ECOGRAPHY

Review

Meta-analysis of Antarctic phylogeography reveals strong sampling bias and critical knowledge gaps

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Ecography
2022: e06312
doi: 10.1111/ecog.06312
Subject Editor and
Editor-in-Chief:
David Nogués-Bravo
Accepted 5 September 2022

Much of Antarctica's highly endemic terrestrial biodiversity is found in small ice-free patches. Substantial genetic differentiation has been detected among populations across spatial scales. Sampling is, however, often restricted to commonly-accessed sites and we therefore lack a comprehensive understanding of broad-scale biogeographic patterns, which could impede forecasts of the nature and impacts of future change. Here, we present a synthesis of published genetic studies across terrestrial Antarctica and the broader Antarctic region, aiming to identify current biogeographic patterns, environmental drivers of diversity and future research priorities. A database of all published genetic research from terrestrial fauna and flora (excl. microbes) across the Antarctic region was constructed. This database was then filtered to focus on the most well-represented taxa and markers (mitochondrial COI for fauna, and nuclear ITS for flora). The final dataset comprised 7222 records, spanning 153 studies of 335 different species. There was strong taxonomic bias towards flowering plants (52% of all floral data sets) and springtails (54% of all faunal data sets), and geographic bias towards the Antarctic Peninsula and Victoria Land. Recent connectivity between the Antarctic continent and neighbouring landmasses, such as South America and the Southern Ocean Islands (SOIs), was inferred for some groups, but patterns observed for most taxa were strongly influenced by sampling biases. Above-ground wind speed and habitat heterogeneity were positively correlated with genetic diversity indices overall though environment was a generally poor predictor of genetic diversity. The low resolution and variable coverage of data may also have reduced the power of our comparative inferences. In the future, higher-resolution data, such as genomic SNPs and environmental modelling, alongside targeting sampling of remote sites and under sampled taxa, will address current knowledge gaps and greatly advance our understanding of evolutionary processes across the Antarctic region.

Keywords: biogeography, genetic diversity, macrogenetics, molecular ecology, phylogeography, polar, Southern Hemisphere, spatial ecology

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Introduction

Our understanding of global biodiversity and biogeographic patterns is increasing, particularly with advances in research methods and techniques (Beheregaray 2008, Leigh et al. 2021). In recent decades, phylogeographic methods, which use genetic variation to infer the diversity and relatedness of different species and populations, have proven especially useful owing to their ability to draw linkages between micro- and macro-evolutionary research (Moore 2001, Kumar and Kumar 2018). Macrogenetic studies examining patterns of intraspecific genetic variations across multiple taxa with larger spatial and temporal scales are, nevertheless, still rare (Leigh et al. 2021). With global environmental change accelerating at an unprecedented rate, we urgently need to understand the larger scale evolutionary patterns that have shaped biodiversity patterns, in order to forecast future changes and manage at-risk ecosystems. The Antarctic region, where endemic biodiversity has evolved in relative isolation (Convey et al. 2008, 2014, 2020), encompasses many of these ecosystems and is facing the concomitant threats of rapid environmental change and increasing connectivity, both between Antarctic and non-Antarctic regions and among sites within the region, as the climate rapidly warms and human activity increases (Convey 2011, Convey and Peck 2019).

The geographic and climatic history of Antarctica has strongly influenced its biodiversity. The isolation of the continent with the breakup of Gondwana led to the evolution of a large number of endemic species which have persisted in Antarctica for millions of years, despite bottlenecks, range shifts and extinctions of many taxa with Pleistocene glaciations (Convey et al. 2008, Vyverman et al. 2010). During glaciations, many Antarctic terrestrial species were restricted to small refugia including ice-free nunataks, geothermal regions and dry valleys, resulting in genetic differentiation (Pugh and Convey 2008, Fraser et al. 2012, 2014). Range expansions during interglacial periods resulted in reduced genetic variation due to founder effects (van de Wouw et al. 2007, Lagostina et al. 2021) and secondary contact of sister taxonomic groups (Nolan et al. 2006, Rogers 2007). Long-distance dispersal during interglacial periods could, however, connect populations, subsequently increasing ranges and genetic diversity. For example, there is mounting evidence for strong genetic connectivity in some taxa between Antarctica and South America via the Scotia Arc (Biersma et al. 2020a, Lagostina et al. 2021, Maroni et al. 2022). Furthermore, many organisms occurring in Antarctica appear to have bipolar or even cosmopolitan distributions (Pisa et al. 2014, Biersma et al. 2017, Kleinteich et al. 2017), which could be a result of interglacial dispersal.

Over 99.5% of Antarctica is covered by ice and its climate is the coldest, driest and windiest on Earth (Convey et al. 2008, Convey 2011), with varied environmental gradients and major spatial and temporal variations (Convey et al. 2014). The current Antarctic terrestrial flora is dominated by lichens and mosses, with just two flowering plant species (*Deschampsia antarctica* and *Colobanthus quitensis*) (Peat et al. 2007, Convey 2011). Most animal groups are small invertebrates such as arthropods, tardigrades and nematodes (Velasco-Castrillón et al. 2014, Chown et al. 2015). These terrestrial taxa are generally distributed around ice-free ecoregions including nunataks and polar deserts, particularly along the Antarctic Peninsula and Scotia Arc (Chown et al. 2015, Convey and Peck 2019). Recent phylogeographic studies have revealed substantial genetic diversity among populations separated by tens to hundreds of kilometres, mostly as a result of the patchiness of habitable environments (e.g. much Antarctic terrestrial biodiversity is found in ice-free 'islands' separated by kilometres of unsuitable habitat, Convey 2013) and the limited dispersal abilities of biota (Stevens et al. 2006, Griffiths and Waller 2016, Convey and Peck 2019, McGaughran et al. 2019). Diverse evolutionary histories exhibited within continental Antarctica (Stevens et al. 2006, 2021, Chown and Convey 2007, Carapelli et al. 2020), and recent classification of areas into Antarctic Conservation Biogeographic Regions (ACBRs, Terauds et al. 2012, Terauds and Lee 2016) has drawn on our existing understanding of Antarctic biogeography.

Antarctic ecosystems are currently facing the combined impacts of rapid warming and escalating human activity (Convey 2013, Convey and Peck 2019, Duffy and Lee 2019). However, a large part of Antarctica remains unsampled, with many taxa and regions understudied (Convey et al. 2014, Convey and Peck 2019). Despite advances in molecular methods, we still have only a limited understanding of the region's genetic diversity because of logistical problems associated with accessing sampling locations and methods – particularly for microbiota and cryptic species (Grant and Linse 2009, Chown et al. 2012). Furthermore, biogeographic research in the Antarctic region to date has generally been piecemeal, focussing on particular locale/s and/or taxa at a time, without much broader scale synthesis. Identifying the drivers of genetic diversity in the Antarctic region is therefore difficult, which will make managing these changing ecosystems especially challenging in the future (Chown and Convey 2007, 2012, Chown et al. 2012, 2015, Leihy et al. 2020).

Here, we provide a broad-scale synthesis of genetic studies from terrestrial Antarctica to assess phylogeographic patterns, determine potential environmental drivers of these patterns, and identify the knowledge gaps for Antarctica's genetic diversity. Specifically, we set out to address the following questions: 1) which terrestrial taxa are well versus poorly represented in existing datasets? 2) what are the broad-scale biogeographic patterns across the Antarctic region? and 3) what are the environmental drivers of diversity patterns? We hypothesised that existing data would predominantly be from flowering plants and macro/mesofauna (insects, springtails and mites) from sampling locations close to research stations, because of the relative ease of sampling for these groups and regions. Biogeographic patterns were expected to vary somewhat among taxonomic groups, although we predicted that in general diversity would be highest around the Antarctic Peninsula due to the more clement environmental conditions in these lower-latitude locations. Lastly, we predicted that

warm temperatures and strong winds would be positively correlated with genetic diversity, as indicated by some prior research (Baird et al. 2019, McGaughran et al. 2019).

Methods

Database construction

A list of genetic studies of Antarctica published prior to 1 November 2021 was compiled from multiple databases (Supporting information). Publications were fetched from four major databases based on Boolean keyword search including four Antarctic keywords and 41 molecular keywords (Supporting information) using R package 'Fulltext' (Chamberlain 2021) with R ver. 3.6.2 implemented in RStudio ver. 1.2.5033 (<www.r-project.org>) and Python ver. 3.8 (Van Rossum and Drake 2009). Search terms and methods were adapted to the specific requirements of each database (Supporting information). Duplicated records were removed, and all abstracts were then manually checked (by two authors) to ensure all records were indeed genetic studies with data from Antarctica and the Southern Ocean (not, for example, studies examining specific anti-inflammatory, antioxidant or antifreeze proteins in Antarctic species). Over 80% of studies were filtered out at this stage. Based on abstracts, the remaining records were categorised according to broad taxon (animal, embryophyte plant, fungi, lichen or algae) and ecosystem types (terrestrial, marine, freshwater). Marine birds including penguins, and marine mammals including pinnipeds were assigned to the marine category due to their high mobility across oceans.

For terrestrial studies, which were the focus of this synthesis, additional publication details (species name, genetic marker, georeferenced sampling locations) were manually extracted. Geographic coordinates were approximated from map figures for locations that had not been georeferenced in the paper (where this was not possible, the record was excluded from the study). Coordinates were then standardised into decimal degrees format. From each study, publicly available database accession numbers for genetic data were manually associated with sampling locations if not readily provided in the publication. Non-Antarctic-focussed publications were only retained if they included genetic data from the Antarctic. Here we defined Antarctica as areas south of 60°S. Authors were contacted for extra information where needed. When authors were unable to provide the requested information, either data were re-analysed to infer locations (e.g. from haplotype maps and networks), or records were excluded. Multiple sequences generated from different genetic markers for the same sample specimens were treated as one record to avoid location duplication. Species names were standardised according to Wauchope et al. (2019), while subspecies and infraspecies were assigned to species level. Records with taxonomic uncertainty were classified to the lowest certain level.

All terrestrial records from the Treaty region of Antarctica (i.e. > 60°S) were assigned to 'Region' groups according to a modified version of the designated Antarctic Conservation Biogeographic Regions (ACBRs; Fig. 1; Terauds et al. 2012, Terauds and Lee 2016). With the exception of the records from the South Shetland Islands, Antarctic Peninsula and Victoria Land, records were assigned to the ACBR in which they were located. The South Shetland Islands, Antarctic Peninsula and Victoria Land each contained a disproportionally high number of records (e.g. South Shetland Islands comprised more than 20% of all records), thus these ACBRs were subdivided (as detailed in Fig. 1) to assess population structures on smaller geographic scales. Studies with sampling locations on both continental Antarctica and on either the Southern Ocean Islands (SOIs) and/or non-Antarctic landmasses (Table 1) were included in order to investigate potential population connectivity with regions outside the continent. Here SOIs included the Falkland Islands, South Georgia and South Sandwich Islands, Marion and Prince Edwards Islands, French Southern and Antarctic Lands (excl. Adélie Land), Heard and McDonald Islands as well as Macquarie and New Zealand sub-Antarctic Islands (Fig. 1). South America, New Zealand, Tasmania and mainland Australia were grouped as 'Non-Antarctic Landmass'. Six regions from the SOIs were assigned based on 'expert-defined bioregions' from Terauds et al. (2012). Density of sampling and distances between sample locations and nearest research stations (source: COMNAP 2017) were calculated using the 'raster' (Hijmans and van Etten 2012) and 'sp' (Pebesma and Bivand 2005) R packages.

Choice of markers and taxa

To enable inter- and intra-population comparisons, the most frequently used molecular markers were chosen separately for animals, plants and lichenised fungi (lichens). Taxonomic groups were excluded if they were only represented by a limited number of sequences (< 10) or were poorly georeferenced. The mitochondrial DNA (mtDNA) cytochrome c oxidase I (COI) gene was chosen for animals, while internal transcribed spacer (ITS) regions from nuclear ribosomal DNA were selected for both plants and lichen. All ITS sequences were further trimmed down to the ITS1 region based on sequence attribute information on GenBank to ensure consistency. The remaining taxonomic groups consisted of 20 animal, seven plant and five lichen genera, within which species represented by data from only one region were excluded from molecular analysis. Taxa that were not represented by ten or more sequences within at least two regions (i.e. an absolute minimum of 20 sequences) were excluded from subsequent analyses. To enable biogeographic comparisons to be made, analyses were performed at genus level when species had distributions that were restricted to a single region. For species that could be analysed at species level (i.e. widely distributed species), we replicated species-level analyses with all species grouped to genus (noting that the genera *Acutuncus*, *Alaskozetes*, *Colobanthus* and *Deschampsia* contain only one species occurring in Antarctica in our database) to examine if the level of grouping affected analyses and results.

Seven animal genera, four plant genera and two lichens were retained for further analysis.

Molecular analysis

Sequences were downloaded from GenBank, BOLD (Barcode of Life Data System) and EMBL (European Molecular Biology Laboratory) in FASTA file format. All sequences were aligned using MUSCLE ver. 3.8.31 (Edgar 2004) with default settings and were manually checked in Geneious Prime ver. 2021.1.1 (<www.geneious.com>). Poorly aligned regions were identified and deleted using Gblocks ver. 0.91b (Castresana 2000). Phylogenetic relationships of each taxon were assessed using maximum likelihood (ML) and Bayesian inference (BI) models without outgroups. The most appropriate substitution models were selected by the AICc of jModeltest ver. 2.1.10 (Supporting information, Guindon and Gascuel 2003, Guindon 2020). ML analysis was performed in PhyML ver. 3.0 (Guindon et al. 2010) with 1000 bootstrap pseudoreplicates. BI phylogenetic trees were constructed using MrBayes ver. 3.2.6 (Ronquist and Huelsenbeck 2003). The Markov chain Monte Carlo (MCMC) simulation was set

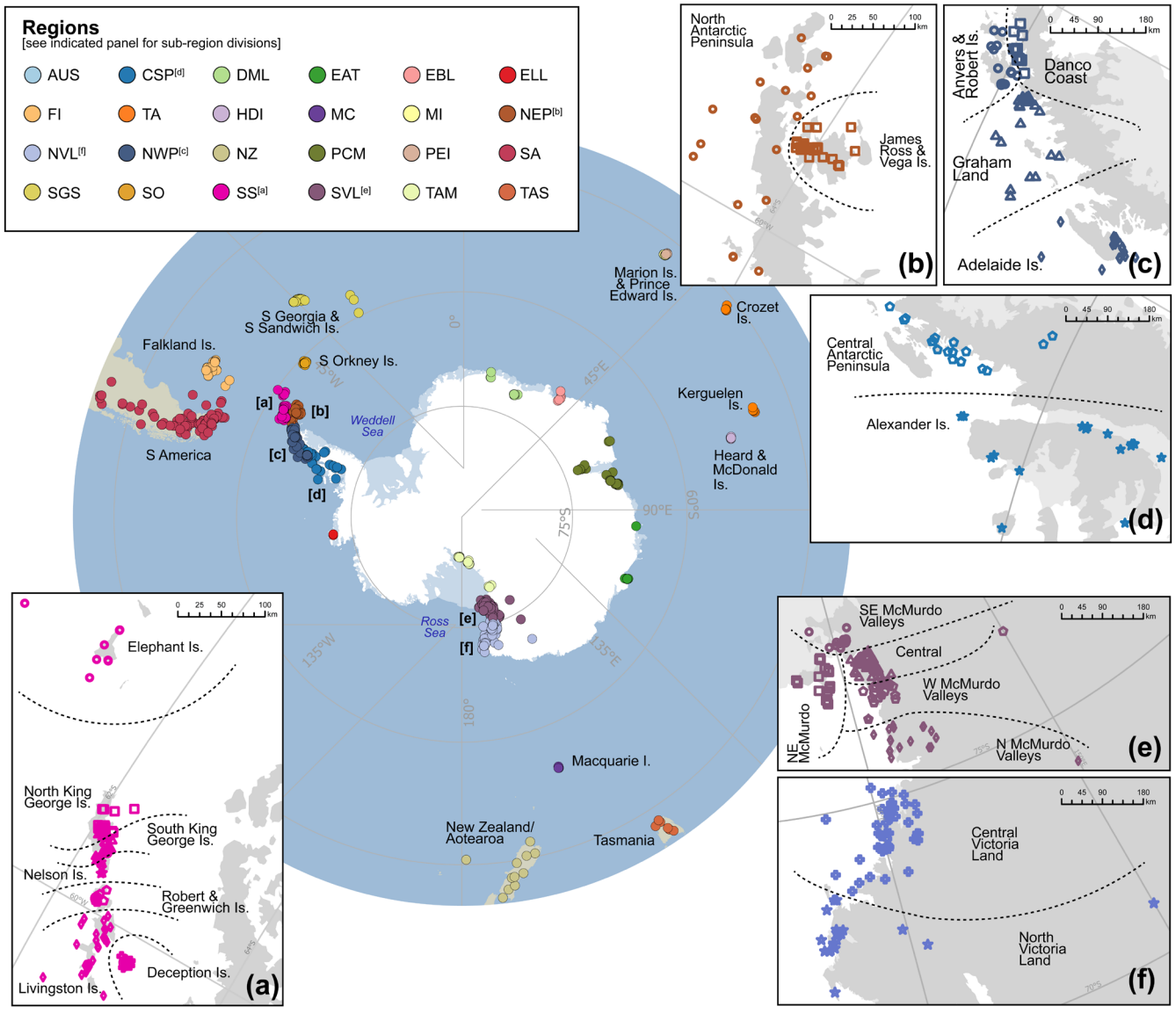

Figure 1. Overview of genetic data distribution and population regions of Antarctic, Southern Ocean Island and non-Antarctic landmass terrestrial taxa (marine records were excluded). Coloured points indicate individual sampling records (details in Supporting information). Regions within the Antarctic Treaty region (> 60°S) were based on a modified version of the ACBRs (Terauds et al. 2012, Terauds and Lee 2016). Southern Ocean Island (SOI) regions were assigned based on 'expert-defined regions' from Terauds et al. (2012). Non-Antarctic Landmasses included South America, New Zealand, Tasmania and mainland Australia. The South Shetlands (a), Antarctic Peninsula (b–d) and Victoria Land (e, f) regions were sub-divided based on past studies (Supporting information), with subdivisions indicated by different shapes and dashed lines.

Table 1. Summary of number of records grouped by taxonomic groups and population regions retained in the dataset of Antarctic terrestrial genetic studies (Supporting information). Studies were retrieved from four major databases using Boolean keywords search with four Antarctic keywords and 41 molecular keywords, and filtered by manually checking. Numbers in bold represent highest number of records among regions.

				Animals (52.73%)					
Population region	Code	No. of records	% Total	Collembola	Arachnid	Hexapoda	Tardigrada	Rotifera	Other animals
Antarctic Biogeographic Regions									
Central south Antarctic Peninsula	CSP	177	0.025	11	30	0	1	0	16
Dronning Maud Land	DML	214	0.030	76	0	0	44	5	0
East Antarctica	EAT	25	0.003	0	0	0	0	6	0
Enderby Land	EBL	55	0.008	0	0	0	6	0	0
Ellsworth Land	ELL	3	0.000	0	0	0	0	0	0
North-east Antarctic Peninsula	NEP	154	0.021	10	10	1	0	3	29
North Victoria Land	NVL	923	0.128	341	122	0	**99**	134	11
North-west Antarctic Peninsula	NWP	733	0.101	225	89	3	0	13	30
Prince Charles Mountains	PCM	149	0.021	0	0	0	19	103	0
South Victoria Land	SVL	1217	0.169	**700**	85	0	4	**217**	**36**
Transantarctic Mountains	TAM	164	0.023	134	0	0	0	0	2
South Orkney Islands	SO	66	0.009	0	3	2	0	7	0
South Shetland Islands	SS	1450	**0.201**	148	8	8	0	1	15
Southern Ocean Islands									
South Georgia and South Sandwich Islands	SGS	216	0.030	14	54	6	0	0	1
Îles Crozet and Îles Kerguelen	TA	82	0.011	12	14	15	0	0	0
Heard and McDonald Islands	HDI	36	0.005	7	10	8	0	0	0
Macquarie Island	MC	46	0.006	15	18	0	0	0	0
Marion Island	MI	712	0.099	355	**217**	**111**	0	0	0
Prince Edward Island	PEI	58	0.008	3	0	55	0	0	0
Falkland Islands	FI	112	0.016	0	0	0	0	0	13
Non-Antarctic Landmass									
Mainland Australia	AUS	15	0.002	1	1	0	0	0	0
Tasmania	TAS	23	0.003	19	0	0	0	0	0
New Zealand	NZ	40	0.006	3	6	0	0	4	0
South America	SA	552	0.076	2	1	20	13	2	1
	Total	**7222**		**2076**	668	229	186	495	154
	% Total			**0.287**	0.092	0.032	0.026	0.069	0.021

(Continued)

Table 1. Continued.

Population region	Code	Embryophyte plants (19.65%)				Lichens	Fungi	Algae
		Bryophytes	*Deschampsia*	*Colobanthus*	Other plants			
Antarctic Biogeographic Regions								
Central south Antarctic Peninsula	CSP	36	2	56	0	14	11	0
Dronning Maud Land	DML	0	0	0	0	4	**84**	1
East Antarctica	EAT	14	0	0	0	4	1	0
Enderby Land	EBL	43	0	0	0	0	0	6
Ellsworth Land	ELL	1	0	0	0	2	0	0
North-east Antarctic Peninsula	NEP	44	0	3	0	9	0	45
North Victoria Land	NVL	75	0	0	0	117	17	7
North-west Antarctic Peninsula	NWP	56	13	63	0	102	23	116
Prince Charles Mountains	PCM	17	0	0	0	4	0	6
South Victoria Land	SVL	38	0	0	0	79	45	13
Transantarctic Mountains	TAM	0	0	0	0	28	0	0
South Orkney Islands	SO	28	7	11	0	2	6	0
South Shetland Islands	SS	**157**	9	175	0	**631**	67	**231**
Southern Ocean Islands								
South Georgia and South Sandwich Islands	SGS	28	14	94	0	0	5	0
Îles Crozet and Îles Kerguelen	FL	21	7	0	7	6	0	0
Heard and McDonald Islands	HDI	1	7	0	3	0	0	0
Macquarie Island	MC	4	0	0	9	0	0	0
Marion Island	MI	4	0	0	25	0	0	0
Prince Edward Island	PEI	0	0	0	0	0	0	0
Falkland Islands	FI	5	10	10	0	14	0	60
Non-Antarctic Landmass								
Mainland Australia	AUS	13	0	0	0	0	0	0
Tasmania	TAS	0	0	0	0	0	0	4
New Zealand	NZ	11	0	0	0	16	0	0
South America	PT	34	**24**	**240**	0	215	0	0
	Total	630	93	652	44	1247	259	489
	% Total	0.087	0.013	0.090	0.006	0.173	0.036	0.068

at 1 000 000 run lengths for most taxa except *Cryptopygus*, *Gomphiocephalus* and *Halozetes* which used 3 000 000 run length due to a larger number of sequences. Sampling frequency of MCMC was 500. Convergence of chains were evaluated in Tracer ver. 1.7.2 (Rambaut et al. 2018) with 25% burn-in. All other settings for both ML and BI were left at default. Trees were reproduced using R package 'ggtree' (Yu 2020).

To investigate overall genetic diversity and structure, sequences of each taxon were further trimmed to equal lengths in Geneious Prime with some sequences excluded due to short size (relative to mean length). Ambiguities were treated as missing data. Three genetic parameters (number of sequences, number of unique haplotypes, number of polymorphic sites) and four diversity metrics (mean number of pairwise differences, nucleotide diversity, haplotype diversity, Theta S) were calculated for every population using Arlequin ver. 3.5.2.2 (Schneider et al. 2010). The demographic history (population expansion and contraction) of each region was analysed using infinite site models with Tajima's D test (Tajima 1989) and Fu's FS test (Fu 1997) with 10 000 permutations performed in Arlequin. For details of each index see Schneider et al. (2010).

For between region differences, hierarchical analysis of molecular variance (AMOVA) was conducted in R using the package 'poppr' (Kamvar et al. 2014) with 10 000 permutations, to examine genetic differentiation among regions and subregions as defined above. Pairwise genetic differentiations were calculated using Nei's Gst (Nei 1973), Jost's D (Jost 2008) and Hedrick's G'st (Hedrick 2005) using R package 'mmod' (Winter 2012). Furthermore, taxa with more than ten unique haplotypes were assigned to clades inferred from BI and ML trees as well as nucleotide divergence value using uncorrected p-distances calculated in R. Within the Antarctic Treaty area (> 60°S), rarefied haplotype richness was calculated for each region/sub-region (Fig. 1) and for each genus (pooled across regions) to investigate the extent of sampling biases on observed haplotype richness relative to expected richness. Rarefaction analyses were performed using the 'iNext' R package (Chao et al. 2014, Hsieh et al. 2020).

Spatial and environmental analysis

To examine the relationship between geographic distance and genetic differentiation, spatial principal component analysis (sPCA, Jombart et al. 2008) and Mantel tests were performed using R packages 'ade4' and 'adegenet'. sPCA uses multivariate methods to summarise spatial patterns of genetic variation among regions by accounting for genetic differentiations and spatial autocorrelations using Moran's index (Moran 1950). The Mantel test examines correlations of genetic distances and geographic distance (Mantel 1967). Both sPCA and Mantel tests were carried out with 10 000 permutations. To investigate potential environmental factors affecting overall diversity patterns within Antarctica and compare patterns of genetic diversity to previously described patterns of species richness, generalised linear mixed models (GLMM) with seven response variables (genetic and structure indices) and 15 predictor variables (Supporting information) were used on overall statistics for all taxonomic groups. Predictors included nine climatic, four geological and one anthropogenic factor (Table 2) that have been suggested to correlate with Antarctic biodiversity patterns (Chown et al. 2015, Convey and Peck 2019) and that have been used previously as predictors of phylogeographic patterns across Antarctica (McGaughran et al. 2019). Latitude was added as a predictor to explicitly model high-level spatial autocorrelation amongst sites. Number of sequences and taxon were treated as random effects to account for potential sampling bias. Fixed effects were scaled and centred to compare effect sizes. For each ACBR region, environmental data were extracted and either the regional sum (for ice-free area and human activity) or regional median (for all other variables) were calculated using spatial overlay implemented in R package 'Raster'. Median was used as a measure of central tendency to reduce the effects of outliers and overdispersal of data. For climatic and geological variables, stepwise AIC was performed and the best models which included both climatic and geological variables were selected. Gaussian, Poisson and Binomial distributions were fitted and assessed using model diagnostic tools

Table 2. The 14 environmental variables used as predictors in generalised linear mixed models to assess potential environmental drivers of genetic diversity of 13 major Antarctic terrestrial taxa.

Variables	Full name	Units	Time period	Source
WORLDCLIM_BIO1	Annual mean temperature	°C	1970–2000	Fick and Hijmans (2017)
WORLDCLIM_BIO5	Max temperature of warmest month	°C	1970–2000	Fick and Hijmans (2017)
WORLDCLIM_BIO6	Min temperature of coldest month	°C	1970–2000	Fick and Hijmans (2017)
WORLDCLIM_BIO12	Annual precipitation	mm	1970–2000	Fick and Hijmans (2017)
MELT	Melt days	days	1979–2020	Picard and Fily (2006)
SOLAR_RAD	Median surface net solar radiation	J m^{-2}	1979–2020	Hersbach et al. (2020)
WIND_SPEED	Median wind speed (10 m above ground)	m s^{-1}	1979–2020	Hersbach et al. (2020)
SLOPE	Median slope	radians	-	Howat et al. (2019)
ASPECT	Median aspect	radians	-	Howat et al. (2019)
RUGOSITY	Median rugosity		-	Howat et al. (2019)
TRI	Terrain ruggedness index		-	Howat et al. (2019)
ELEV	Median elevation	m	-	Howat et al. (2019)
AREA_M2	Total ice-free area	m^2	-	Terauds and Lee (2016)
HUMAN_DENSITY	Density of human activity points	points/m^2	-	Leihy et al. (2020)

including residuals against predicted values, overdispersion check and pseudo R^2 values. GLMM were conducted separately for fauna and flora to examine if there were any differences between larger taxonomic groups. Additional GLMM analyses, following the same model selection process, were performed using rarefied haplotype richness (± upper/lower confidence limits) values as response variables (Supporting information) and taxonomic group as a random factor to examine if expected richness can provide additional insight into the relationships between genetic diversity and environmental factors.

Results

Overview

The final dataset contained a total of 7222 records (individual samples), which spanned 153 studies of 335 different species (Table 1, Supporting information). Animals comprised over half of total records (53%), more than twice the number of embryophyte plant records (20%), while the other 27% included lichens, fungi and algae. Among 13 major taxonomic groups, Collembola (springtails) had the highest number of records, making up almost a third of the total, followed by lichens (17%) and Arachnids (mites, 9%). Among geographical regions, South Shetland Islands had the highest number of records (20%), followed by southern Victoria Land (17%) and northern Victoria Land (13%). Springtails were the most studied taxa in South Victoria Land, while most of the records for lichens were in the South Shetland Islands.

Both the Antarctic Peninsula and Victoria Land had a high number of records (Fig. 2), although records from the Peninsula were closer to the research stations than those from Victoria Land (Fig. 2d). More than 95% of continental Antarctica had no record of genetic sequences of the 13 major taxonomic groups examined here. Over 70% of sampling locations were within 50 km of their nearest research stations, while nearly half were within 10 km. The sampling locations furthest away from research stations were at Ellsworth Land, approximately 878 km from any research base.

Across all studies, 71 different genetic markers were used, with 65 (42 %) studies using only one marker. The use of multiple markers was more common for studies on plants and lichens than animals (Supporting information), and the most markers used in a single study was seven (ID 308; Saługa et al. 2018). COI was the most-used marker for animals, comprising 63% of total animal records (Supporting information). For plants, ITS comprised the highest proportion of plant and lichen records (38%). SSU (ribosomal small subunit, 18S), LSU (ribosomal large subunit, 28S) and plastid genes and their associated spacers were also commonly used. Their total number of records surpassed those that used ITS, but there was not sufficient sequence replication within species to allow meta-analysis.

Molecular analysis

Population overview

2836 sequences were retained for molecular analysis, including 2286 from animals and 550 from plants and lichens (Table 3). Overall, *Cryptopygus* spp. springtails had the highest number of sequences and the most widespread distributions. Within the Antarctic region (Continental Antarctica, South Shetland Islands and South Orkney Islands), *Schistidium antarctici* moss was represented in eight regions, the highest among all species. Within animal groups, only *Cryptopygus* and *Friesea* springtails had data from populations across larger regions including the Peninsula and Victoria Land. For plants and lichens, two out of six taxa (*Schistidium* and *Umbilicaria*) had data from populations spanning larger regions, particularly *Schistidium* which had data from Ellsworth Land and eastern Antarctica.

Cryptopygus springtails had the highest number of observed haplotypes (Table 3) while *Colobanthus quitensis* had the lowest number of observed haplotypes either among all regions or within Antarctica. Rarefaction analyses indicated that current sampling insufficiently captures haplotype diversity, with observed haplotype diversity across Antarctic regions often substantially lower than the estimated richness (Supporting information).

Genetic diversity and differentiation

For most taxa, regions along the Antarctic Peninsula showed higher genetic diversity than other regions according to the four diversity metrics (mean number of pairwise difference, nucleotide diversity, haplotype diversity, Theta S), and there was a generally negative relationship between diversity and latitude within the Peninsula (Supporting information). Animals showed high diversity in Victoria Land in terms of species diversity, although each species had restricted distributions at either southern (SVL) or northern Victoria Land (NVL) except *Stereotydeus* mites, which had higher diversity in NVL. *Acutuncus* tardigrades, in contrast to other taxa, showed higher diversity in Dronning Maud Land (DML). Furthermore, non-Antarctic regions, particularly South America (SA), generally had higher diversity than Antarctic regions, except islands in the Scotia Arc which mostly had lower diversity compared to SA and the Peninsula (including the South Shetland Islands).

No species had haplotypes shared among all regions (Antarctica and non-Antarctic) or regions within the Antarctic. Because of the large numbers of haplotypes within taxa, broad-scale patterns were primarily assessed on higher-level (clade) differences except for *Colobanthus*, which had fewer than ten unique haplotypes. Clades were inferred from phylogenetic trees as well as uncorrected p-distance values for each taxon (Supporting information). For animals, COI clades were generally classified where uncorrected p-distances were at least 2%, except for *Halozetes*, *Stereotydeus* and *Cryptopygus* spp. for which we used a 10% threshold due to these taxa comprising multiple sub-species. For plants and lichens, ITS clades were generally separated by 0.1–2.0% in

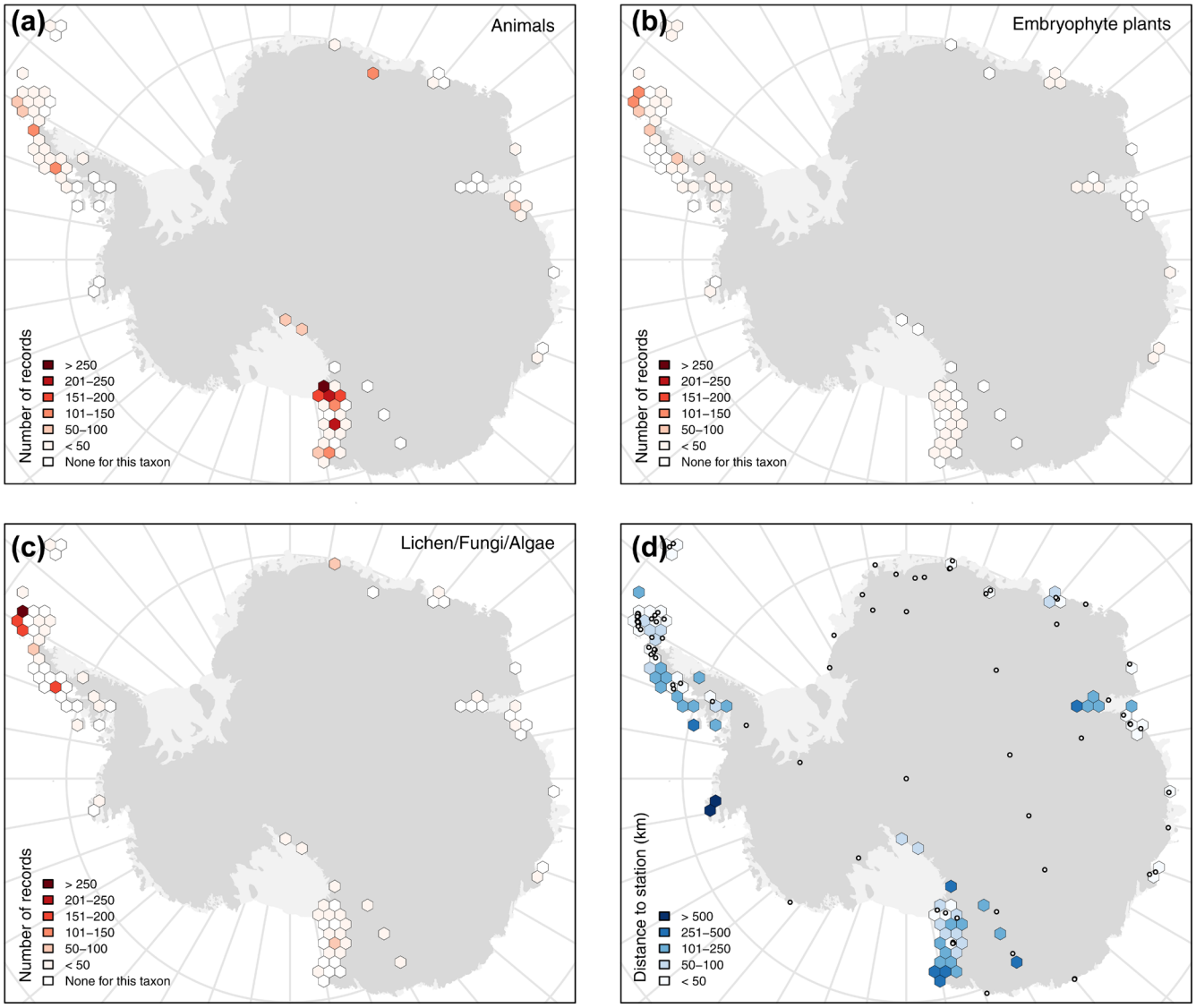

Figure 2. Geographic patterns of numbers of genetic records of (a) animals, (b) embryophyte plants and (c) lichen/fungi/algae in the Antarctic region and (d) associated sampling distance to nearest research stations (hollow circles), from 153 Antarctic terrestrial phylogenetic studies. Values were calculated in 100 km^2 cells (zero values not shown).

uncorrected p-distances. Six taxa (*Acutuncus*, *Stereotydeus*, *Gomphiocephalus*, *Deschampsia*, *Umbilicaria* and *Usnea*) had clades that included samples from all regions.

Overall, animals showed relatively strong phylogenetic structure, with high levels of differentiation among regions, while plants and lichens were less differentiated. Hierarchical AMOVA (Supporting information) showed more structural differentiation at smaller scales (between individuals and subregions) than larger scales (between regions). Most animal taxa did not share haplotype clades across regions except on the Peninsula (Supporting information, Fig. 3a). Within the Peninsula, there was usually one single clade, except *Alaskozetes*, which had distinct clades on the Peninsula with high genetic distances (> 10%, Fig. 3b). Only *Acutuncus* tardigrades shared clades across larger regions (Fig. 3c), however each region exhibited different proportions of two major clades with high pairwise distance. For plants and lichens, clades were generally geographically widespread, shared among regions across Antarctica and even between Antarctica and South America (Supporting information, Fig. 4a and b). Similarly to animals, they generally had large differentiations between Antarctica and non-Antarctic regions, although some taxa (e.g. *Bryum*) also had shared clades (Fig. 4c). The overall AMOVA differentiation results were consistent with haplotype patterns. The genus-level analysis provided similar results with species-level analyses (Supporting information) and did not alter any of the overarching patterns observed in species-level analyses (for example, AMOVA results for *Bryum argenteum* indicated 18.6% variation between regions and 81.0% variation within samples while comparative results for *Bryum* spp. were 25.2% and 75.4%, respectively, with all results statistically significant). Broad-scale biogeographic

Table 3. Summary table of genetic data of 13 Antarctic terrestrial (Continental Antarctica, South Shetland Islands, South Orkney Islands) taxa retained for phylogeographic analysis. Numbers in parentheses indicate counts in all regions including Antarctica, Southern Ocean Islands (SOIs) and non-Antarctic landmasses. Non-Antarctic data were only retained if each respective study also included samples from Antarctica. Estimated haplotypes were calculated using rarefaction of haplotype richness within Antarctica.

Taxa	Marker	No. of sequences	Length (bp)	No. of regions	No. of observed haplotypes	No. of estimated haplotypes
Tardigrada						
Acutuncus antarcticus	COI	87 (87)	554	3 (3)	25 (25)	168
Arachnida						
Alaskozetes antarcticus	COI	89 (101)	494	9 (5)	42 (49)	103
Halozetes spp.	COI	48 (367)	476	8 (3)	17 (162)	27
Stereotydeus spp.	COI	228 (228)	399	2 (2)	66 (66)	143
Collembola						
Cryptopygus spp.	COI	495 (699)	495	15 (6)	206 (276)	296
Friesea spp.	COI	125 (129)	478	4 (3)	19 (23)	28
Gomphiocephalus spp.	COI	675 (675)	463	2 (2)	87 (87)	88
Bryophyta						
Bryum argenteum	ITS1	62 (74)	526	11 (6)	21 (30)	148
Schistidium antarctici	ITS1	59 (65)	566	9 (8)	22 (35)	43
Angiosperms						
Deschampsia antarctica	ITS1	14 (34)	591	4 (3)	10 (25)	44
Colobanthus quitensis	ITS1	99 (194)	536	8 (5)	5 (7)	5
Lichens						
Umbilicaria spp.	ITS1	30 (30)	174	6 (6)	15 (15)	91
Usnea spp.	ITS1	126 (175)	165	5 (3)	23 (38)	56

patterns were similar at a genus level as at species level, with sub-Antarctic islands generally differentiated from Antarctic populations, and regional differentiation within Antarctica. Additionally, the genera *Acutuncus*, *Alaskozetes*, *Colobanthus* and *Deschampsia* contain only one species occurring in Antarctica in our database. Thus, results from the original analyses (Table 3) remain the focus of subsequent interpretation and discussion.

Spatial and environmental analysis

Mantel tests indicated isolation by distance in *Alaskozetes* based on Nei's Gst, and in *Cryptopygus*, *Bryum*, *Deschampsia* and *Umbilicaria* based on Jost's D and Hedrick's G'st (Supporting information). The sPCA highlighted that there were significant spatial structures in global scores (positive spatial autocorrelation) of *Halozetes* ($p = 0.008$, $R = 0.297$), which showed clear distinction between Antarctic and non-Antarctic regions (Supporting information). However, both tests are sensitive to sampling efforts, thus results need to be interpreted with caution.

Gaussian distribution was applied to all GLMM models according to best model fit compared to Poisson and negative binomial distributions (Supporting information). Wind speed showed the strongest positive relationship for three out of five diversity indices. Temperature of the warmest month (bio5) and solar radiation each showed negative correlation with one index (no. of polymorphic sites, nucleotide diversity respectively), while median elevation and ice-free area each exhibited positive correlation with one index (haplotype diversity, Nei's Gst respectively). However, all marginal R^2 values were lower than conditional R^2 values, indicating strong contributions of random effects (number of sequences and taxonomic group). Therefore, results need to be interpreted with caution. Wind speed also had the strongest positive relationship with three diversity indices of animals (Supporting information) with medium effect sizes (0.2–0.4), while for plants and lichens elevation showed the strongest positive correlations with medium effect sizes (Supporting information). For rarefied haplotype richness, no models showed significant relationships between environmental variables and estimated richness values. While marginal R^2 was still lower than conditional R^2, both showed medium (> 0.2) to strong (> 0.5) fits (Supporting information).

Discussion

Status of Antarctic terrestrial genetic research

As predicted, existing genetic data were mostly from flowering plants and macro/mesofauna close to research stations. Mosses and lichens have also received considerable phylogeographic research attention, though when compared to angiosperms they remain understudied, relative to their known high abundance and richness across the Antarctic region (Table 1). For animals, research efforts have focussed on conspicuous macro/mesofauna, which is also consistent with the greater attention given to the patterns of charismatic breeding vertebrates (Pertierra et al. 2020). Genetic data for insects were relatively sparse, which can be attributed to there being only one insect species native to Antarctica, and data for this species are quite comprehensive with a full genome sequenced (Kelley et al. 2014). Observed bias towards the

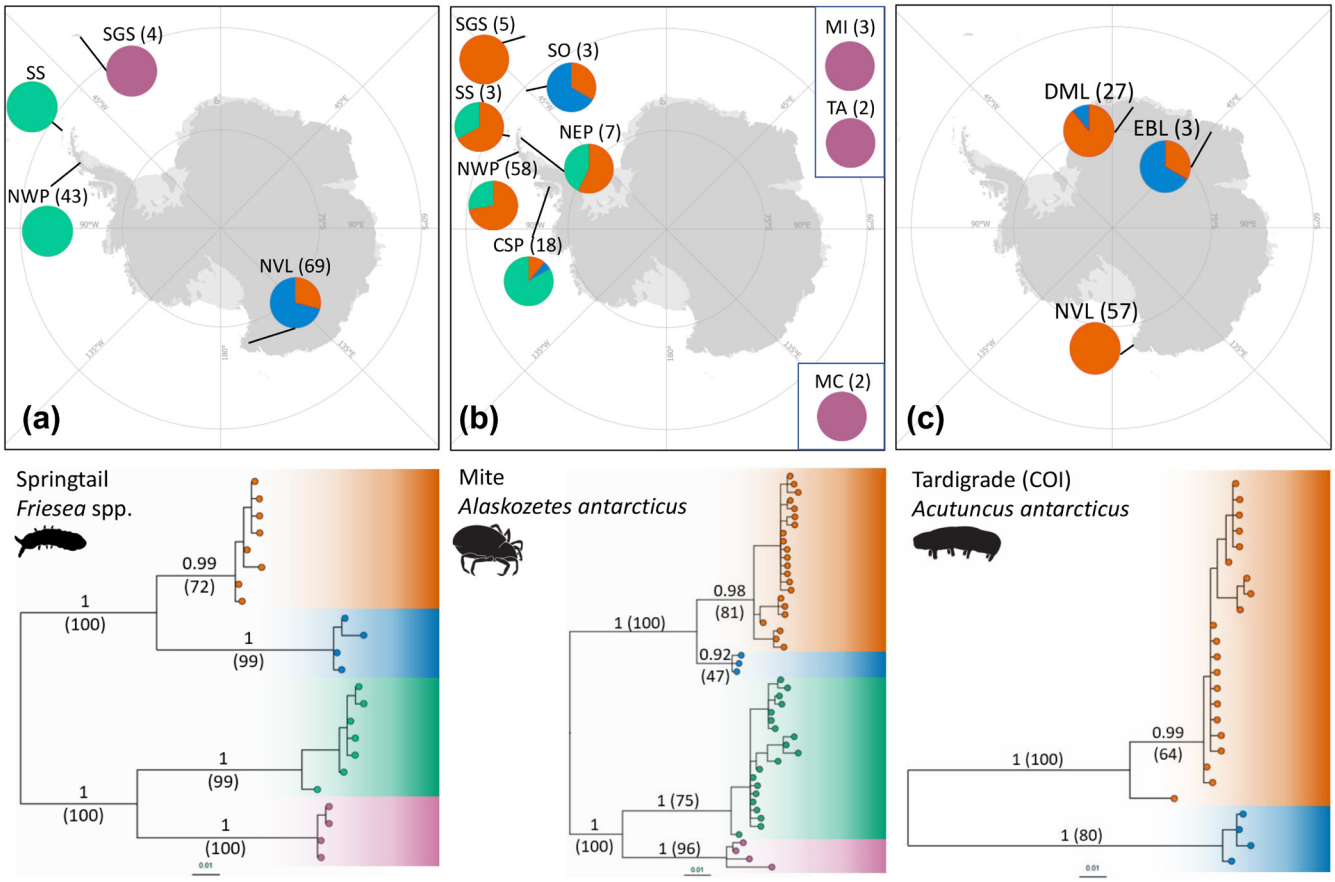

Figure 3. Phylogeographic relationships of major clades of animals (a) *Friesea* spp., (b) *Alaskozetes antarcticus* and (c) *Acutuncus antarcticus* for mitochondrial marker COI. Pie charts represent the relative frequency of each haplotype clade in each region. Numbers in parentheses indicate number of sequences in each region. Numbers on tree branches are Bayesian posterior probabilities (above branches), with maximum likelihood bootstrap values in parentheses.

Peninsula region might be the result of the relatively intensive sampling effort in that part of Antarctica, with many research bases (at least 45 bases along the Peninsula and nearby islands) and visits from research vessels, and the relatively mild climate (average above 1°C in summer). There are fewer research bases in Victoria Land, but the relatively large area of ice-free ground around the Dry Valleys has also received considerable research attention. Conversely, East Antarctica and Dronning Maud Land have been the focus of relatively few genetic studies, and those primarily on mosses, lichens, tardigrades and rotifers.

For most of Antarctica's terrestrial biota, our results highlighted that phylogenetic and population genetic research remains quite scarce and fragmented. The extreme environment of Antarctica is not only difficult for many organisms to inhabit, but also hinders large-scale sampling efforts, and many parts of Antarctica remain unsurveyed (Convey et al. 2014, Convey and Peck 2019, Leihy et al. 2020). The focus of many genetic studies has not been on broad-scale population comparisons; a large proportion of genetic studies have instead focussed on functional genomics of microorganisms in Antarctica for bioprospecting (Martínez-Rosales et al. 2012, Duarte et al. 2018). Furthermore, marine vertebrates such as teleost fish have received a disproportionate level of research interest in relation to their cold-adaptation abilities and associated genes (Fletcher et al. 2001, Giordano et al. 2012).

Fortunately, the widespread adoption of open science principles means that most (though not all – see Methods and below discussion around data accessibility limitations) genetic sequence data that do exist are publicly available, which enables analysis of metadata and knowledge gaps. With technological advances, the methods and complexities of genetic studies in Antarctica are improving. Random amplified polymorphic DNA (RAPD) fingerprinting was commonly used in early studies to examine genetic variation within and among populations (Selkirk et al. 1997). DNA barcoding, which can provide taxonomic diversity information for relatively low cost and time (DeSalle and Goldstein 2019), has also been widely used. The vast majority of studies retrieved by our search used PCR and Sanger sequencing to generate data from one or a few markers, targeting common barcoding (e.g. COI) genes or other well-known parts of the genome. A few Antarctic studies have used newer approaches, such as genotyping by sequencing (McGaughran et al. 2019) and other forms of high-throughput genomic sequencing (Czechowski et al. 2017), but these studies as yet only

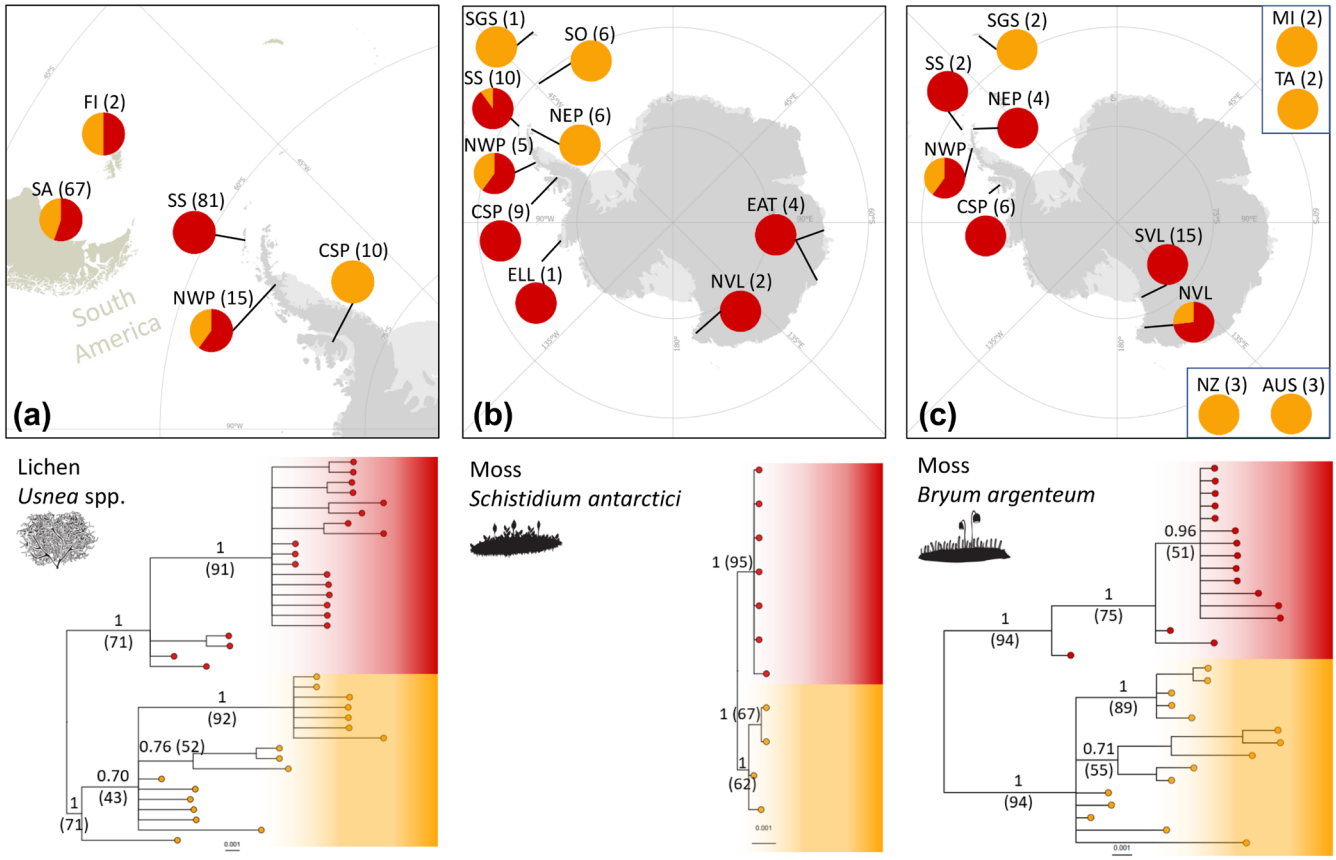

Figure 4. Phylogeographic relationships of major clades of plants and lichens: (a) *Usnea* spp., (b) *Schistidium antarctici* and (c) *Bryum argenteum* for nuclear ITS1. Pie charts represent the relative frequency of each haplotype clade in each region. Numbers in parentheses indicate number of sequences in each region. Numbers on tree branches are Bayesian posterior probabilities with maximum likelihood bootstrap values in parentheses.

represent a tiny component of Antarctic genetic research. These new genomic methods are, however, proving to be powerful tools for population and diversity research, and although they were once more expensive (Narum et al. 2013), these days they are competitively priced with respect to more traditional methods. Given the quite low diversity detected across large spatial scales in Antarctica using single markers (Fig. 3, 4, Supporting information), future research should prioritise high-resolution genomic sequencing, which can provide greater insights into intraspecific diversity and connectivity in the Antarctic (McGaughran et al. 2019).

Biogeographic patterns

Our results indicate that sampling biases exist and could be a confounding factor when examining the relatively high genetic diversity across the SOIs and Antarctic Peninsula (versus higher latitude regions). With current data it is not possible to fully decouple this sampling bias from the effects of climatic, geological and anthropogenic drivers of biogeographic patterns, which themselves often align with sampling patterns (Fig. 2, Supporting information). Nevertheless, our hypotheses of biological connections between the Antarctic and South America were supported, particularly for plants and lichens (Fig. 4, Supporting information). Meanwhile, animals in Victoria Land exhibited quite high genetic diversity and little evidence of connections to other regions. Our meta-analyses thus indicate somewhat different evolutionary histories for flora versus fauna in Antarctica, with floral diversity mainly concentrated in more northern regions, whereas animals show signs of persistence in multiple regions including more southern locations.

High genetic diversity in Antarctic Peninsula and/or Victoria Land

The high genetic diversity exhibited in the Antarctic Peninsula and Victoria Land is consistent with many other phylogenetic studies and is likely more than an artefact of sampling bias concentrated in the region (Fig. 2), although both regions have relatively more suitable environments for both fauna and flora to survive compared to other parts of Antarctica (Convey and Peck 2019). As high genetic diversity is often associated with long-term vicariant evolution and inferred potential refugia during Pleistocene glacial periods (Hewitt 2004, Fraser et al. 2012, Lau et al. 2020), both regions have been suggested to contain multiple glacial refugia, with a

relatively large proportion of ice-free areas and higher mean annual temperatures, as well as geothermal regions, allowing organisms to persist (Chown and Convey 2007, Pugh and Convey 2008, Fraser et al. 2012, 2014, McGaughran et al. 2019). Dispersal events during interglacial periods have been proposed (McGaughran et al. 2019, Zaccara et al. 2020, Lagostina et al. 2021), including among refugia, resulting in range expansion and the occurrence of lineages from different clades within regions.

The apparent genetic connectivity of Antarctic flora (here including plants and lichens based on Singh et al. 2018) among some regions indicates long-distance dispersal has occurred, although determining the direction and timing of dispersal events would require higher resolution data. Flora in Antarctica might readily disperse with wind and oceanic rafting (Biersma et al. 2020b), or zoochory with birds (Parnikoza et al. 2018). Some species are able to survive extreme environmental conditions for long periods, even centuries (Parnikoza et al. 2011, Cannone et al. 2017), although the overall more northern distributions of flora reflect their physiological limitations to better conditions of temperature, soil nutrients, liquid water availability and sunlight (Peat et al. 2007, Singh et al. 2018). The limited evidence for genetic connectivity of animals, on the other hand, may indicate restricted movement between regions. Although animals have higher individual mobilities on very small spatial scales, passive dispersal on larger scales via e.g. wind (Muñoz et al. 2004, McGaughran et al. 2019) and water (Hawes et al. 2008) might not be survivable for many taxa. Patterns of species turnover for plants and animals across the Southern Ocean region have been previously noted and attributed to these contrasting dispersal capabilities (Leihy et al. 2018). Furthermore, geographic barriers such as mountain ranges, glaciers and waterways can extend the distances a species would need to travel between ice-free regions, which could be considerably longer than direct geographic distances between two regions (Zink 1997). Models might, therefore, fail to capture some isolation-by-distance signals, particularly for Antarctica with its geographically complex island-like habitats.

One exception to the pattern of restricted lineage distribution in animals was the tardigrade *Acutuncus antarcticus*, which had widespread clades (Fig. 3c). Tardigrades are known for their ability to withstand extreme environmental conditions, and one study found that they were able to recover and reproduce after being frozen for over 30 years (Tsujimoto et al. 2016). Such hardiness could enhance long-distance dispersal capacity as well as in situ persistence through challenging periods. The Enderby Land population of *A. antarcticus* showed high genetic diversity compared to all other animal populations and had low values for population neutrality tests, suggesting this region may have been a glacial refugium. Indeed, previous studies have suggested that part of Enderby Land remained ice-free since at least the Pliocene and retained freshwater systems (Bayly et al. 2003, Pugh and Convey 2008). Tardigrade species of the genus *Mesobiotus* have also recently been shown to have discrete genetic lineages within Antarctica, indicative of an Antarctic radiation following isolation from other continents (Short et al. 2022).

Phylogenetic studies have frequently revealed or hinted at unrecognised species in terrestrial Antarctica, and many species previously thought to be widespread around the continent have later been resolved as multiple species/genera with more restricted distributions, such as *Cryptopygus* and *Friesea* springtails (Torricelli et al. 2010, Greenslade 2018, Carapelli et al. 2020, Stevens et al. 2021). Our results highlight this diversity, and the large divergences detected within some species could also support calls for more taxonomic work, for example in *Acutuncus* and *Gomphiocephalus*. Antarctic terrestrial flora, in contrast to fauna, generally showed low genetic variation, which highlights the need for a concerted molecular and taxonomic revision of these genera and their species delimitations, particularly for lichens (7 *Umbilicaria* spp. and 6 *Usnea* spp. were included in this study). However, Lücking et al. (2021) noted that species delimitations in lichens are affected by many factors such reproductive strategies and symbiotic components, and often high-resolution phylogenomic approaches (such as RADseq) are needed to reveal genetic differences; the lower-resolution ITS1 marker used here might be unable to differentiate species.

High Southern Hemisphere diversity and connectivity

Although for taxa with distributions in South America there was in general a strong signal of connectivity – or at least relatively recent dispersal – to (or from) terrestrial Antarctica, most groups showed a strong differentiation between Antarctica and other non-Antarctic regions. This distinction has been observed in many previous studies (Mortimer et al. 2011, Biersma et al. 2018, Baird et al. 2021, Stevens et al. 2021). Animals exhibited stronger differentiation between Antarctica and SOIs than plants and lichens, which could be due to lower long-distance dispersal abilities of flightless invertebrates (Hopkin 1997, Convey et al. 2014).

The SOIs include young, volcanic islands such as Heard Island and South Sandwich Islands, old uplifted continental crust such as Macquarie Island, as well as parts of submarine plateaux such as Marion Island or the continental crust such as islands around the Scotia Arc (Quilty 2007). They range in age from as young as a few hundreds of thousands of years, to > 100 Ma, and are mostly separated by thousands of kilometres of ocean (Quilty 2007, Moon et al. 2020). Most of the islands were, at least partially, covered by ice during the Pleistocene glacial periods (Hodgson et al. 2014). Strong circumpolar winds, currents and fronts in the Southern Ocean have been suggested to facilitate dispersal of organisms between islands (Muñoz et al. 2004, Moon et al. 2017, Leihy et al. 2018), but to inhibit southward colonisation to continental Antarctica (Fraser et al. 2012), although occasional southward dispersal via both sea and air is possible (Fraser et al. 2018, Baird et al. 2021). The genetic patterns within islands were likely driven by volcanic and glacial events as well as environmental variabilities (Moon et al. 2017). For instance, 162 observed haplotypes of *Halozetes* mites were

analysed in this research, the second highest amongst all taxa (Table 3). However, seven out of the nine identified clades (70% of all haplotypes) were found only in the SOIs, which indicated some recent connections among islands but not between the islands and continental Antarctica (Supporting information). Glacial refugia and volcanic activity have been suggested to have promoted divergence within islands, for example Marion Island (Mortimer et al. 2012).

Antarctic terrestrial flora generally had strong connections with South America and islands along the Scotia Arc (e.g. South Georgia, South Orkney, Fig. 4, Supporting information). Studies have suggested that many current lineages in Antarctica could have originated from South American glacial refugia (Biersma et al. 2020a), consistent with our results showing higher diversity levels at lower latitudes. However, vicariant evolution in the Antarctic has also been inferred (Biersma et al. 2017, 2018, 2020a, Zaccara et al. 2020, Lagostina et al. 2021), and some lineages may have even dispersed northward, contrary to most southward colonisation hypotheses (Convey et al. 2000, Lagostina et al. 2021). Our focus here on taxa found in the Antarctic region meant that this study did not include all genetic records from South America and thus was not able to address such questions in-depth.

Wind and habitat heterogeneity may promote diversity

As predicted, wind was inferred to be one of the key environmental parameters affecting genetic diversity in Antarctica, particularly for animals. Wind is one of the major dispersal mechanisms for many Antarctic terrestrial fauna (Hopkin 1997, Mortimer et al. 2011, McGaughran et al. 2019), and while long-distance dispersal of animals was not strongly supported in our results, wind may nevertheless facilitate dispersal across the 'island-like' habitat of ice-free patches within Antarctic biogeographic regions, promoting hybridisation and gene flow. Nevertheless, some studies have suggested that dispersal of Antarctic animals may still be limited at very small spatial scales, particularly around Victoria Land (Collins et al. 2019, 2020, Carapelli et al. 2020). Meanwhile, geographic barriers can extend the actual dispersal distances a species would need to travel, which could be considerably longer than straight-line geographic distances between two regions (Zink 1997), particularly in Antarctica due to the widespread ice sheets. Plants and lichens also utilise wind for dispersal but as they appear to disperse more effectively than animals (Muñoz et al. 2004, Casanovas et al. 2013, Lagostina et al. 2021), they might more easily maintain population connectivity across larger regions (Fig. 4, Supporting information) and achieve species turnover across the SOIs (Leihy et al. 2018). Kling and Ackerly (2021) recently demonstrated how wind has shaped the evolutionary patterns of trees across the globe, with stronger winds facilitating genetic connectivity, which further highlights the importance of wind-driven dispersal in plants more broadly.

Habitat heterogeneity (measured by elevation, slope, aspect, rugosity, terrain ruggedness) also exhibited significant correlations with various diversity indices, although to a lesser extent than wind. This correlation has been demonstrated in many other ecosystems around the world (Ortego et al. 2012, Engler et al. 2014, Manel et al. 2020), but not so much in the Antarctic region due to lack of small scale analysis. Furthermore, habitat heterogeneity is also related to temperature and wind differences on varying scales (from microhabitat to regional climate), and small 'near the ground' differences have been suggested to be a major driver of diversity (Geiger et al. 2003, Potter et al. 2013). Strong local adaptation and selective sweeps may also contribute to genetic diversification due to the distinct and dynamic local environment of Antarctica, although most demonstrations of these effects are from microbiome and protein studies (Hawes et al. 2011, Rengefors et al. 2015). Temperature surprisingly did not show a strong relationship with overall genetic diversity, although there were some subtle effects. This result could be due to the ubiquitous extreme temperature conditions across the region, though it may also be a reflection of the relatively coarse temperature data used and the low variance explained by fitted models. Furthermore, the observed relationships may be affected by the derived environmental data from ACBR boundaries, which only included ice-free areas. Finer-scale analysis was not, however, possible with the resolution of genetic and environmental data currently available. Sampling bias, indicated by the difference between expected and observed haplotype richness across both regions and genera, may also be confounding analyses.

Present gaps and future priorities

Although our findings help summarise phylogeographic patterns and processes for Antarctic terrestrial species, they also highlight inadequacies and omissions in existing datasets. We encountered considerable challenges in compiling information, including but not limited to access to data and metadata (there is no standardised requirement for data sharing, although databases have been developed in an attempt to improve this; Deck et al. 2017), filtering processes, and data retrieval. Several studies that had produced data that could have given insights into biogeographic patterns were not able to be included. For example, many studies of fungi, algae and their symbionts were not included because the research papers and data sets did not record which sequence came from which location (these studies tended to be focussed on community composition rather than biogeography). Meanwhile, studies that did not publish (or provide on request) full sets of sequence data, but instead released only unique/novel haplotypes, had to be excluded from our analyses to minimise sampling bias (Paz-Vinas et al. 2021). We also identified potential issues with some sequence data, for example when BLAST results indicated the amplicon was probably not the target taxon, we opted to conservatively exclude some sequences. Taxonomic ambiguities also prevented inclusion of some data sets, for example for soil microfauna such as

nematodes. Such groups constitute important components of Antarctica's biodiversity (Chown et al. 2015); resolving the taxonomic and data archiving issues for past and future work on these taxa would greatly enhance our capacity to research the drivers of evolution in Antarctica.

Sampling intensity across much of Antarctica is remarkably low (Fig. 2) and obtaining data from an array of species from less-sampled regions should be a key priority for future research (Box 1). Low sample sizes for some regions and taxa, as noted in other studies (McGaughran et al. 2019, Cakil et al. 2021) has likely affected our analyses. In particular, the low sample sizes from regions beyond the Peninsula and Victoria Land could mean we are drastically underestimating the true genetic diversity of some parts of Antarctica. Although data were not available for direct comparison, qualitative comparisons against species occurrence records across Antarctica (Chown et al. 2015, Leihy et al. 2020) indicate that the molecular data synthesised here represent a tiny subset of described biodiversity. The inconsistency of genetic records for taxa and regions may over or underestimate the actual diversity levels, though rarefaction analyses suggest that observed diversity is currently an underestimate of expected diversity across all genera and regions. Additionally, the genus-level analyses (Supporting information) for taxa that could not be resolved to species may have led to further underestimation of genetic diversity and the metrics used to describe it. This undersampling is consistent with research in the Arctic, where harsh conditions have constrained sampling efforts to areas close to research stations, while regions further afield receive less attention (Metcalfe et al. 2018). Comparing sampling effort and the locations of Antarctic facilities (Fig. 2), it is clear that a similar bias applies to the Antarctic region.

Box 1. Recommendations for future priorities of Antarctic phylogeographic research

1) A sampling focus on under-represented invertebrate groups, mosses and lichens.
2) A sampling focus on regions beyond the Peninsula and Victoria Land, such as Eastern Antarctica, the Transantarctic Mountains and Dronning Maud Land.
3) Using advanced genetic and genomic technologies with higher resolutions to enable more insightful inferences of species delimitation and population differentiation. Importantly, whether using traditional or modern genetic approaches, methods should as far as possible be comparable among studies, and data sets properly archived with detailed meta-data.
4) Obtaining detailed environmental data to enable fine-scale modelling to assess the relationships between distribution, diversity and environmental factors, particularly under future climate trajectories.

Many genetic studies on terrestrial taxa in Antarctica have used different markers, or different gene regions, making broad-scale comparative research difficult. Here, we re-analysed only one marker for plants, and one for animals, as there was insufficient data from other markers to enable a meaningful meta-analysis. For animals, although the COI marker is considered to have high resolution for species discrimination, primer binding regions are not necessarily highly conserved (Deagle et al. 2014), and COI may fail to detect species when there is introgressive hybridisation, over-splitting and incomplete lineage sorting (Chee 2015). Similarly, although ITS is widely used for flora, there may be issues related to identification when encountering pseudogenes or homogenisation of DNA repeats (Álvarez and Wendel 2003). Evolutionary rates also vary across markers and time periods, confounding both cross-taxon (Heads 2005, Guindon 2020), and intraspecific (Nietlisbach et al. 2012, Alban et al. 2021) comparisons when different markers are used. The inherent differences between COI and ITS, the two most prevalent markers in our faunal and flora data, respectively, make all but the most superficial comparisons of evolutionary patterns in the Antarctic region extremely difficult. Microsatellites, multiple markers or the use of advanced genomic methods, along with morphological analyses, would increase confidence in examining species and population differentiation (Ouborg 2010, Padial et al. 2010).

Alongside the direct impacts of warming and human activity (Duffy and Lee 2019, Siegert et al. 2019), non-native species could also threaten Antarctic biodiversity and disrupt established biogeographic patterns. Previously uninhabitable areas may soon become available to species with the requisite physiological tolerances to cold and desiccation (Lee et al. 2017, Gutt et al. 2021), and although oceanic barriers are challenging to cross, they are not impenetrable (Fraser et al. 2018, Cárdenas et al. 2020, Bartlett et al. 2021, Lagostina et al. 2021, Maroni et al. 2022). Developing an understanding of the physical and evolutionary processes that shape diversity and distributions in Antarctica will be critical for building useful models to forecast and help manage Antarctic ecosystems into the future. Although there remain many gaps to be filled and future research priorities to be pursued (Box 1), our results help to show what existing data can tell us about broad biogeographic patterns and drivers in Antarctica.

Acknowledgements – We thank the authors who provided extra information and assistance with the database construction, including (in surname alphabetical order): Prof. Steven Chown, Dr Claudia Coleine, Prof. Peter D. Crittenden, Assoc. Prof. Marie-Laure Guillemin, Prof. Ian D. Hogg, Dr Soon Gyu Hong, Dr Angela McGaughran, Assoc. Prof. Lorena Rebecchi, Prof. Jason E. Stajich and Prof. Bettine Jansen van Vuuren.

Funding – This work was supported by the New Zealand Antarctic Science Platform (grant no. MBIE ANTA1801) and a Royal Society of New Zealand Rutherford Discovery Fellowship (grant no. RDF-UOO1803) to CIF, via an Honours scholarship to XPL. GAD and CIF were supported by a Royal Society of New Zealand Te Apārangi Marsden Fund grant (grant no. MFP-20-UOO-173). LRP was supported by Biodiversa ASICS funding (EU-Biodiversa ASICS project).

Author contributions

Xiaoyue P. Liu: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Grant A. Duffy**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Resources (equal); Supervision (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **William S. Pearman**: Data curation (equal); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Luis R. Pertierra**: Formal analysis (supporting); Methodology (supporting); Resources (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Ceridwen I. Fraser**: Conceptualization (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Resources (equal); Supervision (lead); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06312>.

Data availability statement

This study used previously published genetic data from diverse studies. All metadata (GenBank accessions, paper references, geolocations etc.) for data used in this study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kprr4xh7p>. This article contains no original data.

Supporting information

The Supporting information associated with this article is available with the online version.

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