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RESEARCH ARTICLE

Effects of dispersal strategy and migration history on genetic diversity and population structure of Antarctic lichens

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Abstract

Aim: The homogenisation of historically isolated gene pools has been recognised as one of the most serious conservation problems in the Antarctic. Lichens are the dominant components of terrestrial biotas in the Antarctic and in high mountain ranges of southern South America. We study the effects of dispersal strategy and migration history on their genetic structure to better understand the importance of these processes and their interplay in shaping population structure as well as their relevance for conservation.

Location: Maritime Antarctic and southern South America.

Methods: Populations of three fruticose lichen species, *Usnea aurantiacoatra*, *U. antarctica* and *Cetraria aculeata*, were collected in different localities in the Maritime Antarctic and southern South America. *Usnea aurantiacoatra* reproduces sexually by ascospores, whereas the other two species mostly disperse asexually by symbiotic diaspores. Samples were genotyped at 8–22 microsatellite loci. Different diversity and variance metrics, Bayesian cluster analyses and Discriminant Analysis of Principal Components (DAPC) were used to study population genetic structure. Historical

migration patterns between southern South America and the Antarctic were investigated for *U. aurantiacoatra* and *C. aculeata* by approximate Bayesian computation (ABC).

Results: The two vegetative species display lower levels of genetic diversity than *U. aurantiacoatra*. Antarctic populations of *C. aculeata* and South American populations of *U. aurantiacoatra* display much stronger genetic differentiation than their respective counterparts on the opposite side of the Drake Passage. *Usnea antarctica* was not found in South America but shows comparably low levels of genetic differentiation in Antarctica as those revealed for *U. aurantiacoatra*. Phylogeographic histories of lichens in the region differ strongly with recent colonisation in some instances and potential in situ persistence during Last Glacial Maximum (LGM) in others. Patterns of genetic diversity indicate the presence of glacial refugia near Navarino Island (South America) and in the South Shetland Islands. ABC analyses suggest that *C. aculeata* colonised the Antarctic from Patagonia after the LGM. Results for *U. aurantiacoatra* are ambiguous, indicating a more complex population history than expressed in the simplified scenarios.

Main Conclusions: Mode of propagation affects levels of genetic diversity, but the location of glacial refugia and postglacial colonisation better explains the diversity patterns displayed by each species. We found evidence for glacial in situ survival of *U. aurantiacoatra* on both sides of the Drake Passage and postglacial colonisation of Antarctica from South America by *C. aculeata*. Maintaining the strong genetic differentiation of Antarctic populations of *C. aculeata* requires strict conservation measures, whereas populations of *U. aurantiacoatra* are exposed to a much lower risk due to their higher diversity and connectivity.

KEYWORDS
approximate Bayesian computation, biodiversity, *Cetraria aculeata*, climate change, conservation, microsatellites, *Parmeliaceae*, *U. aurantiacoatra*, *Usnea antarctica*

1 | INTRODUCTION

Antarctica began to separate from South America over 40 million years ago (Scher & Martin, 2006). The opening of the Drake Passage, today separating the continents by 900 km, was completed about 28 Mya (Lawver & Gahagan, 2003). In addition to the strong spatial isolation the Antarctic Circumpolar Current (ACC) and atmospheric circulation patterns provide substantial barriers against colonisation of the Antarctic from the north (Fraser et al., 2018). Consequently, levels of endemism are high (between 35% and 100% in different organismal groups, Rogers, 2007). Within the Antarctic, biotas are widely separated by large ice sheets and restricted to small ice-free areas covering only 0.3% of the continent (Convey & Stevens, 2007) leading to distinct biogeographical structure (Chown & Convey, 2007; Peat et al., 2007; Terauds et al., 2012). As a result, patterns of genetic diversity in Antarctic organisms have been shaped by isolation and recolonisation, allopatric divergence amongst populations, founder events and the occasional occurrence of secondary contact zones (Domaschke et al., 2012; Nolan et al., 2006; Rogers, 2007) but above all by limited migration and gene flow due to the strong fragmentation of habitable areas and reduced dispersal abilities of many organisms. Therefore, strong local and regional genetic differentiation has been observed in most Antarctic terrestrial organisms (Chong et al., 2015; Courtright et al., 2000; McGaughran et al., 2010; Skotnicki et al., 2004; van de Wouw et al., 2008). Together with high levels of endemism, this is evidence for long-standing survival of terrestrial and lacustrine organisms in glacial refugia (Convey & Stevens, 2007; de Wever et al., 2009; Green et al., 2011; Jones et al., 2013) perhaps concentrated around areas of geothermal activity (Fraser et al., 2014). From a biological perspective, the Antarctic thus presents an assemblage of widely spaced "habitat islands" (Bergstrom & Selkirk, 1997) with sufficiently long continuity to support considerable genetic diversity (Convey et al., 2014).

The Western Antarctic region, particularly the Antarctic Peninsula and the Bellingshausen Sea, has until recently been subject to rapid regional warming (Turner et al., 2005). The ensuing glacial retreat exposes so far uninhabited disturbed ground, potentially favouring the establishment of invasive species (Chown et al., 2012;

Sancho et al., 2017). Moreover, higher temperatures alleviate physiological stress, and the increase in available habitat leads to larger population sizes and reduced competition as witnessed by 5-fold to 25-fold increases in local abundance of indigenous plants over a few decades (Fowbert & Lewis Smith, 1994). Simultaneously, human impact on Antarctic ecosystems is growing, because of increased scientific activities (>100 research facilities in the Antarctic Treaty area) and rising numbers of tourists with multiple landings in different Antarctic regions. Both activities facilitate propagule movement into Antarctica and amongst different habitats and bioregions. Together with an expansion of habitable terrain, this facilitates the breakdown of dispersal barriers and the merging of genetically isolated populations (Chown et al., 2015). The potential genetic homogenisation of gene pools that are now highly differentiated has been identified as a serious threat to Antarctic biodiversity (Hughes & Convey, 2010; Terauds et al., 2012) and "one of the most significant conservation problems in the Antarctic" (Chown & Convey, 2007). Consequently, there is a growing need to reassess and monitor the extent of Antarctica's biological isolation and the genetic structure of its biota (Fraser et al., 2018).

Lichens, symbioses of heterotrophic fungi (mycobionts) and autotrophic green algae and/or cyanobacteria (photobionts) play a dominant role in the Antarctic terrestrial vegetation. Of the more than 400 reported species, 34% are endemics, indicating isolation of lichen biotas over geological timescales. The other species are mostly cosmopolitan or bipolar (Garrido-Benavent & Pérez-Ortega, 2017); many are found in southern South America. Global distribution patterns and molecular phylogenetic analyses suggest that some of the more widespread species evolved in the Antarctic and colonised South America and the Arctic from there (Søchting & Castello, 2012), whilst others migrated from the Northern Hemisphere southwards into Patagonia and Antarctica (Fernández-Mendoza & Printzen, 2013). Lichens display different reproductive and dispersal strategies that may affect their dispersal abilities and gene flow between isolated populations. Small-sized meiotic and mitotic fungal spores are generally considered ideal vehicles for long-distance dispersal by wind (Tibell, 1994) whilst asexual propagules (soredia, isidia or thallus fragments) containing both symbionts may facilitate the establishment on newly exposed substrata. Human-induced gene flow between Antarctic lichen populations and increased migration rates between South America and Antarctica would be of immediate conservation concern, because both would change the genetic composition of Antarctic lichen populations and endanger the survival of genetically isolated and locally adapted lineages.

Information about the spatial genetic structure of lichens in the region is therefore urgently needed to assess possible future effects of local human activities and global temperature increase on Antarctic terrestrial vegetation. We present here population genetic data on three fruticose lichen forming fungi reported from South America and the Maritime Antarctic: *Usnea aurantiacoatra* reproducing sexually via ascospores and two species with mostly symbiotic, asexual dispersal: *U. antarctica* with soredia and *Cetraria aculeata* mostly dispersing by thallus fragments. *Usnea antarctica* and *U. aurantiacoatra* belong to the *Neuropogon* group of *Usnea*. Most species of this group occur in southernmost South America, Australasia and Antarctica and have likely evolved there (Jørgensen, 1983; Wirtz et al., 2008, 2012). *Cetraria aculeata* is a bipolar lichen species that colonised Antarctica from Patagonia during the Pleistocene (Fernández-Mendoza & Printzen, 2013). Therefore, these three species are representative taxa to study the effects of dispersal strategy and population history on the genetic structure of Antarctic lichens and assess the likely effects of climate change and human impact on them. Our main research questions can be summarised as follows:

- Do the large distance between southern South America and Antarctica and the isolation of ice-free areas within the Antarctic result in genetic isolation of lichen populations or are natural levels of dispersal high enough to connect gene pools within the region?
- Do differences in dispersal strategy have an impact on the genetic diversity and structure?
- What are the effects of immigration history and potential glacial survival on the genetic structure of Antarctic lichens?
- What are the conservational consequences of our findings, particularly a possible breakdown of genetic isolation as a result of regional climate change or human-mediated transfer of propagules?

2 | MATERIALS AND METHODS

2.1 | Sample collection and DNA extraction

Sampling covered a wide range of localities in the Maritime Antarctic (61–64°S) and southern South America (50–55°S) (see localities in S1), including the Falkland Islands (hereafter "Falkland"). Most samples were collected between 2015 and 2018. A few populations sampled between 2007 and 2014 and cryo-conserved at Herbarium Senckenbergianum (FR) were added to the dataset. For most analyses, samples from different nearby stands (e.g. on the same island) were pooled into "localities," The data sets comprised: 10 localities/22 stands/441 individuals for *U. aurantiacoatra*, 6 localities/20 stands/370 individuals for *U. antarctica* and 10 localities/16 stands/266 individuals for *C. aculeata*. For further details on sampling locations see Supplementary Table S1.

Total DNA was extracted from young terminal branches. Branches were ground with the Bead Ruptor 24 (Omni International Inc.), and DNA was extracted with the GeneOn BioTech Plant Kit (BGgreen Biotech) according to the manufacturer's instructions.

2.2 | Microsatellite analyses and genetic diversity

Samples *of Usnea aurantiacoatra* and *U. antarctica* were genotyped using 21 and 22 microsatellites markers, respectively. The identification of the two *Usnea* species was confirmed with a Discriminant Analysis of Principal Components (DAPC) based on

microsatellite markers as reported in Lagostina et al. (2018). Eight consistently amplifying markers were used for *Cetraria aculeata*. Detailed information on primers and PCR amplification can be found in Lagostina et al. (2017) and Lutsak et al. (2016). PCR amplicons were electrophoresed using an Applied Biosystems 3730 sequencer, with the LIZ 600 (*Usnea* sp.) or LIZ 500 (*C. aculeata*) size standards (Applied Biosystems, Waltham, Mass., USA). Allele sizes were manually scored using the Geneious 10 microsatellites tool (Kearse et al., 2012).

Allele frequencies and genetic diversity (Shannon's information index) were calculated using the software GenAlEx 6.503 (Peakall & Smouse, 2006, 2012) for the three species. To eliminate the impact of unequal sample sizes on observed allelic richness, we applied rarefaction (Kalinowski, 2004) using the program HP-Rare, v. 6 June 2006 (Kalinowski, 2005) and a sample size of *Nmin−1*. Tests for clonal population structure and differentiation amongst populations using Jost's D were calculated with the software GenoDive 2.0b23 (Meirmans & Van Tienderen, 2004). Clones in each population were detected using a stepwise mutation model, discarding null alleles and assessed based on the number of genotypes, with 999 permutations randomising alleles over individuals over all populations.

2.3 | Clustering analysis

Individuals of each species were clustered into gene pools using STRUCTURE 2.3.4 (Falush et al., 2003; Pritchard et al., 2000). The analyses were based on 10 serial runs for each number of clusters (*K*) between 1 and 10. Admixture models used a uniform alpha prior, independent allele frequencies and no prior population information. All analyses were run for 5×10^5 generations after a burn-in of 25×10^4 generations. To estimate the optimal number of admixture clusters, we used the summary likelihood statistics ΔK proposed by Evanno et al. (2005) through the website POPHELPER v1.0.10 (Francis, 2016, www.pophelper.com). The number of clusters was chosen as the value of *K* where ΔK reached its first minimum. Results of the 10 runs for each species were summarised using CLUMPP (Jakobsson & Rosenberg, 2007) and printed out through the web interface of POPHELPER v1.0.10. We also applied DAPC using the R package adegenet 2.1.0 (Jombart, 2008; Jombart & Ahmed, 2011) to validate the clusters detected by STRUCTURE. Analyses were run with 25 (*Cetraria aculeata*), 30 (*Usnea antarctica*) and 60 (*U. aurantiacoatra*) retained principal components. To allow a direct comparison of results, we chose the same numbers of *K* (genetic groups) as used in the STRUCTURE analysis.

2.4 | Estimation of historical gene flow between South America and Antarctica

To interpret patterns of gene flow between South America and Antarctica in a historical context, we compared different colonisation scenarios for *C. aculeata* and *U. aurantiacoatra* by approximate Bayesian computation (ABC) as implemented in DIYABC 2.1.0 (Cornuet et al., 2014). *Usnea antarctica* was not found by us in southern South America and hence was excluded from this analysis. In order not to overparameterize the models, whilst still allowing the definition of meaningful historical scenarios, we pooled samples of *C. aculeata* into four (South America incl. Falkland, King George, Elephant, Antarctic Peninsula) and those of *U. aurantiacoatra* into six regions (Navarino, rest of Chile, Falkland Islands, King George, Livingston and Elephant Island). Four scenarios assuming preglacial and postglacial colonisation of Antarctica from South America and vice versa were tested for both species. In addition, we tested scenarios, in which populations with higher than average genetic diversity resulted from admixture between South American and Antarctic populations (Table 1). For *C. aculeata* this model assumed that a postglacial admixture event between Elephant Island and South American populations gave birth to the population on King George Island. Usnea aurantiacoatra showed similarly high levels of genetic diversity on Navarino and Livingston Island. We therefore tested two scenarios in which the Livingston Island population arose due to postglacial admixture between Navarino and King George Island, and admixture between Livingston Island and Chilean populations led to the Navarino Island population.

Preliminary runs with default priors were carried out to optimise posterior distributions of effective population sizes N_i and colonisation times t_i. To assess the impact of prior choice on the results, the analyses were then run twice for each species using slightly different priors. The first analysis used uniform priors with minimum and maximum values individually selected according to the preliminary analyses. The second analysis used normally distributed priors with minimum and maximum as above, the mean set to half the max value and standard deviation set to half the mean value. Mutation rates of SSR markers in lichens are poorly studied. We therefore used the default settings of DIYABC for mutation model parameters in all analyses, except for the mean coefficient P which was set to follow a uniform distribution with min and max of 0.1–0.8. Details on model parameters can be found in Table 2.

Posterior distributions of parameters were estimated based on 1% out of 5×10^6 (*C. aculeata*) or 6×10^6 (*U. aurantiacoatra*) simulated data sets closest to the observed data set. Posterior probabilities of scenarios were obtained (1) as the proportion of each scenario in the 500 most similar subsets and (2) based on logistic regression on linear discriminant analysis components of the most similar 1% of simulated data sets. We used mean number of alleles and Fst as summary statistics to evaluate priors and mean genic diversity, mean size variance and $(d\mu)^2$ genetic distance amongst populations for model checking. Posterior and prior predictive errors were inferred based on 1000 pseudo-observed data sets (pods) and the 500 most similar subsets (direct approach) or the 1% data sets closest to the pods (logistic regression approach).

TABLE 1 Assumptions of historical gene flow models compared in the ABC analysis

	Cetraria aculeata	*Usnea aurantiacoatra*
Scenario 1:	Glacial survival in South America	Strong isolation of Falkland Islands due to early split before LGM
Colonisation of Antarctica from South America after LGM	Postglacial colonisation of King George Island from South America	Postglacial colonisation of Chile, Livingston and Deception Islands from Navarino Island
	Later colonisation of Antarctic Peninsula and Elephant Island with strong founder effects	Later "stepping stone" colonisation of King George and Elephant Island
Scenario 2:	Postglacial colonisation of South America, Elephant Island and Antarctic Peninsula from King George Island with strong founder effects	Postglacial colonisation of Navarino and Falkland Islands from Livingston Island
Colonisation of South America from Antarctica after LGM	Rapid postglacial diversification in South America	Strong isolation of Falkland due to founder effect
		Later colonisation of Chile from Navarino and "stepping stone" colonisation of KGI and Elephant Island from Livingston Island
Scenario 3:	Pre-glacial colonisation of King George Island from South America	Glacial survival on Livingston and Navarino Island
Colonisation of Antarctica from South America before LGM	Glacial survival on both sides of the Drake Passage with higher Ne in South America	Strong isolation of Falkland due to colonisation before LGM
	Postglacial colonisation of Elephant Island and Antarctic Peninsula from King George Island with strong founder effects	Postglacial colonisation of Chile from Navarino Island and of KGI and Elephant Island from Livingston Island
Scenario 4:	Pre-glacial colonisation of South America from King George Island	Glacial survival on Livingston and Navarino Island
Colonisation of South America from Antarctica before LGM	Glacial survival on both sides of the Drake Passage with higher Ne in South America	Postglacial colonisation of Chile and Falkland from Navarino
	Postglacial colonisation of Elephant Island and Antarctic Peninsula from King George Island	Strong isolation of Falkland due to founder effect
		Postglacial "stepping stone" colonisation of KGI and Elephant Island from Livingston Island
Scenario 5:	Pre-glacial colonisation of Elephant Island from South America	Pre-glacial colonisation of KGI from Navarino Island
Most diverse antarctic population admixed from South American and neighbouring Antarctic populations	Glacial survival on both sides of the Drake Passage	Glacial survival on Navarino Island and KGI
	High diversity on KGI because of postglacial admixture	High diversity on Livingston Island because of postglacial admixture
	Postglacial colonisation of Antarctic Peninsula from Elephant Island	Postglacial colonisation of Chile and Falkland from Navarino and colonisation of Elephant Island from KGI

(Continues)

TABLE 1 (Continued)

	Cetraria aculeata	*Usnea aurantiacoatra*
Scenario 6:		Pre-glacial colonisation of Chile from Livingston Island
Population on Navarino Island admixed from Livingston Island and Chile		Glacial survival on Livingston Island and in Chile
		High diversity on Navarino Island because of postglacial admixture
		Postglacial colonisation of Falkland Islands from Navarino Island and "stepping stone" colonisation of KGI and Elephant Island from Livingston Island

Scenarios were specified to best explain patterns of genetic diversity and isolation inferred in preliminary analyses.
Abbreviation: LGM, Last Glacial Maximum.

3 | RESULTS

3.1 | Genetic diversity

We sampled 22 stands of *Usnea aurantiacoatra* and 16 stands of *Cetraria aculeata* in southern South America, Falkland, and the Maritime Antarctic as well as 20 stands of *U. antarctica* in the South Shetland Islands and the Antarctic Peninsula (Figure 1). We confirmed identification of *Usnea antarctica* and *U. aurantiacoatra* with a DAPC analysis (Figure S2 in supplementary material). All of the supposed samples of *U. antarctica* from South America were identified as *U. aurantiacoatra*.

For *Cetraria aculeata* the final dataset comprised 2128 alleles (n = 266 × 8 loci) including 19 null alleles. For *U. antarctica* we analysed 8140 alleles (n = 370 × 22 loci) including 41 null alleles and for *Usnea aurantiacoatra* we scored 9261 alleles (n = 441 × 21 loci) including 164 null alleles. *Usnea aurantiacoatra* had the highest total number of alleles (232), with the highest mean number of observed (7.476) and effective alleles (4.016) recorded on Navarino Island in South America followed by Livingston Island in the Antarctic (7.238; 2.725, Table 3). The highest mean number of private alleles was observed on Livingston Island (0.857) followed by Navarino Island (0.762). The Shannon information index was highest on Navarino (1.490) with rather similar values around 1.0–1.1 on Livingston, King George and Falkland. None of the diversity metrics showed a clear latitudinal pattern. In *Cetraria aculeata* the highest observed number of alleles (4.750) was also found on Chile, Navarino, and decreased to the north and south. The highest effective number of alleles (2.902) was detected in a stand in Chile, and the observed (1.250) and effective number of alleles (ca. 1.0) was lowest on Elephant Island and near Primavera Base on the Antarctic Peninsula. Private alleles were detected in all South American populations (except Falkland) and on King George Island but not on Elephant Island and on the Antarctic Peninsula. In *Usnea antarctica* the observed (effective) mean number of alleles ranged between 4.682 (1.954) on Livingston and 1.591 (1.238) on Deception Island. Private alleles were recorded in all the sampling areas except for Deception Island.

Every individual of *U. aurantiacoatra* belonged to a different clone. Hence, there was no evidence for clonal structure of populations (Table 4). In *C. aculeata* there was strong evidence for clonal reproduction. The 133 samples from South America and Falkland belonged to 113 different clones (Supplementary Table S3), whilst all individuals from Elephant Island belonged to the same multilocus genotype and samples from King George Island and Primavera on the Antarctic Peninsula were dominated by a single clone. GenoDive also inferred significant clonal population structure in *U. antarctica* although the number of clones was almost as high as expected.

3.2 | Genetic structure

Antarctic populations of *C. aculeata* were strongly differentiated from each other and from South American localities. The highest value of Jost's *D* (0.502) was observed between Primavera base and Tierra del Fuego (Table 5). South American localities were poorly differentiated (*D* values ranging between 0.003 and 0.131). The highest differentiation in *U. aurantiacoatra* was observed between localities in South America and Falkland (0.495 between Navarino and Falkland 1). Antarctic localities of *U. aurantiacoatra* were poorly differentiated (Jost's *D* 0.021–0.075). Those of *U. antarctica* showed similarly low differentiation (between 0.007 and 0.095), only for Deception Island *D* exceeded 0.2.

The STRUCTURE analysis showed different geographic structure in all three species (Figure 2). For all datasets, the optimal number of clusters was inferred as K = 4. Antarctic populations of *C. aculeata* display extreme regional genetic structure with different gene pools on the Antarctic Peninsula, King George and Elephant Islands. The gene pool on Elephant Island is also relatively common in South America, where it co-occurs with a fourth gene pool that is absent from Antarctica. South American populations show no strong differences in gene pool composition. Populations of *U. aurantiacoatra* in Falkland and Navarino Island are dominated by local gene pools that are absent elsewhere. A third gene pool is largely restricted to Antarctica. About half of the samples from Livingston Island belong to a fourth gene pool

TABLE 2 Historical demographic parameters for *Cetraria aculeata* and *Usnea aurantiacoatra* used in the ABC analysis

Parameters	Abbreviation	Priors, analysis 1	Priors, analysis 2
Cetraria aculeata			
Current effective population sizes	N1	uniform [10; 100.000]	normal [10; 100.000]
	N2, N4	uniform [10; 20.000]	normal [10; 20.000]
	N3	uniform [10; 50.000]	normal [10; 50.000]
Effective population sizes after postglacial colonisation events or LGM bottlenecks	N1b	uniform [10; 6.000]	normal [10; 6.000]
	N2b, N4b	uniform [10; 1.000]	normal [10; 1.000]
	N3b	uniform [10; 3.000]	normal [10; 3.000]
Effective population sizes before LGM	N1c	uniform [10; 100.000]	normal [10; 100.000]
	N3c	uniform [10; 50.000]	normal [10; 50.000]
Effective population sizes after pre-glacial colonisation events	N1d	uniform [10; 40.000]	normal [10; 40.000]
	N3d	uniform [10; 20.000]	normal [10; 20.000]
Successive postglacial colonisation events	t1	uniform [10; 5.000]	normal [10; 5.000]
	t2	uniform [10; 8.000]	normal [10; 8.000]
End of LGM bottleneck	t3	uniform [10; 10.000]	normal [10; 10.000]
Onset of last glaciation	t4	uniform [10; 12.000]	normal [10; 12.000]
Pre-glacial colonisation events	t5	uniform [10; 14.000]	normal [10; 14.000]
Duration of population size bottlenecks	db	uniform [10; 5.000]	normal [10; 5.000]
Usnea aurantiacoatra			
Current effective population sizes	N1	uniform [10; 80.000]	normal [10; 80.000]
	N2	uniform [10; 30.000]	normal [10; 30.000]
	N3, N6	uniform [10; 24.000]	normal [10; 24.000]
	N4	uniform [10; 120.000]	normal [10; 120.000]
	N5	uniform [10; 160.000]	normal [10; 160.000]
Effective population sizes after postglacial colonisation events or LGM bottlenecks	N1b	uniform [10; 40.000]	normal [10; 40.000]
	N2b, N4b	uniform [10; 10.000]	normal [10; 10.000]
	N3b	uniform [10; 5.000]	normal [10; 5.000]
	N5b	uniform [10; 1.000]	normal [10; 1.000]
	N6b	uniform [10; 12.000]	normal [10; 12.000]
Effective population sizes before LGM	N1c	uniform [10; 80.000]	normal [10; 80.000]
	N2c	uniform [10; 30.000]	normal [10; 30.000]
	N3c	uniform [10; 24.000]	normal [10; 24.000]
	N5c	uniform [10; 160.000]	normal [10; 160.000]
Effective population sizes after pre-glacial colonisation events	N1d, N2d, N3d	uniform [10; 10.000]	normal [10; 10.000]
Successive postglacial colonisation and admixture events	t1	uniform [10; 2.000]	normal [10; 2.000]
	t2	uniform [10; 6.000]	normal [10; 6.000]
	t3	uniform [10; 8.000]	normal [10; 8.000]
End of LGM bottleneck	t4	uniform [10; 10.000]	normal [10; 10.000]
Onset of last glaciation	t5	uniform [10; 12.000]	normal [10; 12.000]
Pre-glacial colonisation events	t6	uniform [10; 14.000]	normal [10; 14.000]
Duration of population size bottlenecks	db	uniform [10; 2.000]	normal [10; 2.000]
Admixture rate	ra	uniform [0.001; 0.999]	normal [0.001; 0.999]

Effective population sizes N1–N6 refer to pooled populations, for *C. aculeata*: South America incl. Falkland Islands (1), Elephant Island (2), KGI (3), Antarctic Peninsula (4); for *U. aurantiacoatra*: Navarino Island (1), Falkland Islands (2), Chile (3), KGI (4), Livingston and Deception Island (5), Elephant Island (6). Additional conditions: Current effective population sizes (N1–N6) and population sizes before LGM larger than those of bottlenecked populations sizes (N1>N1b; N1c>N1b, N1d; N2>N2b; N2c>N2b, N2d; N3>N3b; N3c>N3b, N3d; N4>N4b; N5>N5b; N5c>N5b, N5d; N6>N6b) and times t1 to t5 succesively larger (t6>t5>t4>t3>t2>t1).

Abbreviation: LGM, Last Glacial Maximum.

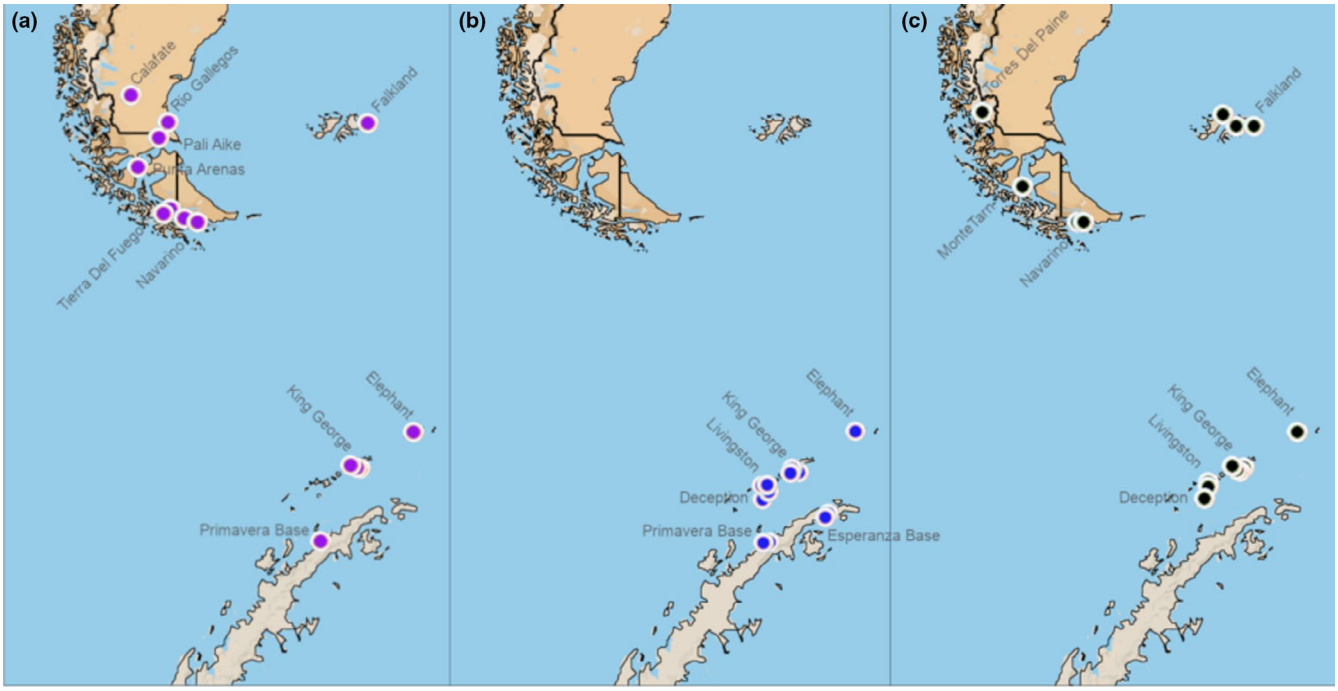

FIGURE 1 Sampling localities of (a) *Cetraria aculeata* (purple), (b) *Usnea antarctica* (blue) and (c) *Usnea aurantiacoatra* (black) [Colour figure can be viewed at wileyonlinelibrary.com]

that also predominates in populations from Mt Tarn and Torres del Paine in Chile. Populations of *U. antarctica* on Livingston and Deception Island are dominated by two gene pools that are virtually absent in other localities. Most samples from Elephant Island and Esperanza belong to a third gene pool that, together with a fourth one, also occurs on King George Island and near Primavera. DAPC resulted in the same clustering, (Figure 3).

3.3 | Historical scenarios of intercontinental gene flow

Since *U. antarctica* was not found by us in southern South America, we studied intercontinental gene flow only in *C. aculeata* and *U. aurantiacoatra* (Figure 4). We investigated five historical scenarios for *C. aculeata* and six for *U. aurantiacoatra* to infer the history of gene flow across the Drake Passage. In *Cetraria*, scenario 1 (postglacial colonisation of Antarctica from South America; see Table 1) received the highest posterior probability irrespective of prior selection and whether obtained by direct estimation or logistic regression. Probabilities ranged between 0.968 (uniform priors, direct approach) and 0.999 (normally distributed priors, logistic regression). The lowest inferred boundary for the 95% confidence interval was 0.814 (uniform priors, direct approach), excluding any of the other scenarios (Table S4). The second most probable scenario 2 (postglacial colonisation of South America from Antarctica) received probabilities of 0.0005–0.024. The posterior predictive error was very low (uniform priors: 0.030–0.036, normally distributed priors: 0.015).

No single historical scenario was well supported for *U. aurantiacoatra*. The posterior probability depended partly on prior selection and strongly on the inference method (direct or by logistic regression). Scenario 2 (postglacial colonisation of South America from Antarctica) was strongly favoured (p = 0.92, 95% CI: 0.8783; 0.9685) when posterior probability was inferred by logistic regression and priors were normally distributed. Otherwise, scenario 1 (postglacial colonisation of Antarctica from South America) received slightly higher support. Scenario 3 (preglacial colonisation of the Antarctic from South America with glacial survival on Navarino and Livingston Island) was only supported when posterior probability was estimated by the direct approach. Preglacial colonisation of South America from Antarctica and the admixture scenarios were poorly supported (p-values of 0–0.096). The posterior predictive error was higher than for *C. aculeata* (uniform priors: 0.261–0.342, normally distributed priors: 0.340–0.413).

4 | DISCUSSION

Although a growing number of studies has been focussing on the phylogeography and genetic diversity of southern South American and Antarctic lichens (e.g. Garrido-Benavent et al., 2018; Ruprecht et al., 2020), restricted access to the Antarctic has so far largely prevented the accumulation of regional-scale data sets. Fine-scale population genetic data on Antarctic lichens, the most important primary producers of Antarctic terrestrial ecosystems, are therefore still largely lacking. Our study provides a first insight into levels of genetic diversity and structure of Antarctic populations and historical intercontinental gene flow of three common Antarctic lichens (*Cetraria aculeata*, *Usnea antarctica*

TABLE 3 Localities of *Cetraria aculeata*, *Usnea antarctica* and *U. aurantiacoatra* investigated in this study, number of individuals, mean number of alleles, effective mean number of alleles, rarefied mean number of alleles, mean number of private alleles, rarefied mean number of private alleles and Shannon information index

Locality	No. of samples	No. of alleles	Effective no. of alleles	No. of alleles (rarefied)	No. of private alleles	No. of private alleles (rarefied)	Information Index
Cetraria aculeata							
Argentina, Calafate	11	2.250 ± 0.366	1.691 ± 0.263	2.14	0.125 ± 0.125	0.45	0.534 ± 0.149
Argentina, Rio Gallegos	12	3.250 ± 0.726	2.301 ± 0.580	2.79	0.125 ± 0.125	0.89	0.789 ± 0.224
Chile, Pali Aike	20	4.000 ± 1.069	2.902 ± 0.961	3.00	0.375 ± 0.183	1.12	0.907 ± 0.247
Chile, Punta Arenas	25	4.250 ± 0.996	2.409 ± 0.674	3.04	0.375 ± 0.263	1.07	0.899 ± 0.193
Chile, Tierra del Fuego	23	4.250 ± 0.773	2.638 ± 0.548	3.09	0.375 ± 0.183	1.50	0.981 ± 0.210
Chile, Navarino	23	4.750 ± 0.977	2.771 ± 0.555	3.44	0.250 ± 0.164	1.33	1.081 ± 0.203
Falkland	19	3.500 ± 0.756	2.426 ± 0.657	2.76	0 ± 0	0.79	0.841 ± 0.194
South America	**133**	**7.875 ± 1.884**	**2.920 ± 0.815**	**4.14**	**4.375 ± 0.885**	**2.66**	**0.525 ± 0.081**
Elephant Island	39	1.250 ± 0.250	1.014 ± 0.014	1.11	0 ± 0	0.06	0.031 ± 0.031
King George Island	51	3.375 ± 1.449	2.483 ± 1.073	2.18	0.500 ± 0.378	0.91	0.541 ± 0.325
Primavera Base	43	1.250 ± 0.164	1.018 ± 0.013	1.10	0 ± 0	0.12	0.037 ± 0.026
Antarctica	**133**	**4.0 ± 0.479**	**2.046 ± 0.463**	**2.27**	**0.500 ± 0.378**	**0.79**	**0.325 ± 0.125**
Usnea antarctica							
Elephant Island	19	2.227 ± 0.246	1.547 ± 0.161	2.00	0.045 ± 0.045	0.11	0,43 ± 0,094
King George Island	100	4.409 ± 0.425	1.808 ± 0.216	2.53	0.818 ± 0.243	0.35	0,645 ± 0,103
Livingston Island	83	4.682 ± 0.485	1.954 ± 0.195	2.80	1.227 ± 0.394	0.48	0,765 ± 0,101
Deception Island	9	1.591 ± 0.107	1.238 ± 0.053	1.58	0 ± 0	0.13	0,262 ± 0,051
Primavera Base	68	3.591 ± 0.454	1.769 ± 0.187	2.36	0.318 ± 0.121	0.29	0,593 ± 0,111
Esperanza Base	91	3.136 ± 0.396	1.712 ± 0.215	2.20	0.227 ± 0.091	0.13	0,517 ± 0,115
Antarctica	**370**	**6773 ± 0.631**	**1.946 ± 0.250**	**n/a**	**6.773 ± 0.631**	**n/a**	**0.352 ± 0.055**
Usnea aurantiacoatra							
Chile, Torres del Paine	14	2.857 ± 0.210	1.899 ± 0.153	2.64	0 ± 0	0.33	0,722 ± 0,077
Chile, Monte Tarn	49	3.810 ± 0.496	2.141 ± 0.316	2.67	0 ± 0	0.32	0,718 ± 0,136
Chile, Navarino	74	7.476 ± 0.770	4.016 ± 0.415	4.58	0.762 ± 0.266	1.15	1,490 ± 0,104
Falkland 1	18	3.095 ± 0.337	1.970 ± 0.180	2.68	0.048 ± 0.048	0.38	0,742 ± 0,098
Falkland 2	18	4.00 ± 0.431	2.642 ± 0.294	3.39	0.190 ± 0.148	0.70	1,011 ± 0,106
Falkland 3	17	3.524 ± 0.394	2.280 ± 0.235	3.01	0.095 ± 0.066	0.59	0,847 ± 0,119

(Continues)

TABLE 3 (Continued)

Locality	No. of samples	No. of alleles	Effective no. of alleles	No. of alleles (rarefied)	No. of private alleles	No. of private alleles (rarefied)	Information Index
South America	**190**	**9.143 ± 0.871**	**3.640 ± 0.372**	**5.66**	**2.048 ± 0.405**	**2.27**	**0.669 ± 0.030**
Elephant Island	18	3.238 ± 0.300	1.995 ± 0.213	2.78	0.095 ± 0.095	0.23	0,753 ± 0,098
King George Island	130	6.476 ± 0.635	2.449 ± 0.275	3.37	0.286 ± 0.101	0.41	1,037 ± 0,106
Livingston Island	77	7.238 ± 0.756	2.725 ± 0.349	3.70	0.857 ± 0.221	0.74	1,141 ± 0,117
Deception Island	26	3.381 ± 0.327	2.013 ± 0.165	2.75	0 ± 0	0.19	0,788 ± 0,089
Antarctica	**251**	**9.000 ± 0.762**	**2.516 ± 0.295**	**4.88**	**1.905 ± 0.436**	**1.49**	**0.521 ± 0.040**

and *U. aurantiacoatra*). The two species of *Usnea* are the most common and dominant lichens in coastal areas of the maritime Antarctic and belong to a group of species that is restricted to the Southern Hemisphere. *Cetraria aculeata*, on the other hand, has colonised the Antarctic coming from the Northern Hemisphere (Fernández-Mendoza & Printzen, 2013). Due to their different modes of propagation, the three species represent a kind of minimal set of taxa to study the impact of reproductive and historical differences on population genetic structure. By including populations from southern South America, we were also able to study the history of intercontinental gene flow in two of the three species. Our results allow us to assess the impact of reproductive mode, colonisation and glacial history on the diversity and spatial structure of these lichen populations. They also provide further insight into dispersal capacities and conservation of Antarctic lichen communities.

4.1 | Impact of reproductive mode on genetic diversity

As expected by population genetic theory (e.g. Bengtsson, 2003), the sexually reproducing *U. aurantiacoatra* shows higher genetic diversity than the mostly asexual *C. aculeata* and *U. antarctica*. Whilst diversity levels are difficult to compare amongst *Cetraria* and *U. aurantiacoatra* due to the different numbers of genotyped loci, results for the two closely related *Usnea* species rely basically on the same set of loci confirming that asexual reproduction reduces genetic diversity in lichens (Grewe et al., 2018; Otálora et al., 2013). The observed clonal population structure in the two mostly asexual species (Table 4) further supports this interpretation. Nevertheless, SSR data discover much higher genetic diversity in these two species than was previously found based on DNA sequences. In *C. aculeata* we found 130 clones and a total of 67 SSR alleles (data not shown) in contrast to only two DNA sequence haplotypes (Domaschke et al., 2012). *Usnea antarctica* displays even higher allelic richness and genetic diversity in our sample. The extremely high genetic diversity in *U. aurantiacoatra* corresponds well with the genotypic richness found in the Mediterranean *Parmelina carporrhizans* (Alors et al., 2017) indicating that this might be a general trend amongst sexually reproducing lichens.

4.2 | Impact of historical factors on population diversity and differentiation

The observed differences in diversity and genetic structure amongst the species studied by us exemplify the important impact of historical factors on the spatial genetic structure of lichens, particularly at the range margins (Eckert et al., 2008). South American populations of *C. aculeata* comprise two to four times higher genetic diversity than Antarctic ones with and without rarefaction, confirming similar results by Domaschke et al. (2012) based on DNA sequence data. In contrast, *U. aurantiacoatra* displays comparable numbers of alleles and private alleles in Antarctic and South American populations and only slightly smaller allelic richness after rarefaction, whilst genetic diversity is equal in both regions.

The genetic differentiation amongst populations shows opposite trends in both species (Figures 2 and 3 and Table 5). Populations of

TABLE 4 Test for clonal population structure performed in GenoDive. Species, number of samples *N*, expected (C_E) and observed (C_O) number of clones (multilocus genotype), percentage % of clones (multilocus genotype), probability *p* of observing this number of clones under random mating

Species	*N*	C_E	C_O	%	*p*
Cetraria aculeata	266	210.734	130.000	51.128	0.001
Usnea antarctica	370	369.329	342.000	7.568	0.001
Usnea aurantiacoatra	441	441.000	441.000	0	1.000

C. aculeata are strongly differentiated in Antarctica, whilst those of *U. aurantiacoatra* show strong differentiation in South America. The *D*-values for both species in these regions resemble the level of differentiation found between geographically isolated populations of *Buellia frigida* in the Queen Maud Mts and other areas in the Ross Sea Region (Jones et al., 2015). In contrast, South American populations of *C. aculeata* and Antarctic populations of *U. aurantiacoatra* are considerably less well differentiated. This suggests that both lichens have different population histories, a conclusion also supported by phylogeographic surveys and distribution data. DNA sequence data indicated that *C. aculeata* originated in the Northern Hemisphere, dispersed into South America during the Pleistocene and hence colonised the Antarctic recently (Fernández-Mendoza & Printzen, 2013). The two *Usnea* species, on the other hand, are assumed to have evolved either in the Antarctic or in southern South America (Jørgensen, 1983; Wirtz et al., 2012). In contrast, populations of *U. aurantiacoatra* from Falkland, Navarino Island and more northern sites in Patagonia are assigned to three distinct gene pools, whereas Antarctic populations are poorly differentiated (Figure 2 and Tables 3 and 5). If, as in *C. aculeata*, stronger differentiation amongst lichen populations indicates a more recent colonisation history, then postglacial recolonisation of sites in Chile and the Falkland Islands by *U. aurantiacoatra* apparently followed a south-north trajectory.

4.3 | Glacial population history

The effects of Pleistocene glacial cycles on the distribution ranges of species and their genetic diversity have frequently been studied in the Northern Hemisphere (Hewitt, 2004). The effects of southern hemispheric glaciations on biota have received less attention, but due to the stronger geographical isolation of Antarctica and the smaller extent of land mass in Southern Hemispere, demographic processes, including range shifts, extinction of populations and recolonisation during glacials and interglacials are likely to differ between these regions (Fraser et al., 2012).

The strong support for scenario 1 in the ABC analysis allows us to temporally constrain the colonisation of Antarctica by *C. aculeata* to the Holocene. The necessary restriction to a few rather simple historical scenarios in ABC prevented us to further differentiate colonisation histories within the Antarctic. However, the combination of ABC analyses, genetic diversity and inference of genetic differentiation allows us to conclusively interpret the population history of *C. aculeata* on both sides of the Drake Passage. The species appears to have reached southern South America during the Pleistocene (Fernández-Mendoza & Printzen, 2013). Moderate levels of gene flow apparently prevented strong genetic differentiation between the South American populations. The relatively high genetic diversity on King George Island indicates that colonisation of the Antarctic may have started in this region with subsequent dispersal to Elephant Island and the Antarctic Peninsula. Alternatively, although postglacial recolonisation from lower latitudes appears to have been extremely rare amongst terrestrial Antarctic taxa (Fraser et al., 2012), the strong genetic isolation between Antarctic populations and the fact that all individuals of *C. aculeata* on Elephant Island belong to a single clone also present near Calafate in Argentina may suggest founder effects during independent colonisation events from South America. This specific scenario was, however, not tested by us. It is interesting that the glacial survival of *C. aculeata* in a refugium on King George Island (scenario 3), and admixture scenario 5, which could also account for the higher genetic diversity on King George Island, received the lowest support of all models. At any rate, the inferred postglacial colonisation of the South Shetland Islands fits nicely with similar results from other organismal groups, for example, the vascular plant *Colobanthus quitensis* (Biersma et al., 2020), the moss *Chorisodontium aciphyllum* (Biersma, Jackson, Bracegirdle, et al., 2018) and the lichen *Pseudephebe minuscula* (Garrido-Benavent et al., 2021) all indicating that colonisation of the Antarctic was a recent event.

The ABC analysis for *U. aurantiacoatra* provided no unequivocal support for any specific scenario, but the admixture scenarios and preglacial colonisation of South America from the Antarctic received only negligible support. The glacial and postglacial history of the species can therefore only tentatively be reconstructed, in part because the results of the ABC seem to contradict observations of genetic diversity and population differentiation. The high genetic diversity of *U. aurantiacoatra* (and *C. aculeata*) on Navarino Island supports the existence of a southern Patagonian refugium as previously postulated for plant and fungal species and lichen photobionts (Eizaguirre et al., 2018; Garrido-Benavent et al., 2018; Sérsic et al., 2011) and is consistent with reconstructions of the Patagonian ice shield indicating that Navarino Island was at least partly ice-free during the Last Glacial Maximum (LGM, Darvill et al., 2014; Glasser & Jansson, 2008).

A second, Antarctic, refugium of *U. aurantiacoatra* and *U. antarctica* is indicated by the higher allelic richness and numbers of private alleles on Livingston and King George Island as compared to Elephant Island, Deception Island or the Antarctic Peninsula. The extension of ice caps and severe environmental conditions during the LGM were once believed to have precluded survival of organisms in polar regions (e.g. Nordal, 1987). Nowadays, the glacial persistence of organisms in the Antarctic is hardly questioned (Biersma, Jackson, Stech, et al., 2018; Pugh & Convey, 2008). Nunataks, perhaps associated with geothermal activities, or debris covering glaciers may have provided refugial habitats (Fickert et al., 2007; Fraser et al., 2014; Garrido-Benavent et al., 2018) and the assumption of a refugium on Livingston Island or King George Island would be consistent with the reconstruction of Nunataks in the region (Ruiz-Fernández & Oliva, 2016; Simms et al., 2011). Indirect evidence for glacial persistence of *Usnea* in the Antarctic also comes from the fact that *U. antarctica*, formerly believed to occur in southern South America, according to our data, is an Antarctic endemic.

Comparative population genetic data on lichens from glacial refugia and formerly glaciated areas are scarce and entirely lacking for Antarctic lichens, but higher genetic diversity and numbers of private alleles in glacial refugia and gradual decrease of diversity with

TABLE 5 Symmetrical matrix of Jost's *D* index of genetic differentiation for A: *Cetraria aculeata*, B: *Usnea antarctica* and C: *U. aurantiacoatra*

Cetraria aculeata	**Argentina, Calafate**	**Argentina, Rio Gallegos**	**Chile, Pali Aike**	**Chile, Punta Arenas**	**Chile, Tierra del Fuego**	**Chile, Navarino**	**Falkland**	**Elephant Island**	**King George Island**	**Primavera Base**
Argentina, Calafate	0	0.115	0.08	0.18	0.106	0.091	0.084	0.136	0.415	0.447
Argentina, Rio Gallegos	0.115	0	0.052	0.012	0.039	0.094	0.003	0.107	0.277	0.392
Chile, Pali Aike	0.08	0.052	0	0.129	0.081	0.122	0.012	0.227	0.291	0.433
Chile, Punta Arenas	0.18	0.012	0.129	0	0.086	0.131	0.064	0.143	0.344	0.408
Chile, Tierra del Fuego	0.106	0.039	0.081	0.086	0	0.104	0.068	0.223	0.412	**0.502**
Chile, Navarino	0.091	0.094	0.122	0.131	0.104	0	0.068	0.254	0.359	0.356
Falkland	0.084	0.003	0.012	0.064	0.068	0.068	0	0.164	0.282	0.338
Elephant Island	0.136	0.107	0.227	0.143	0.223	0.254	0.164	0	0.419	0.486
King George Island	0.415	0.277	0.291	0.344	0.412	0.359	0.282	0.419	0	0.244
Primavera Base	0.447	0.392	0.433	0.408	**0.502**	0.356	0.338	0.486	0.244	0

Usnea antarctica	**Elephant Island**	**King George Island**	**Livingston Island**	**Deception Island**	**Primavera Base**	**Esperanza Base**
Elephant Island	0	0.007	0.069	**0.263**	0.04	0.034
King George Island	0.007	0	0.054	0.242	0.03	0.027
Livingston Island	0.069	0.054	0	0.206	0.095	0.074
Deception Island	**0.263**	0.242	0.206	0	0.241	0.259
Primavera Base	0.04	0.03	0.095	0.241	0	0.034
Esperanza Base	0.034	0.027	0.074	0.259	0.034	0

Usnea aurantiacoatra	**Chile, Torres Del Paine**	**Chile, Mount Tarn**	**Chile, Navarino**	**Falkland 1**	**Falkland 2**	**Falkland 3**	**Elephant Island**	**King George Island**	**Livingston Island**	**Deception Island**
Chile, Torres Del Paine	0	0.24	0.434	0.383	0.291	0.328	0.158	0.163	0.093	0.226
Chile, Mount Tarn	0.24	0	0.359	0.462	0.378	0.406	0.118	0.166	0.15	0.168
Chile, Navarino	0.434	0.359	0	**0.495**	0.436	0.477	0.375	0.356	0.372	0.373
Falkland 1	0.383	0.462	**0.495**	0	0.208	0.173	0.366	0.374	0.332	0.403
Falkland 2	0.291	0.378	0.436	0.208	0	0.104	0.261	0.313	0.215	0.312
Falkland 3	0.328	0.406	0.477	0.173	0.104	0	0.307	0.353	0.292	0.379
Elephant Island	0.158	0.118	0.375	0.366	0.261	0.307	0	0.021	0.059	0.065
King George Island	0.163	0.166	0.356	0.374	0.313	0.353	0.021	0	0.064	0.069
Livingston Island	0.093	0.15	0.372	0.332	0.215	0.292	0.059	0.064	0	0.075
Deception Island	0.226	0.168	0.373	0.403	0.312	0.379	0.065	0.069	0.075	0

Overall highest value in bold.

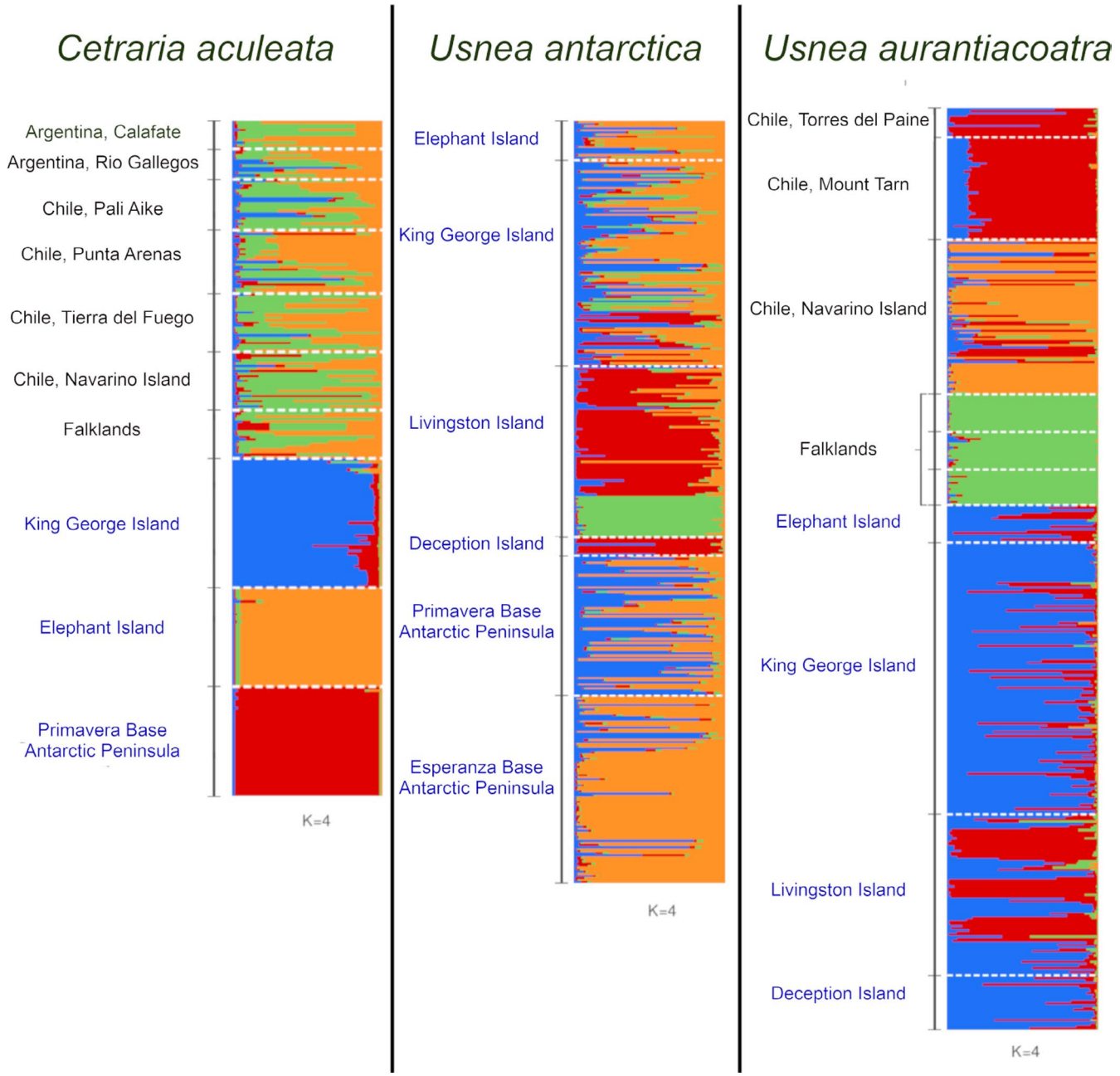

FIGURE 2 Assignment of individuals of the three species to $K = 4$ gene pools obtained by Structure. Populations are arranged from North to South and separated with white dotted lines. The height of each colour in a bar corresponds to the estimated probability with which the individual belongs to the respective gene pool. [Colour figure can be viewed at wileyonlinelibrary.com]

increasing distance from these areas have been observed in some Northern Hemispheric species (Allen et al., 2018; Printzen et al., 2003; Scheidegger et al., 2012). The lower diversity levels on the Falkland Islands and in Chile north of Navarino Island as well as on Elephant and Deception Island might therefore characterise these populations as more recently colonised from refugial populations on both sides of the Drake Passage. The strong support under one of the combinations of priors and probability inference methods for scenario 2, postulating postglacial colonisation of Navarino Island from the Antarctic (Figure 4h), seems strangely at odds with the exceptionally high diversity found on Navarino Island.

The inconclusive outcome of ABC analyses for *U. aurantiacoatra* might potentially result from strong recent gene flow erasing historical signal in the data. Results from the cluster analyses, however, make this interpretation unlikely. Firstly, the presence of local gene pools on Falkland and Navarino Island is evidence of overall restricted gene flow in our data set. Although populations in northern Chile share their major gene pool with Livingston and Elephant Island, this gene pool has a frequency of only 20% on Navarino. Its exchange between South American and Antarctic populations could hardly have erased all historical signal from our data set. Moreover, Navarino Island is situated on a straight line between

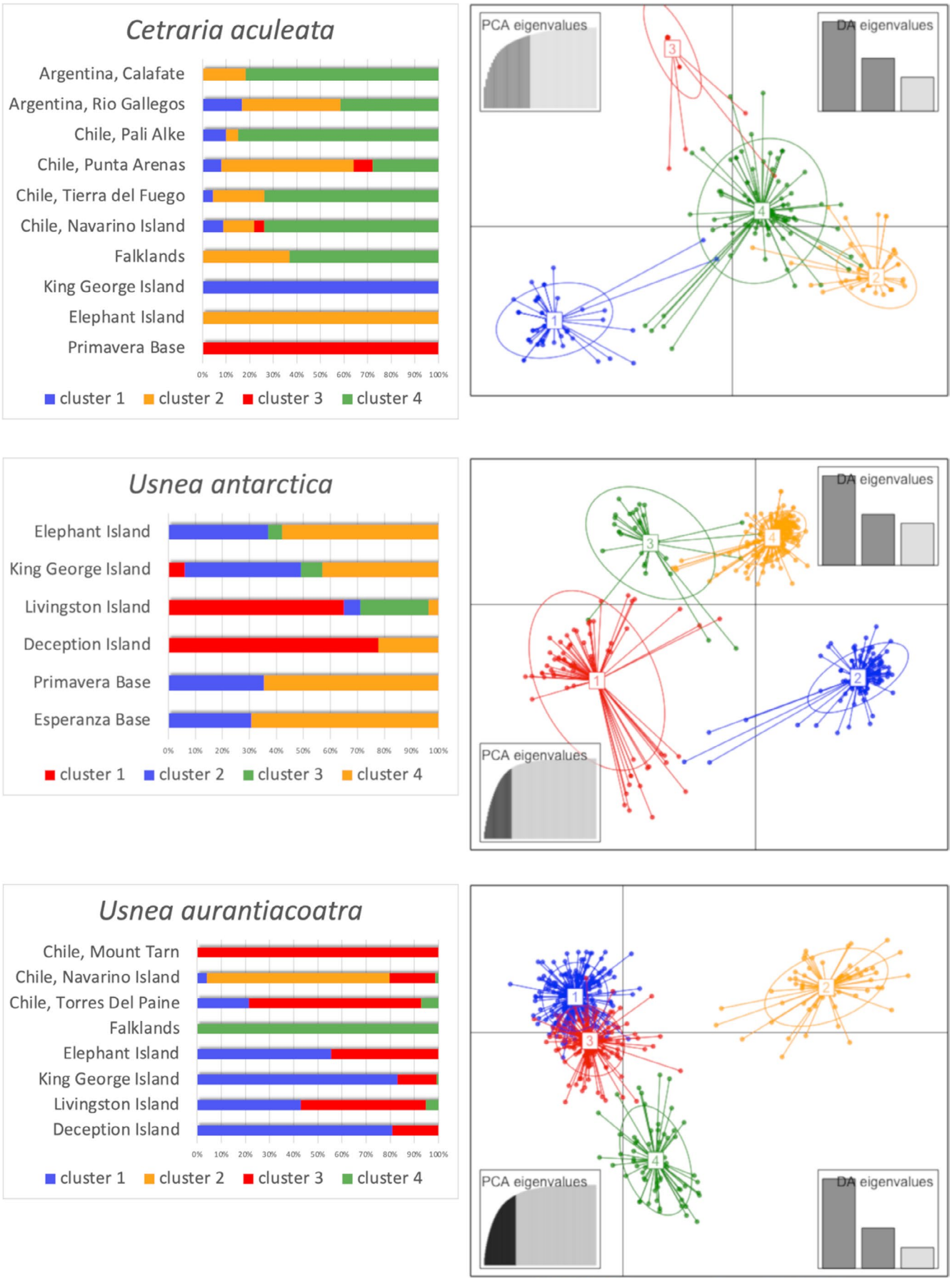

FIGURE 3 Clustering of samples after Discriminant Analysis of Principal Components (DAPC) analysis (right) for $K = 4$ and frequency of clusters in geographical locations for *Cetraria aculeata*, *Usnea antarctica* and *U. aurantiacoatra* [Colour figure can be viewed at wileyonlinelibrary.com]

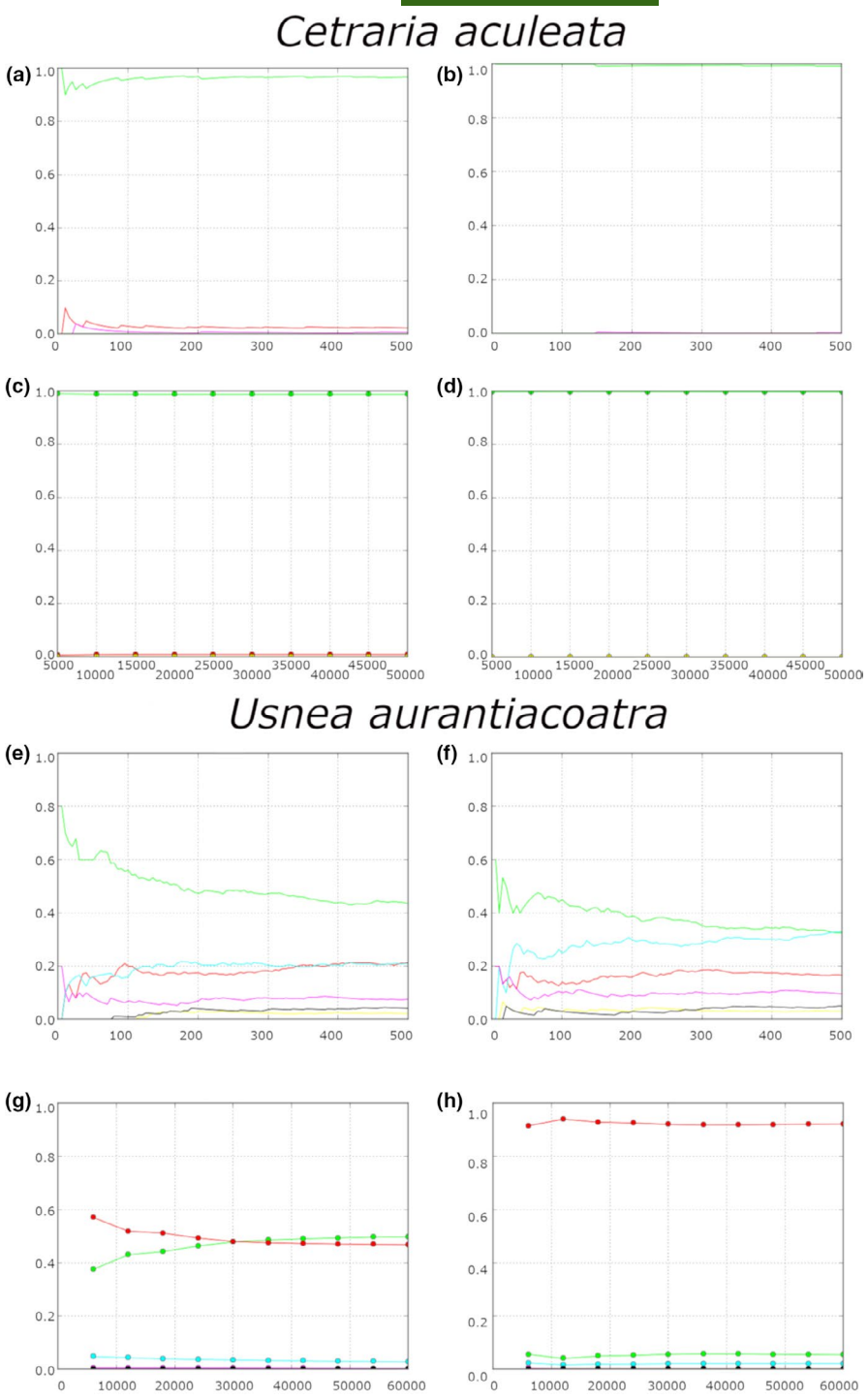

FIGURE 4 Results of the ABC analyses. Relative support for historical scenarios under different combinations of priors and probability inference methods. Left column: uniform priors; right column: normally distributed priors. For details see Table 2. (a, b, e, f) Direct inference of posterior probablity as the proportion of each scenario in the 500 most similar subsets. (c, d, g, h) Probability inferred by logistic regression on linear discriminant analysis components of the most similar 1% of simulated data sets (50.000 for *C. aculeata*, 60.000 for *U. aurantiacoatra*) [Colour figure can be viewed at wileyonlinelibrary.com]

northern Chilean and Antarctic populations. It is therefore unlikely that strong recent gene flow from South America into the Antarctic would not have affected its genetic composition more strongly. Potential gene flow from the Antarctic into South America must have been restricted to the rarer of the two Antarctic gene pools, which, moreover, only occurs on Livingston Island. This also speaks against high levels of gene flow. We regard it as much more likely that this gene pool survived in refugia on Navarino and Livingston Island and played a major role in postglacial recolonisation of northern Chilean populations but not in the Antarctic. Apparently, the glacial history of the species in the region is more complex than expressed in our ABC scenarios and its resolution requires a more extensive geographical sampling.

The diverging levels of genetic diversity of *U. antarctica* and *U. aurantiacoatra* populations on Livingston and Deception Island merit some attention. Both islands are close to each other, and Deception Island, the most active volcano in the area, was probably not glaciated during the LGM (Guillemin et al., 2018; Simms et al., 2011). The absence of private alleles and low diversity on Deception Island could result from recent volcanic eruptions in 1967, 1969 and 1970

that strongly reduced the size of lichen populations (Lewis Smith, 1984), but are more likely an artefact resulting from low sample sizes.

Finally, our data do not indicate whether the gradually declining levels of genetic diversity in *C. aculeata* resulted from postglacial recolonisation of northern localities from the Navarino refugium or persistence in smaller local refugia. The more pronounced diversity gradient in *U. aurantiacoatra* and the lack of private alleles in northern Chile at Torres del Paine and Mt. Tarn suggest more pronounced population size bottlenecks during the LGM. As a saxicolous subalpine species, *U. aurantiacoatra* likely had more restricted glacial habitats than the terricolous lowland *Cetraria*. Alternatively, founder effects during post-glacial recolonisation from the Navarino refugium may account for the strongly reduced genetic diversity in these populations.

4.4 | Intercontinental gene flow and consequences for conservation

Due to its geographical distance from other continents and the strong effects of the ACC, Antarctica is considered the biologically most isolated continent. As judged from levels of endemism, the degree of isolation varies strongly with the taxonomic group considered (Barnes et al., 2006), and such data for terrestrial organisms are still very scarce. Distribution patterns of bryophytes and lichens on sub-Antarctic islands are indeed correlated with the prevailing wind patterns indicating directional long-distance colonisation (Muñoz et al., 2004). For some lichens and bryophytes with bipolar distribution, long-distance dispersal mediated by migratory birds has also been demonstrated (Garrido-Benavent & Pérez-Ortega, 2017; Lewis, Behling, et al., 2014; Lewis et al., 2014). The wide geographical ranges of many lichens and genetic similarities amongst widely separated populations have sometimes been interpreted as evidence for ongoing long-range dispersal, even between continents (Geml et al., 2010). But although numerous lichen species occur in South America and Antarctica, our data do not confirm dispersal of lichens across the Drake Passage on short time scales. Since we could not confirm the presence of *U. antarctica* in South America, this species might be an Antarctic endemic that never managed to cross the Drake Passage. *Usnea aurantiacoatra* apparently survived the LGM in separate refugia north and south of the Drake passage, whilst the high genetic differentiation of peripheral Antarctic populations of *C. aculeata* suggests very recent dispersal from King George Island or rare colonisation events from South America, both with strong founder effects.

The invasion of alien species and propagule transfer into Antarctica has been a major concern of conservationists (Hughes & Convey, 2010) and is regarded as "one of the most significant conservation problems in the Antarctic" (Chown & Convey, 2007). The increasing risk of accidental introduction of invasive species and genetic homogenisation of Antarctic gene pools is due to two interacting factors. Whilst global warming is beginning to change the ACC and associated aerial currents (Chown et al., 2015; Fraser et al., 2018) exposes so far uninhabited, disturbed ground and alleviates physiological stress, growing numbers of researchers and tourists in the region act as possible vectors for propagules. Although our results do not indicate any immediate threat to the genetic composition of lichen populations, they suggest that *C. aculeata* and *U. aurantiacoatra* are exposed to different risks. Conservation measures for Antarctic organisms should therefore consider the different population histories and spatial genetic structure of the species. The genetically diverse and poorly differentiated Antarctic populations of the two *Usnea* species are apparently experiencing high natural levels of gene flow. On this background, additional human transfer of propagules will have comparatively little impact (and would be difficult if not impossible to detect). Care should be taken, though, to prevent introduction of South American gene pools currently not present in the Antarctic. The genetically poor and highly differentiated populations of *C. aculeata* require stronger conservation measures to avoid the introduction of alien genotypes and homogenisation of gene pools. The different distributional patterns of both species in South America, a result of their different population histories, exacerbate this problem. *Usnea aurantiacoatra* only occurs in small and isolated patches and prefers higher elevations, reducing the risk of accidental introduction into Antarctica, for example, by tourists. In contrast, *C. aculeata* is much more widespread in South America and also grows at lower elevations, for example, around the airport of Rio Gallegos (Fernández-Mendoza, pers. comm.). It therefore has a much higher chance to be transferred by Antarctic visitors.

5 | CONCLUSIONS

This is one of the first studies to evaluate the effects of dispersal strategy and migration history on genetic diversity and population structure of Antarctic lichens. As expected, levels of genetic diversity are lower in the two mostly asexual species but patterns of differentiation are affected by population history rather than reproductive mode. Both the northern immigrant *C. aculeata* and the (sub)Antarctic *U. aurantiacoatra* show higher levels of genetic differentiation in marginal than central populations. Diversity hotspots for both species suggest the existence of glacial refugia on Navarino Island and Livingston or King George Island, where also *U. antarctica* displays highest diversity. Although we found no convincing evidence for ongoing gene flow from southern South America into the Maritime Antarctic, the strong genetic structure of *C. aculeata* calls for protective measures to avoid gene flow between isolated populations.

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DATA AVAILABILITY STATEMENT

Three microsatellites datasets are deposited in Pangaea. Lagostina, Elisa (2019): List of number of microsatellite repeats for fungus specific locus in stands of Cetraria aculeata, Usnea antarctica and U. aurantiacoatra. PANGAEA, https://doi.org/10.1594/PANGAEA.906884.

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REFERENCES

Allen, J. L., McKenzie, S. K., Sleith, R. S., & Alter, S. E. (2018). First genome-wide analysis of the endangered, endemic lichen *Cetradonia linearis* reveals isolation by distance and strong population structure. *American Journal of Botany*, *105*(9), 1556–1567.

Alors, D., Dal Grande, F., Cubas, P., Crespo, A., Schmitt, I., Molina, M. C., & Divakar, P. D. (2017). Panmixia and dispersal from the Mediterranean Basin to Macaronesian Islands of a macrolichen species. *Scientific Reports*, *7*, 40879.

Barnes, D. K. A., Hodgson, D. A., Convey, P., Alle, C. S., & Clarke, A. (2006). Incursion and excursion of Antarctic biota: Past, present and future. *Global Ecology and Biogeography*, *15*, 121–142.

Bengtsson, B. O. (2003). Genetic variation in organisms with sexual and asexual reproduction. *Journal of Evolutionary Biology*, *16*(2), 189–199.

Bergstrom, D. M., & Selkirk, P. (1997). Distribution of bryophytes on subantarctic Heard Island. *Bryologist*, *100*(3), 349–355.

Biersma, E. M., Jackson, J. A., Bracegirdle, T. J., Griffiths, H., Linse, K., & Convey, P. (2018). Low genetic variation between South American and Antarctic populations of the bank-forming moss *Chorisodontium aciphyllum* (Dicranaceae). *Polar Biology*, *41*(4), 599–610.

Biersma, E. M., Jackson, J. A., Stech, M., Griffiths, H., Linse, K., & Convey, P. (2018). Molecular data suggest long-term *in situ* Antarctic persistence within Antarctica's most speciose plant genus, *Schistidium*. *Frontiers in Ecology and Evolution*, *6*, 77.

Biersma, E. M., Torres-Díaz, C., Molina-Montenegro, M. A., Newsham, K. K., Vidal, M. A., Collado, G. A., Acuña-Rodríguez, I. S., & Convey, P. (2020). Multiple late-Pleistocene colonisation events of the Antarctic pearlwort *Colobanthus quitensis* (Caryophyllaceae) reveal the recent arrival of native Antarctic vascular flora. *Journal of Biogeography*, *47*(8), 1663–1673.

Chong, C. W., Pearce, D. A., & Convey, P. (2015). Emerging spatial patterns in Antarctic prokaryotes. *Frontiers in Microbiology*, *6*, 1058–1071.

Chown, S. L., Clarke, A., Fraser, C. I., Cary, S. C., Moon, K. L., & McGeoch, M. A. (2015). The changing form of Antarctic biodiversity. *Nature*, *522*(7557), 431–438.

Chown, S. L., & Convey, P. (2007). Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society*, *362*(1488), 2307–2331.

Chown, S. L., Huiskes, A. H. L., Gremmen, N. J. M., Lee, J. E., Terauds, A., Crosbie, K., Frenot, Y., & Bergstrom, D. A. (2012). Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *PNAS*, *109*(13), 4938–4943.

Convey, P., Chown, S. L., Clarke, A., Barnes, D. K. A., Bokhorst, S., Cummings, V., Ducklow, H. W., & Wall, D. H. (2014). The spatial structure of Antarctic biodiversity. *Ecological Monographs*, *84*(2), 203–244.

Convey, P., & Stevens, M. I. (2007). Antarctic Biodiversity. *Science*, *317*(5846), 1877–1878.

Cornuet, J. M., Pudlo, P., Veyssier, J., Dehne-Garcia, A., Gautier, M., Leblois, R., Marin, J. M., & Estoup, A. (2014). DIYABC v2.0: A software to make Approximate Bayesian Computation inferences about population history using Single Nucleotide Polymorphism, DNA sequence and microsatellite data. *Bioinformatics*, *30*(8), 1187–1189.

Courtright, E. M., Wall, D. H., Virginia, R. A. et al (2000). Nuclear and mitochondrial DNA sequence diversity in the Antarctic nematode *Scottnema lindsayae*. *Journal of Nematology*, *32*(2), 143–153.

Darvill, C. M., Stokes, C. R., Bentley, M. J., & Lovell, H. (2014). A glacial geomorphological map of the southernmost ice lobes of Patagonia: The Bahía Inútil – San Sebastián, Magellan, Otway, Skyring and Río Gallegos lobes. *Journal of Maps*, *10*, 500–520.

De Wever, A., Leliaert, F., Verleyen, E., Vanormelingen, P., Van der Gucht, K., Hodgson, D. A., Sabbe, K., & Vyverman, W. (2009). Hidden levels of phylodiversity in Antarctic green algae: Further evidence for the existence of glacial refugia. *Proceedings of the Royal Society*, *276*(1673), 3591–3599.

Domaschke, S., Fernández-Mendoza, F., García, M. A., Martín, M. P., & Printzen, C. (2012). Low genetic diversity in Antarctic populations of the lichen *Cetraria aculeata* and its photobiont. *Polar Research*, *31*, 17353.

Eckert, C. G., Samis, K. E., & Lougheed, S. C. (2008). Genetic variation across species' ranges: The central-marginal hypothesis and beyond. *Molecular Ecology*, *17*(5), 1170–1188.

Eizaguirre, J. I., Peris, D., Rodríguez, M. E., Lopes, C. A., De Los Ríos, P., Hittinger, C. T., & Libkind, D. (2018). Phylogeography of the wild Lager-brewing ancestor (*Saccharomyces eubayanus*) in Patagonia. *Environmental Microbiology*, *20*(10), 3732–3743.

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software Structure: A simulation study. *Molecular Ecology*, *14*, 2611–2620.

Falush, D., Stephens, M., & Pritchard, J. K. (2003). Inference of population structure: Extensions to linked loci and correlated allele frequencies. *Genetics*, *164*, 1567–1587.

Fernández-Mendoza, F., & Printzen, C. (2013). Pleistocene expansion of the bipolar lichen *Cetraria aculeata* into the Southern hemisphere. *Molecular Ecology*, *22*(7), 1961–1983.

Fickert, T., Friend, D., Grüninger, F., Molnia, B., & Richter, M. (2007). Did debris-covered glaciers serve as Pleistocene refugia for plants? A new hypothesis derived from observations of recent plant growth on glacier surfaces. *Arctic, Antarctic, and Alpine Research*, *39*(2), 245–257.

Fowbert, J. A., & Lewis Smith, R. I. (1994). Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. *Arctic and Alpine Research*, *26*(3), 290–296.

Francis, R. M. (2016). POPHELPER: An R package and web app to analyze and visualize population structure. *Molecular Ecology Resources*, *17*(1), 27–32.

Fraser, C. I., Morrison, A. K., McC Hogg, A., Macaya, E. C., van Sebille, E., Ryan, P. G., Padovan, A., Cameron, J., Valdivia, N., & Waters, L. M. (2018). Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. *Nature Climate Change*, *8*, 704–708.

Fraser, C. I., Nikula, R., Ruzzante, D. E., & Waters, J. M. (2012). Poleward bound: Biological impacts of Southern Hemisphere glaciation. *Trends in Ecology & Evolution*, *27*(8), 462–471.

Fraser, C. I., Terauds, A., Smellie, J., Convey, P., & Chown, S. L. (2014). Geothermal activity helps life survive glacial cycles. *PNAS*, *111*(15), 5634–5639.

Garrido-Benavent, I.., de los Ríos, A., Fernández-Mendoza, F., Pérez-Ortega, S. (2018). No need for stepping stones: Direct, joint dispersal of the lichen-forming fungus *Mastodia tessellata* (Ascomycota) and its photobiont explains their bipolar distribution. *Journal of Biogeography*, *45*(1), 213–224.

Garrido-Benavent, I., & Pérez-Ortega, S. (2017). Past, present, and future research in bipolar lichen-forming fungi and their photobionts. *American Journal of Botany*, *104*(11), 1660–1674.

Garrido-Benavent, I., Pérez-Ortega, S., de los Ríos, A., Mayrhofer, H., and Fernández-Mendoza, F. (2021). Neogene speciation and Pleistocene expansion of the genus *Pseudephebe* (Parmeliaceae, lichenized fungi) involving multiple colonizations of Antarctica. *Molecular Phylogenetics and Evolution*, *155*, 107020.

Geml, J., Kauff, F., Brochmann, C., & Taylor, D. L. (2010). Surviving climate changes: high genetic diversity and transoceanic gene flow in two arctic–alpine lichens, *Flavocetraria cucullata* and *F. nivalis* (Parmeliaceae, Ascomycota). *Journal of Biogeography*, *37*(8), 1529–1542.

Glasser, N., & Jansson, K. (2008). The glacial map of southern South America. *Journal of Maps*, *4*(1), 175–196.

Green, T. G. A., Sancho, L. G., Türk, R., Seppelt, R. D., & Hogg, D. (2011). High diversity of lichens at 84°S, Queen Maud Mountains, suggests preglacial survival of species in the Ross Sea region, Antarctica. *Polar Biology*, *34*(8), 1211–1220.

Grewe, F., Lagostina, E., Wu, H., Printzen, C., & Lumbsch, H. T. (2018). Population genomic analyses of RAD sequences resolves the phylogenetic relationship of the lichen-forming fungal species *Usnea antarctica* and *Usnea aurantiacoatra*. *MycoKeys*, *113*, 91–113.

Guillemin, M. L., Dibrasquet, H., Reyes, J., & Valero, M. (2018). Comparative phylogeography of six red algae along the Antarctic Peninsula: Extreme genetic depletion linked to historical bottlenecks and recent expansion. *Polar Biology*, *41*(5), 827–837.

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transaction of the Royal Society London*, *Series B*, *359*(1442), 183–195.

Hughes, K. A., & Convey, P. (2010). The protection of Antarctic terrestrial ecosystems from inter- and intra-continental transfer of non-indigenous species by human activities: A review of current systems and practices. *Global Environmental Change*, *20*(1), 96–112.

Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23*(14), 1801–1806.

Jombart, T. (2008). Adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*, 1403–1405.

Jombart, T., & Ahmed, I. (2011). Adegenet 1.3-1: New tools for the analysis of genome-wide SNP data. *Bioinformatics*, *27*, 3070–3071.

Jones, T. C., Hogg, I. D., Wilkins, R. J., & Green, T. G. A. (2013). Photobiont selectivity for lichens and evidence for a possible glacial refugium in the Ross Sea region, Antarctica. *Polar Biology*, *36*(6), 767–774.

Jones, T. C., Hogg, I. D., Wilkins, R. J., & Green, T. G. A. (2015). Microsatellite analyses of the Antarctic endemic lichen *Buellia frigida* Darb. (Physciaceae) suggest limited dispersal and the presence of glacial refugia in the Ross Sea Region. *Polar Biology*, *38*(7), 941–949.

Jørgensen, P. M. (1983). Distribution patterns of lichens in the Pacific Region. *Australian Journal of Botany*, *Supplementary Series*, *13*(10), 43–66.

Kalinowski, S. T. (2004). Counting alleles with rarefaction: Private alleles and hierarchical sampling designs. *Conservation Genetics*, *5*, 539–543.

Kalinowski, S. T. (2005). hp-rare 1.0: A computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes*, *5*, 187–189.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., & Drummond, A. (2012). Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*(12), 1647–1649.

Lagostina, E., Dal Grande, F., Andreev, M., & Printzen, C. (2018). The use of microsatellite markers for species delimitation in Antarctic *Usnea* subgenus *Neuropogon*. *Mycologia*, *110*(6), 1047–1057.

Lagostina, E., Dal Grande, F., Ott, S., & Printzen, C. (2017). Fungus-specific SSR markers in the Antarctic lichens *Usnea antarctica* and *U. aurantiacoatra* (*Parmeliaceae*, Ascomycota). *Applications in Plant Sciences*, *5*(9), 1700054.

Lawver, L. A., & Gahagen, L. M. (2003). Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *198*, 11–37.

Lewis, L. R., Behling, E., Gousse, H., Qian, E., Elphick, C. S., Lamarre, J. F., Bêty, J., Liebezeit, J., Rozzi, R., & Goffinet, B. (2014). First evidence of bryophyte diaspores in the plumage of transequatorial migrant birds. *PeerJ*, *2*, e424.

Lewis, L. R., Rozzi, R., & Goffinet, B. (2014). Direct long-distance dispersal shapes a New World amphitropical disjunction in the dispersal-limited dung moss *Tetraplodon* (Bryopsida: Splachnaceae). *Journal of Biogeography*, *41*(12), 2385–2395.

Lewis Smith, R. I. (1984). Colonization and recovery by cryptogams following recent volcanic activity on Deception Island, South Shetland Islands. *British Antarctic Survey Bulletin*, *62*, 25–51.

Lutsak, T., Fernández-Mendoza, F., Greshake, B., Dal Grande, F., Ebersberger, I., Ott, S., & Printzen, C. (2016). Characterization of microsatellite loci in the lichen-forming fungus *Cetraria aculeata* (*Parmeliaceae*, Ascomycota). *Applications in Plant Sciences*, *4*(9), 1600047.

McGaughran, A., Torricelli, G., Carapelli, A. et al (2010). Contrasting phylogeographical patterns for springtails reflect different evolutionary histories between the Antarctic Peninsula and continental Antarctica. *Journal of Biogeography*, *37*(1), 103–119.

Meirmans, P. G., & Van Tienderen, P. H. (2004). GENOTYPE and GenoDive: Two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes*, *4*(4), 792–794.

Muñoz, J., Felicisimo, M., Cabezas, F. et al (2004). Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science*, *304*(5674), 1144–1147.

Nolan, L., Hogg, I. D., Stevens, M. I., & Haase, M. (2006). Fine scale distribution of mtDNA haplotypes for the springtail *Gomphiocephalus hodgsoni* (Collembola) corresponds to an ancient shoreline in Taylor Valley, continental Antarctica. *Polar Biology*, *29*(10), 813–819.

Nordal, I. (1987). Tabula rasa after all? Botanical evidence for ice-free refugia in Scandinavia reviewed. *Journal of Biogeography*, *14*(4), 377–388.

Otálora, M. A. G., Salvador, C., Martínez, I., & Aragón, G. (2013). Does the reproductive strategy affect the transmission and genetic diversity of bionts in cyanolichens? A case study using two closely related species. *Microbial Ecology*, *65*(2), 517–530.

Peakall, R., & Smouse, P. E. (2006). GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, *6*(1), 288–295.

Peakall, R., & Smouse, P. E. (2012). GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research—An update. *Bioinformatics*, *28*(19), 2537–2539.

Peat, H. J., Clarke, A., & Convey, P. (2007). ORIGINAL ARTICLE: Diversity and biogeography of the Antarctic flora. *Journal of Biogeography*, *34*, 132–146.

Printzen, C., Ekman, S., & Tønsberg, T. (2003). Phylogeography of *Cavernularia hultenii*:Evidence of slow genetic drift in a widely disjunct lichen. *Molecular Ecology*, *12*(6), 1473–1486.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959.

Pugh, P. J. A., & Convey, P. (2008). Surviving out in the cold: Antarctic endemic invertebrates and their refugia. *Journal of Biogeography*, *35*(12), 2176–2186.

Rogers, A. D. (2007). Evolution and biodiversity of Antarctic organisms: A molecular perspective. *Philosophical Transactions of the Royal Society B*, *362*(1488), 2191–2214.

Ruiz-Fernández, J., & Oliva, M. (2016). Relative paleoenvironmental adjustments following deglaciation of the Byers Peninsula (Livingston Island, Antarctica). *Arctic, Antarctic, and Alpine Research*, *48*(2), 345–359.

Ruprecht, U., Fernández-Mendoza, F., Türk, R., & Fryday, A. M. (2020). High levels of endemism and local differentiation in the fungal and algal symbionts of saxicolous lecideoid lichens along a latitudinal gradient in southern South America. *Lichenologist*, *52*(4), 287–303.

Sancho, L. G., Pintado, A., Navarro, F., Ramos, M., De Pablo, M. A., Blanquer, J. M., Raggio, J., Valladares, F., & Green, T. G. A. (2017). Recent warming and cooling in the Antarctic peninsula region has rapid and large effects on lichen vegetation. *Scientific Reports*, *7*(1), 5689.

Scheidegger, C., Bilovitz, P. O., Werth, S., Widmer, I., & Mayrhofer, H. (2012). Hitchhiking with forests: Population genetics of the epiphytic lichen *Lobaria pulmonaria* in primeval and managed forests in southeastern Europe. *Ecology and Evolution*, *2*(9), 2223–2240.

Scher, H. D., & Martin, E. E. (2006). Timing and climatic consequences of the opening of Drake Passage. *Science*, *312*(5772), 428–430.

Sérsic, A. N., Cosacov, A., Cocucci, A. A., Johnson, L. A., Pozner, R., Avila, L. J., Sites, J. W. Jr, & Morando, M. (2011). Emerging phylogeographical patterns of plants and terrestrial vertebrates from Patagonia. *Biological Journal of the Linnean Society*, *103*(2), 475–494.

Simms, A. R., Milliken, K. T., Anderson, J. B., & Wellner, J. S. (2011). The marine record of deglaciation of the South Shetland Islands, Antarctica since the Last Glacial Maximum. *Quaternary Science Reviews*, *30*(13–14), 1583–1601.

Skotnicki, M. L., Mackenzie, A. M., Ninham, J. A., & Selkirk, P. M. (2004). High levels of genetic variability in the moss *Ceratodon purpureus* from continental Antarctica, subantarctic Heard and Macquarie Islands, and Australasia. *Polar Biology*, *27*(11), 687–698.

Søchting, U., & Castello, M. (2012). The polar lichens *Caloplaca darbishirei* and *C. soropelta* highlight the direction of bipolar migration. *Polar Biology*, *35*(8), 1143–1149.

Terauds, A., Chown, S. L., Morgan, F. et al (2012). Conservation biogeography of the Antarctic. *Diversity Distributions*, *18*(7), 726–741.

Tibell, L. B. (1994). Distribution patterns and dispersal strategies of Caliciales. *Botanical Journal of the Linnean Society*, *116*(3), 159–202.

Turner, J., Colwell, S. R., Marshall, G. J., Lachlan-Cope, T. A., Carleton, A. M., Jones, P. D., Lagun, V., Reid, P. A., & Iagovkina, S. (2005). Antarctic climate change during the last 50 years. *International Journal of Climatology*, *25*(3), 279–294.

van de Wouw, M., van Dijk, P., & Huiskes, A. H. L. (2008). Regional genetic diversity patterns in Antarctic hairgrass (*Deschampsia antarctica* Desv.). *Journal of Biogeography*, *35*(2), 365–376.

Wirtz, N., Printzen, C., & Lumbsch, H. T. (2008). The delimitation of Antarctic and bipolar species of neuropogonoid *Usnea* (*Ascomycota*, *Lecanorales*): A cohesion approach of species recognition for the *Usnea perpusilla* complex. *Mycological Research*, *112*(4), 472–484.

Wirtz, N., Printzen, C., & Lumbsch, H. T. (2012). Using haplotype networks, estimation of gene flow and phenotypic characters to understand species delimitation in fungi of a predominantly Antarctic *Usnea* group (Ascomycota, Parmeliaceae). *Organisms Diversity and Evolution*, *12*(1), 17–37.

BIOSKETCH

Elisa Lagostina obtained her PhD at the Senckenberg Research Institute and Natural History Museum Frankfurt (Germany) and Goethe University Frankfurt (Germany). Her PhD research is focused on population genetics and conservation of Antarctic lichens. She is interested in the study of microorganism relationships and symbiosis, gene flow and conservation of biodiversity.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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