterning in relation to ecological and geographical parameters. We found annual precipitation and broader temperature ranges (temperature heterogeneity) to be the major drivers of genera richness across the desert and that elevation to be the most important predictor of reproductive mode. We, firstly, show that even under extreme environmental conditions, niches in soil ecosystems can sustain stable and diverse invertebrate communities, but, secondly, find that some areas show signs of simple food webs.

2 RESULTS

In this study, we aimed to analyze different regions of the Atacama and thus established localities and sampling sites in major areas of the desert: (1) the Altiplano area (Tarapacá region) is more humid and known for supporting more vegetation than the hyperarid core of the Atacama (Bull et al., 2016), (2) the area around the Quebrada de Aroma (Tarapacá region) has moderately alkaline soils with increasing gypsum as altitude decreases and harbors several microorganism taxa such as Proteobacteria and Actinobacteria (Knief et al., 2020b), (3) the San Francisco area - further on referred to as Eagle Point (Antofagasta region) - is home to several bacterial species with predominant firmicutes taxa (Maza et al., 2019), (4) the Salar de Huasco (Tarapacá region) experiences high UV radiation, salinity and arsenic concentrations supporting several microbial taxa (Castro-Severyn et al., 2021; Arndt et al., 2020) as well as three flamingo species, a nearly threatened puma species and several other vertebrates (de Bienes Nacionales, 2022), (5) the Paposo area (Antofagasta region) receives water in the form of fog (called camanchaca), it harbors plant species-rich fog oases (known as loma formations) (Moat et al., 2021; Contreras et al., 2023) and is an area of high endemism (Jerez, 2000; Pizarro-Araya and Jerez, 2004; Arndt et al., 2020) and the (6) Totoral area (Atacama region) is composed of sand dunes where endemic plants of the Apocynaceae family (Morales, 2013), as well as reptiles and birds can be found. In order to analyze patterns of biodiversity in the hyper-arid Atacama Desert using nematodes as a model for soil organisms, we sampled, identified, sequenced and studied diversity at different levels. We analyzed diversity at the haplotype, genera, family, and community level including life-history characteristics such as feeding types and reproductive modes. We used linear models as well as a random forest approach to assess the factors that contribute the most to the genera richness and reproductive mode patterns across the desert.

2.1 A rich diversity of roundworms persists in the Atacama

We collected 393 nematode morphotypes from 112 samples collected along six localities throughout the Atacama Desert (Fig 1 B, supplementary Fig S1). Collected nematodes were then sequenced (”Methods”) with a percentage of high quality base pairs above at least 20 (HQ 20 %), 386 sequences from different morphotypes were kept for further analysis. More specifically, we analyzed a total of 39 nematodes from the Altiplano locality, 37 from the Aroma locality, 163 from the Eagle Point locality, 44 from the Paposo locality, 26 from the Salars locality (Salars) and 77 for Totoral dunes locality. Our sampling also included sites where no nematodes could be found (Fig 1 B). These sites are used as reference for environmental conditions under which nematodes do not seem to persist. We classified the nematodes into 21 families and 36 genera, illustrating a rich diversity of roundworms flourishing in the Atacama. Seven families were found in the Altiplano as well as the Aroma locality, nine families were found in Eagle Point, 12 in the Salars, eight in Totoral Dunes and ten in Paposo (Fig 3 B). We observed that some generalist families were ubiquitously found, whereas others were geographically restricted. Cephalobidae were present in all localities, whereas representatives of families Panagrolaimidae and Qudsianematidae were

found in five of the localities (all except for the Salars). The family Anguinidae was uniquely found in the Eagle Point locality. The families Trichistomatidae and Mermithidae were unique to the Salars locality. Tylencholaimidae was uniquely found in the Paposo locality and Acuariidae in Altiplano.

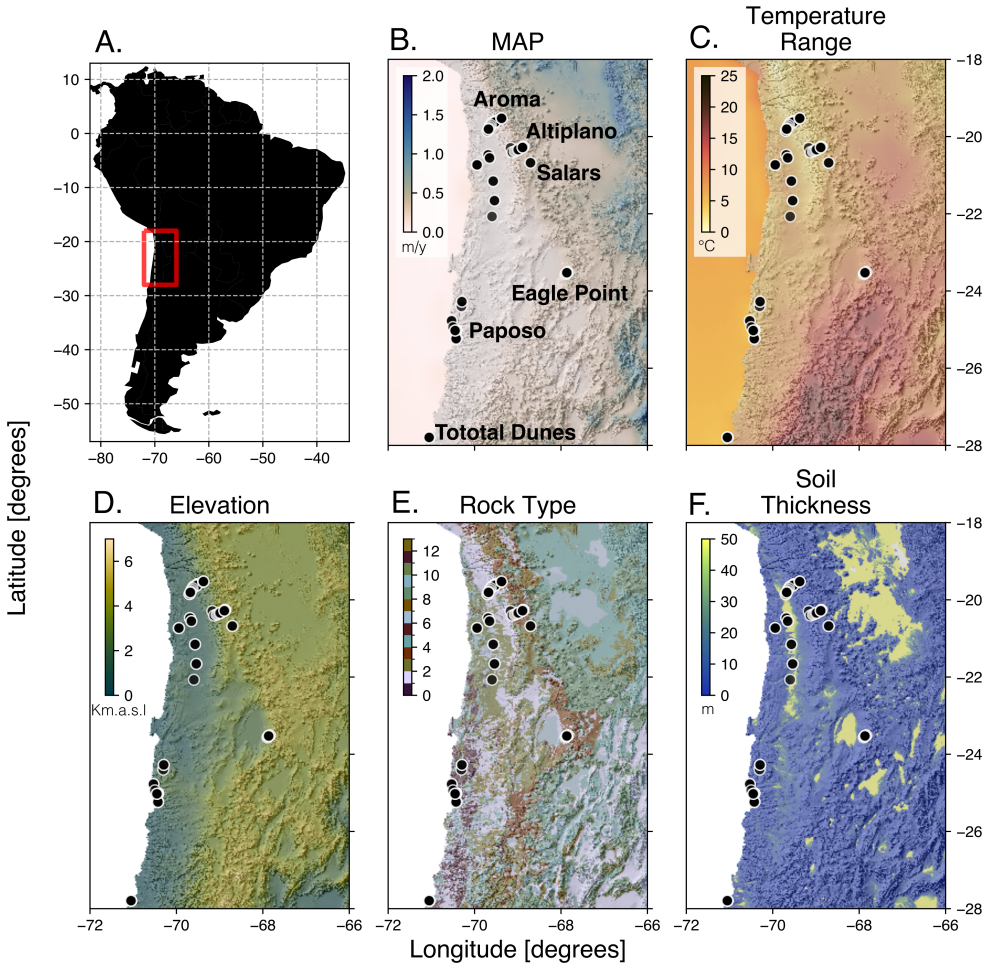

Figure 1. Environmental variables analyzed in the Atacama Desert to predict genera richness across the desert. Rock type is defined as lithological classes from (Hartmann and Moosdorf, 2012) (see supplementary table S18).

2.2 Genetic diversity and haplotype uniqueness differs between nematode taxa

Given the diversity of retrieved nematode genera and the disparity between ubiquitous and regionally restricted taxa, we wanted to analyze patterns of biogeography on the genetic level. We assessed haplotype clustering and genetic diversity (π, θ) for seven taxonomic groups using 18S rRNA (table 1). We studied genetic diversity in two manners: per taxonomic group including all habitats, and per habitat analyzing one taxonomic group at a time.

There were between 17 to 166 segregating sites for the different soil nematodes in our networks (supplementary table S8) and we identified differences in haplotype structure and clustering at the genera and family levels (supplementary figures S3 - S7). For the genera *Acrobeloides*, *Acrobeles* and *Panagrolaimus* we found 24, 22 and 20 different haplotypes respectively (table 1). For the families included in the order Dorylamida and the superfamily Aphelenchoidea, 16 haplotypes were identified

Table 1. Summary of the different taxonomic groups used to create haplotype networks. The number of haplotypes, total π and total θ are specified, sorted from low to high π. Genetic diversity is estimated per site.

Taxonomic group	Haplotypes	Total π	Total θ
Plectidae	10	0.00633	0.00993
Alaimidae	2	0.01145	0.01504
Acrobeloides	24	0.01278	0.02192
Dorylamida	16	0.01611	0.01456
Acrobeles	22	0.02877	0.02654
Panagrolaimus	20	0.05788	0.04221
Aphelenchoidea	16	0.11199	0.08095

respectively. The family Plectidae was composed of ten different haplotypes. For Alaimidae, only one haplotype was found and is shared in three habitats (table 1). Overall, we were not able to find any distinct geographical clustering of haplotypes based on the networks, i.e. individual haplotypes were present in geographically distant localities. We found genetic diversity at the genera level to be the highest for *Panagrolaimus* (π = 0.05788 , θ = 0.04221 , Fig 2A) and the lowest for *Acrobeloides* (π = 0.01278, θ = 0.02192). At the family level, the highest genetic diversity was found for Aphelenchoidea (π= 0.11199, θ = 0.08095, Fig 2B), and the lowest was found for Plectidae (π = 0.00633, θ = 0.00993).

To better understand the possible effect of geography on genetic distance, we calculated the genetic distance as Euclidean distance and compared it to the geographic distance of the different localities. Using Mantel statistics based on Spearman's rank correlation (ρ). For *Panagrolaimus* a significant ($p < 0.05$) isolation-by-distance pattern could be found (r = 0.6, p = 0.041667, 119 permutations), no pattern was found for other taxa analysed. With this approach, it appears that geographically distant haplotypes of *Panagrolaimus* are also genetically more distant in their 18S rRNA region. Specifically for this genus, we see the highest diversity in the Eagle Point (π=0.06548) and the lowest in Totoral Dunes where only one haplotype was found for several individuals (supplementary table S9). These results showcase the high variability of genetic diversity within soil nematode taxa in the Atacama Desert and in relation to their habitat.

2.3 The nematode community composition varies between habitats

We assessed soil nematode community composition variation in the six localities employing the Jaccard similarity index at the family level. We found the Aroma and Eagle Point localities to share the highest proportion of families (J=0.78) followed by Altiplano and Aroma (J=0.75). Conversely, we observed the least amount of shared families between Eagle Point and the Totoral Dunes (J=0.21) and the Salars locality when compared to Totoral Dunes (J=0.25)(Fig 3-A). As expected under the isolation-by-distance model, community composition appears to become more dissimilar with increased geographical distance, between the different localities (Mantel statistic based on Spearman's rank correlation ρ, r 0.5153 , p = 0.048611 , 719 permutations). We were interested to know if a co-occurence analysis of families would identify a specific geographical pattern, but using 82 family pairs (108 pairs were removed due to unique presence in specific localities) could not retrieve a signal.

2.4 Soils in the Atacama are dominated by different categories of nematodes

We wanted to use nematodes as indicators of soil condition throughout different habitats in the desert by assessing their different functional groups. We categorized nematodes into different feeding types, as well as into the colonizer-persister series based on common life-history characteristics reported in literature and assigned using the NINJA application (Sieriebriennikov et al., 2014). Nematodes that are r-strategists (c-p1 colonizer) are considered indicators of resource availability and unstable environments, whereas those that are k-strategists (c-p5 persister) are consider indicators of food web complexity and more stable habitats (Bongers and Ferris, 1999). We found that the different habitats show a different structure regarding nematode functional groups. Despite the presence of nematodes belonging to all colonizer-persister categories (c-p) across the desert, r-strategists (categories c-p1 and c-p2) are predominant in the Altiplano locality (57.2 % of families found in the locality) as well as in the Aroma and Totoral Dunes localities. Whereas k-strategists (categories c-p4 and c-p5) were the predominant type of families in the Paposo and

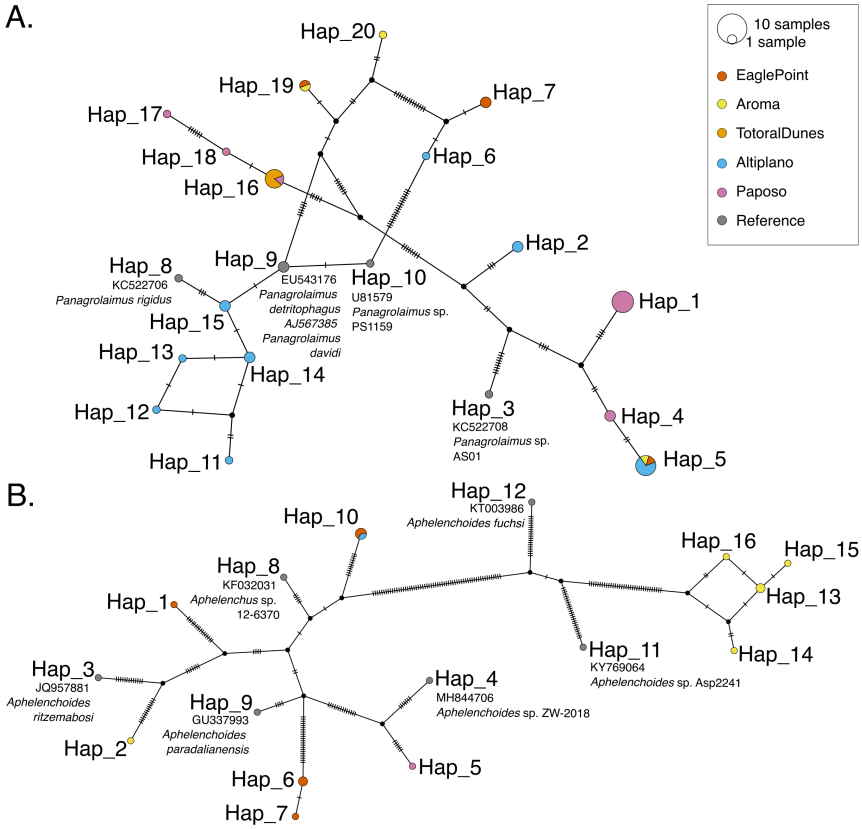

Figure 2. A. Haplotype network of *Panagrolaimus* based on 18S rRNA sequences. B. Haplotype network of Aphelenchoidea based on 18S rRNA sequences. Color refers to sampling locations. Reference sequences were retrieved from the curated 18S-NemaBase (Gattoni et al., 2023). Accession number and species name is written next to the respective node of haploytpe (abbreviated to "Hap"). Vertical hatchmarks indicate the number of differences from one node to the next.

Salars localities (supplementary table S11). By assessing the different feeding types of the nematodes analysed, we found that most families in the different habitats are bacterivores and omnivores (41.2% and 20.1% respectively). The remaining nematode families were categorized as predators, fungivores and herbivores (18.7%, 14.4% and 5.6% respectively)(Fig 3-B). Families with unicellular eukaryotic feeding type (UEF) were not found in this study (supplementary table S12). A structuring of the different soil habitats regarding feeding types is apparent, as the Salars only harbor bacterivore, predatory and omnivore families whereas other areas as Totoral Dunes have a more diverse feeding type assemblage with herbivores, fungivores, bacterivores, predators and omnivores present (Fig 3-B).

2.5 Climate and latitude determine soil biodiversity in the Atacama

To understand driving forces and constraints of nematode taxonomic biodiversity across the Atacama desert more globally, we used a modeling approach incorporating environmental data. We first aimed to predict genera richness and found that the best predictive model using a probabilistic approach incorporated soil thickness and range of temperature. The model showed the highest Akaike weight (0.4709556) and a statistically significant slope for both environmental variables (table 2) which indicates that nematode genera richness in the Atacama Desert could be related to reduced soil thickness and more climate heterogeneity, here represented as the range of temperature. To account for variation across localities in our predictions, we further assessed genera richness using linear mixed effect models specifying the sampling locality as a random effect. Our analysis confirmed that sampling localities had a significant influence on the modeling process, suggesting that spatial variation plays a crucial role in shaping the observed patterns, potentially due to underlying environmental heterogeneity between the different locations. Incorporating locality effects into the models was therefore essential to capture

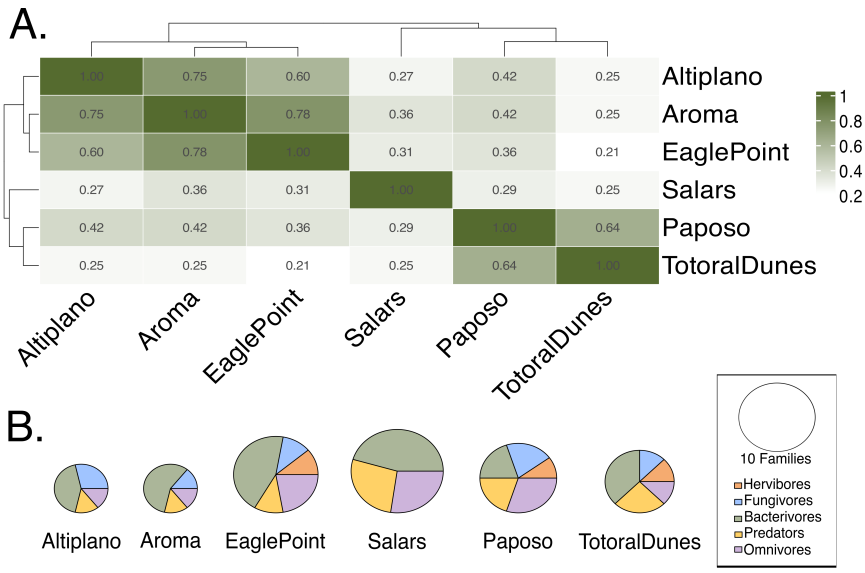

Figure 3. A. Jaccard similarity index of families found in six localities. B. Number of families found per locality represented by the size of the circles, the proportion of families found with the different feeding types is represented in the pie chart by the different colors.

the ecological drivers of genera richness given our dataset. With this approach, we then found that the best predictive model incorporated mean annual precipitation and range of temperature, representing the seasonal thermal amplitude an organism experiences within a given area (temperature heterogeneity). The preferred model showed the highest Akaike weight (0.5263228) and a statistically significant slope for the intercept and both climatic variables (equation 1)(table 2 - B).

To further validate the results of the tested linear models, we implemented a random forest approach. With this approach we found that the most important variables for genera richness prediction in our analysis were elevation, mean annual precipitation, latitude and range of temperature (Supplementary Table S16). This corroborates that mean annual precipitation and range of temperature, in congruence with the linear models, have a strong consistent influence on genera richness prediction. With the three approaches we found that less genera are predicted to occur in the hyper-arid core of the desert (e.g zero for the region of Pampa del Tamarugal), and more genera are predicted to occur, for instance, in the Altiplano region (Fig 4 A). Notably, temperature heterogeneity was a consistent predictor of genera richness across all modeling approaches tested. Additionally, mean annual precipitation was identified as a significant predictor in both linear mixed-effects models and random forest analyses, highlighting the role of climate for shaping genera richness.

$$\begin{aligned} genera\ richness = & -3.723925 + 0.015028 * precipitation \\ & + 0.688582 * temperature\ range \end{aligned} \tag{1}$$

2.6 Reproductive mode association to environmental variables

The theory of geographical parthenogenesis predicts an excess of asexual taxa in marginal habitats. Given our findings of taxonomically structured nematode communities in different regions of the Atacama Desert, we wanted to test for the specific life-history trait of parthenogenesis (asexual reproduction) using our modeling approach. We established single-worm cultures for a representative subset of our samples. Ten out of the eighteen cultures showed nematodes with parthenogenetic reproduction, i.e. no presence of males and successful propagation from a single unfertilized female. The remaining seven cultures showed sexual reproduction, i.e. presence of males (supplementary Fig S2-G) and no propagation from single females. Sexual strains showed a propagation rate of 0% from single unfertilized females cultures, whereas the asexual strains' propagation rate was 83.3% ($\pm$10.48%). We initially tested variables of

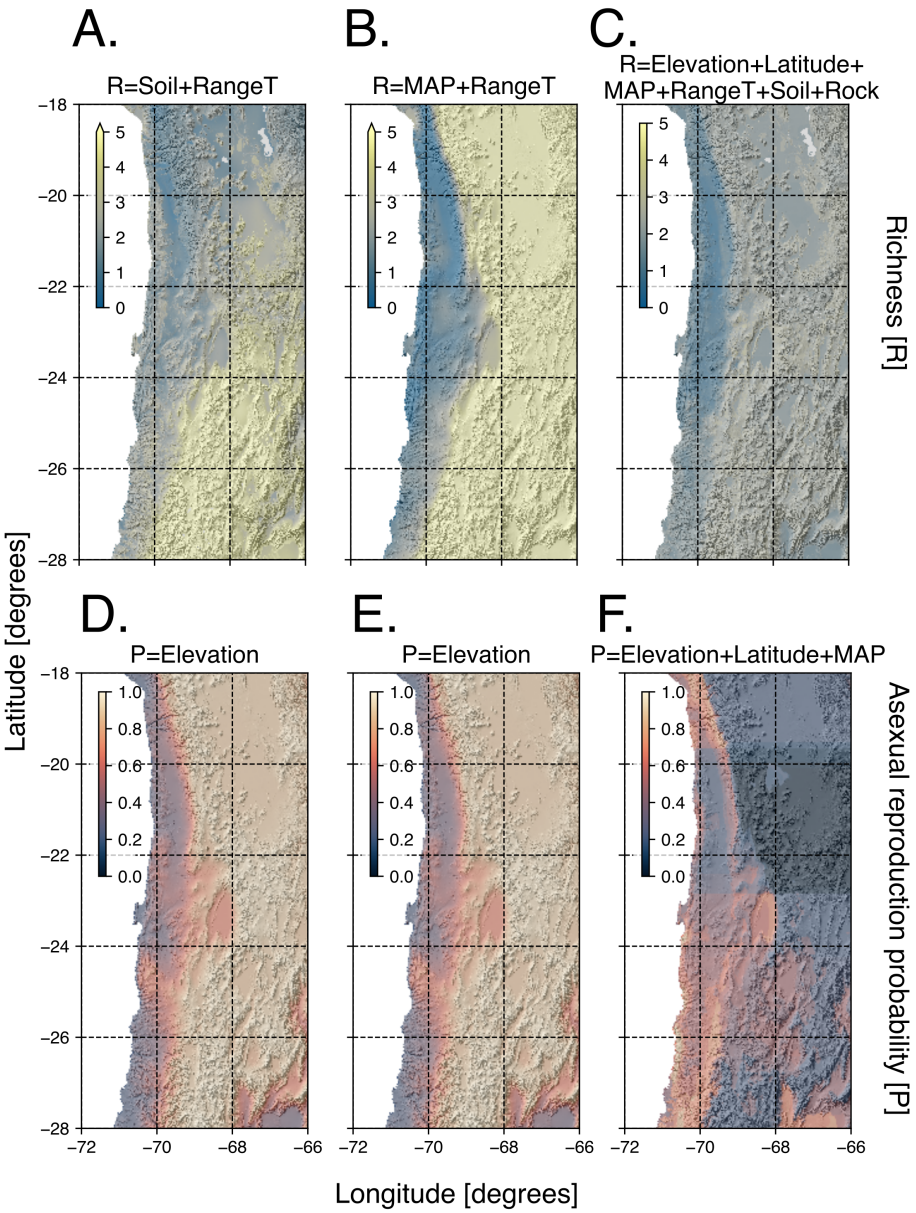

Figure 4. Model predictions for genera richness and probability of a nematode being asexually reproducing in the Atacama Desert. In the upper panel (A) shows genera richness (R) as predicted by soil thickness and range of temperature using a generalized linear model, (B) shows genera richness as predicted by mean annual precipitation implementing linear mixed-effects model, (C) displays predicted genera richness implementing a random forest approach. In the lower panel (D and E) display the probability of a nematode being asexually reproducing (P) as predicted by elevation using a generalized linear model and generalized mixed-effects model respectively, (F) shows the probability of being asexually reproducing implementing random forest.

A.

Least squares model genera richness				
Parameters	Value	SE	t-value	p-value
Intercept	-0,0411977	0,5056251	-0,081479	0,9352
Slope_soil_thick	-0,4978359	0,1252874	-3,973551	<0,005*
Slope_rangetemperature	0,4417225	0,1099234	4,018457	<0,005*

B.

Linear mixed effect model genera richness					
fixed effects	Parameters	Value	SE	t-value	p-value
	Intercept	-3,296081	1,3105763	-2,514986	0,0135*
	Slope_MAP	0,012731	0,0023134	5,503008	<0,005*
	Slope_rangetemperature	0,652375	0,2329109	2,800965	0,0062*
random effects	Parameters	Stdev			
∼1 — Locality	Intercept	0,0086093			
	Residual	1,079537			

C.

Generalized linear model reproductive mode				
Parameters	Value	SE	t-value	p-value
Intercept	-1,2907594	0,8565084	-1,507	0,1218
Slope_elevation	0,0008667	0,0004077	2,126	0,0335*

D.

Generalized linear mixed effect model reproductive mode					
fixed effects	Parameters	Value	SE	z-value	p-value
	Intercept	-1,2907594	0,8585562	-1,503	0,1327
	Slope_elevation	0,0008667	0,0004082	2,123	0,0337*
random effects	Parameters	Stdev			
∼1 — Locality	Intercept	<0,001			
	Residual	<0,001			

Table 2. Summary statistics of the selected models based on Akaike weights for predicting genera richness (A and B) and the likelihood of asexual reproductive mode (C and D). Models B and D incorporate locality as a random effect to account for potential bias arising from variations in sampling locations.

elevation and latitude as predictors of reproductive mode along with mean annual precipitation and range of temperature, the former two to test for common variables associated with geographical parthenogenesis, the later two given their effect on genera richness prediction from our linear mixed-effects and random forest models. We tested generalized linear models as well as generalized mixed-effects models to account for the effect of sampling locality (supplementary tables S20 and S21). In addition, we used a model including vegetation coverage (supplementary Fig S12, supplementary table S19). The best predictive model for reproductive mode incorporated only elevation showing the highest Akaike weight and a statistically significant slope (table 2 C), while, for example, plant association did not show any effect on the prediction of reproductive mode. We also tested the effect of sampling locality on the prediction of reproductive mode and found, in congruence with the previous approach, that the model incorporating only elevation was preferred (table 2 D). Our validation of these linear models with a random forest approach supports that increasing elevation is the main driver for asexual reproductive mode (represented as 1) evolution in soil nematodes in the Atacama(supplementary table S17). Our models show that the likelihood of nematode taxa being asexual is greater at higher elevations than in lower ones (e.g. coastal area)(Fig.4). To account for variation across localities in our predictions, we further assessed genera richness using generalized linear mixed effect models specifying the sampling locality as a random effect, in this case we found that the sampling localities have no significant effect on the likelihood of a reproductive mode.

3 DISCUSSION

Altered soil characteristics, along with increasing temperatures, will have an impact on community dynamics and species abundance, especially in times of accelerated global change (Jones et al., 2017; Zablocki et al., 2016; Prather et al., 2012). Dry lands cover around 40% of the Earth's land surface (Cartereau et al., 2022). These areas are projected to increase in aridity as a consequence of climate change (on Climate Change , IPCC). Desertification processes, as an example, soil erosion, acidification and salinization, have affected over 12% of dry lands already (Burrell et al., 2020), partly due to changing precipitation patterns (Várallyay, 2010). Understanding soil biodiversity and species distribution in present-day desert environments could provide a model for further studies on the effect of desertification and resilience of soil ecosystems. Using nematodes as a model system, we analyzed which factors shape soil biodiversity in an extreme environment, the Atacama Desert in northern Chile. While aridity generally characterizes the Atacama Desert, we found that nematode diversity shows patterning throughout different niches (e.g. sand dunes, saline lake-shore sediments, fog oases), as well as in relation to ecological and geographical parameters. We identified mean annual precipitation and latitude to be the major predictors of genera richness in the desert. Furthermore, elevation was identified as the primary predictor of reproductive mode. Additionally, the characterization of nematodes as indicators of soil condition, based on their life cycle characteristics, revealed that some niches are stable (taxa that are sensible to pollutants and disturbance) while others exhibit signs of a poor soil food web with high tolerance to

pollutants and disturbance. Here we describe for the first time the biogeographic patterns of nematodes focusing on their diversity, life-history and community composition in the Atacama Desert, where studies on soil organisms, such as roundworms, are still scarce (Marín et al., 2021; Gadea, 1963).

Atacama soils harbors a rich nematode diversity. We analyzed diversity from the haplotype level (genetic diversity) to community level patterns (genera richness and Jaccard similarity at the family level). We report that the Atacama Desert is home to at least 36 different genera of nematodes grouped in 21 families, spread across various habitats. We identified cosmopolitan nematode families, including members of Cephalobidae and Panagrolaimidae, which have been documented in other desert environments such as the Namib Desert (Marais et al., 2019; Treonis et al., 2024), the Judean Desert (Steinberger et al., 2001), the Mojave Desert (De Ley et al., 1999, 2001), and the Monte Desert (Shahina and De Ley, 1997). These families have also been reported in the arid region of Arica in the Atacama Desert (Jimenez Roco, 1972). We found both families in most analyzed areas and aimed to assess the genetic differences among individuals from different localities and their relationship to ecological, geological and geographical factors. Particularly for the family Panagrolaimidae, all sequenced individuals belonged to only one genus (*Panagrolaimus*), which displayed an isolation-by-distance pattern (IBD). We were able to detect this pattern in *Panagrolaimus* specifically, as we found a high enough proportion of sexually reproducing individuals present in our samples (asexually reproducing species do not have gene flow and thus by default show separation). A possible explanation for IBD is limited dispersal, which has been reported to be lower in nematodes of this genus when compared to other species in a laboratory setting (Kreuzinger-Janik et al., 2022). Generally, dispersal is lower for below ground organisms when compared to above ground taxa (Berg et al., 2010). Dispersal can be mediated by wind in small invertebrates like nematodes (Ptatscheck et al., 2018), but the effect of wind dispersal has not been studied to date in the Atacama.

Soil biodiversity in the Atacama is highly structured and in parts sensitive to disturbance. By examining communities at both the haplotype and family levels across different desert niches, we identified distinct local patterns. For example, the Jaccard similarity analysis revealed distinct communities in Salars compared to other regions. The influx of freshwater from complex underground aquifers into high-altitude wetlands, along with elements like lithium and arsenic, high salt concentrations, and seasonal fluctuations, contribute to the formation of these unique ecosystems (Al-Jawad et al., 2024; Paquis et al., 2023; Castro-Severyn et al., 2021). Microbial life, proposed as the dominant life form in this area, displays density and structure changes through dry and wet seasons (Paquis et al., 2023), which in consequence can have an effect on the nematode community in the area (Muschiol et al., 2015), given that most families found in the wetlands were bacterivores. Differences in the taxa found in the different areas can also provide information on the complexity of the soil food web, both the salars and Paposo were dominated by persisters that are described to be more sensitive to environmental disturbance and often have a narrow ecological amplitude. Even if these indicators are developed in communities of agricultural soils (Bongers, 1990), which are expected to differ significantly from the oligotrohpic desert soils, the relative difference in the proportion of persisters among the here investigated localities ($\approx$ 10% more than colonizers), highlights the sensitivity of food webs in the salars and Paposo. This aligns to observed and reported threats to these ecological niches that are mining, plant extraction, pasture beyond the area's capacity, truck transit with dangerous materials, uncontrolled tourism and habitat loss due to vehicle transit off roads (Carrasco-Lagos et al., 2015).

In contrast, in Altiplano, Totoral Dunes, and Aroma the dominant groups were colonizers that are described to be more resistant to adverse environmental conditions in agricultural soils, indicating poor soil food web function in the absence of some feeding types (Bongers and Bongers, 1998; Du Preez et al., 2022). Even if the here investigated soils cannot compare to eutrophic agrigultural conditions, the relative dominance in colonizers in comparison to the soils from the salar and Paposo localities, indicate altered food web function in Apltiplano, Totoral Dunes and Aroma. Sand dune systems, such as Totoral Dunes, have already been reported to be dominated by coloniser taxa due to their broad ecological range, with high abundances of the family Cephalobidae throughout coastal sand dunes (Ruiz-Cuenca and Abolafia, 2021, 2023).

Soil community diversity patterns across the Atacama Desert are primarily shaped by climate. To further understand if broader scale patterns could be found for the soil communities, we implemented a genera richness modeling approach. In isolated areas such as the Atacama Desert, comprehensive field studies that encompass the entire area are challenging due to the desert's complex topography and large

terrain extension. Modeling approaches provide a simplified representation of real-world phenomena (Weisberg, 2007)specifically for multifaceted scenarios, as we observed in the Atacama. These models are thus an excellent tool to disentangle the driving factors of species and community distributions by incorporating the complex interplay of ecological, geographical and edaphic factors (Guisan and Zimmermann, 2000).

Our results highlight the key role of climate, particularly mean annual precipitation and temperature heterogeneity, in shaping nematode genera richness. Precipitation, as a proxy for water availability, is a well-established driver of soil biodiversity across various taxa, including protists, bacteria, fungi, arachnids, rotifers, and nematodes (Zhang et al., 2023). In desert environments, higher precipitation can enhance biodiversity by improving nutrient availability and soil moisture (Hu et al., 2022). Specifically, in the Atacama Desert, it has been linked to species distribution and habitat suitability in beetles (Zúñiga-Reinoso et al., 2021) and increased microbial diversity at higher elevations (Knief et al., 2020a).

Soil nematodes, like other invertebrates (Schratzberger et al., 2019), rely on the thin water film between soil particles for movement, making water availability crucial (Yeates, 2004). While some can survive dry conditions through anhydrobiosis (Ricci, 1998; Leeuwenhoek, 1702; Rebecchi et al., 2019), active nematodes depend on precipitation to sustain mobility and biodiversity. Increased precipitation has also been linked to shifts in nematode communities, particularly an increase in bacterial-feeding nematodes, likely due to a rise in bacterial biomass (Chen et al., 2014).

Beyond precipitation, we found that temperature heterogeneity (seasonal temperature variation) also influences genera richness in the Atacama Desert. While temperature fluctuations are known to shape community dynamics, their precise role in food web interactions remains incompletely understood (Zander et al., 2016). Temperature heterogeneity has been identified as a key factor in population structure (Stager et al., 2021), a driver of increased protist densities (Hammill and Dart, 2022), and a contributor to significant community dissimilarities (Robinson et al., 2018). Variations in climate across localities may create distinct micro-niches, fostering the establishment of diverse biological communities.

Although not identified as the primary drivers of nematode diversity in our study, latitude, elevation, and edaphic factors (such as soil thickness and rock type) may still influence community diversity in the extreme environment of the Atacama Desert. These edaphic factors have been proposed as key regulators of soil biodiversity by shaping various environmental conditions, including weathering processes, soil pH, clay formation, water infiltration, and retention capacity (Ott, 2020; Geroy et al., 2011). Plant coverage and type can also play an important role in supporting nematode diversity, as plants have been found to be biodiversity hotspots in desert ecosystems for both microorganisms (that serve as food source for nematodes) and invertebrates (Treonis et al., 2022; Jones et al., 2023). However, fine scale analysis of soil and plant properties are not included this study and should be consider in future work.

Latitude, widely recognized as a major determinant of taxonomic diversity, is central to the concept of the latitudinal diversity gradient (LDG) (Fischer, 1960; Wallace, 1878). While the LDG has been empirically observed across numerous taxa (Qian et al., 2024; Economo et al., 2018; Hillebrand, 2004), its underlying mechanisms remain unclear. Latitude often interacts with other ecological and climatic factors, making it difficult to disentangle its direct effects from confounding influences (Saupe, 2023; Rapoport, 1975; Gaston, 2000; Rosenzweig, 1992).

While climate appears to be the primary driver of nematode biodiversity in the Atacama Desert, it is important to acknowledge that this conclusion is based on the current dataset and represents an initial assessment of potential taxa distribution across this complex landscape. A more comprehensive understanding of biodiversity in the region will require systematic sampling with an increased sample size, particularly capturing diversity in high-altitude and southern areas of the desert that remain difficult to access.

Moreover, the broad patterns identified through different modeling approaches do not account for fine-scale habitat heterogeneity (e.g., water bodies, specific plant associations, or areas with persistent shade), which likely contribute to the availability of distinct ecological niches for nematodes. Despite these limitations, our analysis provides a valuable framework for understanding the potential distribution of nematode taxa in this extreme environment. By offering an initial biogeographic perspective, this study serves as a foundation for future research and targeted field experiments, ultimately enhancing our knowledge of nematode biodiversity in the Atacama Desert.

Asexual nematodes are more prevalent in higher altitudes in the Atacama. The hypothesis of geographical parthenogenesis posits that at high latitudes, high altitudes and in extreme environments,

asexually reproducing taxa are more prevalent when compared to sexually reproducing ones (Vandel, 1928; Alonso-Marcos et al., 2019; Kearney, 2005; Horne and Martens, 1998; Law and Crespi, 2002). Testing for this hypothesis allowed us to investigate how the relationship between taxa richness and complex biological traits (reproduction) evolved within some nematodes under globally extreme environmental conditions, finding that with increasing elevation, soil nematodes in the Atacama are more likely to reproduce asexually than sexually is supported by the Red Queen Hypothesis (RQH). RQH suggests that in environments with high biotic interactions, sexual taxa are at advantage, while in harsh conditions with lower interactions, such as high altitudes, asexually reproducing taxa are more prevalent (Van Valen, 1973; Hartmann et al., 2017). While our findings appear to indicate that even in an environment with generally harsh (or extreme) conditions, as the Atacama Desert, parthenogenetic taxa are most successful at the margins, we note that larger sampling sizes across multiple taxa will be needed for our understanding of geographical parthenogenesis as a phenomenon in nature. At the very least our data on the reproductive mode of soil nematodes demonstrates that the evolution of biological traits is influenced by ecological, edaphic and geographic conditions in very stable environments, like the Atacama. On a large time-scale the Atacama shows a remarkable climatic stability (aridity for over 150 Ma), showing no significant latitudinal movement since the late Jurassic (Hartley et al., 2005). However, on shorter time-scales climatic variation is present, our results reveal nematode diversity across different levels of biological organization but do not provide insights into abundance, that eventually can be highly variable across seasons (e.g., during the Altiplano rainfall season). Nevertheless, we expect that taxonomic diversity remains relatively stable throughout the year for the localities and sampling points analyzed, given that several taxa are capable of undergoing anhydrobiosis.

In summary, soils of the Atacama Desert are home to a diverse fauna of nematodes. While ecological strategies follow regional-local patterns (e.g colonizer-persister distribution), reproductive strategies and genera richness follow a global trend. Even in a system that is seen as an extreme on the environmental scale, diverse communities are distributed along the desert with more genera rich communities in areas with higher precipitation and lower latitudes. Remarkably, asexual taxa appear to be more prominent in the marginal ranges of high altitudes. Future research should prioritize systematic sampling to evaluate the robustness of the model-derived predictions we present in this study.

Our study highlights the necessity of biodiversity and ecosystem health assessments to understand the territory's biological uniqueness. The Atacama has been historically explored for its notable mineral

richness, consequently mining has been a common activity throughout the desert, threatening the stability of unique ecosystems and the communities that protect and manage these territories (Zanetta-Colombo et al., 2022). Focusing on biodiversity research in the Atacama Desert would not only guide our understanding of biological evolution but also our understanding of the limits to life under global change.

4 MATERIAL AND METHODS

4.1 Sampling, extraction and morphological identification

Samples were taken in six different localities across the desert. Here we define a locality as an environmentally distinct area, identified based on visible ecological and landscape features. We determined them based on direct field observation and previously defined priority sites in (Dunai et al., 2020), considering factors such as dominant vegetation, presence of water bodies and landforms while considering habitat suitability for nematodes. We named the localities as Altiplano (ALT), Aroma (ARO), Eagle Point (EPT), Salar de Huasco and Laguna Grande (Salars), Paposo (PAP) and Totoral Dunes (TDT). Sampling in the protected Salar de Huasco was conducted under the authorization (09/2023) of the Corporación Nacional Forestal (CONAF). In this study, 7 samples from Altiplano, 11 samples from Salars, 15 samples from Paposo, 20 samples from Totoral Dunes, 23 samples from Aroma and 21 samples from the Eagle point were analyzed (Supplementary tables S1 - S6). Other areas sampled where no nematodes were found and are not part of the defined localities are later on included in the modeling process (Supplementary Table S7).

Soil samples of approximately 500g were taken in the different locations using a shovel, from the upper 10-30 cm of each site and stored in zip-lock bags. Samples taken near to plants corresponded to sediment approximately 10 cm away from the plant stem, or from plant litter in the case of Paposo. They were initially checked for the presence/absence of nematodes on-site by extracting a portion from the soil samples using seeding trays with one layer Kimberly-Clark Kimtech science precision wipes 7551. Trays were flooded from the bottom and samples were allowed to re-hydrate overnight. The water was

then filtered through sieves of 80 and 120 μm. Nematodes were collected on petri dishes and examined using a Zeiss Stemi 2000 microscope, this procedure was also followed in a laboratory setting for further morphological and molecular work.

Adult nematodes were morphologically identified using a Zeiss Axioplan 2 light microscope and further examined at 10X, 20X and 40X following multiple diagnostic features as shown in supplementary Fig S2. Examined individuals were categorized as morphotypes to account for morphological variation within nematode families. Morphotype representatives for each family found on the samples were stored in 10μl of nuclease-free water and stored at -20 degrees Centigrade for further processing.

4.2 DNA extraction, barcoding and sequence processing

DNA extraction was performed on whole single individual nematodes using a modified version of the HotSHOT DNA extraction method (Montero-Pau et al., 2008). PCR was performed using the Cytiva PuReTaq Ready-To-Go™ PCR Beads or REDTaq® ReadyMix™ PCR-mix. The genetic marker 18S rRNA was amplified using the forward (CGCGAATRGCTCATTACAACAGC) and reverse (GGGCG-GTATCTGATCGCC) primers described in (Floyd et al., 2005), targetting the V2, V3 and V4 regions. The thermocycling conditions used were: denaturation at 94 °C for 5 min, 35 cycles of amplification (94 °C for 30 s; 54 °C for 30 s; 72 °C for 70 s), followed by a final extension at 72 °C for 5 min. Gel electrophoresis was performed (1.5% gel) to assess the amplicons. PCR products were purified using the Exo-CIP™ Rapid PCR Cleanup Kit (NEB - E1050L). DNA samples were submitted for sequencing to Eurofins Genomics and Genewiz.

Sequences were analyzed using Geneious Prime® (v. 2024.0.5). Only sequences with at least 20% high-quality bases (HQ%) were kept for further processing. Sequences were trimmed at the ends (regions with more than 1% chance of an error per base) and sequence similarity was analyzed using BLAST+ (v. 2.12.0) implementing the curated 18S-NemaBase (Gattoni et al., 2023) using the blastn function incorporated in Geneious Prime. Best hits were assigned according to the lowest E-value and a high percentage of identity.

4.3 Genetic diversity and haplotype uniqueness

Nematode families represented by five or more 18s rRNA sequences from different samples and present in more than one locality were used to generate haplotype networks. Sequences were grouped based on their sequence similarity to reference sequences of the curated 18S-NemaBase database (Gattoni et al., 2023), identified to family and if possible genus level. Due to lack of resolution in the sequences, some haplotype networks were created based on family level instead of genus level. The grouped sequences were aligned (multiple alignments) using Clustal Omega (v. 1.2.3). Short sequences (<300 bp) or with lack of overlap were removed. Alignments were manually trimmed in Geneious prime according to sequence overlap. Trimmed and curated alignments were used as input for DnaSP (v. 6.12.03) (Rozas et al., 2017) to calculate nucleotide diversity (π) and the Watterson's estimator (θ). Haplotype data files were created in DnaSP and according to this trait matrices defining the occurrences of the different haplotypes were generated and then used as input for PopART (v. 1.7) (Leigh and Bryant, 2015). Haplotype networks were constructed using the TCS inference method (Clement et al., 2002). Networks were finalized using Inkscape (v. 1.3.2). Sequence sets were defined in DnaSP to estimate π for each location where enough sequences were present.

4.4 Community composition throughout the Atacama

We estimated the Jaccard disimilarity index (β diversity) using presence/absence data of families found in 6 localities (Altiplano, Aroma, Eagle Point, Salars, Paposo and Totoral Dunes), here we analyzed aggregates communities per locality and don't discriminate by soil sample (bag). We used the vegan package (v 2.6-4) (Oksanen et al., 2024) and visualized the results inverted (Jaccard similarity) as a heatmap using pheatmap (v. 1.0.12) (Kolde, 2019) in R. We further on analyzed family co-occurrence using the cooccur function of the cooccur package (v. 1.3) (Griffith et al., 2016). To test for isolation-by-distance patterns, we estimated distance between all combinations of sampling localities on centroids using the sf (v. 1.0-16) (Pebesma, 2018; Pebesma and Bivand, 2023) and geodist (v. 0.1.0) (Padgham and Sumner, 2024) packages. Following, a mantel test was performed comparing Jaccard dissimilarity to geographical distance using the mantel function of the vegan package with the Spearman's rank correlation ρ. The nucleotide diversity for each location of the different groups was also tested for

isolation-by-distance patterns using the same approach. Nucleotide diversity was transformed to genetic distance by estimating the Euclidean distance using the base R package stats (R Core Team, 2023a).

4.5 Nematodes as soil indicators

Presence-absence information at the Family level for each locality was used as input for the application NINJA: Nematode INdicator Joint Analysis (Sieriebriennikov et al., 2014). We assessed the coloniser-persister structure assemblage of soil nematode families found in the Atacama Desert as well as the feeding type composition in each of the sampling localities.

4.6 Modeling ecological constraints of nematode biodiversity

We evaluated climatic (environmental, e.g. precipitation) and geomorphological (edaphic and geographic, e,g. topographic complexity and latitude respectively) variables as predictors for genera richness in the Atacama Desert. We tested 57 probabilistic models using generalized least squares linear regression from the package nlme (v. 3.1) (Pinheiro and Bates, 2000; Pinheiro et al., 2024) on R and 57 linear mixed effect models using lme from the package nlme, using the sampling localities as a random effect. Data of genera presence in the Atacama Desert was obtained as described in the previous sections through morphological and genetic identification. The geomorphological variables evaluated were elevation, topographic complexity, curvature, soil thickness, rock type and latitude (supplementary table S13). We obtained elevation data from a digital elevation model at 15 arc sec resolution (Tozer et al., 2019) and calculated a) topographic complexity as the standard deviation of elevation in a coarser 0.01 degree resolution grid (Roell et al., 2021) and b) curvature as the second derivative of elevation with respect to the aspect in a 3x3 grid (Evans, 2013) as implemented in the RichDEM package (v. 0.0.3) (Barnes, 2016) in Python. Soil thickness and rock-type data were obtained from publicly available datasets compiled respectively by Pelletier et al. (2016) and Hartmann and Moosdorf (2012). The evaluated climatic variables were mean annual temperature, mean annual precipitation, temperature range, and precipitation range. Here, 'range' is defined as the difference between seasonal (rather than daily) minimum and maximum values, serving as a proxy for climatic heterogeneity. Temperature and precipitation data were obtained from the openly accessible Chelsea version 2 climate dataset (Karger et al., 2017, 2021). A correlation matrix plot was obtained using the cor and corrplot functions from the corrplot package (v. 0.92) (Wei and Simko, 2021) o assess variable correlations ($> |0.65|$) (Supplementary Fig. S9), only a representative variable from highly correlated pairs was included in the analysis to avoid redundancy. We furhter conducted a principle component analysis using the prcomp function of the stats package (v. 4.3.2) (R Core Team, 2023b), the PCA was visualized using the factoextra package (v. 1.0.7)(Kassambara and Mundt, 2020) in R. We log-transformed soil thickness and topographic complexity (supplementary Fig S8) to fulfill model assumptions. Bioinformatic pipelines were optimized using ChatGPT.

We evaluated a total of 114 models, including null models (Supplementary Tables S14 and S15), which incorporated various combinations of selected predictive variables. Half of the tested models were least squares models (GLS), while the other half accounted for the same variables but included localities as a random effect to control for influence of the localities (linear mixed effect models - LME). The variables were selected based on two criteria: 1) variables should not display strong correlation with each other, and 2) the variable contribution to explain the variability along the first and second principal components must be high and among the top variables (supplementary figures S10 and S11). Furthermore, the residuals of each model fit were visually evaluated and a variance structure adjustment was performed where necessary following Zuur et al. (2009). The preferred predictive models per approach (GLS and LME) were then selected based on the Bayesian information criterion (BIC) and further estimation of Akaike weights (wm) (Anderson et al., 2000), as the latter provides the probability that a model is the best model according to the set of models tested and the experimental data (Portet, 2020). The preferred predictive models were then used to obtain a map representing the possible nematode diversity in terms of genera richness. We further on tested variable importance of the previously used variable set using the machine learning algorithm Random Forest using the package randomForest (v. 4.7-1.1) (Liaw and Wiener, 2002) to validate the results obtained in the linear models. Training and testing set were created using the rsample (v. 1.2.1). The model was then evaluated using caret (v. 6.0-94).

4.7 Reproductive mode determination and association to environmental variables

Laboratory cultures were established from nematodes extracted from the soil samples. Worms were propagated on nematode growth medium (NGM) plates containing *E. coli* strain OP50 as a food source.

Single-strain established cultures were analyzed morphologically to identify males and females of a strain. Cultures with only females were categorized as possible parthenogens and cultures with both males and females present were categorized as possible gonochoristhic. In addition, single juvenile stage nematode cultures were propagated (to ensure no mating) to determine the reproductive mode of the strains as described in (Lewis et al., 2009). Between 5 to 30 single juvenile cultures were set up for reproductive mode corroboration per strain. We consider asexual cultures where larvae grew into adults and laid eggs without fertilization from a male.

Models testing elevation, precipitation and mean annual precipitation as predictors for reproductive mode (sexual or asexual). Environmental data was collected as in the previous section. Two model types were employed: (a) a logistic regression analysis using the glm function from the stats package in R (v. 4.3.2), with a binomial family distribution ($family = binomial$), and (b) a generalized linear mixed-effects model, implemented with glmer from the lme4 package (v. 1.1-36), incorporating localities as a random effect to account for spatial variability in the samples. Following, additional models were tested including vegetation coverage and percentage of phanerophytes estimated for the samples where reproductive mode could be assessed. Plant identification was done through morphological identification. The same approach for evaluating variable importance using Random Forest was implemented as described in the previous section (genera richness).

AUTHOR CONTRIBUTIONS

O.H, A-M.W and P.H.S. designed the research. M.L.A. facilitated sampling and provided resources. L.V.,L.P, N.W and A.Su performed the research. L.V, L.P., A.St and E.A-T analyzed the data. L.V., L.P., O.H, A-M.W and P.H.S.wrote the paper

ACKNOWLEDGMENTS

We would like to thank Julian Pfeiffer, Siwen Ding, Julia Caro-Valenzuela, Thalia Sotiropoulos for their support. We would like to thank the Comunidad Lickan Antay de Toconao and the Comunidad Indígena Aymara Laguna del Huasco for allowing us in their territory as well as the Corporación Nacional Forestal (CONAF) for providing the authorization (09/2023) for Salar de Huasco. We would like to highlight the importance of collaborating with local indigenous communities. This allows researchers to learn from their ancestral knowledge on the territories that have been under their management and protection for generations. This ancestral knowledge, enriches scientific understanding, and in turn the data produced can inform and enhance the management of their territories. Such approach ensures high quality scientific output that can reach beyond the academic community and have direct impact on society. This research was conducted under the DFG funded project B08 in the CRC1211 [grant number 268236062] awarded to P. Schiffer and A-M Waldvogel and the grant ANID/Milenio/ICN2021_044 awarded to M.L.A.

DATA AVAILABILITY

All raw data used for analysis in this manuscript can be found in Zenodo (https://doi.org/10.5281/zenodo.14930774). Sequencing data is available on GenBank with accession numbers PQ587582-PQ587967. All the code implemented in the data analysis can be found on github (https://github.com/lauraivillegasr/BiogeographyDesert) and will be available as a reproducible run on CodeOcean (10.24433/CO.6395549.v2).

REFERENCES

Acosta, E., Fincke, V., Nitsche, F., and Arndt, H. (2023). Novel cercozoan and heterolobosean protists from the rhizosphere and phyllosphere of two endemic cacti from the atacama desert. *European Journal of Protistology*, 91:126034.

Al-Jawad, J., Ford, J., Petavratzi, E., and Hughes, A. (2024). Understanding the spatial variation in lithium concentration of high andean salars using diagnostic factors. *Science of The Total Environment*, 906:167647.

Alonso-Marcos, H., Nardi, F. D., Scheffknecht, S., Tribsch, A., Hülber, K., and Dobeš, C. (2019). Difference in reproductive mode rather than ploidy explains niche differentiation in sympatric sexual and apomictic populations ofpotentilla puberula. *Ecology and Evolution*, 9(6):3588–3598.

Alvial, I. E., Orth, K., Durán, B. C., Álvarez, E., and Squeo, F. A. (2012). Importance of geochemical factors in determining distribution patterns of aquatic invertebrates in mountain streams south of the atacama desert, chile. *Hydrobiologia*, 709(1):11–25.

Anderson, D. R., Burnham, K. P., and Thompson, W. L. (2000). Null hypothesis testing: Problems, prevalence, and an alternative. *The Journal of Wildlife Management*, 64(4):912.

Anthony, M. A., Bender, S. F., and van der Heijden, M. G. A. (2023). Enumerating soil biodiversity. *Proceedings of the National Academy of Sciences*, 120(33).

Arndt, H., Ritter, B., Rybarski, A., Schiwitza, S., Dunai, T., and Nitsche, F. (2020). Mirroring the effect of geological evolution: Protist divergence in the atacama desert. *Global and Planetary Change*, 190:103193.

Bardgett, R. D. and van der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, 515(7528):505–511.

Barnes, R. (2016). *RichDEM: Terrain Analysis Software*.

Berg, M. P., Kiers, E. T., Driessen, G., Van Der Heijden, M., Kooi, B. W., Kuenen, F., Liefting, M., Verhoef, H. A., and Ellers, J. (2010). Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, 16(2):587–598.

Bongers, T. (1990). The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia*, 83(1):14–19.

Bongers, T. and Bongers, M. (1998). Functional diversity of nematodes. *Applied Soil Ecology*, 10(3):239–251.

Bongers, T. and Ferris, H. (1999). Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology and Evolution*, 14(6):224–228.

Borgonie, G., García-Moyano, A., Litthauer, D., Bert, W., Bester, A., van Heerden, E., Möller, C., Erasmus, M., and Onstott, T. C. (2011). Nematoda from the terrestrial deep subsurface of south africa. *Nature*, 474(7349):79–82.

Boström, S. and Holovachov, O. (2013). Description of one new species of heterocephalobellus rashid, geraert and sharma, 1985 (rhabditida: Cephalobidae) from kelso dunes, mojave national preserve, california, usa and usno, argentina. *Journal of Nematode Morphology and Systematics*, 16:161–166.

Bull, A. T., Asenjo, J. A., Goodfellow, M., and Gómez-Silva, B. (2016). The atacama desert: Technical resources and the growing importance of novel microbial diversity. *Annual Review of Microbiology*, 70(1):215–234. PMID: 27607552.

Burrell, A. L., Evans, J. P., and De Kauwe, M. G. (2020). Anthropogenic climate change has driven over 5 million km^2 of drylands towards desertification. *Nature Communications*, 11(1).

Carrasco-Lagos, P., Moreno, R., Figueroa, A., Espoz, C., and de la Maza, C. (2015). *Sitios Ramsar de Chile*. Secretaría Regional Ministerial (SEREMI) del Medio Ambiente de la Región Metropolitana, Facultad de Ciencias, Centro de Investigación e Innovación para el Cambio Climático y Centro Bahía Lomas de la Universidad Santo Tomás, Facultad de Ciencias Forestales y Conservación de la Naturaleza de la Universidad de Chile, Corporación Nacional Forestal (CONAF).

Cartereau, M., Leriche, A., Baumel, A., Ondo, I., Chatelain, C., Aronson, J., and Médail, F. (2022). Global bioregionalization of warm drylands based on tree assemblages mined from occurrence big data. *Frontiers of Biogeography*, 14(4).

Castro-Severyn, J., Pardo-Esté, C., Mendez, K. N., Fortt, J., Marquez, S., Molina, F., Castro-Nallar, E., Remonsellez, F., and Saavedra, C. P. (2021). Living to the high extreme: Unraveling the composition, structure, and functional insights of bacterial communities thriving in the arsenic-rich salar de huasco altiplanic ecosystem. *Microbiology Spectrum*, 9(1).

Chai, R., Mao, J., Chen, H., Wang, Y., Shi, X., Jin, M., Zhao, T., Hoffman, F. M., Ricciuto, D. M., and Wullschleger, S. D. (2021). Human-caused long-term changes in global aridity. *Npj Clim. Atmos. Sci.*, 4(1).

Chen, D., Cheng, J., Chu, P., Hu, S., Xie, Y., Tuvshintogtokh, I., and Bai, Y. (2014). Regional-scale patterns of soil microbes and nematodes across grasslands on the mongolian plateau: relationships with climate, soil, and plants. *Ecography*, 38(6):622–631.

Clement, M., Snell, Q., Walke, P., Posada, D., and Crandall, K. (2002). Tcs: estimating gene genealogies. In *Proceedings 16th International Parallel and Distributed Processing Symposium*. IEEE.

Contreras, M. J., Leal, K., Bruna, P., Nuñez-Montero, K., Goméz-Espinoza, O., Santos, A., Bravo, L., Valenzuela, B., Solis, F., Gahona, G., Cayo, M., Dinamarca, M. A., Ibacache-Quiroga, C., Zamorano,

P., and Barrientos, L. (2023). Commonalities between the atacama desert and antarctica rhizosphere microbial communities. *Frontiers in Microbiology*, 14.

de Bienes Nacionales, M. (2022). Crea parque nacional "salar del huasco", en la regiÓn de tarapacÁ. deja sin efecto los ds n° 24 de 2019 y n° 5 de 2022, no tramitados. *Ley 19300*.

De Ley, I., Baldwin, J., De Ley, P., Mundo-Ocampo, M., Nadler, S., and Gebre, M. (2001). Acromoldavicus mojavicus n. sp. (nematoda: Cephaloboidea) from the mojave desert, california. *Nematology*, 3(4):343–353.

De Ley, I., De Ley, P., Baldwin, J., Mundo-Ocampo, M., and Nadler, S. (1999). Three new species of nothacrobeles (nemata: cephalobidae) from the mojave desert. *J Nematol*, 4:482–97.

De Ley, P. (2014). Past and present highlights of nematode research in the mojave desert. *Mojave National Preserve Science Newsletter*, 4:5–10.

Döge, J. d. S., de Oliveira, H. V., and Tidon, R. (2015). Rapid response to abiotic and biotic factors controls population growth of two invasive drosophilids (diptera) in the brazilian savanna. *Biological Invasions*, 17(8):2461–2474.

Du Preez, G., Daneel, M., De Goede, R., Du Toit, M. J., Ferris, H., Fourie, H., Geisen, S., Kakouli-Duarte, T., Korthals, G., Sánchez-Moreno, S., and Schmidt, J. H. (2022). Nematode-based indices in soil ecology: Application, utility, and future directions. *Soil Biology and Biochemistry*, 169:108640.

Dunai, T. J., Melles, M., Quandt, D., Knief, C., and Amelung, W. (2020). Whitepaper: Earth – evolution at the dry limit. *Global and Planetary Change*, 193:103275.

Economo, E. P., Narula, N., Friedman, N. R., Weiser, M. D., and Guénard, B. (2018). Macroecology and macroevolution of the latitudinal diversity gradient in ants. *Nature Communications*, 9(1).

Edgington, S., Buddie, A., Moore, D., France, A., Merino, L., and Hunt, D. (2010). Heterorhabditis atacamensis n. sp. (nematoda: Heterorhabditidae), a new entomopathogenic nematode from the atacama desert, chile. *Journal of Helminthology*, 85(4):381–394.

Eduardo Palma, R., Marquet, P. A., and Boric-Bargetto, D. (2005). Inter- and intraspecific phylogeography of small mammals in the atacama desert and adjacent areas of northern chile. *Journal of Biogeography*, 32(11):1931–1941.

Eshel, G., Araus, V., Undurraga, S., Soto, D. C., Moraga, C., Montecinos, A., Moyano, T., Maldonado, J., Díaz, F. P., Varala, K., Nelson, C. W., Contreras-López, O., Pal-Gabor, H., Kraiser, T., Carrasco-Puga, G., Nilo-Poyanco, R., Zegar, C. M., Orellana, A., Montecino, M., Maass, A., Allende, M. L., DeSalle, R., Stevenson, D. W., González, M., Latorre, C., Coruzzi, G. M., and Gutiérrez, R. A. (2021). Plant ecological genomics at the limits of life in the atacama desert. *Proceedings of the National Academy of Sciences*, 118(46).

Evans, I. S. (2013). Land surface derivatives: history, calculation and further development. *Proceedings of geomorphometry*, pages 16–20.

Fischer, A. G. (1960). Latitudinal variations in organic diversity. *Evolution*, 14(1):64.

Floyd, R., Rogers, A. D., Lambshead, P. J. D., and Smith, C. R. (2005). Nematode-specific pcr primers for the 18s small subunit rrna gene. *Molecular Ecology Notes*, 5(3):611–612.

Gadea, E. (1963). Nota sobre nematodos muscícolas de atacama (chile). *Miscelanea Zoologica*, 1-5.

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, 405(6783):220–227.

Gattoni, K., Gendron, E. M. S., Sandoval-Ruiz, R., Borgemeier, A., McQueen, J. P., M. Shepherd, R., Slos, D., O. Powers, T., and L. Porazinska, D. (2023). 18s-nemabase: Curated 18s rrna database of nematode sequences. *Journal of Nematology*, 55(1).

Geroy, I., Gribb, M., Marshall, H., Chandler, D., Benner, S., and McNamara, J. (2011). Aspect influences on soil water retention and storage. *Hydrological Processes*, 25(25):3836–3842.

Griffith, D. M., Veech, J. A., and Marsh, C. J. (2016). cooccur: Probabilistic species co-occurrence analysis inr. *Journal of Statistical Software*, 69(Code Snippet 2).

Guisan, A. and Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135(2–3):147–186.

Gómez-Silva, B. and Batista-García, R. A. (2022). The atacama desert: A biodiversity hotspot and not just a mineral-rich region. *Frontiers in Microbiology*, 13.

Hakobyan, A., Velte, S., Sickel, W., Quandt, D., Stoll, A., and Knief, C. (2023). Tillandsia landbeckii phyllosphere and laimosphere as refugia for bacterial life in a hyperarid desert environment. *Microbiome*, 11(1).

Hammill, E. and Dart, R. (2022). Contributions of mean temperature and temperature variation to

population stability and community diversity. *Ecology and Evolution*, 12(2).

Hartley, A. J., Chong, G., Houston, J., and Mather, A. E. (2005). 150 million years of climatic stability: evidence from the atacama desert, northern chile. *Journal of the Geological Society*, 162(3):421–424.

Hartmann, J. and Moosdorf, N. (2012). The new global lithological map database glim: A representation of rock properties at the earth surface. *Geochemistry, Geophysics, Geosystems*, 13(12).

Hartmann, M., Štefánek, M., Zdvořák, P., Heřman, P., Chrtek, J., and Mráz, P. (2017). The red queen hypothesis and geographical parthenogenesis in the alpine hawkweed hieracium alpinum (asteraceae). *Biological Journal of the Linnean Society*, 122(4):681–696.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163(2):192–211.

Hörandl, E. (2006). The complex causality of geographical parthenogenesis. *New Phytologist*, 171(3):525–538.

Horne, D. J. and Martens, K. (1998). Geographical parthenogenesis in european non-marine ostracods: post-glacial invasion or holocene stability? *Hydrobiologia*, 391(1/3):1–7.

Hu, Y., Li, X., Guo, A., Yue, P., Guo, X., Lv, P., Zhao, S., and Zuo, X. (2022). Species diversity is a strong predictor of ecosystem multifunctionality under altered precipitation in desert steppes. *Ecological Indicators*, 137:108762.

Jerez, V. (2000). Diversidad y patrones de distribución geográfica de insectos coleópteros en ecosistemas desérticos de la región de antofagasta, chile. *Revista chilena de historia natural*, 73(1).

Jimenez Roco, M. (1972). Contribución al conocimiento de los nematodos del departamento de arica. (segunda parte). *IDESIA*, 2:53–58.

Jones, D. L., Fuentes, B., Arenas-Díaz, F., Remonsellez, F., van Hall, R., Atkinson, B. S., Mooney, S. J., and Bol, R. (2023). Life at the extreme: Plant-driven hotspots of soil nutrient cycling in the hyper-arid core of the atacama desert. *Soil Biology and Biochemistry*, 184:109128.

Jones, L. M., Koehler, A., Trnka, M., Balek, J., Challinor, A. J., Atkinson, H. J., and Urwin, P. E. (2017). Climate change is predicted to alter the current pest status of globodera pallida and g. rostochiensis in the united kingdom. *Global Change Biology*, 23(11):4497–4507.

Jordan, T. E., Kirk-Lawlor, N. E., Blanco, N., Rech, J. A., and Cosentino, N. J. (2014). Landscape modification in response to repeated onset of hyperarid paleoclimate in the atacama desert, chile. *Geological Society of America Bulletin*, 126(3-4):1016–1046.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., and Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4(1).

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., and Kessler, M. (2021). Chelsa v2.1 (current).

Kassambara, A. and Mundt, F. (2020). *factoextra: Extract and Visualize the Results of Multivariate Data Analyses*. R package version 1.0.7.

Kearney, M. (2005). Hybridization, glaciation and geographical parthenogenesis. *Trends in Ecology and Evolution*, 20(9):495–502.

Knief, C., Bol, R., Amelung, W., Kusch, S., Frindte, K., Eckmeier, E., Jaeschke, A., Dunai, T., Fuentes, B., Mörchen, R., Schütte, T., Lücke, A., Klumpp, E., Kaiser, K., and Rethemeyer, J. (2020a). Tracing elevational changes in microbial life and organic carbon sources in soils of the atacama desert. *Global and Planetary Change*, 184:103078.

Knief, C., Bol, R., Amelung, W., Kusch, S., Frindte, K., Eckmeier, E., Jaeschke, A., Dunai, T., Fuentes, B., Mörchen, R., Schütte, T., Lücke, A., Klumpp, E., Kaiser, K., and Rethemeyer, J. (2020b). Tracing elevational changes in microbial life and organic carbon sources in soils of the atacama desert. *Global and Planetary Change*, 184:103078.

Kolde, R. (2019). *pheatmap: Pretty Heatmaps*. R package version 1.0.12.

Kreuzinger-Janik, B., Gansfort, B., Traunspurger, W., and Ptatscheck, C. (2022). It's all about food: Environmental factors cause species-specific dispersal. *Ecosphere*, 13(10).

Lal, R., Negassa, W., and Lorenz, K. (2015). Carbon sequestration in soil. *Current Opinion in Environmental Sustainability*, 15:79–86.

Law, J. H. and Crespi, B. J. (2002). The evolution of geographic parthenogenesis in timema walking-sticks. *Molecular Ecology*, 11(8):1471–1489.

Leeuwenhoek, V. (1702). On certain animalcules found in the sediment in gutters of the roofs of houses.

(No Title), 2:207.

Leigh, J. W. and Bryant, D. (2015). ¡scp¿popart¡/scp¿: full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, 6(9):1110–1116.

Lewis, S. C., Dyal, L. A., Hilburn, C. F., Weitz, S., Liau, W.-S., LaMunyon, C. W., and Denver, D. R. (2009). Molecular evolution in panagrolaimus nematodes: origins of parthenogenesis, hermaphroditism and the antarctic species p. davidi. *BMC Evolutionary Biology*, 9(1).

Liaw, A. and Wiener, M. (2002). Classification and regression by randomforest. *R News*, 2(3):18–22.

Ma, J., Wang, G., Sun, S., Li, J., Huang, P., Guo, L., Li, K., and Lin, S. (2024). Most high mountainous areas around the world present elevation-dependent aridification after the 1970s. *Earths Future*, 12(5).

Marais, E., Maggs-Kölling, G., Sherman, C., Doniger, T., Liu, R., Tripathi, B. M., and Steinberger, Y. (2019). Profiling soil free-living nematodes in the namib desert, namibia. *Journal of Arid Land*, 12(1):130–143.

Marshall, D. J., Krug, P. J., Kupriyanova, E. K., Byrne, M., and Emlet, R. B. (2012). The biogeography of marine invertebrate life histories. *Annual Review of Ecology, Evolution, and Systematics*, 43(1):97–114.

Marín, C., Rubio, J., and Godoy, R. (2021). Chilean blind spots in soil biodiversity and ecosystem function research. *Austral Ecology*.

Maslen, N. and Convey, P. (2006). Nematode diversity and distribution in the southern maritime antarctic—clues to history? *Soil Biology and Biochemistry*, 38(10):3141–3151.

Maza, F., Maldonado, J., Vásquez-Dean, J., Mandakovic, D., Gaete, A., Cambiazo, V., and González, M. (2019). Soil bacterial communities from the chilean andean highlands: Taxonomic composition and culturability. *Frontiers in Bioengineering and Biotechnology*, 7.

Moat, J., Orellana-Garcia, A., Tovar, C., Arakaki, M., Arana, C., Cano, A., Faundez, L., Gardner, M., Hechenleitner, P., Hepp, J., Lewis, G., Mamani, J.-M., Miyasiro, M., and Whaley, O. Q. (2021). Seeing through the clouds – mapping desert fog oasis ecosystems using 20 years of modis imagery over peru and chile. *International Journal of Applied Earth Observation and Geoinformation*, 103:102468.

Montero-Pau, J., Gómez, A., and Muñoz, J. (2008). Application of an inexpensive and high-throughput genomic dna extraction method for the molecular ecology of zooplanktonic diapausing eggs. *Limnology and Oceanography: Methods*, 6(6):218–222.

Morales, J. F. (2013). "sinopsis de las apocynaceae s. str.: (apocynoideae y rauvolfioideae) de chile". *Darwiniana, nueva serie*, 1(1).

Muschiol, D., Giere, O., and Traunspurger, W. (2015). Population dynamics of a cavernicolous nematode community in a chemoautotrophic groundwater system: Cavernicolous nematode community. *Limnology and Oceanography*, 60(1):127–135.

Nisa, R. U., Tantray, A. Y., Kouser, N., Allie, K. A., Wani, S. M., Alamri, S. A., Alyemeni, M. N., Wijaya, L., and Shah, A. A. (2021). Influence of ecological and edaphic factors on biodiversity of soil nematodes. *Saudi Journal of Biological Sciences*, 28(5):3049–3059.

Nitsche, F., Carduck, S., von Ameln, J., Mach, N., Dorador, C., Predel, R., Rueckert, S., and Arndt, H. (2023). Gregarines from darkling beetles of the atacama desert, atacamagregarina paposa gen. et sp. nov. from scotobius and xiphocephalus ovatus sp. nov. from psectrascelis (coleoptera, tenebrionidae). *European Journal of Protistology*, 90:126008.

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H. B. A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M. O., Lahti, L., McGlinn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C. J., and Weedon, J. (2024). *vegan: Community Ecology Package*. R package version 2.6-6.

on Climate Change (IPCC), I. P. (2023). *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Ott, R. F. (2020). How lithology impacts global topography, vegetation, and animal biodiversity: A global-scale analysis of mountainous regions. *Geophysical Research Letters*, 47(20).

Padgham, M. and Sumner, M. D. (2024). *geodist: Fast, Dependency-Free Geodesic Distance Calculations*. R package version 0.1.0.

Paquis, P., Hengst, M. B., Florez, J. Z., Tapia, J., Molina, V., Pérez, V., and Pardo-Esté, C. (2023). Short-term characterisation of climatic-environmental variables and microbial community diversity in a

high-altitude andean wetland (salar de huasco, chile). *Science of The Total Environment*, 859:160291.

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10(1):439–446.

Pebesma, E. and Bivand, R. (2023). *Spatial Data Science: With applications in R*. Chapman and Hall/CRC.

Pelletier, J. D., Broxton, P. D., Hazenberg, P., Zeng, X., Troch, P. A., Niu, G., Williams, Z., Brunke, M. A., and Gochis, D. (2016). A gridded global data set of soil, intact regolith, and sedimentary deposit thicknesses for regional and global land surface modeling. *Journal of Advances in Modeling Earth Systems*, 8(1):41–65.

Pereira, C. S., Lopes, I., Sousa, J. P., and Chelinho, S. (2015). Effects of nacl and seawater induced salinity on survival and reproduction of three soil invertebrate species. *Chemosphere*, 135:116–122.

Pinheiro, J., Bates, D., and R Core Team (2024). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-165.

Pinheiro, J. C. and Bates, D. M. (2000). *Mixed-Effects Models in S and S-PLUS*. Springer, New York.

Pizarro-Araya, J., Alfaro, F. M., Ojanguren-Affilastro, A. A., and Moreira-Muñoz, A. (2021). A fine-scale hotspot at the edge: Epigean arthropods from the atacama coast (paposo-taltal, antofagasta region, chile). *Insects*, 12(10):916.

Pizarro-Araya, J. and Jerez, V. (2004). Distribución geográfica del género gyriosomus guérin-méneville, 1834 (coleoptera: Tenebrionidae): una aproximación biogeográfica. *Revista chilena de historia natural*, 77(3).

Portet, S. (2020). A primer on model selection using the akaike information criterion. *Infectious Disease Modelling*, 5:111–128.

Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, J. M., Bloch, C. P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T. A., Parsons, S., and Joern, A. (2012). Invertebrates, ecosystem services and climate change. *Biological Reviews*, 24(4):840–856.

Ptatscheck, C., Gansfort, B., and Traunspurger, W. (2018). The extent of wind-mediated dispersal of small metazoans, focusing nematodes. *Scientific Reports*, 8(1).

Qian, H., Dai, Z., and Wang, J. (2024). Strong evidence for latitudinal diversity gradient in mosses across the world. *Plant Diversity*, 46(4):537–541.

R Core Team (2023a). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team (2023b). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rapoport, E. (1975). *Areografía, estrategias geográficas de las especies*. Fondo de Cultura Económica.

Rebecchi, L., Boschetti, C., and Nelson, D. R. (2019). Extreme-tolerance mechanisms in meiofaunal organisms: a case study with tardigrades, rotifers and nematodes. *Hydrobiologia*, 847(12):2779–2799.

Ricci, C. (1998). Anhydrobiotic capabilities of bdelloid rotifers. *Hydrobiologia*, 387/387:321–326.

Robinson, S. I., McLaughlin, B., Marteinsdóttir, B., and O'Gorman, E. J. (2018). Soil temperature effects on the structure and diversity of plant and invertebrate communities in a natural warming experiment. *Journal of Animal Ecology*, 87(3):634–646.

Roell, Y. E., Phillips, J. G., and Parent, C. E. (2021). Effect of topographic complexity on species richness in the galápagos islands. *Journal of Biogeography*, 48(10):2645–2655.

Rosenzweig, M. L. (1992). Species diversity gradients: We know more and less than we thought. *Journal of Mammalogy*, 73(4):715–730.

Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J. C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. E., and Sánchez-Gracia, A. (2017). Dnasp 6: Dna sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution*, 34(12):3299–3302.

Ruiz-Cuenca, A. and Abolafia, J. (2021). Comparative study of four known species of the genus acrobeles von linstow, 1877 (nematoda, cephalobidae) with 'single' and 'double' cuticle from coastal dunes in spain. *Journal of Helminthology*, 95.

Ruiz-Cuenca, A. N. and Abolafia, J. (2023). Prevalence and distribution of nematodes from coastal sand dunes in the iberian peninsula. *Coasts*, 3(3):263–279.

Satjarak, A., Piotrowski, M. J., Graham, L. E., Trest, M. T., Wilcox, L. W., Knack, J. J., Cook, M. E., and Arancibia-Avila, P. (2021). Microscopic and metagenomic evidence for eukaryotic microorganisms associated with atacama desert populations of giant equisetum. *American Fern Journal*, 111(2).

Saupe, E. E. (2023). Explanations for latitudinal diversity gradients must invoke rate variation. *Proceedings of the National Academy of Sciences*, 120(33).

Schiffer, P. H., Danchin, E. G., Burnell, A. M., Creevey, C. J., Wong, S., Dix, I., O'Mahony, G., Culleton, B. A., Rancurel, C., Stier, G., Martínez-Salazar, E. A., Marconi, A., Trivedi, U., Kroiher, M., Thorne, M. A., Schierenberg, E., Wiehe, T., and Blaxter, M. (2019). Signatures of the evolution of parthenogenesis and cryptobiosis in the genomes of panagrolaimid nematodes. *iScience*, 21:587–602.

Schratzberger, M., Holterman, M., van Oevelen, D., and Helder, J. (2019). A worm's world: Ecological flexibility pays off for free-living nematodes in sediments and soils. *BioScience*, 69(11):867–876.

Shahina, F. and De Ley, P. (1997). Two new species of cephalobidae from valle de la luna, argentina, and observations on the genera acrobeles and nothacrobeles (nematoda: Rhabditida). *Fundamental and Applied Nematology*, 20(4):329–347.

Sieriebriennikov, B., Ferris, H., and de Goede, R. G. (2014). Ninja: An automated calculation system for nematode-based biological monitoring. *European Journal of Soil Biology*, 61:90–93.

Stager, M., Senner, N. R., Swanson, D. L., Carling, M. D., Eddy, D. K., Greives, T. J., and Cheviron, Z. A. (2021). Temperature heterogeneity correlates with intraspecific variation in physiological flexibility in a small endotherm. *Nature Communications*, 12(1).

Steinberger, Y., Liang, W., Savkina, E., Meshi, T., and Barness, G. (2001). Nematode community composition and diversity associated with a topoclimatic transect in a rain shadow desert. *European Journal of Soil Biology*, 37(4):315–320.

Tozer, B., Sandwell, D. T., Smith, W. H. F., Olson, C., Beale, J. R., and Wessel, P. (2019). Global bathymetry and topography at 15 arc sec: Srtm15+. *Earth and Space Science*, 6(10):1847–1864.

Treonis, A. M., Marais, E., and Maggs-Kölling, G. (2024). Soil nematode communities vary among populations of the iconic desert plant, welwitschia mirabilis. *Pedobiologia*, 103:150943.

Treonis, A. M., Marais, E., and Maggs-Kölling, G. (2022). Nematode communities indicate diverse soil functioning across a fog gradient in the namib desert gravel plains. *Ecology and Evolution*, 12(6).

Van Valen, L. (1973). A new evolutionary theory. *Evolutionary Theory*.

Vandel, A. (1928). La parthénogénèse géographique: contribution à l'étude biologique et cytologique de la parthénogénèse naturelle. *Bulletin Biologique de la France et de la Belgique*, 62:164–281.

Voigt, C., Klipsch, S., Herwartz, D., Chong, G., and Staubwasser, M. (2020). The spatial distribution of soluble salts in the surface soil of the atacama desert and their relationship to hyperaridity. *Global and Planetary Change*, 184:103077.

Várallyay, G. (2010). The impact of climate change on soils and on their water management. *Agronomy Research - Special Issue II*, pages 385–396.

Wall, D. H., Bardgett, R. D., Behan-Pelletier, V., Herrick, J. E., Jones, T. H., Ritz, K., Six, J., Strong, D. R., and van der Putten, W. H. (2012). *Soil Ecology and Ecosystem Services*. Oxford University Press, United Kingdom.

Wallace, A. R. (1878). *Tropical nature, and other essays*. Macmillan & Co., London & New York.

Ward, D. (2016). *The Biology of Deserts*. Oxford University Press.

Wei, T. and Simko, V. (2021). *R package 'corrplot': Visualization of a Correlation Matrix*. (Version 0.92).

Weisberg, M. (2007). Forty years of 'the strategy': Levins on model building and idealization. *Biology and Philosophy*, 21(5):623–645.

Whitford, W. G. and Steinberger, Y. (2021). Chihuahuan desert soil biota. *Open Journal of Ecology*, 11(09):581–595.

Wood, J. R., Díaz, F. P., Latorre, C., Wilmshurst, J. M., Burge, O. R., González, F., and Gutiérrez, R. A. (2019). Ancient parasite dna from late quaternary atacama desert rodent middens. *Quaternary Science Reviews*, 226:106031.

Xi, H., Feng, Q., Zhang, L., Si, J., Chang, Z., Yu, T., and Guo, R. (2016). Effects of water and salinity on plant species composition and community succession in ejina desert oasis, northwest china. *Environmental Earth Sciences*, 75(2).

Yeates, G. W. (1970). Two terrestrial nematodes from the mcmurdo sound region, antarctica, with a note on anaplectus arenicola killick, 1964. *Journal of Helminthology*, 44(1):27–34.

Yeates, G. W. (2003). Nematodes as soil indicators: functional and biodiversity aspects. *Biology and Fertility of Soils*, 37(4):199–210.

Yeates, G. W. (2004). *Ecological and behavioural adaptations.*, page 1–24. CABI Publishing.

Zablocki, O., Adriaenssens, E. M., and Cowan, D. (2016). Diversity and ecology of viruses in hyperarid desert soils. *Applied and Environmental Microbiology*, 82(3):770–777.

Zander, A., Bersier, L., and Gray, S. M. (2016). Effects of temperature variability on community structure in a natural microbial food web. *Global Change Biology*, 23(1):56–67.

Zanetta-Colombo, N. C., Fleming, Z. L., Gayo, E. M., Manzano, C. A., Panagi, M., Valdés, J., and Siegmund, A. (2022). Impact of mining on the metal content of dust in indigenous villages of northern chile. *Environment International*, 169:107490.

Zeppilli, D., Leduc, D., Fontanier, C., Fontaneto, D., Fuchs, S., Gooday, A. J., Goineau, A., Ingels, J., Ivanenko, V. N., Kristensen, R. M., Neves, R. C., Sanchez, N., Sandulli, R., Sarrazin, J., Sørensen, M. V., Tasiemski, A., Vanreusel, A., Autret, M., Bourdonnay, L., Claireaux, M., Coquillé, V., De Wever, L., Rachel, D., Marchant, J., Toomey, L., and Fernandes, D. (2017). Characteristics of meiofauna in extreme marine ecosystems: a review. *Marine Biodiversity*, 48(1):35–71.

Zhang, J., Feng, Y., Maestre, F. T., Berdugo, M., Wang, J., Coleine, C., Sáez-Sandino, T., García-Velázquez, L., Singh, B. K., and Delgado-Baquerizo, M. (2023). Water availability creates global thresholds in multidimensional soil biodiversity and functions. *Nature Ecology amp; Evolution*, 7(7):1002–1011.

Zhang, K., Shi, Y., Cui, X., Yue, P., Li, K., Liu, X., Tripathi, B. M., and Chu, H. (2019). Salinity is a key determinant for soil microbial communities in a desert ecosystem. *mSystems*, 4(1).

Zhang, X., Ferris, H., Mitchell, J., and Liang, W. (2017). Ecosystem services of the soil food web after long-term application of agricultural management practices. *Soil Biology and Biochemistry*, 111:36–43.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., and Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer New York.

Zúñiga-Reinoso, A. and Predel, R. (2019). Past climatic changes and their effects on the phylogenetic pattern of the gondwanan relict maindronia (insecta: Zygentoma) in the chilean atacama desert. *Global and Planetary Change*, 182:103007.

Zúñiga-Reinoso, A., Ritter, B., and Predel, R. (2021). The colonization of the puna and atacama biogeographic province by sister clades of psectrascelis (coleoptera: Tenebrionidae): Synchronous expansion without spatial overlap. *Journal of Biogeography*, 48(8):1930–1940.