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High vagility facilitates population persistence and expansion prior to the Last Glacial Maximum in an antarctic top predator: The Snow petrel (*Pagodroma nivea*)

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Abstract

Aims: Pleistocene glacial cycles have had profound effects on the distribution and genetic diversity of high latitude species, which can vary with species-specific traits, such as vagility. Demographic responses of antarctic flying seabirds to the same events remain unassessed. We addressed this knowledge gap by studying the genetic population connectivity and demographic history of a flying seabird endemic to Antarctica, the Snow petrel. We hypothesize that their high vagility due to flight may represent an advantage over non-flying seabirds in enduring past climate variation.

Location: Approximately 3,000 km of coastline in East Antarctica, covering three areas in Mac. Robertson Land, Princess Elizabeth Land and Wilkes Land. An inland location was also sampled at the Prince Charles Mountains, Mac. Robertson Land.

Taxon: Snow petrel (*Pagodroma nivea*).

Methods: We sampled 93 individuals and sequenced a total of 5,412 base pairs, including two mitochondrial genes, four anonymous nuclear loci and a nuclear intron. We used frequentist and Bayesian approaches to examine population genetic structuring and an Extended Bayesian Skyline Plot method to infer the demographic history of the species in the study area. In addition, evidence of exposed bedrock during glacial periods was summarized in maps of the studied area representing potential refugia for the species.

Results: Differentiation indexes, genetic clustering and haplotype networks suggest long-term population connectivity for Snow petrels across the study area, with no evidence for reliction into refugia that were genetically isolated. Significantly, population expansions pre-dated the Last Glacial Maximum (LGM), but only where there was evidence of ice-free areas during this period.

Main conclusions: The high vagility of Snow petrels may have been advantageous for access to foraging areas and supported large populations despite the harsh conditions during the LGM. Our results highlight that species-specific traits can exert a strong influence on demographic responses to the same environmental events.

KEYWORDS
Antarctica, gene flow, historical demography, seabirds, snow petrels

1 | INTRODUCTION

The Pleistocene epoch (*c.* 2.5 Ma to 11.5 ka) was characterized by climatic oscillations that drove cyclic population contractions and expansions of many plant and animal species (Hewitt, 2000). Understanding species' responses to climate change in the past is important to understand evolutionary processes such as species radiations, adaptations or extinctions (Hewitt, 2004). In addition, such understanding is relevant to inform model projections of species' responses to the current and projected climate change and, hence, relevant for conservation of biodiversity. Congruent patterns of genetic structure and diversity among species have been essential to understand species distribution changes in response to climate change in temperate regions (Hewitt, 2000, 2004). However, it has been recognized that responses to climate variation can be influenced by idiosyncrasies of the species or regions under study (Stewart, Lister, Barnes, & Dalén, 2010; Taberlet, Fumagalli, Wust-Saucy, & Cosson, 1998). This can be due to large variation in the nature of refugia where populations persisted during adverse environmental conditions, variable duration of confinement to those refugia, as well as the individual species' resilience to climate change (Stewart et al., 2010). Species' intrinsic resilience depends on factors such as the dispersal ability, physiological tolerance, genetic diversity and adaptive capacity. Therefore, genetic signatures of past demographic changes may differ among species, highlighting the importance of assessing a wide range of taxa before any generalizations are made.

Investigating species' demographic responses to glacial–interglacial cycles is important for cold-adapted species that may be highly vulnerable to contemporary global warming. A study in arctic and alpine habitats found evidence for population expansions during glacial periods and subsequent interglacial population contractions in four species of small mammals (Lanier, Gunderson, Weksler, Fedorov, & Olson, 2015). This is in contrast to the paradigm of contractions during Pleistocene glaciations and post-glacial expansions out of refugia in temperate regions (Hewitt, 2000, 2004). In Antarctica, historical demography has been assessed in relatively few species, with emphasis on marine top and meso-predators, particularly penguins and mammals (Corrigan et al., 2016; Vianna et al., 2017; Younger, Emmerson, & Miller, 2016).

Pleistocene glacial cycles had profound effects on the distribution and genetic diversity of antarctic marine predators (reviewed in Younger, Emmerson, et al., 2016). Even the highly cold-adapted Emperor penguin (*Aptenodytes forsteri*) was forced into isolated refugia as evidenced by three extant mitochondrial lineages that diverged during the Last Glacial Maximum (LGM) *c.* 20 ka (Younger, Clucas, et al., 2015). Currently, these Emperor penguin lineages are mixing over extensive areas (≥8,000 km of coastline), facilitated by the high dispersal capability of the species and the lack of oceanographic barriers (Younger, Clucas, et al., 2015). Similarly, within the *Pygoscelis* penguins, Adélies (*Pygoscelis adeliae*) show evidence of two historically isolated mitochondrial lineages that are now admixed (Ritchie, Millar, Gibb, Baroni, & Lambert, 2004), and the two subspecies of Gentoo penguins (*Pygoscelis papua papua* and *Pygoscelis p. ellsworthii*) likely diverged in allopatry during or just after the LGM (Clucas et al., 2014; Ritchie et al., 2004; Younger, Emmerson, Southwell, Lelliott, & Miller, 2015). Deglaciation and the emergence of new breeding and foraging areas after the LGM have also been invoked to explain the population expansions of various antarctic marine top predators including penguins and seals (Clucas et al., 2014; Corrigan et al., 2016; De Bruyn et al., 2009; Peña et al., 2014; Trucchi et al., 2014; Younger, Emmerson, et al., 2015; Younger, Clucas, et al., 2015).

While seabirds are highly sensitive to climate change (Jenouvrier, 2013), and there is higher species richness among flying than non-flying seabirds in Antarctica, as yet there has been no formal investigation into whether flying seabirds show signatures of isolation in glacial refugia, and subsequent population expansions. Genetic studies on past demographics of flighted seabirds are scarce in the Antarctic continent; to our knowledge only one study includes samples collected in Antarctica (Ritz et al., 2008). This study on the southern skua complex (*Catharacta* spp.) shows a connection between the diversification of this seabird group and antarctic glaciations. The authors hypothesize that *Catharacta maccormicki*, the only skua species with a wide distribution in Antarctica, survived the glacial maximum in situ, but the species showed low mitochondrial phylogeographical structure and divergence times estimated under an isolation with migration model among continental populations post-date the LGM. All sampled populations of the southern skua complex, both in the continent and Sub-Antarctic Islands (SAI), showed signs of expansions but event dates were not estimated. Post-glacial re-colonization of Antarctica from SAI has been shown for penguins and seals (De Bruyn et al., 2009; Peña et al., 2014), but flighted seabirds, such as petrels that can nest on nunataks (exposed rock of a ridge) or rapidly access open-ocean polynyas to feed, could persist in local refugia throughout recent glacial periods (Fraser, Nikula, Ruzzante, & Waters, 2012).

Snow petrels (*Pagodroma nivea*) are small seabirds endemic to Antarctica and its surrounding islands. They have a circumpolar distribution and breed in rock cavities on ice-free land along the coastline or as far as 440 km inland (Goldsworthy & Thomson, 2000). Geographical variation in Snow petrels' body size led to the description of two subspecies (Bonaparte, 1857), but the taxonomic status of the two morphs (small and large) and their distributions remain controversial. Jouventin and Viot (1985) proposed that a cline exists between the two morphs, ranging from the Balleny Islands (66°55′S, 163°45′E), the only location where the large type occurs exclusively, to Davis station (68.58°S, 77.96°E), more than 4,000 km to the west, where the small morph occurs exclusively (Figure 1a, thick-shaded coastline). Only the small morph occurs across the rest of the distribution range. Jouventin and Viot (1985) suggested that the two morphs diverged from a common ancestor when populations were isolated during glaciations, and that the present-day area of coexistence constitutes a region of secondary contact. This appears plausible given that glaciations drove genetic differentiation in flying seabird populations in the Northern Hemisphere (Liebers, de Knijff, & Helbig, 2004), as well as in SAI (Techow et al., 2010). Furthermore, palaeoecological studies using radiocarbon dating of solidified stomach oil (mumiyo) demonstrate that this species endured the LGM on the Antarctic continent but not in all locations of contemporary colonies (Hiller, Wand, Kampf, & Stackebrandt, 1988; Thor & Low, 2011). For example, the Bunger Hills (Queen Mary Land) were colonized *c.* 10 ka (Verkulich & Hiller, 1994) while breeding colonies in Dronning Maud Land have existed since *c.* 37 ka (Figure 1).

Due to their persistence in Antarctica through the LGM and the morphological variation within the species, Snow petrels constitute a good model to test whether antarctic flying seabirds also exhibit signatures of isolation in refugia during the LGM and subsequent population expansion, as has been observed for other antarctic marine predators. Our goal is to determine the spatial structuring of genetic variation in the species in East Antarctica, and to test for signatures of change in population distribution and size through time. We hypothesize that the high vagility of the Snow petrels due to their ability to fly may represent an advantage over non-flying seabirds in enduring past climate variation.

2 | MATERIALS AND METHODS

2.1 | Sampling

Wing sets of deceased Snow petrels were collected over four consecutive summer seasons from 2012 to 2016 near the Australian Antarctic stations of Casey in Wilkes Land, Davis in Princess Elizabeth Land, and Mawson (67.6°S, 62.86°E) in Mac. Robertson Land, covering approximately 3,000 km of coastline in East Antarctica (Figure 1). Hereafter we refer to these sites as Casey, Davis and Mawson regions. In addition, three individuals were sampled inland at the Prince Charles Mountains, Mac. Robertson Land (Figure 1). Wing sets were collected in proximity of established breeding colonies and stored at −18°C for future analysis. For a subset of wings preserved in good condition from each region (Mawson $N = 17$, Davis $N = 25$ and Casey $N = 16$) we measured wing length (WL) with a steel ruler, from carpal joint to the tip of longest primary, to assess morphological variation among regions. In order to test the hypothesis that individuals at Casey have longer wings than at the other collection sites, the mean WL between pairs of regions was compared via one-sided Student's t tests for the Casey/Mawson and Casey/Davis pairs. A two-sided t test was used to test weather WL is different between Mawson/Davis regions. These t tests were implemented in R 3.4.1.

2.2 | Study area and potential refugia

Snow petrels depend on ice-free areas to breed during the summer; therefore, areas that remained ice free during glacial periods represent potential refugia for the species. Maps of exposed bedrock during the LGM across the study area were generated using a variety of evidence from field studies delimiting ice extent, most recently summarized by Mackintosh et al. (2014). Key supporting data include cosmogenic dating and weathering limits that provide a limit on ice elevations and extent at Framnes Mountains (Mackintosh et al.,

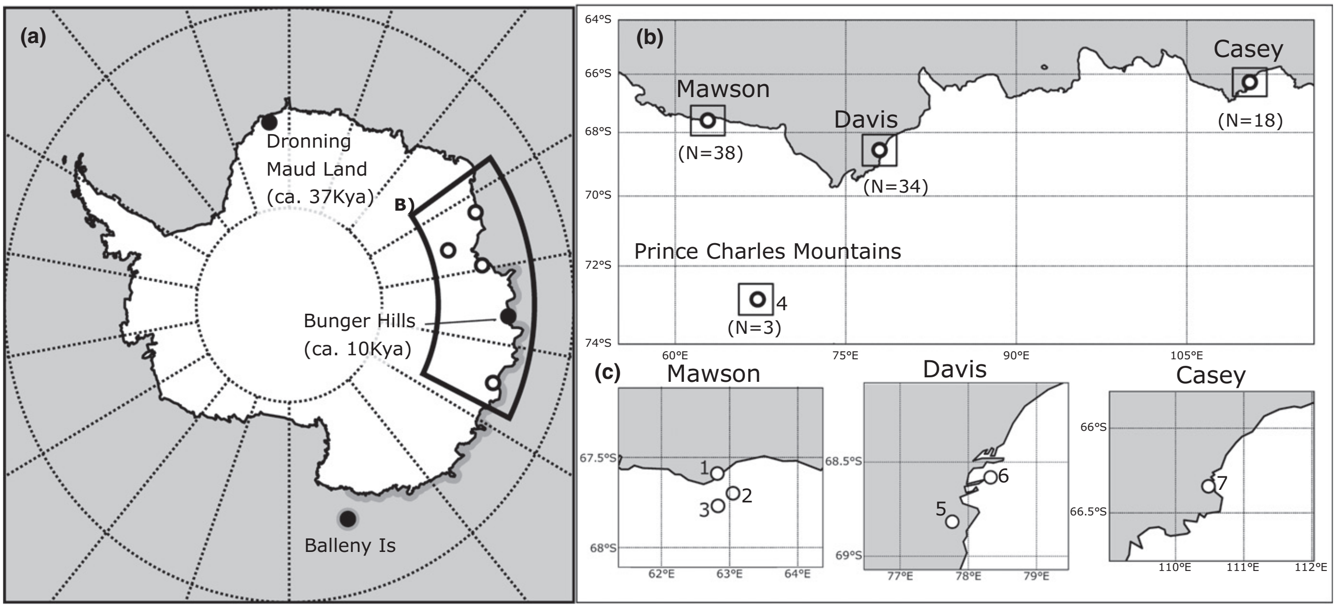

FIGURE 1 (a) Study area in East Antarctica. The box indicates the domain in (b), white circles are the sampling regions for this study, black circles indicate locations from published radiocarbon dating studies (Thor & Low, 2011; Verkulich & Hiller, 1994). (b) Four sample regions and their sampling sizes, (c) Sampling sites: 1. Béchervaise Island (62.82°E, −67.59°S), 2. Mount Henderson (63.05°E, −67.7°S), 3. Rumdoodle (62.83°E, −67.77°S), 4. Prince Charles Mountains (68.18°E, −73.11°S), 5. Hop and Filla islands (77.7°E, −68.81°S), 6. Crooked Lake (78.38°E, −68.62°S), 7. Ardery Island (110.45°E, −66.37°S). The thick-shaded coastline indicates the body size cline for the species, going from "large" at Balleny Islands to "small" at Davis region. With the exception of the Balleny Islands, the small morph occurs throughout the species' range

2007), northern Prince Charles Mountains (White, Fink, & Gore, 2011) and Larsemann Hills (Kiernan et al., 2009), distribution and age of fluvial terraces at Bunger Hills (Gore et al., 2001), and continuous sedimentation in lakes during the LGM at Larsemann Hills (Hodgson et al., 2001). The extent of the ice grounding line is mapped from the RAISED compilation (Bentley et al., 2014), which primarily relies on bathymetry and sediment studies that provide good evidence of ice expansion across the continental shelf at Mac. Robertson Land (Harris & O'Brien, 1998; Mackintosh et al., 2011) and in Prydz Bay (Domack et al., 1998).

Geomorphic evidence of ice-free areas at the LGM indicates the presence of key potential refugia at several sites in Mac.Roberston Land (encompassing Mawson), Princess Elizabeth Land (encompassing Davis) and near the Denman Glacier (Figure 2). Nunataks 200 m above the ice surface were present at David Range at Framnes Mountains (Mackintosh et al., 2007). Low ice elevations along major ice outlets such as the Lambert Glacier/Amery Ice Shelf and Denman glaciers meant that most of the present-day Amery Oasis, along with the central core of Larsemann and Bunger Hills remained ice free (Gore et al., 2001; Hodgson et al., 2001; White et al., 2011). In contrast, LGM ice advanced across all of Windmill Islands and nearby outcrops along the Wilkes Land coast (encompassing Casey, Figure 2b), as evidenced by glacial sediments and erratics deposited in these areas (e.g. Kirkup, Melles, & Gore, 2002).

The presence of potential refugia remains less certain in some parts of the study area. First, significant outcrops along Mac. Robertson Land coast may have escaped glaciation, but have not been subjected to field studies to determine LGM ice heights. Here, the Casey Range may have been high enough to have remained a nunatak based on LGM ice elevation at the nearby David Range (Mackintosh et al., 2007). LGM ice streams drain the continental shelf, and may have produced ice surfaces low enough that part of Stillwell Hills and Scullin Monolith remained ice free. The other major area of uncertainty is Vestfold Hills, where LGM ice extent has been well studied, but remains controversial (e.g. Adamson & Pickard, 1986; Gibson, Paterson, White, & Swadling, 2009; Gore & Colhoun, 1997).

2.3 | Genetic data collection

Muscle tissue (*c*. 25–50 mg) was dissected from an individual's wing and genomic DNA was extracted using a Qiagen DNeasy Blood and Tissue kit following the manufacturer's instructions. The DNA of 93 individuals was used to PCR amplify two mitochondrial markers: the cytochrome *b* gene (Cytb; Kocher et al., 1989), and the second subunit of the nicotinamide adenine dinucleotide dehydrogenase gene (ND2; Sorenson, Ast, Dimcheff, Yuri, & Mindell, 1999), as well as five nuclear markers: one intron (24972; Backström, Fagerberg, & Ellegren, 2008) and four anonymous nuclear loci (Pema1, 5, 7 and 13; Silva, Duarte, & Coelho, 2011). Primers and PCR details are described in Supporting Information Table S1.1 in Appendix S1. All fragments were amplified and sequenced in both directions via Sanger sequencing at the Australian Genome Research Facility. Sequences were assembled, aligned, and edited using Geneious R9.1 (Kearse et al., 2012). Haplotypes for nuclear alleles with multiple heterozygous SNPs were determined using PHASE version 2.1.1 (Stephens, Smith, & Donnelly, 2001). Input files for PHASE were created using SEQPHASE (Flot, 2010). Phases and genotypes with posterior probabilities of >90% were retained. Five independent runs of 10,000 iterations were conducted to check for convergence, and we used the result from the run with the best average value for "goodness-of-fit".

2.4 | Population genetic diversity and structure

Diversity indexes – that is, the number of segregating sites, haplotype and nucleotide diversities per locus and by region – were calculated using DNASP 5.10 (Librado & Rozas, 2009). To compare genetic diversity among regions, we calculated the haplotype diversity (X_H) and nucleotide diversity (π_R) ratios, as the ratios between diversity in the region over diversity in the total sample (Mardulyn, Mikhailov, & Pasteels, 2009), as implemented in SPADS 1.0 (Dellicour & Mardulyn, 2014). Differences in average nucleotide and haplotype diversities among regions were tested with a one-way ANOVA implemented in R 3.4.1. We used DNASP to perform Tajima's *D* (Tajima, 1989) and Fu's F_S (Fu, 1997) tests of mutation-drift equilibrium. Both *D* and F_S statistics are sensitive to changes in population size, and they are expected to be significantly different from zero and negative when the population has undergone a recent expansion or is experiencing purifying selection, or positive when the population has undergone a bottleneck or is experiencing overdominance selection.

Population genetic structure was quantified as global φ_{ST}, using 10,000 permutations to compute the *p*-value for the statistic, based on concatenated mitochondrial DNA and individually for each of the nuclear markers. These tests were implemented in SPADS. In addition, analysis of molecular variance (AMOVA) was performed by hierarchically grouping individuals according to their sampling sites within regions (Mawson, Davis and Casey); the Prince Charles Mountains individuals were excluded given the low sample size (N = 3). Pairwise F_{ST} was calculated between all pairs of regions and among all regions based on the concatenated mitochondrial DNA and for each of the nuclear markers. These analyses were implemented in SPADS, using 10,000 random permutations to test statistical significance. To visualize the relationship among different sequences, we estimated haplotype networks for each locus using the TCS method (Clement, Posada, & Crandall, 2000) as implemented in PopArt (http://popart.otago.ac.nz).

To test whether genotypes on one locus are independent from genotypes at the other loci, we used a linkage disequilibrium tests (*G*-tests) for each pair of loci as implemented in GENEPOP (Raymond & Rousset, 1995). We used the Bayesian approach implemented in the program STRUCTURE 2.3 (Pritchard, Stephens, & Donnelly, 2000) to examine the structuring of genetic variation among individuals based on their nuclear genotypes (sequences were coded as alleles for each of the five nuclear loci). The co-ancestry of each individual to a number of genetic groups (*K*) was estimated under a LOCPRIOR model (Hubisz, Falush, Stephens, & Pritchard, 2009) with admixture and

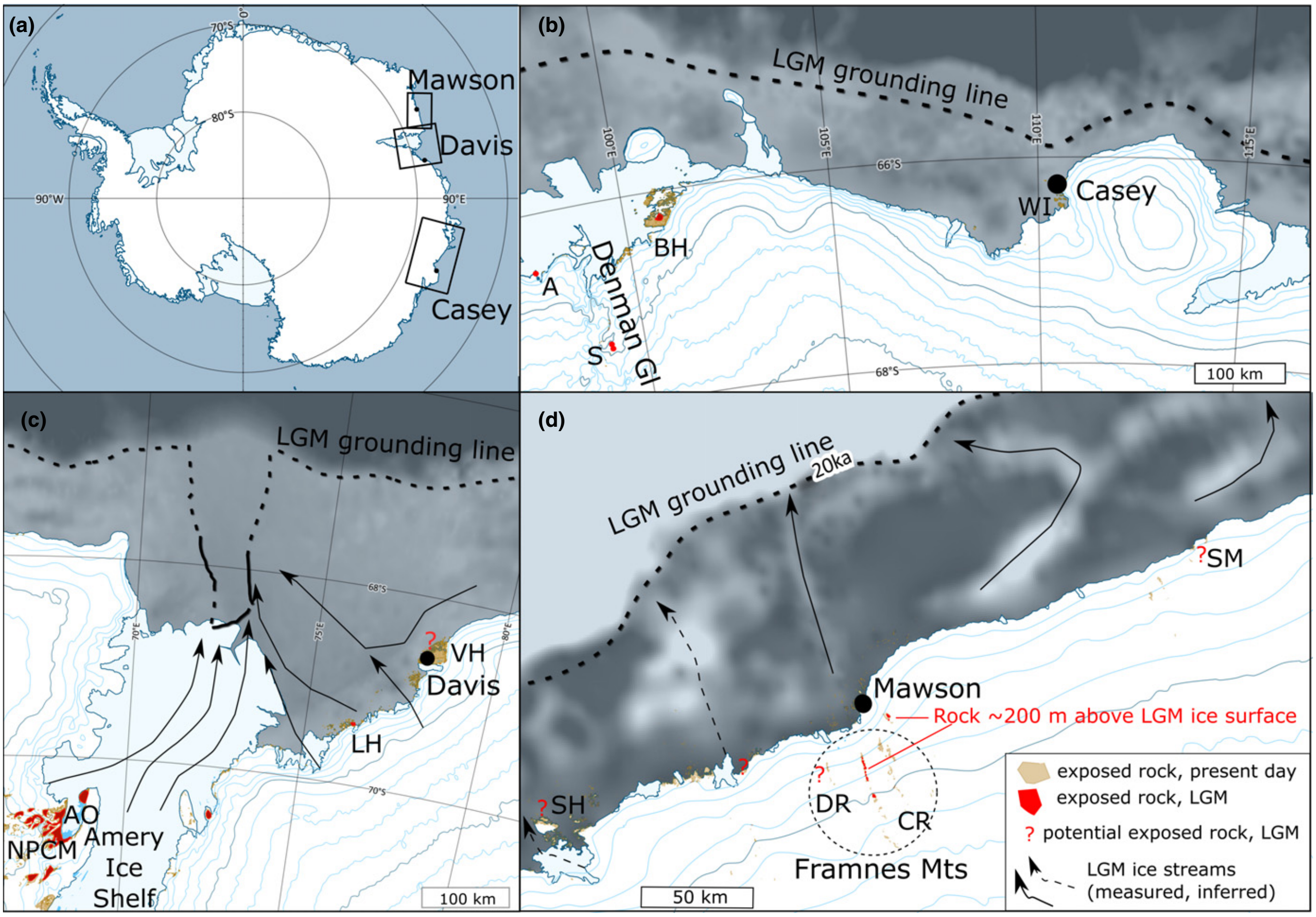

FIGURE 2 Map of exposed bedrock during LGM. (a) Antarctic continent, the three boxes indicate the domain used to map each region. (b) Casey region (Wilkes Land), A = Alligator Island, S = Mt Strathcona, BH = Bunger Hills, WI = Windmill Islands. (c) Davis region (Princess Elizabeth Land), VH = Vestfold Hills, LH = Larsemann Hills, AO = Amery Oasis, NPCM = Northern Prince Charles Mountains. (d) Mawson region (Mac.Roberton Land), SH = Stilwell Hills, CR = Casey Range, DR = David Range, SM = Scullin Monolith [Colour figure can be viewed at wileyonlinelibrary.com]

correlated allele frequencies. Three iterations were run for each *K* (*K* from 1 to 6), and each run consisted of 3×10^6 Markov chain Monte Carlo (MCMC) iterations with a burn-in length of 3×10^5 iterations. To estimate the most likely value for *K*, we used the posterior probability method (Pritchard et al., 2000) and observed the bar plots obtained for each run with different values of *K* (individual membership coefficient plot). In order to compare results using the data as concatenated nuclear sequences (SNPs) rather than alleles for each loci, we used a mixture analysis with linked loci as implemented in BAPS 6.0 (Corander & Tang, 2007). Three independent analyses were run, with *K* ranging from 1 to 6 and three replicates for each *K*.

2.5 | Historical demography

Historical variation in effective population size was tested using the Coalescent Extended Bayesian Skyline Plot (EBSP) method implemented in BEAST2 (Bouckaert et al., 2014). Given that EBSP assumes panmixia and that the sampling scheme can affect the inference of historical demographic reconstructions (Grant, 2015), the analysis was carried out organizing the samples in two different schemes to assess possible bias: (a) individually by region: Mawson (*N*= 38), Davis (*N*= 34) and Casey (*N*= 18), and (b) with individuals from all regions pooled (*N*= 90). For both schemes we used mitochondrial and nuclear markers. We used a strict clock model and substitution rates were set to 0.0189 and 0.0036 substitutions/site/Ma for the mitochondrial markers (Weir & Schluter, 2008) and the nuclear markers (Axelsson, Smith, Sundström, Berlin, & Ellegren, 2004) respectively. The best substitution model fitting each marker was selected using the Bayesian Information Criteria (BIC) in JModelTest (Guindon & Gascuel, 2003). To ensure convergence, three independent runs were performed for each dataset and the results combined using LogCombiner 2.4.7 (Drummond & Rambaut, 2007). Each run comprised 1×10^9 MCMC iterations for Mawson, Davis and the pooled samples and 2×10^9 iterations for Casey samples. In all cases, the initial 10% of iterations were discarded as burn-in. Adequate mixing of the MCMC was examined using Tracer 1.6 (Rambaut, Suchard, Xie, & Drummond, 2015) and runs were optimized until resulting effective sample sizes were >200. Visualization of the demographic history posterior employed the R script provided by the BEAST2 authors at https://www.beast2.org/tutorials/. We used a generation time of 20 years (Chastel, Weimerskirch, & Jouventin, 1993) to present the resulting effective population sizes (N_e) as the number of individuals.

Commonly, the flat portion of the EBSP preceding a deflection is interpreted as a period of stability. However, simulations have indicated that contemporary populations may not bear imprints of ancient population history due to the loss of haplotype lineages (Grant, 2015), for example, during successive population contractions. To avoid the over-interpretation of the skyline plots, we plotted the distribution of coalescent events on gene trees over time to determine the time range (*x*-axis) for which population dynamics are informed by those events (any portion of the posterior distribution outside this time range is informed by the prior distribution only).

3 | RESULTS

3.1 | Population diversity

A total of 5,412 bp was sequenced, including: two mitochondrial genes cytochrome *b* (889 bp) and ND2 (975 bp), four anonymous nuclear loci (619, 715, 742 and 617 bp) and a nuclear intron (855 bp). Sequence data are available at https://data.aad.gov.au/metadata/records/AAS_4184_Spsequences. The mitochondrial sequences included 42 variable sites which defined 34 haplotypes. The nuclear loci combined included a total of 157 SNPs defining 13–54 haplotypes per locus. Haplotype networks were similar for all loci, with one or a few high-frequency haplotypes shared across regions and several haplotypes less frequent and sometimes unique to a region (Supporting Information Figure S1.1 in Appendix S1). Nucleotide diversity ratios were similar across regions: Mawson π_R = 1.06, Davis π_R = 0.86 and Casey π_R = 1.1, and no significant differences in average nucleotide diversity were found among regions (one-way ANOVA, F = 0.021, p = 0.97). Likewise, haplotype diversity ratios were similar across regions: Mawson X_H = 0.4, Davis X_H = 0.3 and Casey X_H = 0.2 and no significant differences in average haplotype diversity were found among regions (one-way ANOVA, F = 0.418, p = 0.66). Both Tajima's *D* and Fu's F_S were negative for all loci across regions (Table 1). Tajima's *D* tests were significant for mitochondrial DNA in all regions (Table 1).

3.2 | Population structure

Low population genetic structuring is indicated by low and non-significant global φ_{ST} based on concatenated mitochondrial DNA and all nuclear markers: φ_{ST} = 0.01 ($p > 0.05$) and 0.007 ($p > 0.05$) respectively. Homologous results were obtained for pairwise F_{ST} among regions, with the exception of Pema 5 where comparisons against Casey were significant (Table 2). Likewise, AMOVA on samples grouped by regions (Mawson, Davis or Casey) was non-significant for all markers except for Pema 5, for which only 3.7% of variance was explained by grouping individuals by region (Table 3). Pairwise F_{ST} among sampling sites is presented in Supporting Information

TABLE 1 Genetic diversity indexes and neutrality tests, by loci and by sampling region

	Mawson					Davis						Casey						PC mountains				
Locus	***n***	***S***	***h***	***π***	***D***	***F*_S**	***n***	***S***	***h***	***π***	***D***	***F*_S**	***n***	***S***	***h***	***π***	***D***	***F*_S**	***n***	***S***	***h***	***π***
Mitoc	38	21	0.82	0.002	−2.2**	−15.4	33	35	0.99	0.002	−2.1*	−27.8	18	20	0.92	0.001	−2.2*	−6.8	2	6	–	–
24972	37	34	0.94	0.004	−1.7	−25.6	30	21	0.93	0.003	−1.3	−18.1	16	14	0.88	0.003	−0.8	−6.9	3	3	0.8	0.001
Pema1	26	24	0.96	0.005	−1.5	−33.4	16	17	0.88	0.004	−1.6	−8.4	14	21	0.94	0.005	−1.6	−12.6	1	2	1	0.003
Pema5	31	15	0.68	0.002	−1.9*	−9.8	23	13	0.78	0.002	−1.4	−8.3	17	10	0.68	0.002	−1.3	−3.2	–	–	–	–
Pema7	29	25	0.83	0.003	−1.7	−12.7	24	28	0.85	0.003	−2.0*	−10.8	16	22	0.85	0.004	−1.6	−7.7	–	–	–	–
Pema13	29	8	0.39	0.001	−1.6	−3.9	21	5	0.37	0.001	−1.9*	−8.5	13	1	0.01	0.0001	−1.2	−1.1	–	–	–	–

n = number of individuals successfully sequenced, *S* = number of variable sites, *h* = haplotype diversity, *π* = nucleotide diversity (per site). *D* and F_S indicate Tajima's *D* and Fu's F_S statistics respectively.

$^*p < 0.05$ and $^{**}p < 0.01$.

Table S1.2 in Appendix S1. No evidence of linkage was found between any pair of loci, results are shown in Supporting Information Table S1.3 in Appendix S1. Posterior probabilities obtained with STRUCTURE indicated no genetic subdivision, and membership coefficient bar plots showed all individuals predominantly assigned to a single group across runs assuming different *K* values (Supporting Information Figure S1.2a in Appendix S1). In agreement with the results obtained with STRUCTURE, the analysis of DNA sequences with BAPS indicated no genetic subdivision (Supporting Information Figure S1.2b in Appendix S1). While we found no evidence of population genetic structure, the individuals sampled at Casey had longer wings than those at Mawson and Davis (Table 2, and Supporting Information Figure S1.3 in Appendix S1).

TABLE 3 AMOVA results per locus

Locus	φ_{SC}	φ_{ST}	φ_{CT}
Mitochondria	0.009	0.014	0.005
24972	0.005	6.8E-4	–0.005
Pema1	0.039*	0.017	–0.022
Pema5	–0.019	0.019	**0.037***
Pema7	0.003	0.005	0.001
Pema13	0.207*	0.095*	–0.141

φ_{SC} = measures the correlation of randomly sampled genotypes among populations within the same region, φ_{ST} = measures the correlation within populations and φ_{CT} = measures the correlation among regions in the total population. Subtle regional genetic differentiation is observed only based on Pema5 (bold).

*$p < 0.05$.

3.3 | Historical demography

The demographic history posteriors obtained with the EBSP suggest that the effective population size at Mawson, Davis and all populations combined increased around two orders of magnitude since 60 ka (Figure 3). In contrast, at Casey the EBSP analysis indicates an expansion of lower magnitude, from 5 to 10 ka (Figure 3).

4 | DISCUSSION

Our results suggest long-term population connectivity for Snow petrels across *c.* 3,000 km of coastline in East Antarctica, representing about 25% of the species' range (Croxall, Steele, McInnes, & Prince, 1995). In the Mawson and Davis areas, population expansions preceded the LGM. This is in contrast to penguin species, including not only Emperor and Adélie, which breed in the same areas as Snow petrels, but also Gentoo, Chinstrap and King penguins that breed in other areas of Antarctica and the sub-Antarctic and expanded only when temperatures increased following the LGM (Peña et al., 2014; Younger, Emmerson, et al., 2016). In contrast to non-flying species, Snow petrels at Davis and Mawson endured the LGM with large effective population sizes; geomorphic evidence of potential refugia during the LGM exists in both regions (Figure 2c,d). In comparison, the effective population size at Casey only expanded after the LGM. This geographical difference in demographic parameters agrees with the expected ice-free areas in the LGM found in the literature (Figure 2), indicating that the region surrounding Casey was likely covered by the ice sheet during the LGM, and that colonization of this area was only possible after the ice retreated. The lack of evidence for divergent genetic lineages in East Antarctica has alternative potential explanations. The presence of multiple refugial populations could be masked by subsequent high population connectivity in East Antarctica, and by a failure of the refugial populations to diverge, especially considering the high effective population sizes during the LGM revealed in this study. Alternatively, extant populations in this area may represent a single genetic stock that recolonized from a glacial refugium elsewhere on the continent. Future genetic studies using higher resolution genomic approaches and involving the complete distribution range of the species may reveal more subtle genetic structuring (e.g. Younger et al., 2017).

Climate variation can influence the genetic structure and demographic history of a species by altering population connectivity patterns and promoting extinctions and founder effects, but such effects depend on characteristics intrinsic to the species. In seabirds, genetic divergence has been associated with foraging segregation, or the species dispersal ability and philopatric behaviours (Friesen, Burg, & McCoy, 2007). Philopatry is expected to promote genetic

TABLE 2 Results for the pairwise genetic and morphological (wing length) comparisons among regions. Pairwise F_{ST} among regions and global F_{ST} based on the concatenated mitochondrial markers and the nuclear markers individually. Statistics and *p*-values for the Student's *t* tests comparing wing lengths among regions show birds at Casey have larger wings

	Mawson versus Davis F_{ST}	Mawson versus Casey F_{ST}	Davis versus Casey F_{ST}	Global F_{ST}
Concatenated mitochondrial	0.012	0.001	0.018	0.011
Intron 24972	0.006	0.004	0.001	0.001
Pema1	0.008	9.000×10^{-4}	0.001	0.004
Pema5	–0.002	0.048*	0.042*	0.025*
Pema7	0.002	6.784×10^{-4}	0.012	0.004
Pema13	0.001	0.008	0.049	0.0138
Wing length comparison *t*-statistic (*df*)	–1.4 (*df* = 22.2)	–3.6 (*df* = 23.3)**	–3.8 (*df* = 34.5)**	

*$p < 0.005$ and **$p < 0.001$.

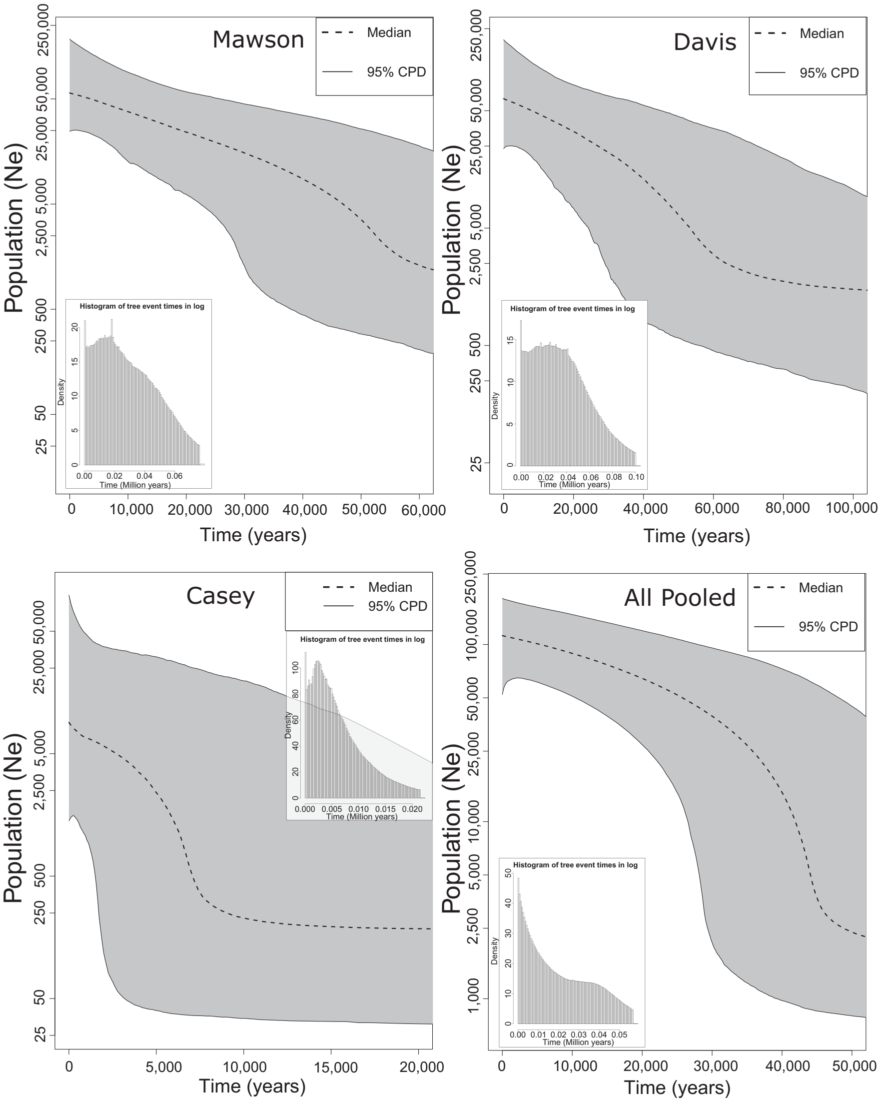

FIGURE 3 Extended Bayesian skyline plots showing the change in effective population size (N_e) over time for each of the three studied regions separately and for all samples pooled. The *Y*-axis scale is logarithmic to show the lower values of N_e. The small graphs within each panel are the histograms including 95% of tree coalescent event times for each of the EBSP runs, used to determine the length of the *x*-axis in each of the skyline plots

differentiation and dispersal ability to facilitate gene flow. The population connectivity found in this study is in agreement with previous ecological studies showing potentially low (13%) philopatric behaviour of Snow petrels (Chastel et al., 1993). However, the relationship between dispersal ability or philopatric behaviour and the resulting signal in population genetic structure is not straightforward. For example, no evidence of genetic structuring has been found for the highly philopatric (and highly vagile) wandering albatross (*Diomedea exulans*) among their breeding colonies in SAI (Milot, Weimerskirch, & Bernatchez, 2008). On the other hand, a highly vagile and also philopatric non-flying seabird, the Gentoo penguin (*Pygoscelis papua*) showed high genetic differentiation among breeding colonies in SAI (Vianna et al., 2017), and no genetic structure among colonies in the Western Antarctic Peninsula (WAP). The same study found that breeding colonies in the SAI had remained stable during the LGM, while the WAP population expanded only after the LGM, possibly recolonizing from SAI (Peña et al., 2014).

Our historical demographic inferences support a Snow petrel population expansion of around two orders of magnitude that precedes the LGM in the Mawson and Davis regions, starting about 60 ka. Ice-free areas existed around both Mawson and Davis at the LGM where Snow petrel populations could have persisted (Figure 2c,d). Palaeoclimate records offer some indication of moderate temperatures for the Davis area during the MIS 3 (Marine oxygen Isotope Stage 3, *c.* 60–25 ka) with ice sheet margins no more advanced than at present (Berg et al., 2016; Hodgson et al., 2001). Although climate records before the LGM for the total study area are incomplete, well dated records in other areas of East Antarctica indicate temperatures leading to the maximum glaciation were c. 5°C colder than at present (Jouzel et al., 2007). Overall, temperature fluctuations before the LGM do not offer a clear link to the timing of the demographic expansion observed in Snow petrels. When data from all regions are pooled, the timing of the expansion is similar, but the magnitude of the expansion is double. Sample size will affect the power of EBSP to infer demographic history (Grant, 2015), whereby small sample sizes can fail to capture the extent of genetic diversity in a recently expanded population, leading to an underestimation of the magnitude of the expansion. The population at Casey expanded more recently (following the LGM) with a lower magnitude of growth than observed in the other regions, which could be affected by the smaller sample size, particularly as these regions are all genetically connected. Alternatively, this could reflect a relatively recent colonization of Casey, especially considering this area was likely covered by the ice sheet during the LGM. Based on radiocarbon dating of mumiyo deposits (Verkulich & Hiller, 1994), recent colonizations (in the last 10 ka) have been reported from the Bunger Hills, even if ice-free areas suitable for nesting occurred nearby during the LGM (Figure 2b, Mackintosh et al., 2014). This suggests that there are different factors other than exposed bedrock (e.g. access to foraging areas) that may have affected local colonization by this species around this area.

Our results indicate that the Snow petrels have been more robust to the LGM than non-flying seabirds breeding in the same areas of East Antarctica. Emperor penguin populations in the Mawson and Davis regions suffered severe bottlenecks during the last glacial cycle and only recovered their numbers *c.* 10 ka (Younger, van den Hoff, Wienecke, Hindell, & Miller, 2016). Similarly, Adélie penguin populations expanded *c.* 14 ka (Younger, Emmerson, et al., 2015), when temperatures increased after the LGM and the ice sheet reached its modern limit. During the LGM, the sea ice extended twice as far north as the present winter extent (Gersonde, Crosta, Abelmann, & Armand, 2005), possibly requiring penguins to walk longer distances to reach the open water at the ice edge where they feed or forcing them to find refugia close to polynyas (Younger, Clucas, et al., 2015; Younger, Emmerson, et al., 2015). On the other hand, demographic reconstructions for a sympatric marine mammal, the Weddell seals (*Leptonychotes weddellii*), indicate that their populations were stable over the past 75,000 years (Younger, van den Hoff, et al., 2016). At higher latitudes, in the South Pacific Ocean, evidence for a population expansion event starting 70,000 years ago has been estimated for the Gould's petrels (*Pterodroma leucoptera*; Iglesias-Vasquez et al., 2017). This suggests a strong resilience to Pleistocene glaciations in this Procellariiform species, despite life history characteristics, such as long generation time and delayed age of maturity, which are shared with the Snow petrels, and that could make them vulnerable to population loss.

Finally, population isolation in refugia during the LGM had been hypothesized to explain the presence of two size morphs of Snow petrels (Barbraud & Jouventin, 1998; Jouventin & Viot, 1985). Barbraud and Jouventin (1998) showed that both morphs of Snow petrels breed at Casey, differing in four morphometric characteristics including WL. Similarly, we found that individuals at Casey had significantly longer wings than those at Mawson and Davis, where the large morph has not been reported. However, the lack of genetic differentiation among regions in our study (differentiation indexes, genetic clustering, haplotype networks) suggest phenotypic variability alone accounts for the observed intraspecific body size variation. Although it is not the purpose of this study to resolve the intraspecific taxonomy of Snow petrels, it is worth noting that subspecies are expected to be represented by well-defined genetic lineages. For example, other subspecies in the Procellariiforms show cytochrome b lineages with 0.6%–0.8% sequence divergence (Cagnon, Lauga, Hemery, & Mouches, 2004; Techow, Ryan, & O'Ryan, 2009); we did not find genetic differentiation using either mitochondrial or nuclear markers associated with geographical location or WL. In the absence of genetic divergence, the question remains whether the observed morphological variation in the species is a result of plasticity or selective processes driving local adaptation. High behavioural plasticity has been observed in other Procellariiforms, for example, Gould's petrels and Providence petrels (*Pterodroma solandri*) populations are genetically similar despite ecological distinctiveness (Iglesias-Vasquez et al., 2017; Lombal et al., 2017).

In conclusion, we show evidence for gene flow among Snow petrel populations over a large area and population growth for long periods (*c.* 60 ka). In terms of the species' past population dynamics, our contribution suggests that the species' high dispersal ability due to flight, may represent an advantage over non-flying seabirds in enduring past climate variation possibly by facilitating the movement of adaptive genes, colonization of new habitats, ability to follow changes in the distribution and availability of resources affected by climate variation. However, we should not become complacent of their future and neglect their conservation since this intrinsic resilience might be insufficient to counteract the environmental impacts of the current unprecedented climate change, as well as the impacts on their terrestrial breeding habitats as human presence and activities in the region increase.

AUTHOR CONTRIBUTIONS

All authors contributed to the writing of the manuscript that was led by CC and CB. CC collected the genetic data and performed the statistical analysis. DW generated the maps of ice-free areas during the LGM. KJM, LME and BW conceived the project and were awarded the AAS grant.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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