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EDITED BY

Alison G Nazareno,
Federal University of Minas Gerais, Brazil

REVIEWED BY

Enrico Alejandro Ruiz,
National Polytechnic Institute, Mexico
Kurt Galbreath,
Northern Michigan University, United States

*CORRESPONDENCE

Abigail C. Jackson
✉ acjackson5@alaska.edu

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Effect of climate history on the genetic structure of an Antarctic soil nematode

Abigail C. Jackson ^{1*}, Steven D. Leavitt ^{1,2},
Dorota Porazinska ³, Diana H. Wall ⁴, Thomas O. Powers ⁵,
Timothy S. Harris ⁵ and Byron J. Adams ^{1,2}

¹Department of Biology, and Evolutionary Ecology Laboratories, Brigham Young University, Provo, UT, United States, ²Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT, United States, ³Department of Entomology and Nematology, University of Florida, Gainesville, FL, United States, ⁴Department of Biology and School of Global Environmental Sustainability, Colorado State University, Fort Collins, CO, United States, ⁵Department of Plant Pathology, University of Nebraska – Lincoln, Lincoln, NE, United States

Historical climate disturbances such as glacial cycling and fluctuating stream, lake, and sea levels strongly influence the distribution and evolutionary trajectories of Antarctic terrestrial species. Antarctic invertebrates, including the ubiquitous sentinel nematode species *Scottnema lindsayae*, are especially sensitive to climate disturbances. We tested hypotheses associated with the historical geographic and population genetic structure of this species as it occurs across the McMurdo Dry Valleys of Antarctica. To reconstruct the influence of climate disturbance and ecological conditions on this species, partial mitochondrial cytochrome c oxidase I gene sequences were analyzed from individual *S. lindsayae* collected from sites across the McMurdo Dry Valleys reflecting opposing gradients of climate disturbance during the Last Glacial Maximum. We found that populations were strongly demarcated by geomorphic barriers, with distinct haplotypes associated with valleys except among valleys that experienced glacial advance and retreat during the LGM. Our work shows that contemporary populations of these animals are strongly structured by prior climate history and reinforced by subsequent ecological conditions. Such findings can be useful for understanding the processes that shape the distribution and abundance of these ecologically important animals and interpreting long-term monitoring of demographic shifts in response to changing climate trends in the McMurdo Dry Valleys.

KEYWORDS

Antarctica, biogeography, climate disturbance, evolution, McMurdo Dry Valleys, population genetics, polar, sentinel species

1 Introduction

Large-scale climate disturbances have lasting effects on ecological conditions and evolutionary change of populations (e.g., Opdam and Wascher, 2004). Climate disturbances create opportunities for stochastic gene flow among populations within a species that are otherwise structured by geography (Moran and Ormond, 2015; Schierenbeck, 2017). The Last Glacial Maximum (LGM; 20–10 kya) caused large-scale extinctions, subsequent expansions, and range shifts apparent in the phylogeography of many species (Hewitt, 1996, 2001; Riddle, 1996; Shafer et al., 2010). Understanding these historical evolutionary responses is important when considering the resilience of ecological communities to climate change (Willis et al., 2010). Mitochondrial DNA has been used extensively to test hypotheses of evolutionary responses to climate disturbances (Avise et al., 1987; Avise, 2009; Hickerson et al., 2010). Utilizing this molecular marker, intraspecific responses to the LGM have been studied across ecosystems and throughout the animal kingdom (Lobon et al., 2016; Khanal et al., 2018; Collins et al., 2019; Guimarães et al., 2022). Climate disturbance events, past and present, are especially influential in the evolutionary patterns of non-vagile species (Malcolm et al., 2002; Normand et al., 2011), and exceptionally so for soil invertebrates faced with extinction by glacial advances during the LGM (McGaughan et al., 2011; Collins et al., 2019, 2020). The extent to which these disturbance events impact the genetic structure of soil invertebrates is less well known.

The extreme Antarctic environment is no exception to climate disturbances that have influenced contemporary biogeography and abiotic conditions (Convey et al., 2014). Though experiencing a relatively stable climate since the mid-Miocene (Sugden et al., 1993; Spector and Balco, 2021; Halberstadt et al., 2022), the LGM created lasting legacies of habitat quality (Campbell et al., 1998; Burkins et al., 2000) and dispersal patterns (Virginia and Wall, 1999; Convey et al., 2014). Work in both terrestrial (Baird et al., 2021) and marine ecosystems (Soler-Membrives et al., 2017) and more specifically on springtails (Stevens and Hogg, 2003; Nolan et al., 2006; Collins et al., 2019, 2020), mites (Marshall and Coetzee, 2000; Brunetti et al., 2021), and mosses (Biersma et al., 2018) have all corroborated the evolutionary impact of the LGM. Among taxonomic groups that have received less attention are Antarctic nematodes. The haplotype diversity of Antarctic soil nematodes has been demonstrated (Courtright et al., 2000; Adams et al., 2007; Velasco-Castrillón and Stevens, 2014). However, the impact of climate disturbance on endemic terrestrial Antarctic biota has yet to be examined using the phylogeographic patterns of broadly distributed nematode species.

The nematode *Scottinema lindsayae* (Timm, 1971) is found across the scant ice-free regions of Antarctica (Freckman and Virginia, 1998; Adams et al., 2014; Velasco-Castrillón and Stevens, 2014). The McMurdo Dry Valleys comprise the largest of these ice-free landscapes (MDVs; 78°S, 162°E; 4,500 km²; Levy, 2013). Freezing temperatures (−18°C; Doran et al., 2002a), low soil moisture (1% water by volume; Campbell et al., 1998), high salinity (~1600 µS/cm; Nkem et al., 2006a), and a truncated growing season (~2 months per

year) reinforce the extreme conditions for life to exist in the MDVs. Under such harsh conditions, terrestrial communities are composed of only a few taxa of soil invertebrates, fungi, and microbial flora (Adams et al., 2014; Dreesens et al., 2014; Feeser et al., 2018). In the 65% of soils suitable for colonization, the communities have minimal functional overlap and are sensitive to climate disturbances (Freckman and Virginia, 1998; Fountain et al., 2014, 2016; Andriuzzi et al., 2018; Franco et al., 2021). In this low diversity ecosystem, *S. lindsayae* is the most common and often the exclusive metazoan in high saline (EC < 700 mS cm^{−1}), low soil moisture (<5%), and high elevation habitats that are inhospitable to other metazoan taxa (Treonis et al., 1999; Nkem et al., 2006a; Poage et al., 2008; Adams et al., 2014; Zawierucha et al., 2019). As a result, populations of *S. lindsayae* are distributed across heterogeneous landscapes, thus providing an ideal system to study the effects of contemporary and historical climate trends on population structure throughout the MDVs. *S. lindsayae* functions as an excellent sentinel of MDVs soil ecosystem structure and functioning for its sensitivity to climate disturbances (Freckman and Virginia, 1997; Doran et al., 2002b; Porazinska et al., 2002; Gooseff et al., 2017; Andriuzzi et al., 2018), indicator of soil habitability (Courtright et al., 2001; Poage et al., 2008), and its disproportionate role in carbon cycling (Barrett et al., 2008; Andriuzzi et al., 2018). As such, the evolutionary response of *S. lindsayae* to past climate disturbances is important for interpreting contemporary responses to ongoing environmental change and sensitivity to future climate disturbances.

The main objective of this study was to identify the phylogeographic response of the sentinel species *S. lindsayae* in the MDVs to historical climate disturbance. We hypothesized that physical and population processes associated with the LGM are responsible for contemporary patterns of nematode distribution and connectivity rather than present day proximal processes shaping phylogeographic patterns. To test the role of historical climate disturbance on the genetic structure of *S. lindsayae*, we focused on three potential drivers: 1) geomorphic barriers that restrict connectivity among populations, 2) legacies of glacial advance and paleolake inundation during the LGM that may have disrupted or homogenized population structure, and 3) contemporary ecological gradients that could shape intraspecific diversity.

2 Materials and methods

2.1 Study system

Scottinema lindsayae (Timm, 1971) is well studied in terms of abundance, distribution, and ecosystem functioning (Figure 1; Adams et al., 2006, 2007, 2014). This species is known to tolerate low soil moisture (<5%; Poage et al., 2008), high salt content (EC < 700 mS/cm; Nkem et al., 2006a; Poage et al., 2008), and high pH (Courtright et al., 2001). Population abundances and life stage diversity are clearly linked to suitable soil habitat (Courtright

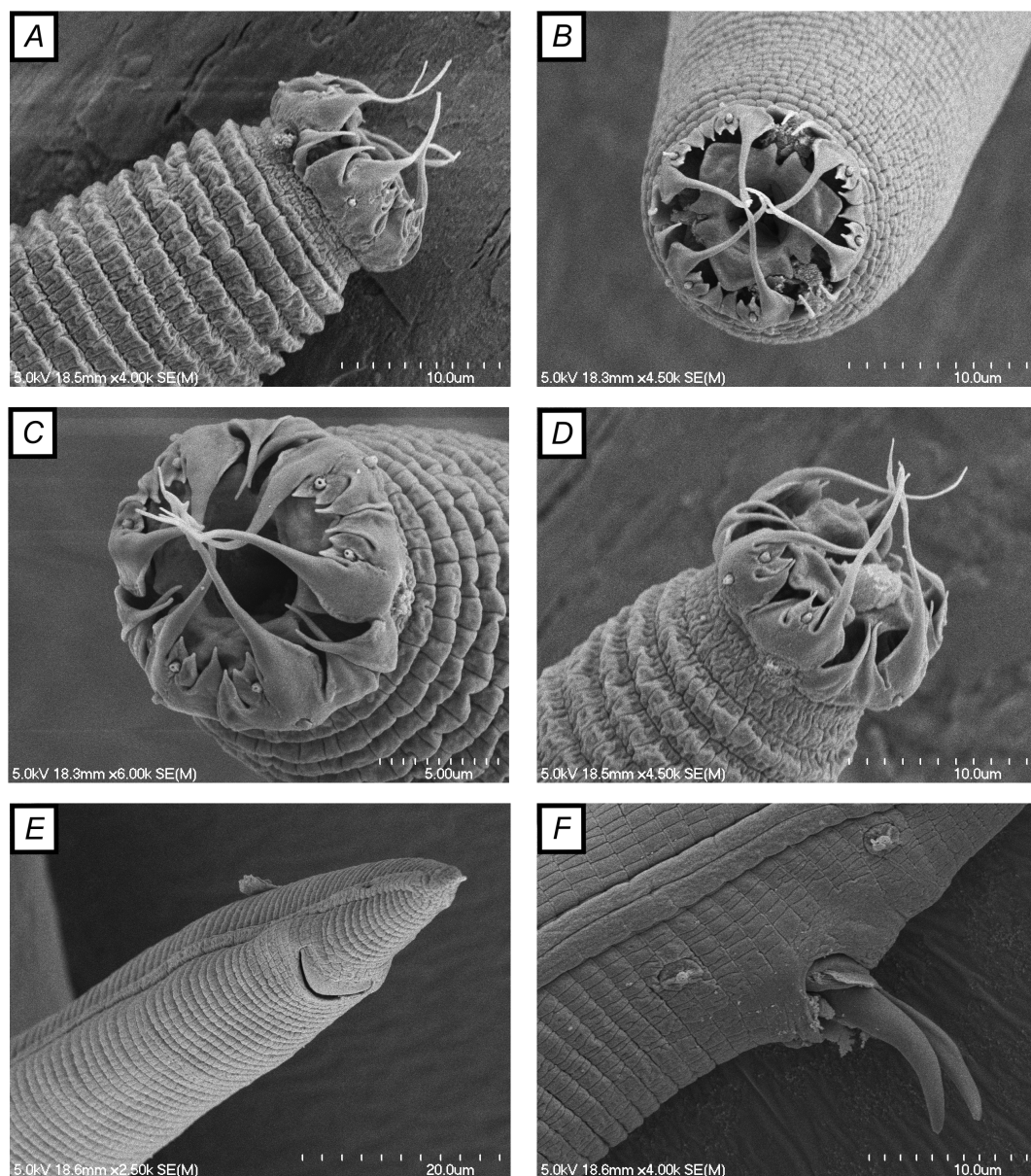


FIGURE 1
Scanning electron microscope images of *S. lindsayae* collected from Garwood Valley. Images (A–D), adult anterior view. Image (E), adult male posterior end. Image (F), adult male with protruding spicula.

et al., 2001; Poage et al., 2008) and respond to contemporary environmental disturbances (Porazinska et al., 2002; Barrett et al., 2008; Andriuzzi et al., 2018).

2.2 Geographic sampling

To study the impacts of opposing disturbance histories during the LGM on nematode populations in the MDVs, we collected soil from 26 sites (Figure 2; Table 1) representing 8 valley systems. Of

note, Taylor Valley is further divided into three well studied lake basins – Fryxell Basin, Hoare Basin, and Bonney Basin – that are distinct in their glacial histories. Of all the sites, 14 represent locations within valleys considered putative undisturbed refugia. These areas of refugia have likely existed as overlapping habitats with suitable abiotic conditions (Convey et al., 2020) throughout recurrent glaciations of the Pleistocene and even through the formation of the MDVs in the mid-Miocene (15–9 mya; Denton et al., 1984, 1993; Sugden et al., 1993; Schäfer et al., 1999). The remaining 12 sites represent locations in the MDVs that were disturbed during the LGM (10–21 kya; Table 1) either by local



FIGURE 2
Map sampling locations for *S. lindsayae* in the McMurdo Dry Valleys. Triangles indicate undisturbed sites (putative refugia), squares represent disturbed sites (impacted by glaciation or paleolake inundation during the LGM). Red diagonal hatching denotes the historical extent of the Ross Sea Drift incursion during the LGM. Each valley or basin is represented by a different color. Where possible we use a consistent color scheme across figures, with darker variants to represent putative refugia when shape-based distinctions were not applicable. Soils collected adjacent to contemporary lakes are referred to as the lake basin they came from.

glacial expansion or paleolake inundation. We chose these sites based on published soil exposure ages (Table 1), proximity to recorded local glacier terminal moraines and paleolake shorelines, and presence of viable *S. lindsayae* communities.

2.3 Soil extraction

We collected 500 g of the top 10 cm of soil at each site using clean plastic scoops and sterile Whirlpak® bags during the Austral

TABLE 1 Sampling site descriptions and locations including the site name, valley or basin system, glacial history (disturbed or undisturbed) during the Last Glacial Maximum, *S. lindsayae* abundances as a proxy for soil habitability, number of individuals sanger sequenced from each site (sample size), latitude and longitude (decimal degrees), elevation (m), and estimated exposure ages based on the existing literature.

Site	Valley	Glacial History	Scottnema abundances (#/kg soil)	Sample Size	Lat	Long	Elevation (m)	Estimated Exposure ages	Citation
Levy Cirque	Beacon Valley	Undisturbed	358	16	-77.7972330	160.6154780	1522	2.3 mya	Schäfer et al., 2000
Beacon Valley, Lower		Undisturbed	3678	13	-77.8067660	160.7177160	1017		
Beacon Valley, Upper		Undisturbed	2320	8	-77.8805330	160.4578160	1386		
Battleship Promontory	Alatna Valley	Undisturbed	147	10	-76.9223500	161.0814330	1241	5 mya	Sugden and Denton, 2004; Margerison et al., 2005; Diaz et al., 2020
Alatna Valley		Undisturbed	1333	13	-76.8946500	161.1391500	981		Calkin, 1964
Hawkings Cirque	Wright Valley	Undisturbed	196	14	-77.5101920	160.5785970	1204		
Labyrinth		Undisturbed	351	7	-77.5500000	161.5166660	767	3 mya	Schäfer et al., 1999; Lewis et al., 2006
Dais		Undisturbed	132	7	-77.5500030	161.1847300	801	4 mya	Schäfer et al., 1999
Lake Brownworth		Disturbed	726	6	-77.4386330	162.7288030	241	26-5 kya	Hall et al., 2001
Mount Suess Peak	Mackay Glacier	Undisturbed	580	7	-77.0366280	161.7101190	970		Sugden and Denton, 2004; Jones et al., 2015
Mount Suess, Lower		Disturbed	3801	16	-77.0182700	161.7343100	517	25-5 kya	
Pegtop Mountain		Disturbed	3047	2	-77.0473530	161.4442960	823	25-5 kya	
Mount Falconer	Fryxell Basin, Taylor Valley	Undisturbed	446	11	-77.5731720	163.1585970	731		Stuiver et al., 1981; Denton et al., 1993; Burkins et al., 2000; Bockheim et al., 2008; Fountain et al., 2014
Gurkha Peak		Undisturbed	2308	9	-77.6509600	163.2515110	917		
Lake Fryxell		Disturbed	110	12	-77.6076940	163.2506830	9	21-12 kya	
Explorers cove		Disturbed	3150	5	-77.5665830	163.4934500	13	10 kya	Anderson et al., 2014; Fountain et al., 2014
Mount Rae	Hoare Basin, Taylor Valley	Disturbed	233	4	-77.6005850	162.8507150	1057		Bockheim et al., 2008
Lake Hoare		Disturbed	3007	11	-77.6349830	162.8888000	129	21-12 kya	Stuiver et al., 1981; Burkins et al., 2000; Hall et al., 2000; Bockheim et al., 2008
Campbell Terrace	Bonney Basin,	Undisturbed	1445	8	-77.6787330	162.5009830	957	120-70 kya	Burkins et al., 2000; Hall et al.,

(Continued)

TABLE 1 Continued

Site	Valley	Glacial History	Scottnema abundances (#/kg soil)	Sample Size	Lat	Long	Elevation (m)	Estimated Exposure ages	Citation
	Taylor Valley								2000; Bockheim et al., 2008
Lake Bonney		Disturbed	470	11	-77.7250000	162.3120000	77	21-12 kya	Stuiver et al., 1981; Burkins et al., 2000; Hall et al., 2000; Bockheim et al., 2008
Miers Valley, high	Miers Valley	Undisturbed	4831	10	-78.1166720	163.7507920	516		
Lake Miers		Disturbed	794	13	-78.1005970	163.8091190	167	26-5 kya	Clayton-Greene et al., 1988; Joy et al., 2017
Garwood Valley, high	Garwood Valley	Undisturbed	1647	7	-78.0379670	163.8748330	581		
Lake Garwood		Disturbed	528	12	-78.0264780	163.8512080	351	26-5 kya	Levy et al., 2013; Joy et al., 2017
Wall Valley	Victoria Valley	Undisturbed	237	10	-77.4955000	160.8651000	1617		
Lake Vida		Disturbed	90	7	-77.3822500	161.8178500	108	300-120 kya	Calkin, 1963; Bockheim and McLeod, 2013; McGowan et al., 2014

Fryxell Basin, Hoare Basin, and Bonney Basin comprise Taylor Valley.

summer between 1996 to 2022. A GPS point of each site was recorded and used for analyses. We transported soils within 48 hours to the Crary Science and Engineering Laboratory at McMurdo Station where they were stored at 4°C until soil invertebrate collection and geochemistry analyses could be performed within 48 hours. We performed a modified sugar centrifugation extraction (Freckman and Virginia, 1993) with a subsample of 100 g to calculate metazoan abundance. We counted soil invertebrates and identified to species, as living or dead, life stage (juvenile or adults), and sex under an inverted microscope (Olympus CKx41, Tokyo, Japan). We measured soil moisture, pH, and electrical conductivity following standard protocols of the MCM LTER project (<https://mcm.lternet.edu/content/soil-elevational-transect-experiment>). Subsequent subsamples of 100 g were extracted in the same way at Brigham Young University to collect individuals of *S. lindsayae* for molecular analyses. All soil samples from which *S. lindsayae* individuals were extracted for this study are archived in the Monte L. Bean Life Sciences Museum frozen soil repository at Brigham Young University. These samples remain available for subsequent morphological, molecular, or ecological analyses. While museum catalog numbers have not yet been assigned, each sample is uniquely identified by its site name and collection metadata. These identifiers, along with sample-specific information sufficient for retrieval, are provided in [Supplementary Table 1](#).

2.4 PCR amplification and sanger sequencing

Following nematode DNA extraction methods of Powers and Harris (1993), we hand-picked individual *S. lindsayae* with an eyelash pick into 10 µl of sterile elution buffer on a cover slip. Using a sterilized 10 µl micropipette tip, we ruptured the nematode by gentle pressure and confirmed the lysate. To a 0.2 ml microcentrifuge tube we pipetted the lysate and 5.2 µl of sterile water used to clean the cover slip. We combined nematode lysate with 2.4 µl each of 20 µM diluted forward primer (COI-Scott-F1: 5'-GTTACAACCTTTTGTGCTTATTCTCTCAC-3') and reverse primer (COI-Scott-R2: 5'-CTGTAAAATAAGCTCGACTRTCWG-3'). Some extractions were performed with an alternative reverse primer with higher fidelity but shorter sequence reads (COI-Scott-R4 5'-GCRTCRTACCTGTTACRTATATRTG-3'). This was done due to lack of successful amplification with the initial primer. We added 15 µl of JumpStart™ REDTaq® ReadyMix™ Reaction Mix (Sigma-Aldrich, DE) to the mixture, vortexed for 30 seconds (sec) to mix, and then placed the mixture into a DNA thermal cycler (Mastercycler X50s, Eppendorf, Germany) with the following cycling parameters: initial denaturation at 94°C for 5 min, 40 cycles of denaturation at 94°C for 30 sec, annealing at 58°C for 30 sec, extension of 0.5°C/sec ramp to 72°C for 90 sec, followed by a final extension at 72°C for 5 min and held at 4°C.

Following PCR amplification, we screened the products on a 1% TAE agarose gel stained with ethidium bromide and visualized with a UV image capture (GelDoc Go, Bio-Rad Laboratories, USA). Successful DNA amplifications were cleaned with a magnetic bead cleaning protocol. We added Mag-Bind® TotalPure NGS (Omega Bio-tek, GA) in a 1.2× concentration to the remaining PCR product, vortexed for 10 min at 2,000 rpm, centrifuged for 5 sec, and followed the standard Omega Bio-tek protocol. We quantified DNA with a Qubit 4 Fluorometer (Invitrogen, USA). Finally, we diluted or concentrated products to 10 ng DNA for Sanger dideoxy sequencing at the Brigham Young University Sequencing Center (Provo, UT).

To ensure highly divergent populations based on COI data did not warrant further investigation as divergent species (Smythe et al., 2019; Ahmed et al., 2022), we sequenced the nuclear Large Ribosomal Subunit (LSU). With the exception of a 52°C annealing step, we used the same DNA template, extraction protocol, PCR cycling parameters, and sequencing chemistry used for the most genetically divergent COI populations: Beacon Valley upper, Lake Bonney, Campbell Terrace, Gurkha Peak, Lake Hoare, Levy Cirque, Mount Rae, Mount Suess peak, and Lake Vida. We used Nadler et al. (2006) primers: forward primer (F-LSU-391: 5'-AG CGGAGGAAAAGAACTAA-3') and reverse primer (R-LSU-501: 5'-TCGGAAGGAACCAGCTACTA-3') to sequence 965 base pair (bp) of the LSU gene.

2.5 Genetic analysis

We verified sequences for the intended loci by comparing them using the NCBI reference database and confirmed the coding sequence did not contain early termination codons, numts (Bensasson et al., 2001), or indels. We aligned sequences in Geneious Prime® 2022.2.2 (<https://www.geneious.com>, New Zealand) using the default settings of MAFT Alignment v7.490. We subsequently trimmed consensus sequences and checked for ambiguities or missing nucleotides using Geneious Prime® 2022.2.2. Out of 838 individual nematodes, 249 yielded successful mtDNA amplicons of 284 base pairs in length which were subsequently aligned and mapped to the reference sequence for further analyses of populations' genetics. The number of sequences processed may not have captured all possible haplotypes (Supplementary Figure 1; Brown et al., 2012). Additionally, 30 LSU sequences, 922 base pairs in length were aligned and mapped to the reference genome. These were found to have no diversity and were not used for downstream analysis. We accessioned the partial COI and LSU sequences in the NCBI GenBank database (OP456699-OP456947 and OP692666-OP692695, respectively).

2.6 Population genetic analyses

All population genetic analyses were conducted using the aligned 284 bp COI mtDNA sequences. We calculated metrics on

haplotype number (Hap), haplotype diversity (h), number of polymorphic sites (P), and nucleotide diversity (π) for each population using ARLEQUIN v3.5.2.2 (Excoffier and Lischer, 2010). To determine the qualitative population structure, we produced median-joining haplotype networks designating the sample site and the valley system using pegas package (Paradis, 2010) and haplotype (Aktas, 2020) following the code provided by Toparslan et al. (2020) using R Studio (R Core Team, 2002). We also constructed a dendrogram stratified by sampling site populations and valley system constructed in poppr 2.9.3 using Nei's D genetic distance measure (Nei, 1972) with 1,000 bootstrap replications. Although the data may have limited power to recover true phylogenetic relationships (Ballard and Rand, 2005), we reconstructed a maximum likelihood phylogenetic tree of all sequences to further represent the evolutionary relationships among sample sites using HKY+F+G4 as the evolutionary model determined the most appropriate for mitochondrial DNA sequence evolution by IQ-tree's model finder (Kalyaanamoorthy et al., 2017; Minh et al., 2020), 10,000 bootstrap resample iterations, and *Acrobeloides varius* COI as the outgroup (Accession number: KX889087.1). The resulting tree was visualized and manipulated using FigTree v1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

To quantitatively assess genetic structure, we calculated pairwise F_{ST} from pairwise nucleotide differences among sites and among valleys. We estimated the statistical significance with 1,000 permutations implemented in ARLEQUIN using the Kimura 2-parameter model (Kimura, 1980). We chose this model because it was most similar to the best fit model (see above). Pairwise uncorrected (p distance) and corrected (Kimura 2P with gamma 4 parameter rate; K2PG4) genetic distances were generated in Molecular Evolutionary Genetic Analysis (MEGA 11.0.13). Finally, we assessed the genetic structure among valleys and sampling sites by performing an analysis of molecular variance (AMOVA) with ARLEQUIN (Kimura 2P distance method) grouping by ten valleys (Table 1).

2.7 Demographic history

To evaluate the demographic history of *S. lindsayae* populations, we calculated Tajima's D and Fu's F_s in ARLEQUIN with 1,000 permutations. These statistics were used descriptively to explore departures from neutral expectations and to support patterns observed in Bayesian skyline plots, particularly regarding recent population expansions (significant negative values) or contractions (positive values). Because these tests were not used for formal hypothesis testing or multiple comparisons, and were interpreted in conjunction with other demographic metrics, we did not apply a multiple testing correction.

To further assess the effect of the LGM disturbance event on *S. lindsayae*, we used Bayesian skyline plots (BSPs) at each valley and for the combined valleys of Taylor, Miers, and Garwood given the lack of significant genetic differentiation and monophyly of the three valleys. BSPs (Drummond et al., 2005) were constructed in BEAST v2.6.7 (Bouckaert et al., 2019) using the following priors:

gamma site model with 4 categories, an HKY empirical evolutionary model as determined by IQ-tree, a strict clock with a molecular rate of 4.7 E -8 substitutions per site per year as determined by the evolutionary rate of *Caenorhabditis elegans* mitochondria DNA (Denver et al., 2000; Xu et al., 2012), and the calculated natural life span of *S. lindsayae* (Overhoff et al., 1993) and the number of days with an average temperature above freezing in the MDVs (Hudson et al., 2022) given that days below freezing pause the life cycle in a cryptobiotic state and must be accounted for in the *in situ* life span of *S. lindsayae*. All models were run with 20,000,000 permutations and reached an ESS score over 200. While mitochondrial DNA is not recommended as the best marker for assuming contemporary population size (Galtier et al., 2009), BSPs provide a rough estimate of effective population size change and are used here in a more relative manner to compare valleys.

2.8 Environmental parameters

To assess the statistical significance of environmental conditions on genetic variation, we analyzed the correlation of intrapopulation genetic differentiation (within population F_{ST}) and haplotype diversity within a population to elevation, soil moisture, electrical conductivity, distance to the coast, and glacial history with generalized linear models in the stats package in Program R (R Core Team, 2002). We then determined the best fitting model based on Akaike Information Criteria adjusted for small sample

size (AIC_C; Akaike, 1973) using AICcmodavg package (Mazerolle, 2020) and MuMIn package (Bartoń, 2022) to average top models. Distance to the coast and elevation were correlated and not considered in the same models. We estimated distance to the coast with GPS and Google Earth Pro. Assumptions for residuals and normalcy were validated on the top model. Top models with a weight (W_i) above 0.05 were averaged and used to calculate the 85% confidence interval of the top parameters to determine the strength of the relationships between ecological conditions and genetic response.

3 Results

3.1 Genetic diversity

We identified high levels of genetic diversity among *S. lindsayae* across all valleys. Of the 249 sequences (~ 12 per site), 55 haplotypes were recovered with 39 (70%) being unique to a sampling site and 41 (75%) being unique to a valley. Haplotypes varied with 52 polymorphic sites (Supplementary Figure 2). The lowest haplotype diversity was found in isolated sites - Beacon Valley Lower, Battleship Promontory, Mount Suess lower, and Pegtop Mountain had one recovered haplotype each. Wright Valley's Dais population had the highest haplotype diversity. Garwood Lake had the highest nucleotide diversity. We found high levels of genetic distance ($\leq 7.4\%$; Table 2; Supplementary Figure 4) for corrected

TABLE 2 Genetic differentiation (F_{ST}) matrix among valley or lake basin calculated in ARLEQUIN using Kimura 2P gamma 4 model.

	Beacon valley	Alatna valley	Wright valley	Mackay glacier	Fryxell basin	Miers valley	Garwood valley	Victoria valley	Hoare basin
Beacon Valley									
Alatna Valley	0.450						Top 15%		
Wright Valley	0.382	0.194					Bottom 15%		
Mackay Glacier	0.726	0.422	0.165						
Fryxell Basin	0.809	0.619	0.502	0.630					
Miers Valley	0.870	0.656	0.534	0.659	0.007				
Garwood Valley	0.638	0.370	0.287	0.470	0.095	0.154			
Victoria Valley	0.582	0.186	0.100	0.369	0.535	0.580	0.290		
Hoare Basin	0.904	0.669	0.540	0.667	0.023	0.040	0.182	0.595	
Bonney Basin	0.931	0.710	0.569	0.707	0.098	0.219	0.245	0.651	0.132

Locations reflect the pooled population from the respective valley or basin. Red-filled cells correspond to F_{ST} values in the bottom 15%. Blue-filled cells correspond to values in the top 15%. All comparisons are statistically significant except for those that are shaded in grey stripes.

TABLE 3 Molecular diversity metrics for each sampling site population including number of sequences (N), number of haplotypes with number of unique haplotypes (Hap()), number of polymorphic sites (P), haplotype diversity (h), nucleotide diversity (π), intra-population genetic differentiation (Kimura 2P F_{ST}).

Population	N	Hap	P	h \pm SD	$\pi \pm$ SD	Within Pop $F_{ST} \pm$ SD
Levy Cirque	16	5 (2)	16	0.450 \pm 0.151	0.0082 \pm 0.0053	2.33 \pm 1.34
Beacon Valley Upper	8	1 (0)	0	0	0.0005 \pm 0.0009	0
Beacon Valley Lower	13	3 (1)	1	0.295 \pm 0.156	0.0005 \pm 0.0009	0.15 \pm 0.23
Battleship Promontory	10	1 (0)	0	0	0	0.00
Alatna Valley	13	4 (2)	12	0.680 \pm 0.112	0.0119 \pm 0.0073	3.37 \pm 1.85
Dais	7	6 (6)	16	0.952 \pm 0.0955	0.0191 \pm 0.0120	5.43 \pm 2.98
Labyrinth	7	2 (0)	14	0.476 \pm 0.171	0.0247 \pm 0.0152	7.03 \pm 3.76
Hawkings Cirque	14	3 (1)	2	0.648 \pm 0.0813	0.0028 \pm 0.0024	0.81 \pm 0.62
Brownworth	6	3 (1)	18	0.600 \pm 0.215	0.0338 \pm 0.0209	9.59 \pm 5.13
Mount Suess Top	7	2 (0)	11	0.571 \pm 0.120	0.0233 \pm 0.0143	6.61 \pm 3.55
Mount Suess Bottom	16	1 (0)	0	0	0	0
Pegtop Mountain	2	1 (1)	0	0	0	0
Wall Valley	10	3 (1)	12	0.644 \pm 0.101	0.0124 \pm 0.0078	3.53 \pm 1.96
Lake Vida	7	5 (1)	28	0.857 \pm 0.137	0.0427 \pm 0.0252	12.10 \pm 6.25
High Miers	10	5 (1)	7	0.844 \pm 0.080	0.0103 \pm 0.0067	2.93 \pm 1.68
Lake Miers	13	5 (2)	21	0.744 \pm 0.087	0.0193 \pm 0.0111	5.47 \pm 2.82
High Garwood	7	3 (1)	5	0.667 \pm 0.160	0.0061 \pm 0.0052	2.03 \pm 1.29
Garwood Lake	12	5 (1)	23	0.727 \pm 0.113	0.0442 \pm 0.0242	12.50 \pm 6.09
Campbell Terrace	8	4 (1)	7	0.643 \pm 0.184	0.0086 \pm 0.0059	2.44 \pm 1.47
Lake Bonney	11	5 (3)	2	0.764 \pm 0.107	0.0022 \pm 0.0021	0.62 \pm 0.53
Mount Rae	4	3 (2)	2	0.833 \pm 0.222	0.0035 \pm 0.0035	1.00 \pm 0.83
Lake Hoare	11	4 (2)	8	0.746 \pm 0.098	0.0146 \pm 0.0089	4.14 \pm 2.23
Lake Fryxell	12	8 (4)	23	0.894 \pm 0.078	0.0192 \pm 0.0112	5.46 \pm 2.83
Mount Falconer	11	6 (4)	20	0.836 \pm 0.089	0.0224 \pm 0.0130	6.35 \pm 3.26
Gurkha Peak	9	3 (0)	5	0.556 \pm 0.165	0.0068 \pm 0.0048	1.92 \pm 1.20
Explorers Cove	5	4 (2)	13	0.900 \pm 0.161	0.0196 \pm 0.0133	5.57 \pm 3.22

SD indicates standard deviation from the mean. Sample sites with lake in the name are soils collected adjacent to contemporary lake shorelines.

K2PG4 genetic distance, differentiation ($F_{ST} \leq 0.996$; [Table 3](#)), and haplotype diversity ($h = 0.926$; [Table 3](#)) across McMurdo Dry Valleys’ nematodes.

From nine sampling sites with high genetic divergence based on COI sequences, 30 LSU sequences were analyzed. These sequences were 100% identical to the reference sequence from [Boström et al. \(2011\)](#), excepting two ambiguous base calls in two individuals. Accession number HM439773.1 (LSU sequence data not shown).

3.2 Phylogeography

Populations of *S. lindsayae* were highly structured in the MDVs based around valley systems and geographic proximity. The haplotype network revealed two high frequency haplotypes

(haplotype 6 and 24; [Figure 3](#)). Haplotype 6 was shared among 13 sites (50% of the sampling sites) and was found in the Lake Brownworth basin and all of the Miers, Garwood and Taylor valley sample sites. Haplotype 24 was found only in Beacon sites, Hawkings Cirque, and Victoria Valley sites (see [Table 1](#) for sites within each valley). In total, 39 haplotypes were restricted to a specific sampling site and the remaining 16 haplotypes were shared among more than one site. Haplotypes 21, 13, 9, 13, and 28 were shared only among the valleys disturbed during the LGM (Taylor, Miers, and Garwood) while haplotypes 30, 3, 54, 48, 4, and 25 were found in the more northerly and undisturbed valleys (Beacon, Alatna, Mackay Glacier, Victoria, and Wright). Only three haplotypes were shared across these two clusters, Haplotypes 23, 10, and 12.

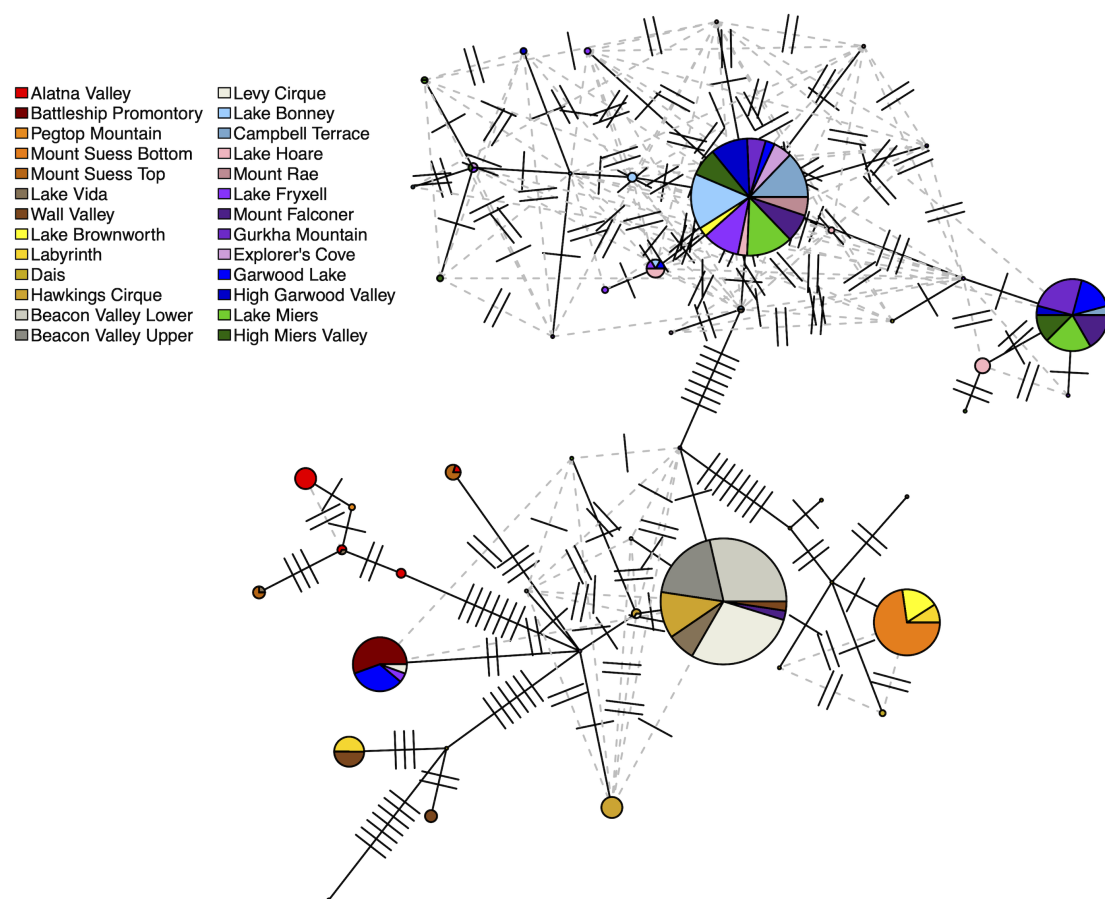


FIGURE 3

Haplotype network depicting haplotype associations and spread among sample site populations. Color corresponds to a sampling site; size of pie slice reflects the number of individuals with the designated haplotype; tick marks indicate a single mutation event distinguishing one haplotype from another. Warmer colors are associated with the northern valleys – Alatna, Mackay Glacier, Victoria, and Wright. The cooler colors designate Taylor, Miers, and Garwood valleys. White and grey designate haplotypes from the westerly isolated Beacon Valley.

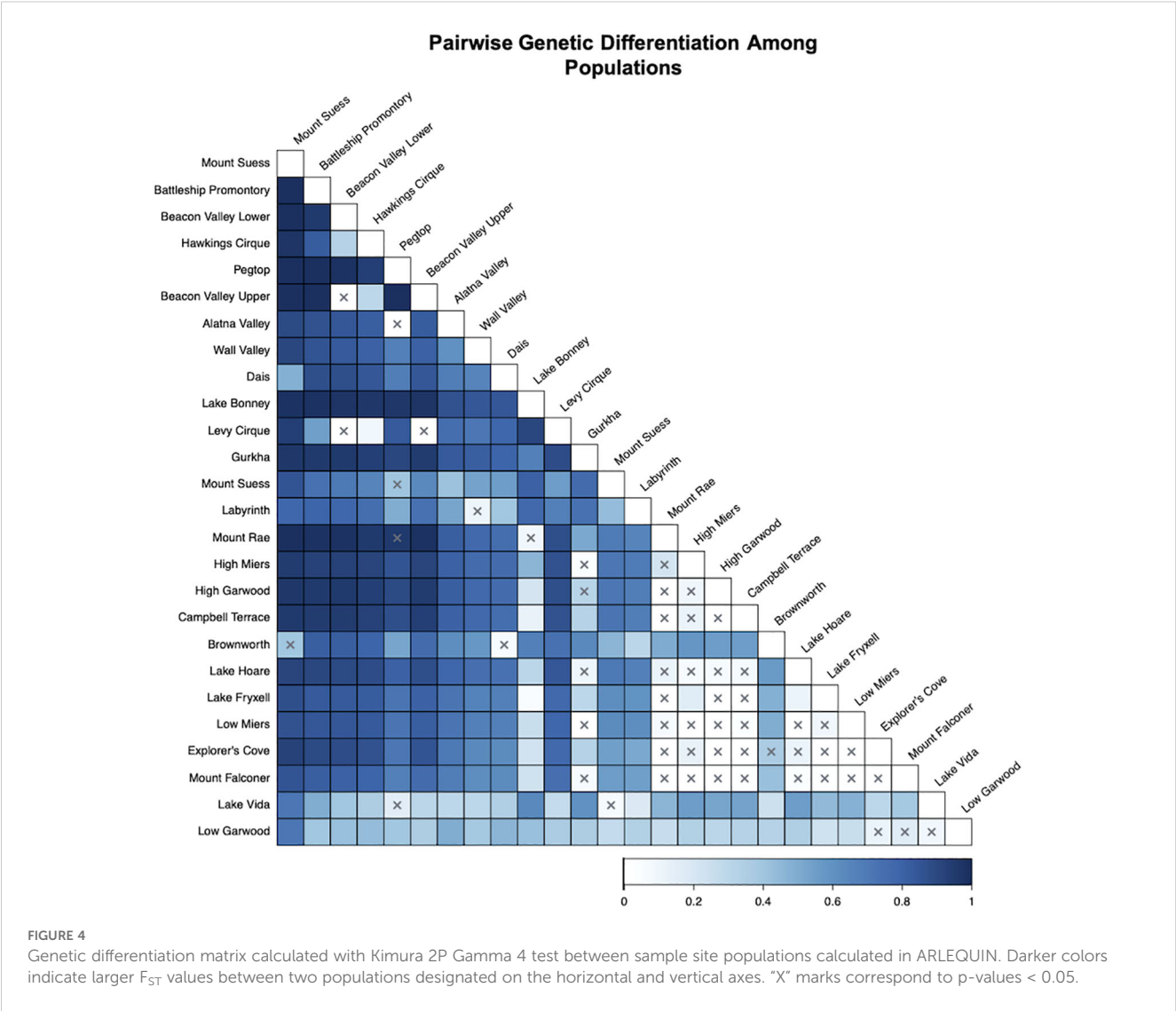
The majority of sampled site populations had high genetic differentiation. Pairwise F_{ST} values ranged from 0.000 to 0.996 among sampling site populations (Figure 4, Supplementary Figure 5). F_{ST} values were highest among the sampling sites from undisturbed valleys (Mount Suess top and bottom, Battleship Promontory, Beacon Valley upper and lower, Levy Cirque, Hawkings Cirque, Pegtop Mountain, Alatna Valley, Wall Valley, Labyrinth, and Dais). Even sites within the same valley system contained statistically significant, high F_{ST} scores. Sample sites from Lake Vida, Taylor, Miers, and Garwood (Mount Rae, Miers mountainside, Garwood mountainside, Campbell Terrace, Lake Hoare, Gurkha Peak, Lake Bonney, Lake Fryxell, Lake Miers, Explorer's Cove, and Lake Garwood) had much lower F_{ST} scores, averaging 0.176. Lake Vida and Lake Garwood populations had lower pairwise genetic divergence across all sampled sites.

Among all valleys, pairwise F_{ST} ranged from 0.007 to 0.931 with all comparisons being significant except for Hoare Basin to Miers Valley, Hoare Basin to Fryxell Basin, and Miers Valley to Fryxell Basin (Table 2, Supplementary Figure 3). The greatest genetic

differentiation was between Beacon and Bonney Basin ($F_{ST} = 0.931$; $p = 0.000$ E-5) and Beacon and Hoare Basin ($F_{ST} = 0.904$; $p = 0.000$ E-5). Pairwise genetic divergence from disturbed valleys – Taylor, Miers, Garwood, and Wright – contained F_{ST} values among the bottom 15%.

Based on the analysis of molecular variance, we found that *S. lindsayae* population structure was not part of a panmictic population as the majority of the variance did not arrive from within populations (Table 4). The majority of the variance was found among valleys (% variance = 41.56.3; $\sigma = 2.72$; $p < 0.00$). Variance among samples within populations accounted for the least variance (% variance = 28.34; $\sigma = 1.85$; $p < 0.00$). This provided evidence that populations were structured by valleys.

The dendrogram constructed with Nei's D and the ML tree additionally validated that populations were structured by valley system (Figure 5, Supplementary Figure 5). Both solutions revealed two broad clusters of populations. Clade B, composed of all sampled populations from Taylor, Miers, and Garwood valleys formed a well-supported monophyletic group (bootstrap support = 99.9%),



suggesting recent shared ancestry and genetic connectivity across these glacially disturbed valleys. In contrast, Clade A, which includes populations from Beacon, Alatna, Victoria, and Wright valleys, represents the best-supported grouping of undisturbed refugial sites. However, nodal support for the monophyly of Clade A is weak, and several internal nodes within the group are also poorly resolved. While this pattern is consistent with broad biogeographic structuring by glacial history, we interpret the

monophyly of Clade A with caution due to limited statistical support.

3.3 Demographic history

Bayesian skyline plots (BSPs) indicated that all populations have experienced recent demographic shifts occurring in the time

TABLE 4 Analysis of molecular variance (ANOVA) indicating population structure is dominated by valley.

Source of variation	d.f.	Sum of squares	Variance components (Σ)	Percentage of variation	p value
Within Populations	223	412.88	1.85	28.34	$p < 0.0001$
Among sites within same valley	16	309.96	1.97	30.11	$p < 0.0001$
Among valleys	9	806.68	2.72	41.56	$p < 0.0001$
Total	248	1529.52	6.53		

Degrees of freedom (df) sum of squares indicate how much of the total variance can be attributed to each source.

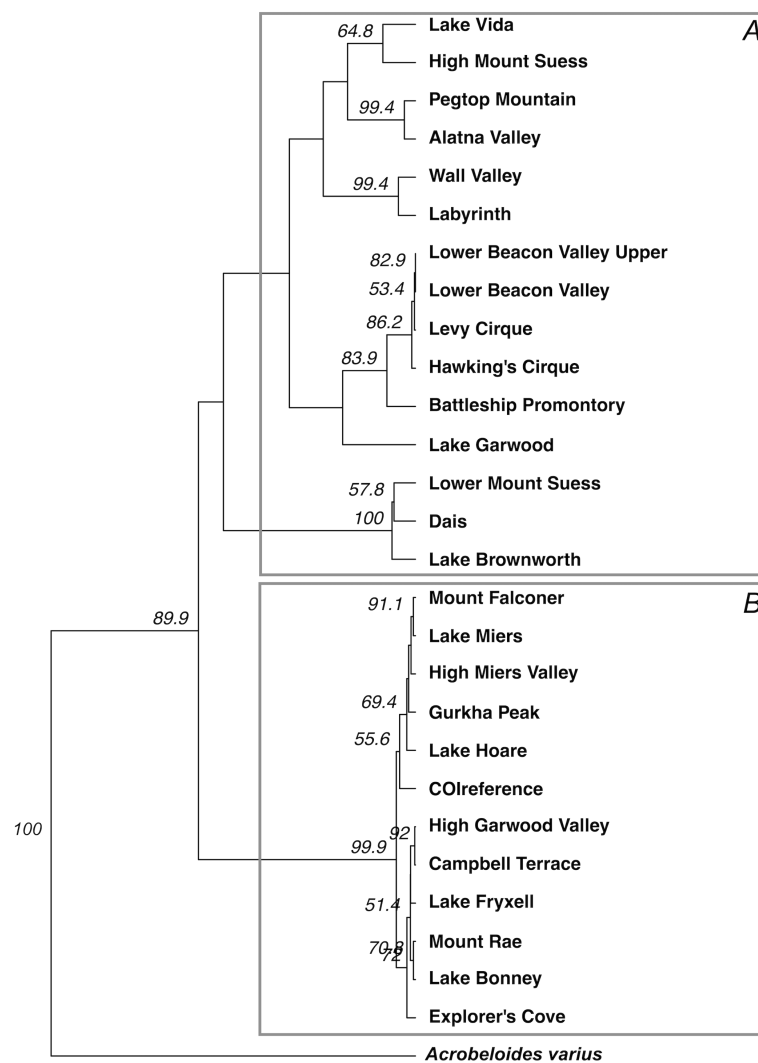


FIGURE 5

Dendrogram of pooled sequences using Nei's D from each sample site population (1,000 bootstrap replicates). The COI sequence of *Acrobeloides varius*, South Korea is used to root the tree. Populations in clade B include those from Taylor Valley sites: Mt Falconer, Gurkha Peak, Explorer's Cove, Lake Fryxell, Campbell Terrace, Lake Bonney, Mt Rae, Lake Hoare, Clade A is composed of sites from Alatna (Alatna Valley and Battleship Promontory), Victoria Valley (Lake Vida and Wall Valley), Mackay Glacier (Mt Suess and Pegtop Mountain), Wright Valley (Lake Brownworth, Dais, Labyrinth, Hawkings Cirque), and Beacon Valley (Lower and Upper Beacon, Levy Cirque).

since the LGM (Figure 6). Small sample sizes or loss of genetic information during population fluctuations may have contributed to the apparent stability of populations prior to the LGM, and may have caused an underestimation of population expansions in the BSPs (Grant, 2015). All undisturbed valleys (Alatna, Mackay Glacier, Victoria, and Wright) except Beacon Valley, shared a pattern of declining effective population size since the time of the LGM (20 kya to present). Conversely, Taylor Valley populations reported an increase in estimated population size following the LGM. Because Taylor, Miers, and Garwood form a monophyletic clade with limited genetic divergence, they were considered a population in BSP and likewise revealed a pattern of population increase around the time of the LGM. Beacon Valley also had a pattern of population increase since the LGM.

Patterns associated with the haplotype network likewise support the pattern of a recent population expansion in Taylor, Garwood,

and Miers with one central haplotype and several satellite haplotypes only one or two mutations removed. Comparatively, the undisturbed northern and western valleys contain haplotypes associated with patterns of long-term isolation associated with several haplotypes with similar frequencies that were several mutations distant.

3.4 Environmental parameters

We ran generalized mixed linear models to test the influence of these environmental conditions (elevation, soil moisture, electrical conductivity, distance to the coast, and glacial history) on genetic diversity and report AIC_C model selection results with AIC_C, weight, delta, and independent variable correlation. We developed 19 models and advanced models with $W_i > 0.05$ for conditional model average

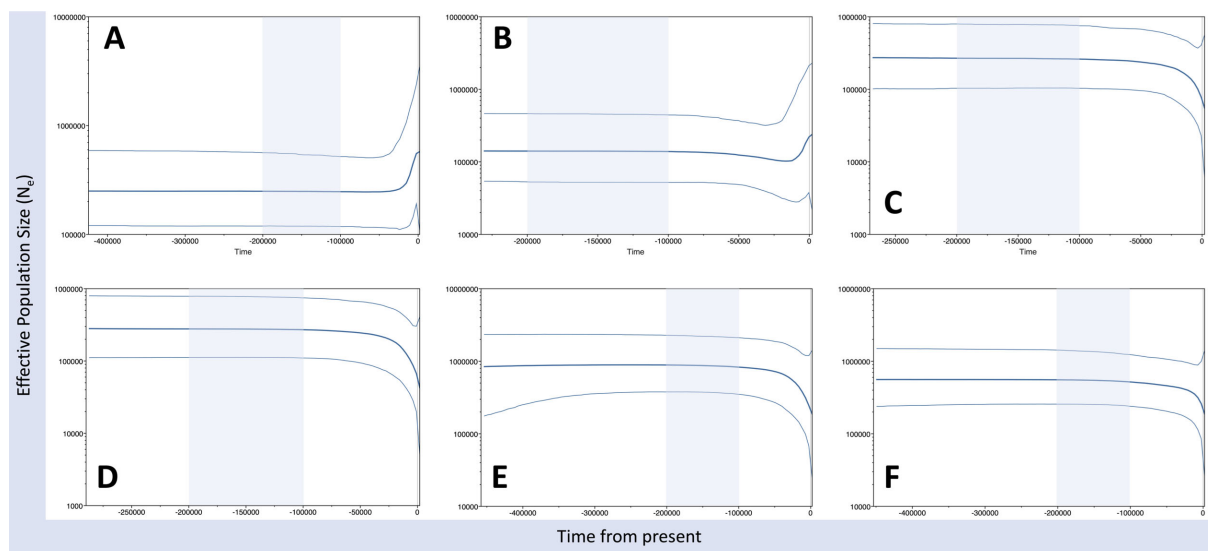


FIGURE 6

Bayesian skyline plots (BSPs) constructed for (A) Taylor, Miers, and Garwood ($n = 71$); (B) Beacon Valley ($n = 37$); (C) Alatna Valley ($n = 23$); (D) Mackay Glacier ($n = 25$); (E) Victoria ($n = 17$); and (F) Wright Valleys ($n = 34$). The x-axis represents time from the present with present day aligned on the right. The time of the LGM is shaded. The y-axis represents the effective population size. The center line is the median estimate. The upper and lower lines indicate highest posterior density intervals.

(Tables 5, 6; full list of models Supplementary Figure 6). Intra-population F_{ST} had a negative relationship with elevation across the top four models ($\beta = -0.006 \pm 0.003$, 85% CI = -0.010 to -0.002, $W_i = 81\%$; Table 5). However, intra-population F_{ST} had a positive relationship with elevation where soils had higher water content ($\beta = 9.15e-4 \pm 4.25e-4$, 85% CI = $2.81e-4$ to $1.55e-3$, $W_i = 37\%$). Soil moisture had a negative relationship with intra-population F_{ST} and was a parameter in three of the top four models ($\beta = -0.590 \pm 0.400$, 85% CI = -1.18 to -0.003, $W_i = 63\%$). Glacial history and electrical conductivity were also parameters in the top models but did not exhibit significant influence over intra-population genetic divergence. Ultimately elevation appears to explain the most variation in intra-population genetic divergence ($R^2 = 0.240$, $p = 0.012$).

Haplotype diversity was influenced by elevation and glacial history. The top model ($W_i = 76\%$) included elevation, glacial history, and their interaction. While the model retained a positive relationship between elevation and haplotype diversity in undisturbed sites, the effect size was modest ($\beta = 7.82 \times 10^{-4}$). This relationship is visually represented in Figure 7, though the trend line appears more pronounced than the spread of data points due to the compressed range of elevation values and limited number of undisturbed high-elevation sites. We interpret this effect as statistically significant but not strongly predictive on its own. The second-best model ($W_i = 19\%$) had simplified parameters that included glacial history and elevation, but not the interaction (Table 6). From these top two models, haplotype diversity had a positive relationship with undisturbed glacial history but not strongly ($\beta = 0.165 \pm 0.248$, 85% CI = -0.200 to 0.531, $W_i = 95\%$), a negative relationship with elevation ($\beta = -0.001 \pm 3.43e-4$, 85% CI = $-1.61e-3$ to $-6.05e-4$, $W_i = 100\%$), and a positive

relationship with elevation when the glacial history is undisturbed ($\beta = 7.82e-4 \pm 3.54e-4$, 85% CI = $2.89e-4$ to $1.28e-3$, $W_i = 76\%$). We included population abundance in a secondary model selection to determine if haplotype diversity or lineage divergence was confounded by abundance of individuals in a site. We found that population abundance was not a parameter in the top models for haplotype diversity. It was among the top two models for intra-population structure but was not significant.

4 Discussion

4.1 Phylogeographic structuring and taxonomic implications

We found that the MDV genetic structure of *S. lindsayae* is demarcated by valley system except where historical climate disturbance has created opportunity for migration and gene flow. Geomorphic barriers like glaciers and intervening mountain ranges have been effective barriers to inferred connectivity, causing accumulation of distinct genetic variations. Glacial recession following the LGM may have aided migration of soil nematodes. We also found that current ecological conditions were able to predict genetic diversity within populations. We found that *S. lindsayae* populations across the MDVs contained highly conserved rRNA sequences across valley systems, most likely indicating this is a single species despite high genetic divergences of the COI gene. Our results are consistent with observations by Courtright et al. (2000) who found a single species and several subpopulations in the MDVs and Velasco-Castrillón and Stevens

TABLE 5 Model selection for within population genetic divergence and ecological conditions.

Within population F _{ST}					
Model parameters		df	AIC _C	Δ	W _i
Elevation + Soil Moisture + Elevation × Soil Moisture		5	139.62	0.00	0.37
Elevation + Soil Moisture		4	141.49	1.87	0.15
Elevation + Glacial History		4	142.34	2.73	0.09
Elevation + EC		4	142.34	2.73	0.10
Model Parameter	Weight %	β	85% CI		
Intercept	100	8.29 ± 2.08	5.24 to 11.3		
Elevation	81	-5.65e-3 ± 2.69e-3	-0.010 to -0.002		
Soil moisture	63	-0.593 ± 0.402	-1.18 to -0.003		
Elevation × soil moisture	37	9.15e-4 ± 4.25e-4	2.81e-4 to 1.55e-3		
Glacial history	32	0.376 ± 2.20	-2.90 to 3.66		
Electrical Conductivity	22	-0.180 ± 1.09	-1.80 to 1.44		

Ecological conditions included elevation (mamsl), soil moisture (%g/g), glacial history, electrical conductivity (EC; dS/m), and distance to the coast (km). We report (top) the models with $W_i > 0.05$ selected from 19 initial models showing each parameter per model (model parameter), degrees of freedom (df), Aikake's Information criterion (AIC_C), difference in AIC_C value compared to top model (Δ), and AIC_C model weight (W_i). Models with $W_i > 0.05$ were judged to contain informative parameters and were included in conditional model averaging (bottom). We report model weight, β estimates, and 85% confidence intervals for conditional averaged parameter estimates from the top models.

TABLE 6 Model selection for haplotype diversity and ecological conditions. Ecological conditions included elevation (mamsl), soil moisture (%g/g), glacial history, electrical conductivity (EC; dS/m), and distance to the coast (km).

Haplotype diversity				
Model parameters	df	AIC _C	Δ	Weight
Elevation + Glacial History + Elevation × Glacial History	5	2.63	0.00	0.76
Elevation + Glacial History	4	5.43	2.80	0.19
Model Parameter	Weight %	β	85% CI	
Intercept	100	0.893 ± 0.108	0.732 to 1.05	
Elevation	100	-1.11e-3 ± 3.43e-4	-0.002 to -6.05e-4	
Glacial History	95	0.165 ± 0.248	-0.200 to 0.531	
Elevation × Glacial History	76	7.82e-4 ± 3.31e-4	2.89e-4 to 0.001	

We report (top) the models with $W_i > 0.05$ selected from 19 initial models showing each parameter per model (model parameter), degrees of freedom (df), Aikake's Information criterion (AIC_C), difference in AIC_C value compared to top model (Δ), and AIC_C model weight (W_i). Models with $W_i > 0.05$ were judged to contain informative parameters and were included in conditional model averaging (bottom). We report model weight, β estimates, and 85% confidence intervals for conditional averaged parameter estimates from the top models.

(2014) who identified limited genetic distance consistent with a single species across the continent. Our study represents a more geographically constrained and detailed synthesis of the population structure of *S. lindsayae* in the MDVs. We found high levels of genetic distance (p distance $\leq 7.4\%$), differentiation ($F_{ST} \leq 0.996$), and haplotype diversity ($h = 0.926$) that identify endemic subpopulations with long-term geographic isolation and population structure excepting large-scale climate disturbance events such as glacial advance and retreat. These results reveal the deterministic processes underlying metazoan population structure and specifically the strong influences of space, climate disturbance, and ecological conditions over genetic patterns.

Our phylogenetic analyses revealed a strongly supported clade (Clade B) composed of populations from valleys disturbed during the LGM, supporting a scenario of post-disturbance recolonization and recent gene flow. Populations from undisturbed valleys clustered into a second group (Clade A), though weak bootstrap support for this clade suggests that its monophyly remains tentative. Interestingly, the poor resolution of deeper nodes within Clade A may reflect a period of rapid diversification among populations in high-elevation valleys that remained isolated through the LGM. This pattern is consistent with long-term geographic isolation followed by early divergence and limited subsequent gene flow. Bayesian skyline plots for these valleys also support this

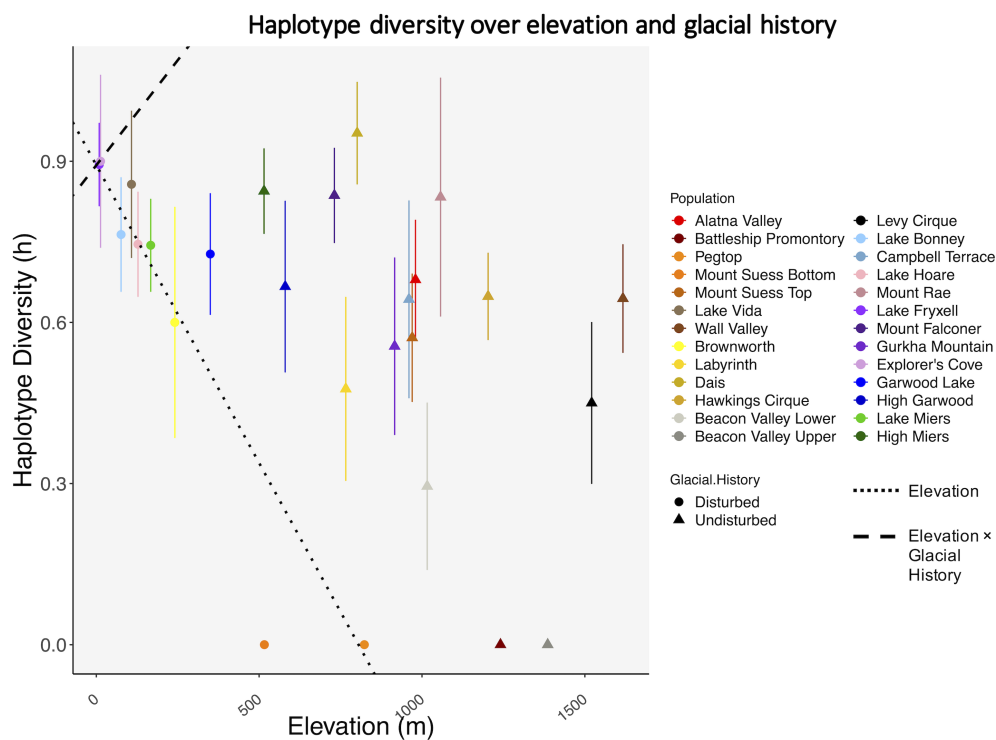


FIGURE 7

Distribution of haplotype diversity across sites by elevation and glacial history. Shapes indicate glacial history (triangles = undisturbed, circles = disturbed); colors represent sampling sites. The dashed line shows the fitted relationship between elevation and haplotype diversity for undisturbed sites, as estimated by the top mixed linear model. While the model indicates a positive relationship, the effect size is modest and visually subtle due to the limited range of high-elevation undisturbed sites. The dotted line shows the relationship for disturbed sites, which was not significant. Haplotype diversity was calculated from COI sequences for each site.

interpretation, showing demographic stability or gradual decline since the LGM—indicative of long-established, independently evolving populations rather than recent expansions. While this lends further support to the refugial history of these populations, the lack of deep phylogenetic resolution underscores the need for future work using multilocus or genomic data to more accurately reconstruct their divergence history and assess potential cryptic speciation.

Notably, the deep divergence among some COI haplotypes, particularly between the two major clades, approaches levels commonly associated with interspecific differences in other nematodes. These patterns raise the possibility that *S. lindsayae*, as currently described, may represent a complex of independently evolving lineages rather than a single cohesive species. While the conserved LSU sequences suggest genetic continuity, the COI divergence is consistent with emerging evidence in other Antarctic invertebrates where mitochondrial lineages reflect cryptic species. This warrants further investigation using multilocus nuclear markers and formal species delimitation analyses to determine whether the divergent lineages identified here correspond to reproductively isolated taxa.

While mitochondrial DNA offers valuable resolution for inferring population structure, we recognize that our reliance on a

single maternally inherited locus imposes limitations. COI does not capture recombination and may be subject to lineage-specific selective sweeps, potentially biasing demographic or phylogenetic inferences. Moreover, mitochondrial markers alone cannot disentangle male-mediated gene flow or provide independent estimates of coalescent times. Though our findings are consistent with other Antarctic metazoan phylogeographic patterns, future studies using nuclear multilocus or genomic datasets (e.g., RADseq or target capture) will be necessary to validate these patterns and resolve fine-scale demographic histories.

4.2 Spatial and temporal patterns of genetic divergence

Using a portion of the mitochondrial COI gene, we found that valley origin, and to a lesser degree geographic proximity, predicted genetic similarity. Frequently, population genetic studies find a strong correlation of genetic distance to geomorphic barriers or geographic distance supporting regionally defined populations (Khanal et al., 2018; Van Der Valk et al., 2018). Populations structured heterogeneously by barriers and distance have been consistently observed throughout Antarctic marine and terrestrial

ecosystems (Convey et al., 2014; Harder et al., 2016) including the MDVs (Stevens and Hogg, 2006; Dreesens et al., 2014; Bennett et al., 2016). Consistent with patterns of Antarctic phylogeography, *S. lindsayae* genetic variance was regionally defined and followed geomorphic barriers.

The strength of geomorphic barriers in shaping population structure is an important consideration in assessing the spatial structure of Antarctic biodiversity. Even on fine scales such as the distance from Wright Valley to Taylor Valley only 20 km apart, populations of *S. lindsayae* were distinct and have evolved significantly high levels of pairwise genetic differentiation and genetic divergence. The intervalley mountain ranges running east to west have the strongest isolating effect on metazoan populations in the MDVs. Results of our AMOVA analysis corroborate this conclusion where we found valley origin to be a strong predictor of genetic variance. While geologic features like mountain ranges and glaciers prevent gene flow, simple geographic distance, to a lesser degree, also increased genetic divergence. Populations close together, in the same valley system, for example, exhibited much lower pairwise genetic differentiation than populations from different valleys that were separated by geomorphic barriers. Wind and water movement are known mechanisms of gene flow among metazoans at the intravalley level in the MDVs and potentially explain the patterns found here (Nkem et al., 2006b; Gooseff et al., 2011; McGaughan et al., 2019; Schulte et al., 2022).

The high degree of intraspecies genetic variation between valleys imply high endemism of valley populations of MDV nematodes (Adams et al., 2007). It is reasonable to find intraspecies variation aligned with geomorphic barriers for non-vagile species like soil nematodes. Given the long-term environmental stability of many of these high elevation refugial valleys and the absence of mechanisms for active dispersal, these patterns are consistent with extended periods of geographic isolation. However, in the absence of formal divergence time estimates, we are not able to assign a specific temporal scale to the origin of this structure. Instead, we interpret the observed patterns as reflecting historical isolation maintained over long durations, disrupted primarily by large-scale events such as glacial advance and retreat during the LGM. Thus, the refugial valleys that remained undisturbed through the LGM contain locally endemic subpopulations that have been evolving independently throughout the Pleistocene. It is likely that other dispersal-limited metazoan taxa of the MDVs are similarly structured by the same valley and geomorphic barriers.

4.3 Climate disturbance legacies

We found that typical patterns of genetic structuring due to geomorphological features (e.g., divergence among valleys) were disrupted by large-scale climate disturbance events, specifically glacial expansion and paleolake inundation during the LGM. It is well established that historical climate is reflected in phylogeographic patterns, including population structures of

organisms in Antarctica where the LGM caused population contractions to local refugia and subsequent recolonization (Rogers, 2007; Keppel et al., 2012; Convey et al., 2020). The impact of the LGM on Antarctic metazoan diversity and population structure has been well documented for mite and springtail species (Demetras et al., 2010; Collins et al., 2019, 2020; McGaughan et al., 2019). Our results corroborate the influence of glacial expansion on phylogeographic patterns in a sentinel Antarctic metazoan. Given the high degree of lineage diversity in the context of phylogenetic reconstruction, our results provide evidence that much of the MDVs have remained habitable through the LGM while those that were inundated by glacial advance and paleolakes – Taylor, Miers, and Garwood – experienced local extinctions and subsequent recolonization.

Our results suggest that the LGM disturbance event may have facilitated connectivity and homogenization of subpopulations as glaciers receded at the end of the LGM. These results are similar to those found in Taylor Valley springtails with lower genetic divergence along the shoreline of paleolake Washburn (Nolan et al., 2006). Similarly, there was less pairwise genetic divergence between populations of *S. lindsayae* from valleys that experienced some degree of disturbance during the LGM indicating a possible mechanism of intervalley gene flow following glacial recession. Additionally, an examination of the relationship among haplotypes suggested two distinct phylogenetic groups, which differs from the conclusions of Courtright et al. (2000) and Adams et al. (2007). The evolutionary pattern of these two clades suggests glaciers shape more than just the geology and geography of the MDVs, but also the distributional patterns of subpopulations. Demographic histories among *S. lindsayae* populations of the MDVs are likely concordant with the timings of glacial and paleolake recession and the progression of habitable soil after the LGM and should be explored in future studies. Bayesian skyline plots support this interpretation by revealing signals of post-LGM population expansion in disturbed valleys (e.g. Taylor, Miers, Garwood), while undisturbed refugial valleys generally show demographic stability or gradual decline. These patterns, drawn from the haplotype network and phylogenetic analysis, suggest that climate disturbance events during the LGM played a large role in shaping the phylogeographic patterns and facilitating intervalley migration, particularly along glacial margins and forefields. While active dispersal across valley systems is unlikely for *S. lindsayae*, historical glacial expansions and retreats, such as the incursion of the Ross Sea Drift, may have temporarily bridged otherwise isolated valleys. These events could have enabled passive migration via continuous ice cover, soil redistribution, or meltwater pathways across low passes. Such mechanisms offer a plausible explanation for the genetic connectivity observed among populations in disturbed valleys. While these results are consistent with historical isolation and post-disturbance recolonization, we note that formal divergence time estimates were not calculated, and future studies using time-calibrated, multilocus data would be necessary to refine the temporal dynamics of these patterns.

Our results indicate that endemic populations are vulnerable to large scale climate disturbances and provides a line of evidence for long-distance dispersal of Antarctic soil nematodes along the margins of receding glaciers and shorelines. The disturbed valley populations exhibit resilience in the face of climate disturbance and ability to recolonize glacial forefields, but forfeit unique genetic lineages as found in undisturbed valleys.

4.4 Environmental constraints on genetic structure

Environmental conditions are important but often overlooked factors in generating phylogeographic patterns (Knowles and Maddison, 2002; Alvarado-Serrano and Knowles, 2014). Results from our analysis of model selection indicated that some ecological drivers may influence intra-population genetic differentiation and haplotype diversity. The abiotic conditions of the MDVs are frequently cited as drivers of species distributions in the MDVs (Hogg et al., 2006; Caruso et al., 2019) and especially when determining the presence of *S. lindsayae* (Poage et al., 2008; Wlostowski et al., 2018; Franco et al., 2021). These studies often utilize elevation (Lee et al., 2019; Bottos et al., 2020), soil moisture (Poage et al., 2008; Van Horn et al., 2013), electrical conductivity (Nkem et al., 2006a), and more recently, glacial history (Magalhães et al., 2012; McGaughan et al., 2014; Chen et al., 2017; Jackson et al., 2022) to characterize deterministic factors of biogeography. To date, studies of how these ecological interactions shape the genetic diversity of MDV soil metazoans have been lacking but are likely significant (Schierenbeck, 2017; Caruso et al., 2019).

Using just a few, but widely tested environmental factors – elevation, soil moisture, distance to the coast, electrical conductivity, and glacial history – we found some factors that were relevant to genetic diversity in this system. The top models for intra-population genetic divergence indicated that elevation and soil moisture were negatively correlated. This trend was reversed when considering the interaction of elevation and soil moisture. Valley floor habitats are the sink to down valley aeolian-transported materials (Diaz et al., 2018). Thus, it follows that lower elevations accumulate intravalley lineages and have more genetic differentiation in any given population. These results indicate higher potential for migration at valley floors through physical processes. Soil moisture is necessary for habitable soil and would be required for wind mediated transport. The negative correlation was surprising but could indicate a more homogenized population where *S. lindsayae* could move further through the interstitial, fluid-filled spaces. Higher elevation soils are typically less conducive for life and sufficient soil moisture provides the first indication that *S. lindsayae* populations can establish at these higher elevations and support relict populations capable of developing higher degrees of within population genetic differentiation. This is consistent with higher elevations, where, mediated by soil moisture, they contain larger variability in community structure (Andriuzzi

et al., 2018). Considering haplotype diversity, we found that elevation was negatively correlated until the disturbance history was considered. Sites at low elevations had higher haplotype diversity perhaps owing to the reasons described above. However, haplotype diversity also increased in high elevation populations that have remained undisturbed, as these sites have been afforded stable habitats and time to develop evolutionary mutations and thus higher haplotype diversity. Such trends provide further support for high-elevation habitats as putative refugia. Environmental and ecological conditions play a role in structuring the genetic diversity of these soil organisms and should be further considered as an important component of long-term monitoring.

Community composition and the distribution of organisms in the MDVs is clearly driven by the environmental and ecological factors responsible for habitat suitability. By extension, it is reasonable to expect that genetic diversity is influenced by these conditions as well. Given the simplified biotic communities, well documented heterogeneous abiotic conditions of the MDVs, and nearly universal distribution of *S. lindsayae*, this system provides a unique opportunity to test the influence of basic abiotic properties like elevation, soil conditions, and geologic history on genetic diversity and structure.

4.5 Conclusions

Our primary aim in this study was to explore the evolutionary response of the sentinel species *S. lindsayae* to historical climate disturbance. We found that climate history had a lasting impact on its population and genetic structure, resulting in demographic shifts and the emergence of distinct, isolated, and endemic subpopulations. Understanding how such patterns arose provides foundational context for interpreting ongoing and future changes. We suggest that future long-term monitoring studies should incorporate a phylogeographic perspective, as this can help identify populations with unique evolutionary histories, inform strategies to preserve existing genetic structure, and predict how climate-driven disturbances may alter the functional and evolutionary trajectories of Antarctic terrestrial ecosystems.

Data availability statement

The full data package is published and available from the Environmental Data Initiative found here: <https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-mcm.269.1> (Jackson et al., 2023).

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

AJ: Conceptualization, Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. SL: Writing – review & editing. DP: Writing – review & editing. DW: Resources, Writing – review & editing. TP: Methodology, Writing – review & editing. TH: Methodology, Writing – review & editing. BA: Conceptualization, Funding acquisition, Methodology, Writing – review & editing, Resources.

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This work is part of a thesis and can be accessed online in accordance with the author's university policy. This is the only form in which it has previously appeared. It can be accessed here: <http://hdl.lib.byu.edu/1877/etd12622> (Jackson, 2022).

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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