Soil biodiversity in the Atacama Desert shows distinct patterns at different diversity levels

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ABSTRACT

Species diversity and distribution, in relation to how they interact with their environment has for long been a major focus of ecological research. Particularly for soil ecosystems, information about geographical patterns of biota is scarce despite the primordial role of soils as ecosystem service providers. The Atacama Desert, the driest non-polar desert on earth, where water is scarce, high salinity patches are frequent and high concentrations of metals are present in water bodies, only specialised taxa can survive. This desert supports some microbial life-forms, plant, vertebrates. Above ground invertebrates have also been reported to occur throughout its extension, but its soils have not been comprehensively analysed. By studying the Atacama as a system with different extreme habitats we aim to better understand and predict resilience of soil organisms in times of global aridification. Nematodes are one of the most important groups of soil organisms in terms of numbers and biodiversity. Here, we investigated diversity of soil nematodes at the genetic, taxonomic, community and life-cycle levels in the Atacama. We find distinct patterns in their assemblages along the different habitats in the desert: dune systems, high altitude mountains, saline lakes, river valleys and fog oases, characterizing some desert soil habitats as stable systems and others as disturbed. We also find that distribution of asexual taxa appears to be in the marginal ranges of high altitudes, and that the distribution of genera richness in the Atacama increases towards the south following a latitudinal diversity gradient, as well as with increasing precipitation. Our work shows that even under extreme environmental conditions healthy soil communities can persist, but we see indicatives of local degradation due to aridification during global change.

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 resilience 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. This 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). The Atacama desert supports diverse microbial life forms, some plants, and a limited number of vertebrate animals (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). Regional environmental patterns are present across the Atacama despite the long term stability of the general geological system (Hartley et al., 2005; Jordan et al., 2014): (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 camanchacas), it harbours 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.

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 their contribution to soil nutrient turnover, carbon sequestration, regulation of bacterial populations among roles in soil ecosystems worldwide, make them an indicator 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 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 transects 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 persistant 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 latitude to be the major drivers of general genera richness across the desert and that elevation was 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 degraded food webs.

2 RESULTS

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 asses 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 194 samples collected along six transects throughout the Atacama Desert (figure 1 B, supplementary figure S1). Collected nematodes were then sequenced ("Methods") with a percentage of high quality base pairs above at least 20 (HQ 20 %). More specifically, we analyzed a total of 39 nematodes from the Altiplano transect, 43 from the Aroma transect, 163 from the Eagle Point transect, 48 from the Paposo transect, 23 from the Salars Transect (Salars) and 77 for Totoral dunes transect. Our sampling also included sites where no nematodes could be found (figure 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 transect, 11 families were found in Eagle Point, 12 in the Salars, nine in Totoral Dunes and ten in Paposo (figure 3 B). We observed that some generalist families were ubiquitously found, wheres others were geographically restricted. Cephalobidae were present in all transects, whereas representatives of families Panagrolaimidae and Qudsianematidae were found in five of the transects (all except for the Salars). The family Anguinidae was uniquely found in the Eagle Point transect. The families Trichistomatidae and Mermithidae were unique to the Salars transect. Tylencholaimidae was uniquely found in the Paposo transect and Acuariidae in Altiplano.

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

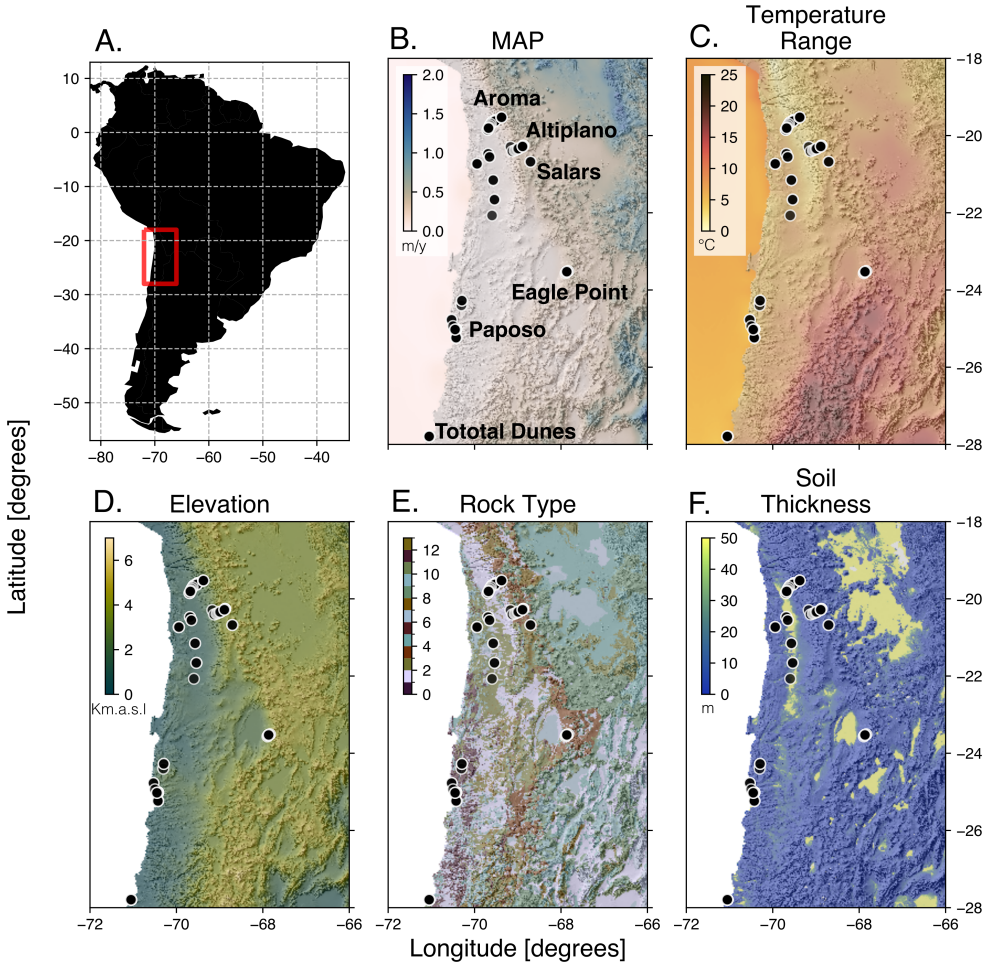

Figure 1. Environmental variables analyzed in the Atacama Desert to predict genera richness across the desert. Rock type is defined as lithological classes from (Hartmann and Moosdorf, 2012) (see supplementary table S10).

genetic diversity in two manners: per taxonomic group including all habitats, and per habitat analyzing one taxonomic group at a time.

for the different taxonomic groups and for the different habitats.

There were between 17 to 166 segregating sites for the different soil nematodes in our networks (supplementary table S1) 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 Dorylamida and Aphelechoidea 16 haplotypes were identified each and 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 geographical clustering of the different haplotypes in the networks, shared haplotypes could be found in geographically distinct habitats. We found genetic diversity at the genera level to be the highest for *Panagrolaimus* (π = 0.05827, θ = 0.04179, figure 2A) and the lowest for *Acrobeloides* (π = 0.01278, θ = 0.02192). At the family level, the highest genetic diversity was found for Aphelenchoididae (π= 0.11199, θ 0.08095, figure 2B), and the lowest was found for Plectidae (π= 0.00633, θ= 0.00993).

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	0.05827	0.04179
Aphelenchoididae	16	0.11199	0.08095

To better understand the possible effect of geography on genetic distance we calculated the latter (Euclidean distance) and compared it to the geographic distance of the different regions with Mantel statistics based on Spearman's rank correlation (ρ). For *Panagrolaimus* a significant ($p < 0.05$) isolation-by-distance pattern could be found ($r = 0.5879$, $p = 0.033333$, 119 permutations). 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 were only one haplotype was found for several individuals (supplementary table S2). 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 randomly varies between habitats

We assessed soil nematode community composition variation in the six transects employing the Jaccard similariy index at the family level. We found the Aroma and Eagle Point transects 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 transect when compared to Totoral Dunes (J=0.25)(figure 3-A). As expected under the isolation-by-distance model, community composition appears to become moderatly more dissimilar with increased geographical distance, between the different transects (Mantel statistic based on Spearman's rank correlation ρ, r 0.5153 , $p = 0.048611$, 719 permutations). We were interested, 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 transects) 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: nematodes that are r-strategists (c-p1 colonizer) are considered indicators of resource availability and degraded 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 analyzed display structuring 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 transect (57.2 % of families found in the transect) as well as in the Aroma and Totoral Dunes transects. Whereas k-strategists (categories c-p4 and c-p5) were the predominant type of families in the Paposo and Salars transects (supplementary table S3). 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)(figure 3-B). Families with unicellular eukaryotic feeding type (UEF) were not found in this study (supplementary table S4). 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 (figure 3-B).

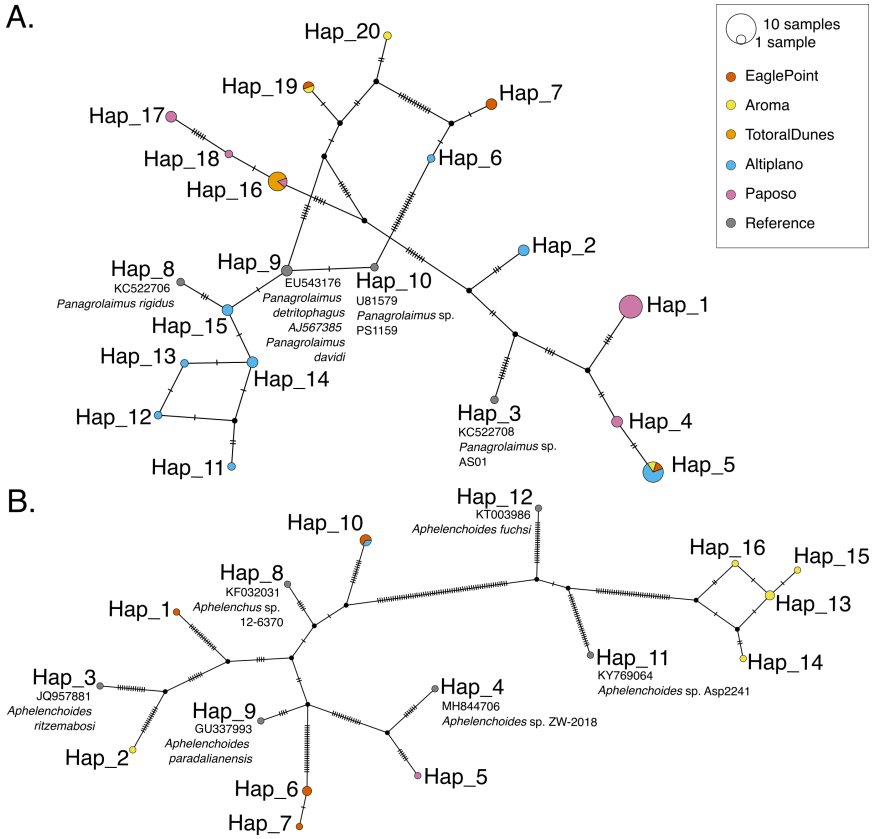

Figure 2. A. Haplotype network of *Panagrolaimus* based on 18S rRNA sequences. B. Haplotype network of Aphelenchoididae based on 18S rRNA sequences. Color refers to sampling locations. Reference sequences were retrieved from the curated 18S-NemaBase (Gattoni et al., 2023). Accession number and species 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.

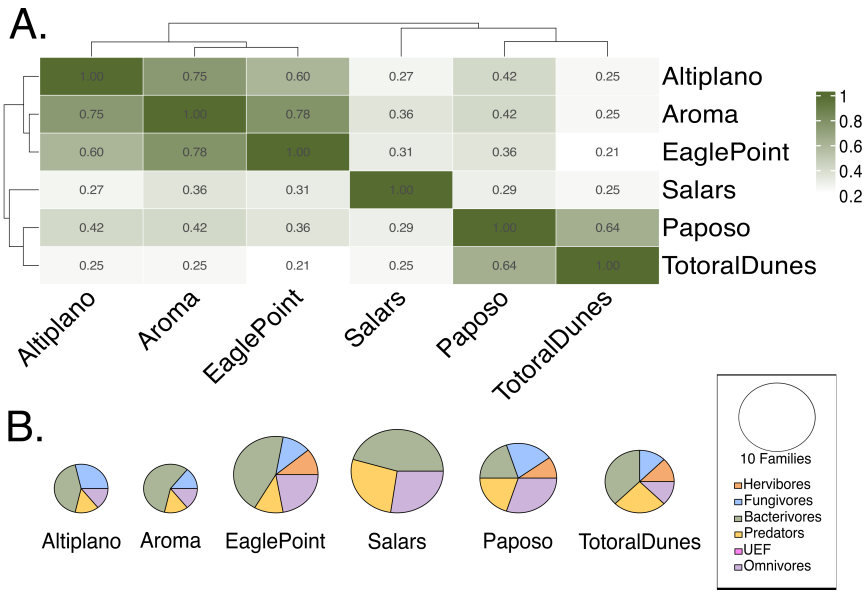

Figure 3. A. Jaccard similarity index of families found in six transects. B. Number of families found per transect represented by the size of the circles, the proportion of families found with the different feeding types is represented in the pie chart by the different colors.

2.5 Precipitation and latitude determine nematode biodiversity

To understand driving forces and constraints of nematode taxonomic biodiversity across the Atacama desert more globally we used a modelling approach incorporating environmental data. We first aimed to predict genera richness and found that the best predictive model using a probabilistic approach incorporated latitude and mean annual precipitation (MAP). The model showed the highest Akaike weight (0.47335) and a statistically significant slope for both environmental variables and the intercept (table 2) which indicates nematode genera richness in the Atacama Desert is related to an increase in precipitation and a decrease in latitude. 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 and latitude (supplementary table S7). This corroborates that mean annual precipitation and latitude, in congruence with the linear models, have a strong consistent influence on genera richness prediction. With both 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 (figure 4 A).

$$\begin{aligned} genera\ richness = &-4.403548 - 0.226990 * latitude \\ &+ 0.026640 * precipitation\ range \end{aligned} \tag{1}$$

Table 2. Summary statistics of (A)the preferred GLS model as determined by Akaike weights for genera richness prediction and (B) the preferred generalized linear model as determined by Akaike weights for likelihood of asexual reproductive mode prediction. Significant values ($p < 0.05$) are indicated with *

	Parameters	Value	SE	t-value	p-value
	Intercept	-3.944688	0.7038593	-5.604370	<0.005*
A.	$Slope_{latitude}$	-0.204889	0.02941174	-6.966230	<0.005*
	$Slope_{MAP}$	0.007444	0.0008188	9.091749	<0.005*

	Parameters	Value	SE	t-value	p-value
B.	Intercept	-1.2907594	0.8565084	-1.507	0.1318
	$Slope_{elevation}$	0.0008667	0.0004077	2.126	0.0335*

2.6 Reproductive mode association to environmental variables

The theory of geographical parthenogenesis predicts an excess of asexual taxa in marginal habitats and finding that nematode communities in different regions of the Atacama desert are taxonomically structured we wanted to test for the specific life-history trait parthenogenesis using our modelling 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 unfertilised female. The remaining seven cultures showed sexual reproduction, i.e. presence of males (supplementary figure S2-G) and no propagation from single females. Sexual strains showed a propagation rate of 0% from single unfertilised females cultures, whereas the asexual strains' propagation rate was 83.3% ($\pm$10.48%). We initially tested variables of elevation and latitude as predictors of reproductive mode along with mean annual precipitation, the former two to test for common variables associated with geographical parthenogenesis, the later given its effect on genera richness prediction from our model (supplementary table S8). In addition, we used a model including vegetation coverage (supplementary figure S12, supplementary table S11). The best predictive model for reproductive mode incorporated only elevation showing the highest Akaike weight and a statistically significant slope(table 2 B), while, for example, plant association did not show any effect on the prediction of reproductive mode. Our validation of this linear model with a random forest approach supports that elevation is the main driver for reproductive mode evolution in soil nematodes in the Atacama (supplementary table S9).

Results for both model approaches are displayed as the probability of taxa reproducing asexually, 0 represents no chance of being asexual (indicating sexual reproduction) and 1 corresponds to 100% chance of reproducing asexually (figure 4).

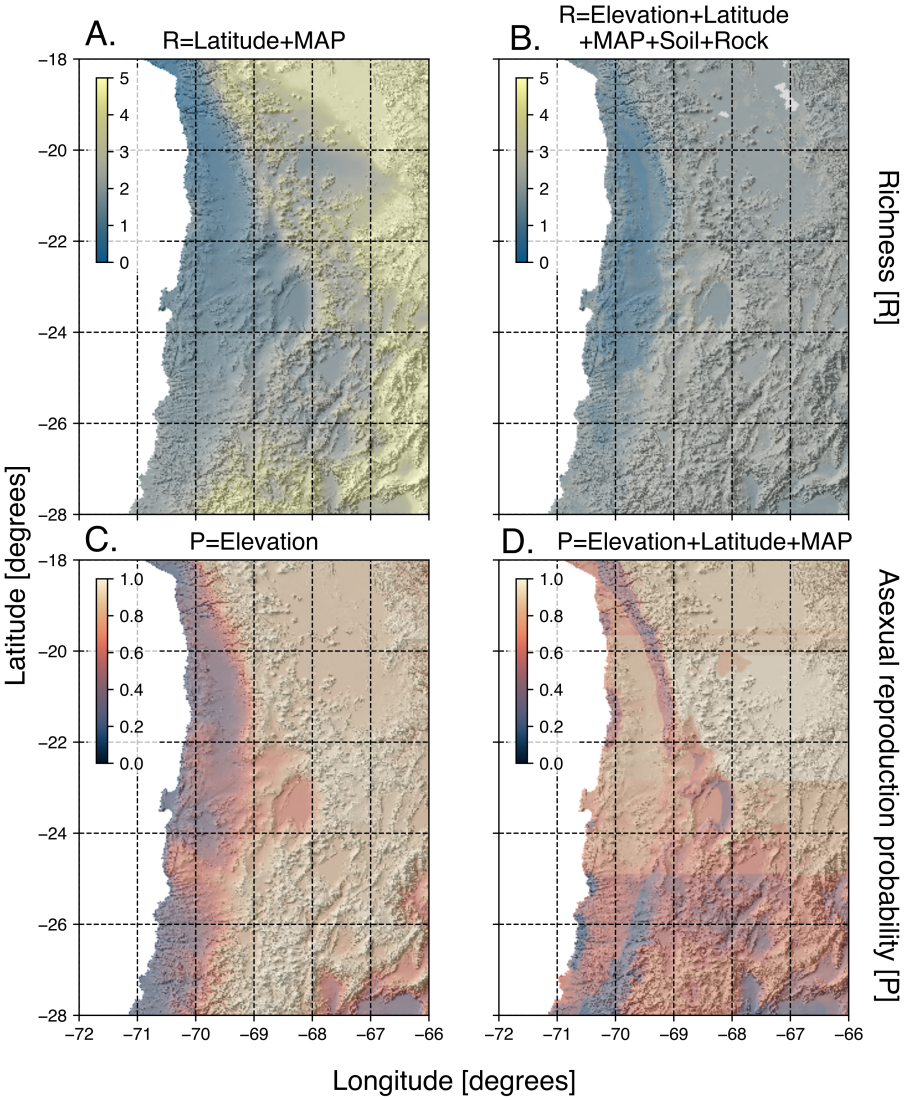

Figure 4. Model predictions for genera richness and probability of a nematode being asexually reproducing in the Atacama Desert. (A) shows genera richness (R) as predicted by latitude and mean annual precipitation using a generalized linear model, (B) shows predicted genera richness implementing a random forest approach, (C) displays the probability of a nematode being asexually reproducing (P) as predicted by elevation using a generalized linear model and (D) the probability of being asexually reproducing implementing random forest.

3 DISCUSSION

Altered soil characteristics, along with increasing temperatures, will have an impact on community dynamics and species abundance, specially in times of accelerated global change (Jones et al., 2017; Zablocki et al., 2016; Prather et al., 2012). Desertification processes, as one example among 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 baseline 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 a region widely regarded as 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 identified 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 while others exhibit signs of a degraded soil food web. 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 locations 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 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 unique communities in the Salar de Huaco and Laguna Grande areas 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 soil food web, both the Salars and Paposo were dominated by persisters that are sensitive to environmental disturbance and often have a narrow ecological amplitude. In contrast, in Altiplano, Totoral Dunes, and Aroma the dominant groups were colonisers that are more resistant to adverse environmental conditions that could indicate degraded soil food web function (Bongers and Bongers, 1998; Du Preez et al., 2022). Sand dune systems, such as Totoral Dunes, have already been reported to be dominated by coloniser taxa due their broad ecological

range, with high abundances of the family Cephalobidae throughout coastal sand dunes (Ruiz-Cuenca and Abolafia, 2021, 2023).

Precipitation and latitude shape soil nematode diversity patterns across the Atacama Desert. 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. In such scenarios, in order to disentangle the driving factors of species and communities distribution, modeling approaches provide a simplified representation of real-world phenomenon(Weisberg, 2007) and can aid in disentangling the interplay of ecological, geographical and edaphic factors (Guisan and Zimmermann, 2000). We found that genera richness is primarily determined by precipitation and latitude. Increased precipitation has been shown to be a biodiversity driver of other organisms in desert environments, given that it regulates nutrient availability in soil as well as water content (Hu et al., 2022). Soil nematodes live in the water film within soil particles and lack of water might hinder their movement (Yeates, 2004). Likewise, rotifers and tardigrades occupy the water film in soil (Schratzberger et al., 2019) and have the ability to enter anhydrobiosis (Ricci, 1998; Leeuwenhoek, 1702). Precipitation as a proxy for water availability in soil also shapes the distribution of other invertebrates. In coleopterans, species ranges and habitat suitability is related to precipitation in the Atacama Desert (Zúñiga-Reinoso et al., 2021). Our results are in line with other nematode studies where mean annual precipitation has been suggested as the predictor of the assemblage structure for nematodes at the regional scale in tropical forests (Shao et al., 2023) and on a global scale (Nielsen et al., 2014) . Previous reports demonstrate that increased precipitation particularly affects soil nematode communities, modulating an increase in abundance of bacterial feeding nematodes, possibly due to the increase in bacterial biomass with increased precipitation (Chen et al., 2014). Our results show that biodiversity increases with decreasing latitude in the Atacama Desert, supporting a latitudinal diversity gradient (LDG) (Fischer, 1960; Wallace, 1878). LDG has been shown empirically for several taxa (Qian et al., 2024; Economo et al., 2018; Hillebrand, 2004), but is not yet well understood on a theoretical level as latitude can be a confounding factor for other mechanisms or variables driving the pattern (Saupe, 2023; Rapoport, 1975; Gaston, 2000; Rosenzweig, 1992).

Asexual nematodes are more prevalent in higher altitudes in the Atacama. Using a species richness modeling approach we used nematodes as indicators to understand regional patterns in the soil ecosystem of the Atacama Desert as an extreme environment aiming to disentangle the driving factors of species and communities distributions. 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 is 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, 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.

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 a extreme environment as a whole, 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 in the marginal ranges of high altitudes.

Our study highlights the necessity of biodiversity and health ecosystem 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 health 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 locations across the desert defined as transects: Altiplano (ALT), Aroma (ARO), Eagle Point (EPT), Salar de Huasco and Laguna Grande (Salars),Paposo (PAP) and Totral Dunes (TDT).Sampling in the protected Salar de Huasco was conducted under the authorization (09/2023) of the Corporación Nacional Forestal (CONAF). Soil samples of aproximately 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. They were initially checked for the presence/absence of nematodes on-site. Nematodes were extracted from soil 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 (look the specification) microscope.

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 figure 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 transect 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 Genious 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). 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 transects (Altiplano, Aroma, Eagle Point, Salars, Paposo and Totoral Dunes) using 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 transects 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 transect 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 transects.

4.6 Modeling ecological constraints of nematode biodiversity

We evaluated climatic (environmental) and geomorphological (edaphic and geographic) 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. 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. 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 climatic variables evaluated were mean annual temperature, mean annual precipitation, range of temperature and range of precipitation (range is defined as the difference between minimum and maximum daily values) (supplementary table S5). 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) to asses variable correlations (supplementary figure S9) as well as 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 figure S8) to fulfil model assumptions. Bioninformatic pipelines were optimized using ChatGPT.

We evaluated a total of 57 models including null models (supplementary table S6), which considered different combinations of a selected number of predictive variables. We selected those variables based on two criteria: 1) variables should not display strong correlation whit 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 three 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 model was 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 model was 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, to ensure no mating, cultures were propagated 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.

Environmental data was collected as in the previous section. Models testing elevation, precipitation and mean annual precipitation as predictors for reproductive mode (sexual or asexual) were performed implementing a logistic regression analysis using the glm function from the package stats in R (v. 4.3.2), using the $family = binomial$. 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

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DATA AVAILABILITY

Code implemented for this study can be found on the github page: https://github.com/lauraivillegasr/BiogeographyDesert , it will be further made available under the capsule number 6395549 in CodeOcean where all scripts can be run to reproduce the analysis.

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