RESEARCH ARTICLE

Rapid radiation of Southern Ocean shags in response to receding sea ice

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Abstract

Aim: Understanding how natural populations respond to climatic shifts is a fundamental goal of biological research in a fast-changing world. The Southern Ocean represents a fascinating system for assessing large-scale climate-driven biological change, as it contains extremely isolated island groups within a predominantly westerly, circumpolar wind and current system. Blue-eyed shags represent a paradoxical seabird radiation—a circumpolar distribution implies strong dispersal capacity yet their species-rich nature suggests local adaptation and isolation. Here we attempt to resolve this paradox in light of the history of repeated cycles of climate change in the Southern Ocean.

Location: Southern Ocean.

Taxa: 16 species and subspecies of blue-eyed shags (Phalacrocoracidae; *Leucocarbo* spp.).

Methods: We use mitochondrial and nuclear sequence data from individuals across the geographical range of the genus to conduct the first comprehensive, time-calibrated phylogenetic analyses and ancestral-range biogeographical reconstructions of the blue-eyed shags.

Results: The origins of many island-endemic lineages are remarkably recent, consistent with a recent high-latitude circumpolar radiation in the Pliocene or Early Pleistocene. This recent sub-Antarctic expansion contrasts with significantly deeper lineages detected in South America and, to a lesser extent, New Zealand. These regions, particularly South America, acted as glacial refugia and sources for multiple waves of post-glacial dispersal.

Main conclusions: The blue-eyed shag paradox is resolved, with at least two waves of dispersal, linked to interglacial cycles, explaining the current distribution and diversity. Descendants of a Pliocene or Early Pleistocene wave of dispersal out of South America survive in the New Zealand region. In contrast, taxa distributed on sub-Antarctic islands originated much later, possibly since the Last Glacial Maximum.

Blue-eyed shags therefore represent a powerful model system—comprising several natural replicates—for studying the early stages of founder-event speciation and adaptation in a Southern-Ocean bird group.

KEYWORDS

biogeography, climate cycles, cormorant, *Leucocarbo*, Southern Ocean, speciation, sub-Antarctic

1 | INTRODUCTION

Understanding how natural populations respond to climatic shifts represents a key goal of biological research in a fast-changing world (Chen et al., 2011; Parmesan & Yohe, 2003). Changes in climate can underpin major shifts in the distribution and diversity of biological assemblages, with glacial–interglacial cycles—such as the repeated series during the Pleistocene Ice Age (2.58–0.01 Mya) (Ehlers et al., 2011)—thought to have driven dramatic changes in species distributions across many regions of the globe (Davis & Shaw, 2001). The biogeographic responses of Northern Hemisphere biota to Quaternary climate shifts, and associated ice-sheet dynamics, are relatively well studied (Hewitt, 2000; Maggs et al., 2008). By contrast, climate-driven shifts involving Southern Hemisphere taxa, especially those inhabiting the Southern Ocean, remain less understood (Cole, Dutoit, et al., 2019; Fraser et al., 2009; Fraser et al., 2010; Fraser et al., 2012).

The Southern Ocean represents a fascinating system for assessing large-scale climate-driven biological change, as it contains multiple groups of extremely isolated oceanic islands within the predominantly westerly wind and current system encircling Antarctica (Fraser et al., 2012). Understanding the evolutionary dynamics of these unique island ecosystems, and of their distinctive endemic taxa, is particularly important in the context of the region's dynamic climatic history. Specifically, geological and biological evidence together indicate that, during recent Pleistocene glacial maxima, several of these outlying island groups (e.g. South Georgia, Kerguelen, Heard, Crozet, Macquarie [itself only ~700,000 years old]) were for thousands of years in the winter sea-ice zone (Figure 1) (Fraser et al., 2009; Gersonde et al., 2005; Trucchi et al., 2014), and in some cases the open ground needed for breeding was covered in glacial ice and snow year round (Hodgson et al., 2014). Indeed, Heard Island was permanently iced over during the Last Glacial Maximum (LGM) (Ehlers et al., 2011).

Major deglaciation events can provide significant ecological opportunities for surviving species (Fraser et al., 2018). Indeed, recent genetic data suggest that some highly dispersive Southern Ocean species or communities have, at different timescales, responded rapidly to colonize newly vacant habitats arising from such climate-driven ecosystem change (Baird et al., 2021; Carrea et al., 2019; Cole, Dutoit, et al., 2019; de Bruyn et al., 2009; Fraser et al., 2009; Fraser et al., 2010; Fraser et al., 2011; Fraser et al., 2012; Fraser et al., 2018; González-Wevar et al., 2017; González-Wevar et al., 2018; González-Wevar et al., 2019; Nikula et al., 2010; Rexer-Huber et al., 2019). In some cases, long-distance dispersal permitted the colonization of islands

that were previously inhospitable, but gene flow remained low between the isolated populations, thus enabling differentiation through drift and selection. Such scenarios are exemplified by the terrestrial Ectemnorhinini weevils and the subtidal limpet genus *Nacella*, which exhibit island-level endemism around the entire Southern Ocean, with divergences dating to the Plio-Pleistocene boundary (~2.58 Mya) and the mid-Pleistocene (0.25–0.6 Mya), respectively (Baird et al., 2021; González-Wevar et al., 2017; González-Wevar et al., 2019).

At the opposite end of the scale, the highly dispersive southern bull kelp (*Durvillaea antarctica*; a keystone intertidal species), and its associated rafting invertebrate communities, exhibit a 'northern richness; southern purity' model whereby disjunct high-latitude sub-Antarctic islands share anomalously low-diversity, circumpolar lineages (Fraser et al., 2009; Fraser et al., 2010; Fraser et al., 2011; Fraser et al., 2012; Fraser et al., 2018; González-Wevar et al., 2018; Nikula et al., 2010). Fraser et al. (2009) hypothesized that these patterns reflect recent passive post-LGM recolonization from ice-free refugia facilitated by circumpolar ocean currents. The intertidal air-breathing limpets *Siphonaria lateralis* and *S. fuegiensis*, which are closely associated with bull kelp, appear to show a more recent dispersal, with an ongoing gene flow among high-latitude sub-Antarctic islands, as evidenced by negligible phylogeographic structure (González-Wevar et al., 2018). Intriguingly, the highly mobile southern elephant seal (*Mirounga leonina*), which exhibits a multiregional refugial pattern (de Bruyn et al., 2009), quickly expanded their range to newly ice-free parts of the Antarctic coast (2500 km from the nearest breeding colony) 8000 years ago, but were extirpated from this region 7000 years later when a grounded ice-sheet returned (see also Obiol et al., 2022; Rexer-Huber et al., 2019). These apparently climate-driven patterns are mirrored to some extent by multispecies demographic analyses of high-latitude penguins, which reveal concordant evidence for simultaneous and rapid post-LGM population expansions associated with exposure of snow-free ground on which to breed (Cole, Dutoit, et al., 2019).

These contrasting biogeographic responses to the Pleistocene glacial–interglacial cycles are underpinned by biology. The gilled *Nacella* limpets can survive subtidally, including on the Antarctic Peninsula (González-Wevar et al., 2017; González-Wevar et al., 2019), and are thus not as affected by sea ice as more intertidal species like southern bull kelp (despite its ability to passively drift onto Antarctic shores; Fraser et al., 2018), air-breathing *Siphonaria* limpets (González-Wevar et al., 2018) or southern elephant seals (de Bruyn et al., 2009).

Blue-eyed shags (*Leucocarbo* spp.) are an ecologically important and species-rich group of philopatric seabirds exhibiting a circumpolar
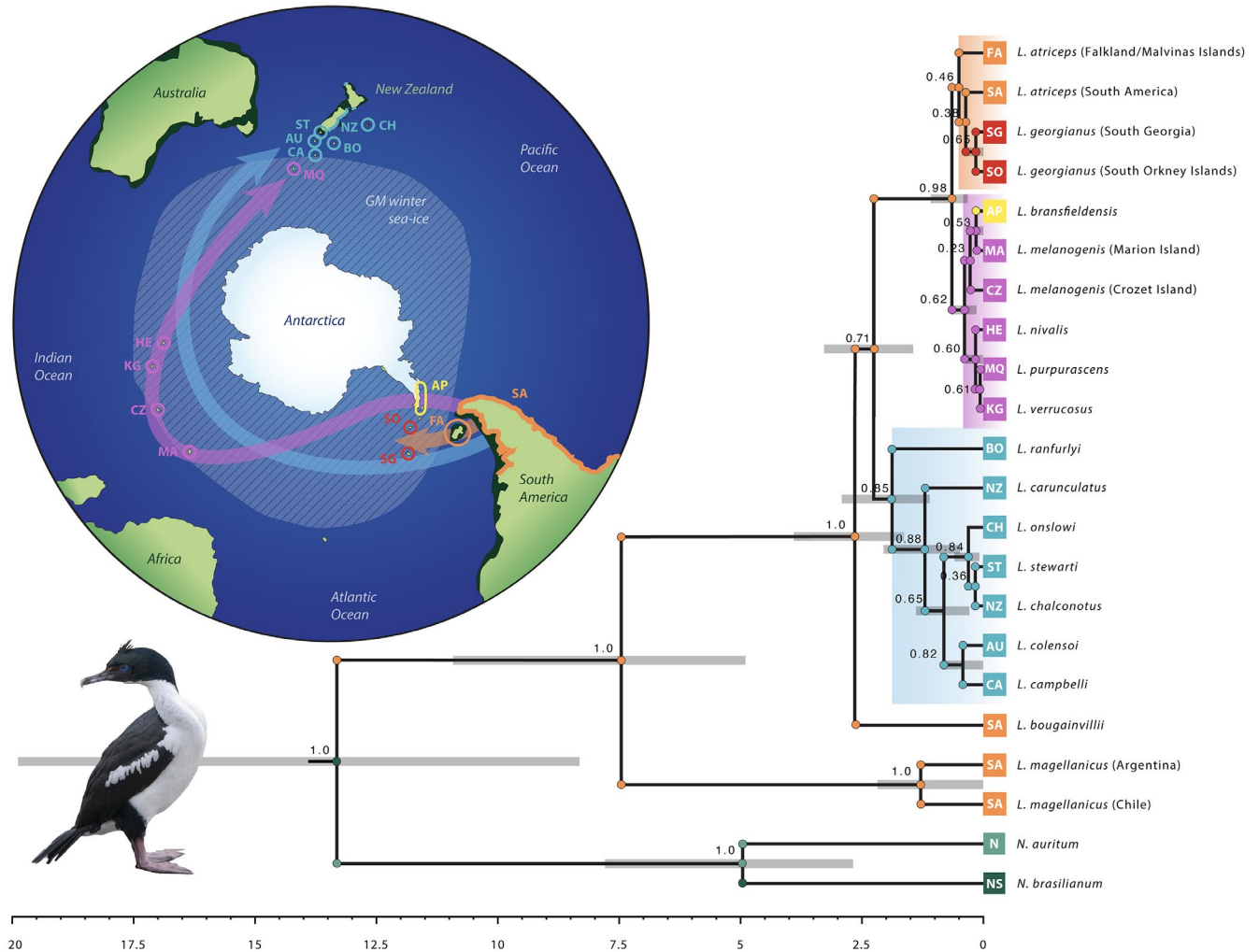
FIGURE 1 Evolutionary history of blue-eyed shags (*Leucocarbo* spp.) in the Southern Ocean. The map depicts inferred postglacial colonization routes (arrows) supported by the dominant westerly winds and eastward flow of the Antarctic Circumpolar Current. The extent of winter sea ice (cross-hatched pattern) and land area (dark green) during the Pleistocene Last Glacial Maximum 29–19 Kya is indicated. Rapid circumpolar expansion and founder-speciation hypotheses are supported by temporal phylogenetic and ancestral biogeographic reconstructions. The time-calibrated species tree is derived from 8.2 kilobases of DNA sequence data (five mitochondrial and five nuclear genes) with *Nannopterum* as the outgroup. Node bars on the phylogeny are 95% HPD of divergence times as indicated on the scale bar (millions of years before present). Node values are Bayesian posterior probability support. Node circles show the ancestral state reconstruction of the geographic distribution based on the DEC + J model. Colours and abbreviations are as follows: Orange: South America; purple/red: High-latitude sub-Antarctic islands; yellow: Antarctic Peninsula; blue: New Zealand region; olive: North America; dark green: South America; FA: Falkland/Malvinas Islands; SA: South America; SG: South Georgia; SO: South Orkney Islands: AP: Antarctic Peninsula; MA: Marion Island; CZ: Crozet Island; HE: Heard Island; MQ: Macquarie Island; KG: Kerguelen Island; CA: Campbell Island; AU: Auckland Island; NZ: Mainland New Zealand; ST: Stewart Island; CH: Chatham Islands; BO: Bounty Islands; N: North America; NS: North and South America. Clade and arrow colours: Orange: South America, South Georgia, South Orkney Islands; purple: Antarctic Peninsula, high-latitude sub-Antarctic islands; blue: New Zealand region

Southern Ocean distribution, with 16 currently accepted species and subspecies (Kennedy & Spencer, 2014; Rawlence et al., 2017). Many of these taxa are endemic to single island groups (Figure 1). Additionally, the small number of lineages that breed on mainland coasts typically exhibit strong phylogeographic structure (Calderón et al., 2014; Kennedy & Spencer, 2014; Rawlence et al., 2015; Rawlence et al., 2017). Preliminary genetic research has suggested that blue-eyed shags comprise two widespread, species-rich clades: a sub-Antarctic clade encompassing South America, Antarctica and high-latitude sub-Antarctic islands; and the other occurring across

the New Zealand region (Figure 1) (Kennedy & Spencer, 2014). Data from the subfossil record and ancient DNA analysis suggests that at least one recently recognized mainland taxon (*L. chalconotus*) has suffered substantial loss of genetic and geographic diversity since human arrival in mainland New Zealand (Rawlence et al., 2015; Rawlence et al., 2016; Rawlence et al., 2017), and that the newly described kōhatu shag (*L. septentrionalis*) became extinct shortly after human arrival in New Zealand (Rawlence et al., 2017).

The broad, species-rich biogeography of *Leucocarbo* presents something of a paradox. Specifically, while the wide Southern Ocean

distribution of the genus, incorporating numerous isolated islands, implies strong dispersal capacity, the presence of numerous single-island endemics suggests that such dispersal ability is insufficient to prevent speciation on these islands. This situation in blue-eyed shags may be somewhat akin to iconic Southern Hemisphere radiations described for penguins (Cole, Ksepka, et al., 2019; Vianna et al., 2020) in which the evolution of island endemics has apparently been underpinned by founder speciation (Waters et al., 2013). The Southern Ocean islands have been heavily impacted by recent glacial cycles (Fraser et al., 2009; Fraser et al., 2012), suggesting that much of their biotic diversity may have evolved relatively recently.

Based on the distinctive Southern Ocean biogeography of *Leucocarbo* shags, we hypothesize that glacial–interglacial transitions have presented crucial opportunities for recent circumpolar range expansion and founder speciation in this group. Here we present the first multigene analysis of *Leucocarbo* that includes all recognized taxa, and use a temporal phylogenetic framework to test for rapid radiation of this unusually species-rich Southern Ocean assemblage.

2 | MATERIALS AND METHODS

2.1 | Specimens, DNA extraction, PCR and sequencing

Tissue, blood or feathers were obtained from a number of sources, covering the geographic distribution of *Leucocarbo* shags (Appendix Table S1.1–1.2). Total genomic DNA was extracted using a phenol/chloroform extraction, a 5% Chelex 100 solution or the Qiagen DNeasy Tissue Kit (Kennedy & Spencer, 2014; Walsh et al., 2013). Negative controls were included with each extraction. For the phylogenetic dataset (using a single location per taxon, except for four taxa where two locations were used and one taxon where three locations were used, see Appendix Table S1.1) DNA was amplified for five mitochondrial genes (12S, overlapping ATPase 8 and 6, ND2, COI) and five nuclear genes (FIB7, PARK7, IRF2, CRYAA and RAPGEF1) (following Kennedy & Spencer, 2014; Kennedy et al., 2019). The phylogenetic dataset's primer details are shown in Table S1 of Kennedy et al. (2019). To investigate within taxon diversity, control region (CR) sequences were amplified for multiple individuals per location (except for two taxa where only a single individual was able to be used, see Appendix Table S1.2) (following Rawlence et al., 2014). Negative controls were included with each PCR. PCR products were purified using the Ultra-Sep Gel extraction kit (Omega) and sequenced on an Applied Biosystems 3730 capillary sequencer. Newly generated sequences for the phylogenetic and CR datasets were added to, and aligned with, those previously published (Kennedy & Spencer, 2014; Rawlence et al., 2014; Rawlence et al., 2017) (see Appendix Tables S1.1-S1.2).

2.2 | Phylogenetic and demographic analyses

The phylogenetic dataset (including two outgroups, the double-crested cormorant *Nannopterum auratum* and the neotropic cormorant *N. brasilianum* [Kennedy & Spencer, 2014; Gill et al., 2021], see Appendix Table S1.1) was divided into nine partitions, five nuclear loci and four mitochondrial loci (the overlapping ATPase 8 and 6 were treated as a single ATPase partition). Models of nucleotide substitution were selected using the Akaike Information Criterion of Modeltest 3.7 (Posada & Crandall, 1998). The models selected for each gene region were as follows: HKY + I for 12S (2st + I), GTR + I for ATPase (6st + I), TIM + G for ND2 (6st + G), TIM + I for COI (6st + I), HKY + I for FIB7 (2st + I), HKY for PARK7 (2st), TrN for IRF2 (6st), HKY for CRYAA (2st) and HKY + I for RAPGEF1 (2st + I). We used StarBEAST2 (v. 0.15.13) implemented in BEAST 2.6.3 (Bouckaert et al., 2019) to jointly infer the *Leucocarbo* species tree along with co-estimation of the mitochondrial and individual nuclear gene trees. We implemented an analytical population size integration model (Bouckaert et al., 2019), unlinked substitution models for all partitions, linked trees for mitochondrial genes and a birth–death tree prior. Strict molecular clocks were used due to the shallow phylogenetic scale encompassed by *Leucocarbo* shags and absence of fossil calibration points within crown-group Phalacrocoracidae (Worthy, 2011); one linked clock for nuclear genes and unlinked clocks for mitochondrial genes. The clock rates for mitochondrial genes were modelled as normal priors with mean substitution rate estimated from rates for terminal nodes 33–39 (i.e. the clade that encompasses *Leucocarbo* and Pelecaniformes, with the most recent common ancestor at node 102) in the phylogeny of Figure S2 of Pacheco et al. (2011). Rates corresponding to terminal nodes 33–39 were obtained from Table S2 of Pacheco et al. (2011). The mean substitution rates in substitutions/site/million years (s/s/Ma) (and standard deviations) used in our analysis were as follows: ND2: 0.00388 s/s/Ma (0.0013); COX1: 0.00232 s/s/Ma (0.0007); ATPase: 0.0029 s/s/Ma (0.0011); and 12S: 0.00145 s/s/Ma (0.0011). Substitution rates for individual nuclear genes were modelled using uninformative 1/X priors. We ran three independent MCMC chains, each run for 50 million steps, sampling every 5000 steps. Additionally, to estimate per species population sizes, analyses were rerun using the linear with constant root populations model (Barido-Sottani et al., 2018; Heled & Drummond, 2010) with the same parameters, but increasing the MCMC chain to 100 million steps, sampling every 10,000 steps. We checked for convergence and sufficient sampling of parameters in Tracer v1.7.1 (Rambaut et al., 2018) and combined individual runs after discarding the first 10% of steps as burn-in in LogCombiner. Maximum clade credibility consensus trees were generated in TreeAnnotator using the median node age. DensiTree v2.2.7 (Bouckaert, 2010) was used to simultaneously visualize all trees post burn-in and generate consensus trees scaled by estimated effective population size.

2.3 | Ancestral range estimation

We estimated the ancestral range of internal nodes of the *Leucocarbo* species tree using the R package BioGeoBears (Matzke, 2013). We implemented three methods of ancestral state estimation with

and without the jump dispersal parameter (J) (Matzke, 2014), and the dispersal probability as a function of the distance parameter (X) (van Dam & Matzke, 2016): dispersal–extinction–cladogenesis (DEC) (Ree & Smith, 2008), dispersal vicariance analysis (DIVA) (Ronquist, 1997) and Bayesian analysis of biogeography (BAYAREA) (Landis et al., 2013). We compared models using corrected Akaike Information Criterion (AICc) and the weighted AICc values. Due to the criticism of +J models (Ree & Sanmartin, 2018), especially regarding statistical comparison to non-+J models, we did not statistically compare models with and without the J parameter. We split the samples into seven biogeographic areas: N) North America, S) South America (including the Falkland/Malvinas Islands), O) South Orkney, South Georgia and the South Sandwich Islands, A) Antarctic Peninsula, K) Kerguelen, Heard, Marion and Crozet Islands, M) Macquarie Island, and Z) New Zealand and the New Zealand sub-Antarctic islands. For models including the +X parameter, pairwise distances between geographic areas were estimated using Google Earth and normalized against the shortest pairwise distance. All analyses were non-stratified with equal transition between areas.

2.4 | Median joining network of mitochondrial control region data

PopArt (Leigh & Bryant, 2015) was used to construct a median joining network of the mitochondrial control region (CR) data. Sites with >5% unidentified states were masked in the analysis.

3 | RESULTS

3.1 | Recent divergence and demographic expansion at high latitudes

Leucocarbo shags form a fully supported monophyletic clade diverging from *Nannopterum* 13.3 Mya (HPD 19.8–8.3 Mya) during the mid-Miocene (Figure 1). All major divergences within the species tree show moderate to strong support (0.71–1.0 posterior probability, PP). The Rock shag (*L. magellanicus*) is sister to the remainder of the genus, the split occurring 7.5 Mya (HPD 10.9–4.9 Mya) during the Late Miocene, whereas the lineage leading to the Guanay shag (*L. bougainvillii*) diverged much more recently 2.6 Mya (HPD 3.9–1.6 Mya) coincident with the onset of the Pleistocene Ice Age 2.58 Mya (Figure 1). Within the Rock shag, there is phylogeographic structure dividing populations from the Atlantic (Argentina) and Pacific (Chile) coasts, dating to 1.3 Mya (HPD 2.2–0.01 Mya) (Figure 1) in agreement with previously reported mitochondrial data (Calderón et al., 2014) and plumage differences (Rasmussen, 1987). However, microsatellite data suggest recent secondary contact and gene flow from the Pacific to Atlantic coasts (Calderón et al., 2014).

The remaining *Leucocarbo* lineage (leading to all the other extant species) split into two major clades 2.3 Mya (HPD 3.3–1.5 Mya) during the Early Pleistocene, shortly after its separation from the

Guanay shag lineage (hence the small inter-nodal distance and only moderate support, PP = 0.71). The first of these clades contains species from the New Zealand region (PP = 0.85), while the second comprises taxa from the sub-Antarctic, including South America (and Falkland/Malvinas Islands), Antarctic Peninsula and high latitude sub-Antarctic islands (PP = 0.98) (Figure 1). Support for the relationships among taxa within these two clades is moderate to low (PP = 0.36–0.88 for the New Zealand clade; PP = 0.23–0.66 for the sub-Antarctic clade). While a strong tree-wide phylogenetic signal is observed for our mitochondrial markers (Appendix Figure S1.1f), the signal among closely related taxa is generally much weaker across the five nuclear markers (Appendix Figure S1.1a–e). Notably, two species for which we have included representatives from multiple populations—*L. atriceps* and *L. melanogenis*—are not always monophyletic in our results. Paraphyly of these taxa is strongly supported by the mitochondrial loci (Appendix Figure S1.1f), but data from the nuclear markers were equivocal (Appendix Figure S1.1a–e), leading to only moderate support for paraphyly in the species tree (Figure 1). These results are emphasized by our DensiTree visualization (Appendix Figure S1.2), which shows congruence or conflict among trees sampled from the posterior. The genetic data do, however, resolve the ambiguity over the taxonomic status of blue-eyed shags on the South Orkney Islands, suggesting these birds are *L. georgianus* and not *L. bransfieldensis* (see Schrimpf et al., 2018).

Phylogenetic analyses revealed substantially deeper divergences among temperate New Zealand *Leucocarbo* lineages relative to those among sub-Antarctic lineages of this genus (Figure 1). Branch lengths in the New Zealand clade are up to four times longer (up to 2 Mya in the Early Pleistocene versus up to 0.5 Mya in the mid-Pleistocene). For instance, while the vast majority of divergence time HPD's among New Zealand taxa substantially predate the LGM, several sub-Antarctic taxa yielded divergence HPDs that are consistent with post-LGM recolonization (Appendix Table S1.3).

Demographic analyses based on the species tree yielded results that visually show stable or increasing population size for blue-eyed shag species in South America, compared to founder-event induced bottlenecks and subsequent population expansions associated with island endemics (Appendix Figure S1.3). The finding of relatively short branch lengths in the sub-Antarctic clade (Figure 1) is consistent with the results of these demographic reconstructions, which reveal recent population expansions in numerous sub-Antarctic lineages following major late-Quaternary bottlenecks (Appendix Figure S1.3). However, recent demographic trajectories are impossible to estimate accurately without population-level data (i.e. comparable loci from multiple individuals per species), and we recommend that future research should explicitly test these demographic hypotheses using genomic data.

The mitochondrial CR dataset comprised 1026 characters, of which 925 were constant, while 83 out of 101 variable characters were parsimony informative. The median-joining network of these fast-evolving mitochondrial CR sequences shows clear separation of Rock shag and Guanay shag haplotypes relative to blue-eyed shag haplotypes distributed throughout the New Zealand region (Figure 2). In many cases, within-taxon diversity is low (e.g. the Campbell (*L. campbelli*), Auckland

(*L. colensoi*), Bounty (*L. ranfurlyi*) and Macquarie (*L. purpurascens*) Islands are each represented by single haplotypes), whereas inter-taxon diversity is high (often over a dozen substitutions separate haplotypes belonging to different taxa). In contrast, taxa within the sub-Antarctic clade tend to be separated by relatively few substitutions, with intra-taxon diversity within this clade generally being equal to or greater than interspecies diversity (e.g. diversity within *L. atriceps* cf. diversity between *L. bransfieldensis* and *L. verrucosus*). The blue-eyed shag CR substitution rate of 3.2 s/s/Ma (95% HPD 0.70–6.57; Rawlence et al., 2015) suggests that divergence dates estimated using these data would be broadly consistent with those determined in our phylogenetic analysis of nuclear and mitochondrial DNA markers.

3.2 | Founder-event speciation

The best-supported BioGeoBears evolutionary scenario for blue-eyed shags, based on our phylogenetic analysis, was a jump dispersal (founder-event speciation)–extinction–cladogenesis (DEC+J) model

(Figure 1, Appendix Table S1.4). Within this model, founder-event speciation (J) was strongly supported (0.027) compared to range expansion (d; 1×10^{-7}). This founder-speciation model reconstructed an ancestral geographic area for *Leucocarbo* of South America, and for all major nodes in the phylogeny. The inferred most-recent common ancestor of the two major clades (New Zealand region and sub-Antarctic) within *Leucocarbo* is from South America, with subsequent circumpolar expansion supported by the Antarctic Circumpolar Current (ACC). The best-supported scenario without a jump parameter was DEC (expansion and speciation) (Appendix Figure S1.4, Table S1.4). In contrast to DEC+J, ancestors at deeper nodes in the phylogeny are inferred to have been geographically widespread, with temporally offset in situ speciation on different islands.

4 | DISCUSSION

Genetic analysis of blue-eyed shags reveals a remarkably shallow evolutionary history among endemic lineages breeding on islands
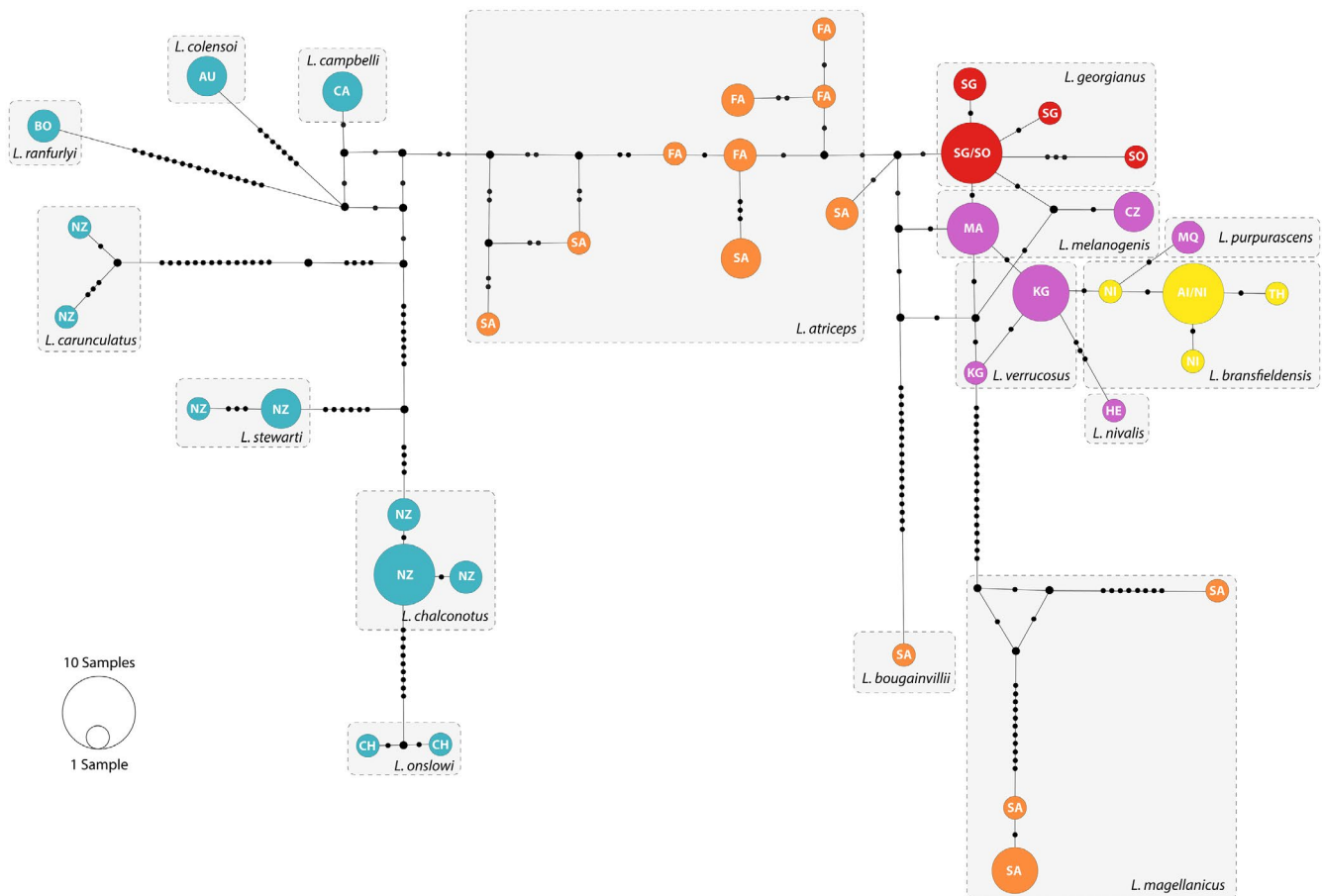
FIGURE 2 Median joining haplotype network of the mitochondrial control region from *Leucocarbo* shags. Circles represent unique haplotypes, with the size of the circle proportional to the number of individuals sharing that haplotype. Black circles represent inferred intermediate haplotypes. Colours (which correspond to those in the map of Figure 1) and abbreviations are as follows: Orange: South America; purple/red: High-latitude sub-Antarctic islands; yellow: Antarctic Peninsula; blue: New Zealand region; FA: Falkland/Malvinas Islands; SA: South America; SG: South Georgia; SO: South Orkney Islands: AP: Antarctic Peninsula; MA: Marion Island; CZ: Crozet Island; HE: Heard Island; MQ: Macquarie Island; KG: Kerguelen Islands; CA: Campbell Island; AU: Auckland Island; NZ: Mainland New Zealand; ST: Stewart Island; CH: Chatham Islands; BO: Bounty Islands

scattered across the vast Southern Ocean, consistent with a recent high-latitude circumpolar radiation (Figure 1). This Pliocene/Pleistocene expansion history of taxa to previously ice-bound, potentially glaciated sub-Antarctic islands is further highlighted by latitudinal contrasts in demographic reconstructions (Appendix Figure S1.3) and echoes recent demographic comparisons of other iconic Southern Ocean seabirds with circumpolar distributions (e.g. Cole, Dutoit, et al., 2019; Trucchi et al., 2014).

4.1 | Postglacial circumpolar expansion

Our results suggest that blue-eyed shags dispersed out of South America during the Late Pleistocene and colonized South Georgia, the South Orkney Islands, the Antarctic Peninsula, and Marion, Crozet, Kerguelen, Heard, and Macquarie Islands. All blue-shag taxa distributed on those islands today—*L. georgianus*, *L. bransfieldensis*, *L. melanogenis*, *L. verrucosus*, *L. nivalis* and *L. purpurascens*—form a well-supported 'sub-Antarctic clade' with *L. atriceps* from South America and the Falkland/Malvinas Islands (PP = 0.98; Figure 1). However, mean node age estimates for most divergences among these taxa postdate 1 Ma, with 95% HPDs that overlap the Holocene (Figure 1; Table S1.3). Furthermore, taxa within the sub-Antarctic clade are not well differentiated in our species-tree analyses (PP = 0.23–0.66)—likely due to a lack of inter-taxon variation at our sampled nuclear loci—and our mitochondrial CR haplotype network reveals that intra-taxon haplotype diversity is generally higher than inter-taxon haplotype diversity (Figure 2). This latter result in particular suggests that phylogenetic reconstructions within this clade may be misled by incomplete lineage sorting (e.g. Suh et al., 2015). Indeed, the mitochondrial DNA sequences of *L. atriceps* from South America and the Falkland/Malvinas Islands (sometimes considered subspecies *atriceps* and *albiventer*, e.g. Strange, 1992) are paraphyletic (Figure 2, Appendix Figure S1.1f), while analyses of other datasets suggest that they represent colour morphs of a single taxon (see Calderón et al., 2014; Malacalza, 1991; Rasmussen, 1994). As a result of incomplete lineage sorting, small sample sizes and non-comprehensive geographic sampling, our node age estimates may only be interpreted as maximum bounds on the foundation of these present-day sub-Antarctic and Antarctic island endemic taxa. The actual foundation events could be much more recent, preceding local taxon-specific bottleneck-driven fixation of deeply divergent alleles inherited from a common genetically diverse source population. Thus, we cannot reject the hypothesis that the modern blue-eyed shag populations on these islands were founded only once climatic conditions improved following the LGM (i.e. <21 ka).

Moreover, post-LGM colonization of southern oceanic sub-Antarctic islands by blue-eyed shags is consistent with several other lines of evidence that suggest that these shags are unlikely to have maintained local breeding colonies during glacial maxima. The open ground on these islands needed by blue-eyed shags for nesting may have been covered by ice and snow during the summer breeding season (Hodgson et al., 2014). In addition, the coasts of many southern oceanic islands (e.g. Kerguelen and Heard Islands) would have been heavily affected by winter sea ice during glacial maxima (Ehlers et al., 2011), most recently during the LGM, which would have extended north of the present-day route of the Antarctic Polar Front (Figure 1; Fraser et al., 2009). Blue-eyed shags are inshore foragers largely dependent on benthic prey species (Cook et al., 2013), which they hunt through pursuit-diving. Encroaching sea ice would therefore have limited their ability to reliably forage inshore. Indeed, extensive sea ice during glacial maxima negatively impacted other coastal benthic and intertidal species (Fraser et al., 2009; González-Wevar et al., 2018; Nikula et al., 2010), and is implicated in the extirpation of some Southern Ocean penguin lineages that depend on coastal ecosystems (Cole, Dutoit, et al., 2019; Cristofari et al., 2018; Trucchi et al., 2014).

The alternative hypothesis for the origin of blue-eyed shag taxa on the southern oceanic sub-Antarctic islands—that they speciated pre-LGM, and colonized their respective islands post-LGM—is not supported by the modern distribution of these taxa, which are endemic to their respective islands. This endemicity contrasts with patterns observed in king penguins, which also likely colonized many of the same islands following the LGM (e.g. Cristofari et al., 2018), but where putative source populations in 'refugia' outside the former extent of glacial sea ice still persist (e.g. Falkland/Malvinas Islands). There is no evidence that the geographic distribution of blue-eyed shag taxa belonging to the sub-Antarctic clade, as currently defined, was ever greater than it currently is. Thus, we argue that a post-LGM origin of these taxa is the most parsimonious explanation for the currently available data.

The phylogeographic patterns observed in the sub-Antarctic clade discussed above—comprising taxa that likely only became established since the LGM—contrast strongly with those observed in its sister clade, which includes blue-eyed shag taxa from the New Zealand region, including the Chatham, Bounty, Auckland and Campbell Islands. Node ages in this well-supported 'New Zealand clade' (PP = 0.85)—including *L. ranfurlyi*, *L. carunculatus*, *L. onslowi*, *L. stewarti*, *L. chalconotus*, *L. colensoi* and *L. campbelli*—are around four times older than those among taxa in its sister clade, with mean ages concentrated during the Early Pleistocene and 95% HPDs that, in most cases, do not overlap the Holocene (Figure 1; Table S1.3). As supported by our phylogeographic analyses, we suggest that members of the New Zealand clade descend from an earlier and independent wave of migration out of South America—during either the Late Pliocene or Early Pleistocene—followed by subsequent isolation and divergence on their respective islands.

It is possible that South Georgia, the South Orkney Islands, the Antarctic Peninsula, and Marion, Crozet, Kerguelen, Heard, and Macquarie Islands were all originally colonized by the same wave of dispersal that founded the taxa comprising the New Zealand clade, but that the resulting populations were repeatedly extirpated during glacial maxima later in the Pleistocene. The modern taxa comprising the New Zealand clade may thus represent relics of a formerly more widespread clade, surviving only because their breeding colonies are located at lower latitudes than the most northerly extent of sea ice

during glacial maxima (Figure 1). This scenario may explain why the Macquarie Island shag (*L. purpurascens*) is a relatively recent derivative within the sub-Antarctic clade rather than the New Zealand clade, despite close geographic proximity (~500 km) of Macquarie Island to New Zealand. Indeed, Macquarie Island was heavily glaciated and impacted by sea ice during glacial maxima (Fraser et al., 2009; Gersonde et al., 2005; Trucchi et al., 2014). This hypothesis of extirpation and re-colonization could be directly tested in the future using ancient DNA from pre-LGM sediments or shag bones excavated from beneath breeding colonies on these sub-Antarctic islands.

It is not clear, in any case, how blue-eyed shags managed to colonize remote island groups, separated by thousands of kilometres, across an expanse of empty ocean. Shag biology suggests a relatively low dispersal capacity—like other species in Phalacrocoracidae, *Leucocarbo* shags have a partially wettable plumage that decreases the layer of insulating air and reduces the energetic costs of diving (Gremillet et al., 2005; Cook & Leblanc, 2007). Blue-eyed shags would not be expected to withstand days or weeks at sea in cold Southern Ocean waters, although facultative hypothermia observed in these shags might enable some tolerance to near-freezing sea-water temperatures (Bevan et al., 1997). Flight performance in this group is also rather limited compared to other avian lineages (Pennycuick, 1989), in part due to their dense bones, which aid in diving. A several thousand-kilometre non-stop flight across the Southern Ocean would therefore seem unlikely, unless driven by some particularly strong and sustained westerly wind and current system. Furthermore, due to the depth of the Southern Ocean, access to benthic prey would be impossible during stopovers on the water surface, although blue-eyed shags are flexible enough to occasionally forage on pelagic fish species (Cook et al., 2013). Indeed, to the best of our knowledge, there is no evidence of any movements of blue-eyed shags of either sex over long distances between remote island groups (e.g. Marchant & Higgins, 1990; Weimerskirch et al., 1985). This absence contrasts with documented dispersal of shags over the shorter distances between the Auckland and Snares Islands in the New Zealand region, a distance of ~365 km (Miskelly, 2001a, 2001b). Based on patterns of dispersal in other seabirds, we hypothesize that females are more likely to disperse than males (e.g. Becker et al., 2008).

We suggest that both waves of blue-eyed shag dispersal from South America into the sub-Antarctic were likely facilitated by the ACC and westerly winds encircling Antarctica (Figure 1; Fraser et al., 2012). This dispersal is likely to be accidental, probably a small number of birds, part of a foraging flock, caught by one of the ferocious storms of the Southern Ocean, but lucky enough to survive and to find land. Dispersing blue-eyed shags may have followed the edge of receding sea-ice following glacial maxima. Such behaviour could have removed the necessity for non-stop overwater dispersal by providing dry areas to land and rest, while still being within range of oceanic islands. Alternatively, or complementarily, ice bergs calved from the Ronne Ice Shelf in Antarctica, which tend to proceed from the Weddell Sea past the Antarctic Peninsula and South Georgia (Ballantyne & Long, 2002; Wagner et al., 2017), may have provided similar stop-over points, allowing blue-eyed shags to raft or island-hop eastward from South America.

4.2 | Founder-event speciation

Our results suggest that many blue-eyed shag taxa arose through founder-event speciation (Figure 1, Appendix Table S1.4), whereby they descend from only a small number of founding individuals. Indeed, mitochondrial CR haplotype frequencies from several island blue-eyed shag species suggest that only a single mitochondrial lineage was represented among their respective founding individuals (Figure 2). Sampled individuals from *L. georgianus*, *L. purpurascens*, *L. nivalis*, *L. verrucosus*, *L. bransfieldensis*, *L. nivalis*, *L. chalconotus*, *L. stewarti*, *L. ranfurlyi*, *L. colensoi* and *L. campbelli* all possess either a single CR haplotype or a single high-frequency haplotype and several low-frequency satellite haplotypes (separated by one to three substitutions). In contrast, continental South American species—*L. atriceps* and *L. magellanicus*—show greater divergence in mitochondrial haplotypes, which are at more dispersed frequencies. Our evolutionary biogeographic reconstructions also strongly support a founder-speciation model (jump dispersal) over a range-expansion model for all major nodes of the *Leucocarbo* phylogeny—the 'jump' parameter is important in modelling founder-event speciation that often characterizes remote archipelagic species (Matzke, 2014; see also Ree & Sanmartin, 2018). In contrast, the best-supported alternative evolutionary scenario lacking such a jump parameter requires widespread ancestors at deeper nodes, which seems biogeographically implausible in this region (Appendix Figure S1.4, Table S1.4).

The Crozet Island shag (*L. melanogenis*) is a notable exception to the pattern of founder-event speciation described above. Originally described from Crozet Island, but also seemingly present on Marion Island (Alexander, 1928; Blyth, 1860; Crawford, 1952; Crawford et al., 2003; Holgersen, 1945; Moseley, 1879; Rand, 1954; Rand, 1956), *L. melanogenis* is paraphyletic in our analyses (Figure 1). Individuals from Marion Island all share a single mitochondrial CR haplotype, which is separated by one substitution from the most frequent *L. georgianicus* and *L. verrucosus* haplotypes (Figure 2). In contrast, all individuals from Crozet Island possess a single haplotype that is separated from the *L. melanogenis* Marion Island haplotype by at least four substitutions. These observations suggest that Crozet Island and Marion Island populations descend from independent founder events, and that the latter population may represent an undescribed taxon. This possibility is consistent with plumage differences observed between blue-eyed shags from those two islands (Rand, 1954).

Founder speciation represents a fascinating feature of archipelagic biogeography globally (Mendelson & Shaw, 2005; Shaw & Gillespie, 2016), and such phenomena may be heavily influenced by density-dependent processes (Shaw & Gillespie, 2016; Waters et al., 2013). While many of the best-known archipelagic radiations have been detected in tropical systems, which have been relatively sheltered from global climatic shifts, our study suggests that such founder-speciation processes may be important even in the vast Southern Ocean (Baird et al., 2021; Cole, Ksepka, et al., 2019; Trucchi et al., 2014), a system heavily impacted by geologically recent glacial cycles. Our blue-eyed shag results also add to increasing evidence for higher rates of diversification in higher latitudes (e.g.

Igea & Tanentzap, 2020; Rabosky et al., 2018; Sun et al., 2020) in contrast to the prevailing view of higher rates at low latitudes (e.g. Cardillo et al., 2005; Ricklefs, 2006).

4.3 | A unique natural laboratory

Intriguingly, the biogeography of blue-eyed shags exhibits a mixture of characteristics seen in both poorly and highly dispersive taxa—they are widely distributed, as expected for highly dispersive taxa, but also display high levels of endemism, as expected for less dispersive taxa (Baird et al., 2021; González-Wevar et al., 2017; González-Wevar et al., 2019; Rexer-Huber et al., 2019). Our results suggest that this combination results from unique aspects of shag biology coupled with dramatic climatic changes that occurred in the Southern Ocean throughout the Pleistocene. Specifically, we propose that Pleistocene glacial maxima repeatedly 'reset' blue-eyed shag speciation on many oceanic islands. While descendants of at least one earlier wave of dispersal survive in New Zealand and surrounding islands, taxa on South Georgia, the South Orkney Islands, the Antarctic Peninsula, and Marion, Crozet, Kerguelen, Heard, and Macquarie Islands, must have colonized those regions after each glacial maxima. However, more comprehensive population-level sampling and high-throughput sequencing of nuclear genetic markers will be needed to unequivocally determine whether the speciation of blue-eyed shags on these islands truly only dates to after the LGM, as we have proposed, rather than after a previous glacial maximum. In any case, stable climatic conditions during the Holocene, and now increasing Anthropocene temperatures, mean that the historical ice-driven cycles of blue-eyed shag extirpation and re-colonization that took place during the Pleistocene are now unlikely to be repeated. The future of these present-day populations in a changing world is unknown.

The unusual combination of traits, described above, makes blue-eyed shags unique among avian groups that breed in the Southern Ocean. Consequently, we exploited this powerful model system for studying speciation at high latitudes—recently isolated island populations of shags provide replicated windows into the early stages of divergence. We note that a recent field guide to seabirds (Harrison et al., 2021) depicts clear differences in adult breeding plumage and skin colouration (e.g. extent of white feathering on the cheek, gular colour, size and colour of the caruncula-tion above the bill) among the various island species, which were based on digital photographs (Peter Harrison pers. comm.). These are likely to be critical in specific-mate recognition and in many cases have likely arisen over relatively short timeframes (perhaps tens-of-thousands of years). Future research using genomic data may illuminate the origins and drivers of these and other pheno-typic differences, and further clarify the fine-scale ancestry and dispersal history of individual island taxa.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and scripts to reproduce the results of this study are available on Data Dryad: https://doi.org/10.5061/dryad.8kprr4xp9. Sequences have been uploaded to GenBank (see Appendix Tables S1.1–S1.2).

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BIOSKETCH

Nic Rawlence is a biologist who uses genetic tools to study evolutionary processes. His work is primarily focused on reconstructing the impacts of climate change and humans on ecosystems through time.

Author Contributions: NJR, JMW, HGS, CET and MK developed the study concept. NJR, ATS, JMW, HGS, KJM and MK designed the project and wrote the initial manuscript. TRC, C-AB, LJN, PGR, LC, PQ, JFM, NR and RAP collected and/or provided the samples. CET, TMK and MK generated the sequence data. ATS, LS, NJR, LD and MK generated the results. TRC, LJN, PGR, LC and RAP helped the design sampling and project directions. All authors contributed to the final manuscript.

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