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Bridging the Scotia Arc: Climate-Driven Shifts in Connectivity of the Freshwater Crustacean *Branchinecta gaini* in Sub-Antarctic and Antarctic Ecosystems

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ABSTRACT

Aim: To integrate the historical and contemporary connectivity of *Branchinecta gaini* (*B. gaini*), in order to better predict future distribution changes within its fragmented, dynamic and isolated habitat range.

Location: The study covers 20 locations of freshwater ecosystems across *B. gaini* distribution within the maritime Antarctic, sub-Antarctic South Georgia, Falkland/Malvinas Islands and southern South America (SSA).

Methods: We used two mitochondrial DNA loci and 7446 SNP markers to assess genetic diversity, population structure and connectivity of *B. gaini*. Additionally, we applied an ensemble ecological niche modelling (ENM) approach to project current and future species distributions under various climate scenarios.

Results: High genetic diversity was found in most sampled locations, with SSA exhibiting the greatest variation in terms of haplotype and nucleotide diversities. Antarctica exhibits short topologies with a limited number of shared haplotypes among its different regions. Overall, there is significant genetic and phylogeographic differentiation among biogeographic regions. Historical demographic analyses indicated population expansion in Antarctic regions but stability in SSA. Contemporary population structure analyses revealed six genetic clusters with limited gene flow and a clear pattern of isolation by distance. Ecological modelling suggested future habitat loss in the sub-Antarctic and potential expansion in Antarctic regions.

Main Conclusions: Our integration of historical and contemporary connectivity potentially provides a solid foundation for the development of conservation strategies, especially in fragile areas with dramatic changes projected. The strong genetic structuring and limited connectivity of *B. gaini* across its range highlight the need for region-specific conservation strategies. These findings emphasise the importance of integrating genetic and ecological approaches to predict species' responses to environmental change and guide conservation strategies for vulnerable Antarctic freshwater ecosystems.

1 | Introduction

Climatic gradients over geological time at different geographic scales and tempos have underpinned the composition and distribution of modern landscapes and their biotas (Norris et al. 2013; Turner 2013). Currently, polar and subpolar regions, both Arctic and Antarctic, show strong evidence of rapid climate change, amplifying the well-documented global trends and affecting terrestrial and freshwater ecosystems, communities and species (Convey 2011; Lee et al. 2017; Quayle et al. 2002, 2003; Spaulding et al. 2010). Maritime Antarctic freshwater habitats are among the fastest-changing environments on Earth (Peck 2005). In particular, the Antarctic Peninsula shows the most significant projected future changes in climate by the end of the current century (Lee et al. 2017). Climate change affects many aspects of ecosystem functions, but not all respond with the same sensitivity to different regional climate scenarios. Research on the resilience of organisms to environmental changes has primarily focused on temperature change, but other environmental factors, including humidity, precipitation, wind-flow patterns on land and ocean currents are also likely to be important (Peck 2005). The Antarctic environment is one of the few large-scale ecosystems worldwide where abiotic factors (e.g., moisture, temperature) are more important than biotic factors (e.g., competition, herbivory, predation) in shaping population structure (Convey 1996; Hogg et al. 2006). In this sense, polar freshwater bodies and their invertebrate fauna may act as early and sensitive detectors of environmental changes, where snow and ice cover variation markedly affects many key ecological variables (Quayle et al. 2002). Additionally, ecological and physicochemical conditions in freshwater environments in the maritime Antarctic can vary markedly over short distances (Butler 1999; Peck 2005). Understanding how multiple climate-related environmental parameters may limit species distributions is essential for predicting how each parameter will affect species and populations over both contemporary and evolutionary timescales.

The freshwater fauna of the maritime Antarctic (a region including the western Antarctic Peninsula and Scotia Arc archipelagos; Convey and Biersma 2024) and sub-Antarctic is a tiny fraction of regional diversity (Terauds et al. 2025). Over millions of years of isolation, this unique biota have evolved and radiated, at the same time evolving varying degrees of tolerance to multiple environmental stresses. As the climate cooled from the mid-Miocene to the Last Glacial Maximum (LGM) during the Quaternary, Antarctic and sub-Antarctic regions experienced multiple cycles of continental- or island-scale ice sheet expansion and contraction, which are widely assumed to have caused severe extinction, leaving a legacy of impoverished Antarctic and sub-Antarctic terrestrial and microbial diversity (Baird et al. 2021; Convey et al. 2020; Pointing et al. 2015; Tytgat et al. 2023). Recent molecular phylogeographic and classical biogeographic studies have overturned a long-held paradigm of complete wipe-out of pre-existing diversity. These studies suggest long-term persistence of perhaps the majority of Antarctica's extant terrestrial and freshwater biota, with estimated persistence ranging from hundreds of thousands to multi-million-year timescales (Baird et al. 2021, Collins et al. 2020, Collins et al. 2023, Convey et al. 2020 and the references therein, Verleyen et al. 2021). In a smaller number of instances, studies have proposed more recent post-glacial dispersal from lower latitudes (Biersma et al. 2020; van de Wouw et al. 2008) and a mixture of both mechanisms (Maturana et al. 2022). In this context, the dispersal capacity of populations in a fragmented and isolated landscape could represent an important evolutionary mechanism determining the structure of contemporary biodiversity.

Animal species commonly respond to climate change by moving towards more suitable regions. Range shift is thus a key element in species histories and is often accompanied by changes in how the genetic diversity is displayed across space and in the dynamics of species interaction within their communities (Hoffmann and Sgro 2011; Parmesan and Yohe 2003; Pauls et al. 2013). Range shifts differ from range expansions, as they involve range retraction at the trailing edge, and are also linked to biological invasions, as the migration of a species beyond their original distribution can impact the communities they invade. Examining intraspecific genetic diversity provides a valuable approach to understanding how past and present climate change has impacted species distribution ranges (Pauls et al. 2013). One of the predicted genetic consequences of range shifts is a reduction in neutral genetic diversity at the leading edge of the changing distribution, since stochastically only a part of the population's overall genetic variation will generally have moved into the newly colonised habitat (Cobben et al. 2011; Pauls et al. 2013). Importantly, this genetic diversity represents the surviving lineages and persisting alleles, while trailing-edge lineages and alleles are more likely to be lost. Thus, the leading edges of natural populations are especially relevant for the long-term conservation of genetic diversity and understanding of species' phylogenetic history and evolutionary potential (Hampe and Petit 2005; Hewitt 2000; Pauls et al. 2013).

Current climate change trends mirror albeit more at more rapid rates, those that occurred after the LGM when species expanded their ranges from ice-age refugia. Most phylogeographic studies provide information on how species reacted to climate change in the past, such as the routes and timeframes of (re)colonisation and identification of refugia. The identification of refugia, often associated with higher and unique

levels of genetic diversity, can also inform on the scale and tempo of past range shifts and help characterise the distribution of genetic diversity through space and time (Hewitt 1996). Therefore, comparison of colonisation of newly available habitats from refugia during interglacial periods with currently expanding range areas may give a means of assessing how long it takes to recover pre-disturbance levels of genetic diversity. This can provide essential insights into assessing species' responses to future climate change, for example how likely a species is to be able to reach projected future habitat under climate change conditions based on its past and present dispersal dynamics (Pauls et al. 2013). This is particularly important in a changing environment, where species are confined to fragmented landscapes and where movement between local populations can affect the persistence and dynamics of entire meta-populations. Models to quantify the potential impacts of 21st century climate change in Antarctica predict that new ice-free areas will emerge across the Antarctic continent, with more than 85% of this change concentrated in the northern Antarctic Peninsula. Moreover, the South Orkney Islands are projected to become completely ice-free, with global temperature rise beyond 2°C leading to a fourfold increase in ice-free area for this bioregion (Lee et al. 2017). Such projections will completely transform our view and understanding of the Antarctic physical environment, from the current intensely insular nature of Antarctic freshwater ecosystems to an increasing emergence of connected habitats for both terrestrial and freshwater biota, potentially leading to profound impacts on genetic and community structure.

Crustaceans are the most diverse and well-documented freshwater invertebrates in Antarctic and sub-Antarctic lakes, overall including representatives of the eight major crustacean orders (Dartnall 2017; Díaz et al. 2019). The most abundant and dominant crustacean species in freshwater habitats in maritime Antarctica are the anostracan *Branchinecta gaini* (*B. gaini*) (Daday 1910) and the copepod *Boeckella poppei* (Mrázek 1910). The Antarctic fairy shrimp, *B. gaini*, is the largest freshwater invertebrate in Antarctic habitats. It inhabits pools and lakes across three Antarctic Conservation Biogeographic Regions (Terauds and Lee 2016), the sub-Antarctic island of South Georgia, southern South America (SSA), including the southernmost portion of the Magellanic Sub-Antarctic ecoregion (MSA), and the oceanic cold temperate Falkland/Malvinas Islands (Hawes 2009; Rosenfeld et al. 2023). Lakes and pools in these regions show extreme seasonality. Smaller and shallower water bodies may freeze in some cases completely to their bases during winter, while larger water masses only freeze at the surface (Laybourn-Parry and Wadham 2014; Walton 2008). Additionally, some smaller water bodies can evaporate entirely as the summer season progresses. Anostracans are well known for their resilience to hostile and highly seasonal environments (Delekto 2003; Lahr 1997; Wharton 2002), and *B. gaini* is a common inhabitant of freshwater bodies across these regions, where maritime Antarctic winter air temperature regularly falls below −30°C for short periods, and monthly averages drop to c. −15°C (Pugh et al. 2002). Moreover, as with other members of its family, its eggs can survive the complete drying out of small pools. This element of the species' life history strategy is key to its success and survival in the extreme and variable Antarctic environment (Peck 2004).

In this study, we integrate historical biogeography, contemporary population genetics and ENM to assess how climate change has shaped and will continue to influence the distribution and genetic structure of *B. gaini*, a key species of Antarctic and sub-Antarctic freshwater habitats. By analysing mitochondrial and SNP markers, we evaluate patterns of genetic diversity, population connectivity and demographic history to infer past colonisation routes and potential refugia. We hypothesise that the current distribution and genetic structure of *B. gaini* reflect historical climate oscillations and are shaped primarily by abiotic environmental variables. Given that range shifts and genetic diversity restructuring are common responses to climate change, we employ an ENM approach to predict *B. gaini*'s distribution under current and future scenarios. This work addresses the urgent call to increase understanding of how biodiversity change is triggered by past and current climate change over time and space, especially in one of the most vulnerable—and under-researched—ecosystems on Earth.

2 | Materials and Methods

2.1 | Datasets for Molecular, Niche Modelling Analyses and Geographic Coverage

The molecular dataset used in this study was compiled from two different sources (1) specimens of *B. gaini* collected from freshwater lakes, ponds and small pools in 20 locations across three biogeographic provinces (Table S1, and Gañán 2023 dataset GBIF) and (2) retrieved sequences from *B. gaini* from additional locations in Antarctica, and *B. granulosa* from Argentinean Patagonia (Table S1). We decided to include these latter sequences since both species are distributed in SSA (but see Rogers et al. 2021), frequently misidentified (see Cohen 1992 for details and Pokorný et al. 2024 for further references) and have not accumulated enough genetic differentiation to consider them two separate species (Pokorný et al. 2024). It is important to notice that we only included genetically closest populations of *B. granulosa* that were in all species delimitation analyses performed by Pokorný et al. (2024) grouped as the same species as *B. gaini*. The occurrence dataset used in the ENM was also compiled from two different sources: (1) new occurrences from *B. gaini* collected during our sampling and (2) published occurrences collated from scientific literature reporting sampling or taxonomic revision of *B. gaini*. The three biogeographic provinces considered in both datasets include the following six regions (see Table S1): (1) SSA, including the Magellanic Subantarctic Ecoregion (Rozzi et al. 2012), Tierra del Fuego and the grassland ecoregion of Argentinean Patagonia (Olson et al. 2001), (2) the core sub-Antarctic island of South Georgia (SGI) including Bird Island and (3) the maritime Antarctic region (MA), including specifically the following regions (i) South Orkney Islands (SOI), (ii) South Shetland Islands (SSI), (iii) western Antarctic Peninsula (WAP) and (iv) northeast Antarctic Peninsula (NEAP). Notice that the Falkland/Malvinas Islands (FMI) were considered only for the occurrence dataset in ENM from published records since we were unable to collect *B. gaini* individuals for genetic analyses. All freshly collected specimens were preserved in a fridge in 95% ethanol. DNA

extractions were carried out using the DNA Blood and Tissue Kit (Qiagen, USA) with a modified protocol for small amounts of tissue Maturana et al. 2021. The quantity and integrity of DNA were measured using Qubit 4 (Thermo, USA).

2.2 | Environmental Data

We extracted 19 bioclimatic variables and the bioscd variable from the CHELSA database (www.chelsa-climate.org, Table S2), with a spatial resolution of approximately 30 arcseconds (~1 km) (Karger et al. 2017). These variables were clipped to the study area, which, in the case of Antarctica, corresponds to ice-free areas. The current ice-free layer was defined using the rock_outcrop_high_res_polygon (Burton-Johnson et al. 2016) from the Antarctic Digital Database (ADD version 7; http://www.add.scar.org). For future projections, we used ice-free area data provided by Lee et al. (2017). To assess multicollinearity among predictor variables, we calculated Pearson correlation coefficients and excluded variables with r-values > 0.75 to ensure the independence of the predictors (Supporting Information S2). The final set of variables included BIO1 (Annual Mean Temperature), BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO12 (annual precipitation), BIO15 (precipitation seasonality) and BIO SCD (snow cover days).

2.3 | DNA Sequences, SNP Calling and Filtering

To address historical and contemporary connectivity across the distribution of *B. gaini*, we conducted analyses using two datasets. For the historical perspective, we used partial fragments of two mitochondrial genes (*cox*1 and 16S rRNA), and for more recent genetic connectivity, we used the Reduce Representation Sequencing (RRS) technique to produce Single Nucleotide Polymorphisms (SNPs). For the historical perspective, we included samples from SSA ($n = 30$), SGI ($n = 31$), and MA ($n = 233$). For the more recent connectivity, we only included samples from SGI ($n = 24$) and MA ($n = 162$). Mitochondrial genes were amplified using PCR (Supporting Information S3). Amplicons were purified and sequenced in both directions by Macrogen Inc. (Santiago, Chile). Alignments were obtained using the standard algorithm of MUSCLE 5.1 (Edgar 2004) implemented in Geneious R10 (https://www.geneious.com). Forward and reverse sequences were manually examined using Phred scores to ensure all sequenced bases matched and were of good quality. For RRS, samples were paired-end sequenced through a genotyping-by-sequencing (GBS) method at the Biotechnology Center in the University of Wisconsin using, after optimisation, the PstI/MspI restriction enzymes. Libraries were prepared using a HiSeq2000 (Illumina, USA) platform. All samples have sequences of a single length (151 bp). After enzyme digestion, it was linked to a barcode adaptor to recognise it *in silico* and libraries were prepared using a HiSeq2000 (Illumina, USA) platform. Reads were visualised in FastQC 0.10.1 for quality checking with a minimum coverage of 25X. SNP calling was carried out with the pipeline Universal Network-Enabled Analysis Kit (UNEAK) in Tassel v. 3 (Lu et al. 2013). We used a minor allele frequency of 0.05, a minimum proportion of sites present of 0.7 and a site minimum call rate of 0.75 to ensure that at least 75% of the individuals in each SNP were covered for at least one tag. After filtering, we estimated Hardy-Weinberg equilibrium (HWE) deviations per locus and per population with Arlequin 3.5.2.2 (Excoffier and Lischer 2010) using 10,000 permutations. p-values were corrected with a false discovery rate (FDR) correction (q-value = 0.05), and SNPs that appeared in HW disequilibrium in at least 60% of the populations were removed from the dataset. This approach ensures the reliability of our inferences regarding population structure, avoiding sequencing artefacts, in alignment with recommended practices for population genetics in non-model organisms (Pearman et al. 2022).

To retain only neutral markers, we used two population differentiation analyses to identify SNPs potentially under diversifying selection. These SNPs were eliminated from the final dataset. The first analysis was performed using the pcadapt v.4.3.3 (Luu et al. 2017) R package. This approach uses a Principal Component Analysis (PCA) to detect population structure. Then, each SNP is regressed at the principal components (PCs) retained. Here, 10 PCs were retained based on their eigenvalues (Cattell 1966). We applied a statistical test to the PCA when regressing SNPs with the PCs, and a cut-off of q-value = 0.05 was selected to assign the outliers. This analysis is not impacted by admixed individuals because pcadapt does not require grouping individuals into populations (Luu et al. 2017). Second, we used an FST outlier approach implemented in Bayescan 2.1 (Foll and Gaggiotti 2008), which uses a Bayesian method to estimate the probability of each locus being under the influence of selection. Considering that such loci tend to be highly differentiated and exacerbate the genetic structure, those identified were not considered for analyses. A total of five separate runs were performed with 500,000 iterations, a 10% burn-in period and a prior odds of 1000 were used. To avoid the occurrence of false positives using both approaches, an FDR correction of q-value = 0.05 was applied. Outliers detected by either or both approaches were eliminated (filtered) from the final dataset, with the aim of highlighting demographic isolation and assessing connectivity patterns. After filtering, a final dataset of 7446 non-outlier SNPs genotyped from 186 individuals was obtained.

2.4 | Historical Genetic Diversity, Structure and Genealogical Reconstruction

Genetic polymorphism levels were determined for both *cox*1 and 16S loci using standard diversity indices, including number of haplotypes (K), number of segregation sites (S), haplotype diversity (H), average number of pairwise differences (Π) and nucleotide diversity (π), using DnaSP v5.10.01 (Librado and Rozas 2009). Genealogical relationships were reconstructed using median-joining haplotype networks in PopART (http://popart.otago.ac.nz). We estimated levels of genetic differentiation for *cox*1 among the six sampled regions through mean pairwise differences (Φ_{ST}, using Kimura-2P genetic distances) and haplotype frequencies (F_{ST}) in ARLEQUIN v3.5.2.2 (Excoffier and Lischer 2010), using 10,000 permutations to assess significance. To test statistical significance of differentiation, we performed a permutation test (20,000 iterations). The p-value for pairwise Φ_{ST} and F_{ST} between populations was corrected using the false discovery rate correction (FDR; Benjamini et al. 2005).

2.5 | Inference of Historical Events on *B. gaini* Population Dynamics

We estimated population dynamics through time for each demographic unit using the Bayesian Skyline Plot (BSP) method implemented in BEAST v2.4.7, based on the *cox*1 marker. We used a population substitution rate of tenfold the evolutionary rate (18% per million years) to estimate the time of expansion of each demographic unit, as this more accurately reflects the rate at which new haplotypes appear (Ho et al. 2008). This better accounts for the time-dependence of molecular evolution at the population level, brings divergence estimates closer to the present and avoids overestimation of recent splits in intraspecific lineages (Ho et al. 2008, 2011). As suggested by these authors, molecular studies at the population level display much higher substitution rates (i.e., within clades) than the mutation rates (i.e., fixed mutations among clades) inferred from phylogenetic analyses. The two independent MCMC calculations were run for 30×10^6 generations (sampled every 1000 iterations), discarding the first 10% of parameter values as burn-in. The convergence of runs was confirmed with Tracer v1.6.

To evaluate the long-term persistence of Antarctic and sub-Antarctic populations of *B. gaini*, we used a DIYABC Random Forest v1.0 (Collin et al. 2021), a supervised machine learning method implemented in an approximate Bayesian computation (ABC) simulation-based method. The ABC-RF approach enables efficient discrimination among scenarios and estimation of the posterior probability of the best scenarios with a lower computation burden. Two different models were built to examine extinction or refugia hypotheses using *cox*1 analyses (for more details, see Supporting Information S4). We first conducted the pre-evaluation scenario and estimation of historical, demographic and mutational posterior distribution to check whether the different proposed models and priors were approximated the target (Cornuet et al. 2010). Additionally, we compared the posterior probabilities of two contrasting scenarios with common priors distributions of effective population sizes (N, N_b), times (t_n) given by the starting and ending dates of the LGM and mutation rates (μ) from closely related taxa (see Supporting Information S5). In the first scenario, we proposed the extinction of populations located south of the Antarctic Polar Front (APF), with subsequent post-glacial recolonisation of the MA and core sub-Antarctic regions from SSA. In the second scenario 2, we proposed an in situ Antarctic refuge or refugees providing intra-regional source(s) of postglacial recolonisation within the MA and core sub-Antarctic South Georgia (see Supporting Information S4).

2.6 | Contemporary Population Structure and Gene Flow

Pairwise F_{ST} comparisons among locations were calculated using Genodive v.3.05 (Meirmans 2020), and significance levels were estimated using 10,000 permutations. Discriminant analysis of principal components (DAPC), in the R package adegenet (Jombart et al. 2010), was used to identify genetic clusters, using the information about the geographical origin of each individual. The function optim.a.score() was used to estimate the optimal number of PCs to retain for the DAPC; here, 9 PCs were retained. The optimal number of clusters for DAPC was estimated with *k*-means clustering, using the Bayesian information criterion (BIC) in the function *find.clusters* using 100,000 iterations, 9 PCs and four discriminant functions. Using Structure 2.3.4 (Pritchard et al. 2000), we evaluated the probability of the assignment of a given individual to a genetic cluster using 10 replicate runs performed in parallel using Strauto (Chhatre and Emerson 2017) with 500,000 MCMC and 10% burn-in. The optimal *k*-values for Structure were estimated using Evanno's method (Evanno et al. 2005) and $\ln(\Pr(X|K))$ values, to identify the k value for which $\Pr(K=k)$ is highest (Pritchard et al. 2000). We considered different *k*-values (e.g., different clustering results) with biological meaning for our discussion (Meirmans 2015; Porras-Hurtado et al. 2013).

We estimated contemporary migration rates between clusters (identified previously with structure analyses) using BA3-SNPs (Mussmann et al. 2019), a modified version of the software BayesAss 3.04 (Wilson and Rannala 2003) for next-generation sequence data. For these estimations, we used 500,000 iterations and a 10% burn-in.

2.7 | Geographic and Environmental Contributions to *B. gaini*'s Genetic Structure

Geographic distance between *B. gaini* populations was calculated using GPS coordinates (latitude and longitude) converted into kilometres with the earth.dist function from the Fossil package (v0.4.0). Environmental variables for each population location were used to compute pairwise Euclidean distances with the *vegdist* function from the Vegan package (v2.6–8). All distance matrices, including the genetic distance matrix, were standardised using the *scale* function to ensure comparability across variables. To evaluate the relative contributions of geographic and environmental factors to contemporary genetic differentiation in *B. gaini*, a Multivariate Matrix Regression with Randomization analysis (MMRR) was performed using the *lgrMMRR* function from the PopGenReport package with 10,000 permutations (Wang et al. 2013). This method allowed us to test the significance and effect size of geographic and environmental predictors on genetic distance. Additionally, pairwise correlations between the genetic distance matrix and each explanatory distance matrix (geographic and environmental) were analysed using Mantel tests implemented in the Vegan package. Mantel tests were performed with Pearson correlation and 10,000 permutations to assess the significance of these relationships. All statistical analyses and visualisations were conducted in R version 4.2.2 (R Core Team 2024).

2.8 | Ecological Niche Modelling

The occurrence dataset comprised our field observations and published records, totalling 56 occurrences of the species across the cold-temperate Falkland/Malvinas Islands, the sub-Antarctic island of South Georgia, the Magellanic sub-Antarctic ecoregion (MSA) and the maritime Antarctic regions (see Table S1). To minimise spatial bias, the dataset was pre-filtered to retain only one occurrence per square kilometre. An ensemble modelling approach was employed using the biomod2 package (Thuiller et al. 2009), implemented in R v. 4.2.3 (R Core Team 2024). The modelling techniques used to predict the distribution of *B. gaini* across the study area included RF, ANN, CTA, GBM, FDA, MARS,

GLM, MAXENT, MAXNET and SER. Model selection was based on True Skill Statistics (TSS ≥ 0.6) (Allouche et al. 2006), Receiver Operating Characteristic (ROC ≥ 0.8) index and the Boyce index (Boyce et al. 2002). The variable importance function assessed each predictor's impact, with higher values signifying greater significance, although interactions were not considered.

To assess potential changes of *B. gaini* distributions due to climate change, projections were created for current and future periods. Specifically, we modelled for the periods 2041–2070 and 2070–2100. Two Shared Socioeconomic Pathways, SSP3-7.0 and SSP5-8.5, were employed to represent different emissions scenarios: a middle-emission, sustainability-focused future and a high-emission, fossil-fuel-intensive future, respectively (IPCC 2021). This enabled comparative analysis of species distribution expansion or contraction under varying climate conditions. QGIS Version 3.40.7 (QGIS Geographic Information System, 2024. QGIS Geographic Information System. Open Source Geospatial Foundation Project http://qgis.osgeo.org) was used to visualise the results, producing distribution maps for the terrestrial environment. These maps show species presence probability, with more intense colours indicating areas of higher likelihood. Binary projections identified suitable habitat areas (binary value = 1) and unsuitable areas (binary value = 0).

3 | Results

3.1 | Contrasting Historical Diversity in *B. gaini* Across Biogeographic Regions

We collected samples from 20 freshwater sites across the species' reported distribution in MA, SGI and SSA (Figure 1; for more detail, see Table S1 and Gañán 2023). We obtained 295 sequences for *cox*1 and 101 for 16S rRNA of 673 and 411 bp, respectively, with no stop codons and no indels. For the *cox*1 dataset (Table 1), levels of haplotype diversity were high for most of the sampling locations ($Hd_{SSA} = 0.94$, $Hd_{SGI} = 0.58$ and $Hd_{MA} = 0.93$). The highest genetic diversity, in terms of nucleotide and haplotype diversity, was for SSA (Table 1). Except for NEAP, localities within MA displayed similar values of genetic diversity. The *cox*1 median-joining network identified

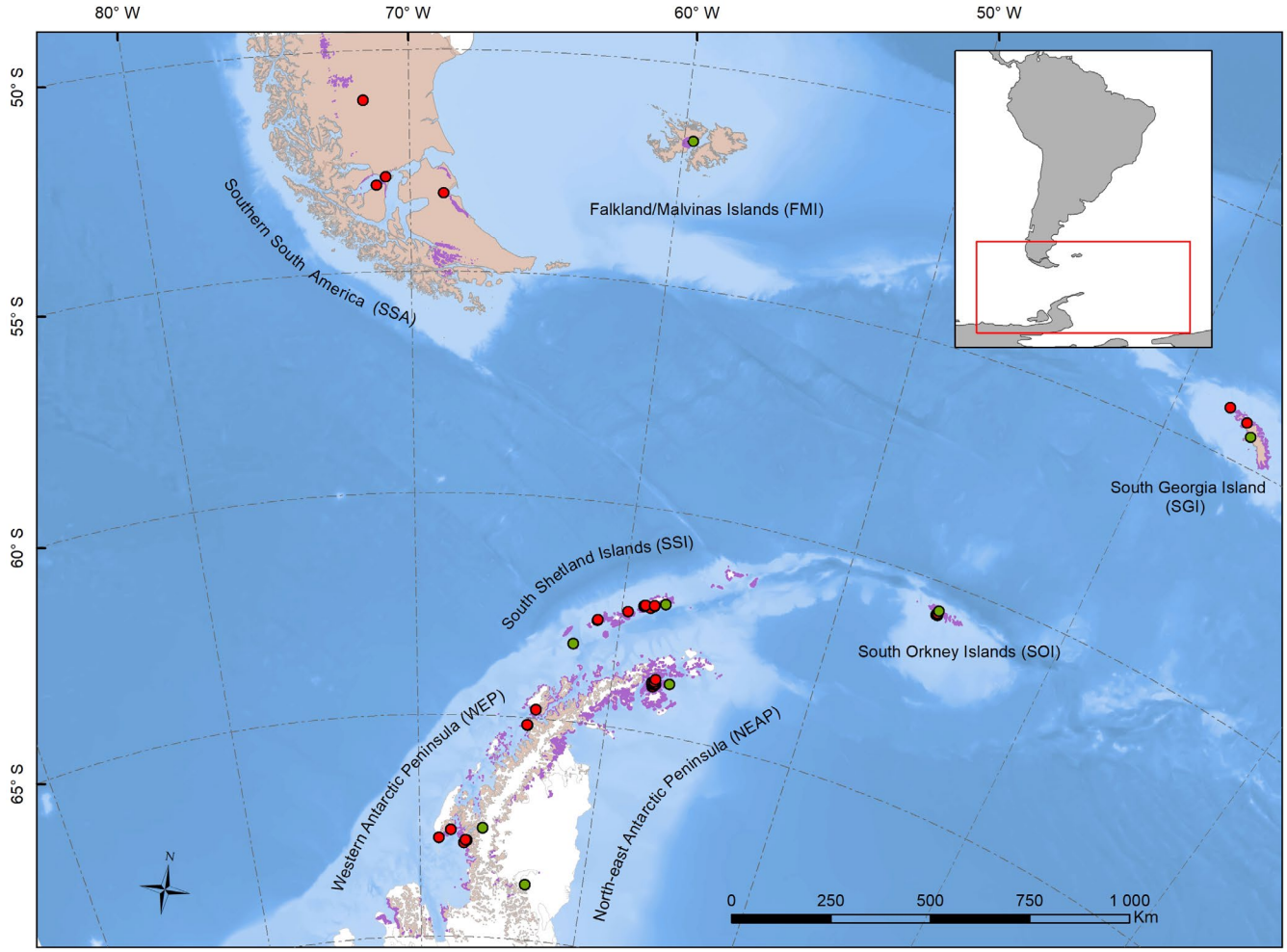

FIGURE 1 | Distribution map of *Branchinecta gaini*. Circles correspond to records of occurrence across their distribution in SSA, the cold-temperate island of the Falkland/Malvinas, the sub-Antarctic Island of South Georgia (SGI) and the Maritime Antarctic (MA). The records were retrieved from published literature (green dots) and our sampling (red dots). Purple area corresponds to the current habitat suitability predicted by the model. This map was created using QGIS v.3.40.7 'Bratislava'. Base layers: Coastline_high_res_polygon, Rock_outcrop_high_res_polygon available from the Scientific Committee for Antarctic Research (SCAR) Antarctic Digital Database (ADD Version 7; http://www.add.scar.org). These data are licensed according to Creative Commons CC-By—data are free to use, modify and redistribute.

TABLE 1 | Diversity indices and neutrality tests for cox1 of *Branchinecta gaini* sampled across three biogeographic provinces.

Biogeographic provinces	Regions	Code	*n*	S	Π	Hd	*K*	π	Tajima's D	Fu and Fs
Southern South America	Tierra del Fuego & Brunswick Grassland (Argentinean Patagonia)	SSA	30	22	4.572	0.938	15	0.007	−0.621	−3.867
Sub-Antarctic islands	South Georgia	SGI	31	5	1.699	0.574	4	0.003	0.967	1.833
Antarctica	South Orkney Island	SOI	50	8	2.167	0.753	8	0.003	0.583	−0.139
	South Shetland Island	SSI	58	16	2.057	0.902	17	0.003	−1.224	−8.801
	West Antarctic Peninsula	WAP	65	20	2.297	0.906	23	0.003	−1.393	−15.891*
	Nort-east Antarctic Peninsula	NEAP	60	20	1.160	0.747	18	0.001	−2.263*	−16.853*
	Maritime Antarctica (SOI, SSI, WAP, NEAP)	MA	233	48	2.379	0.932	58	0.004	−2.072*	−69.169*

Abbreviations: Π, mean number of pairwise differences; π, nucleotide diversity; Hd, haplotype diversity; *K*, number of haplotypes; *n*, number of sequences; S, segregation sites.
*$p < 0.05$.

77 distinct haplotypes, 71 of which were private from each region (Figure 2). The network displays distinct haplogroups with only six shared haplotypes exclusively within MA (SOI, SSI, NEAP, WAP). SSA presented the most extended genealogy, characterised by low frequency haplotypes. In contrast, all regions sampled across MA exhibited a more contracted network, with fewer mutation steps among haplotypes (Figure 2). Within MA, the sampling regions display similar genetic diversity indices and genealogies (insets Figure 2); however, only the Antarctic Peninsula (both WAP and NEAP) exhibited significant neutrality indices (Table 1). The 16S rRNA locus had lower global genetic diversity (Supporting Information S6), with 12 distinct haplotypes, two of which were shared among the different sampled locations except for SSA, which exhibited the greatest diversity (Supporting Information S7). Overall, *B. gaini* displayed strong genetic and phylogeographic structure across sampled areas, with all Φ_{ST} and F_{ST} values being highly significant (Table S8).

3.2 | Historical Biogeographical Events

Bayesian Skyline Plots analyses provided historical population dynamics patterns for MA (SOI, NEAP, SSI, WAP), SGI, and SSA. For MA and SGI, we observed signals of postglacial past demographic changes (population expansion), in contrast with SSA, in which we did not detect population expansion (Figure 3). We compared the posterior probabilities of two historical scenarios, reflecting either the extinction of Antarctic populations, with subsequent postglacial colonisation from SSA (Scenario 1), or the persistence of Antarctic populations in situ refugia (Scenario 2) and intraregional recolonisation within MA. Our results indicate that Scenario 1 was the most likely scenario with a high posterior probability (pp = 0.85, see Supporting Information S9).

3.3 | Contemporary Population Diversity and Structure

We obtained a total of 8751 SNPs from 186 individuals of *B. gaini* across SGI and MA from the SNP calling, after applying filters of minimum count (0.75), minimum proportion of sites present (0.7), minor allele frequency (0.01) and Hardy-Weinberg Equilibrium (HWE). Between Bayescan and pcadapt, we detected 1305 SNPs showing strong or very strong evidence of being potentially under diversifying selection and, in consequence, were removed from the dataset. Finally, 7446 putatively neutral non-targeted SNPs were used to evaluate the spatial genetic structure and contemporary gene flow between SGI and MA sampling locations.

In accordance with the results from the mDNA sequence data, significant geographic structure was present between the different sampling locations (Table S1). With similar levels of genetic diversity (Table 2), three different approaches based on individuals (Structure), allele frequency (F_{ST}) and sampled locations (DAPC), consistently identified six well-defined clusters: Cluster 1 for SGI, Cluster 2 for SOI (from HEY to EMR), Cluster 3 for the SSI King George Island and Robert Island (from WUJ to CPP), Cluster 4 for SSI Livingston Island (LVG), Cluster 5 for NEAP (RSS) and Cluster 6 for the southern part of WAP (from RTR to AVN). It is noteworthy to mention that the Structure software detected an optimal number of groups of $k = 6$ (Evanno's method and DeltaK), in agreement with DAPC, F_{ST} pattern and geographic distribution criteria. There was almost no admixture detected within the 13 populations sampled across SGI and MA. Locations showing some evidence of admixture were Heywood Lake (HEY) in SOI and lakes from King George Island and Robert Island (WUJ, FLD, COPP) (Figure 4c). The populations of SGI, NEAP, LVG and SAP appear as isolated groups with almost no signal of admixture.

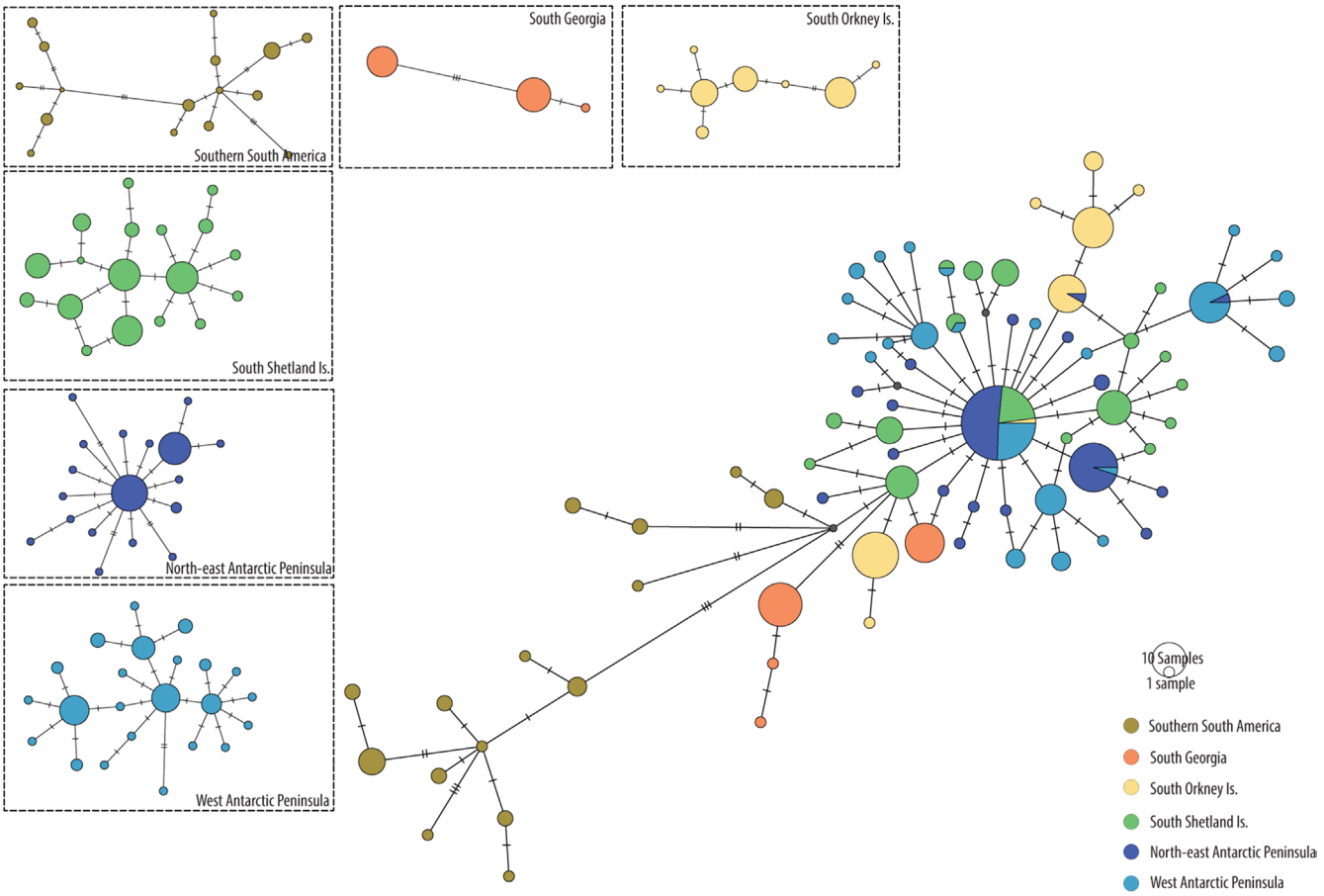

FIGURE 2 | Haplotype network for *Branchinecta gaini* based on 294 mtDNA *cox1* sequences spanning the species' distribution. A neighbour-joining network illustrating the distribution of haplotypes across lakes in SSA, sub-Antarctic South Georgia and within maritime Antarctica. Circle sizes are proportional to haplotype frequency. The length of the connectors is proportional to the number of mutational steps. Locations from the different geographic regions are indicated on Figure 1.

3.4 | Gene Flow

Considering the results described above, the dataset was subdivided into six genetic groups for gene flow estimations: (i) SGI, (ii) all lakes from SOI, (iii) one SSI cluster containing lakes from Fildes Peninsula and Thomas Point (KGI) and Coppermine Peninsula, Robert Island, (iv) a second SSI cluster from Livingston Island (LVG), (v) James Ross Island, NEAP and (vi) all lakes from the southern part of WAP (Figure 4b). Very low levels of contemporary gene flow between these groups were estimated by BayesAss. Less than 1% of individuals in each population correspond to contemporary migrants derived from other regions (Figure 4b), with most contemporary gene flow occurring within each cluster rather than between them (Figure 4b).

3.5 | Environmental Variables Modulating Genetic Distance

The MMRR regression-based model revealed a significant positive relationship between geographic and genetic distance ($\beta D = 0.73$, $p < 0.001$). Conversely, no significant association was found between environmental and genetic distance ($\beta E = -0.16$, $p > 0.05$). While the overall MMRR model, incorporating both predictors, was significant ($p < 0.001$), it explained only 32% of the genetic variation. Consistently, the correlation-based Mantel test supported these findings, revealing a moderate but significant correlation between *B. gaini* genetic distance and geographic distance confirmed ($r = 0.43$, $p = 0.004$, Figure 5), whereas no correlation was detected between genetic and environmental distances ($p = 0.750$, Figure 5).

3.6 | Ecological Niche Modelling

The ENM showed high values for the ROC (0.97), Boyce (0.80) and TSS (0.85) indices, indicating the robustness of the model for predicting the distribution of *B. gaini*. Of the six macroenvironmental variables included in the model, the maximum temperature of the warmest month (BIO5) contributed most to the ENM (43%), followed by snow cover days (BIO SCD, 24%) and annual precipitation (BIO12, 15%). Together, these three variables explained 81.4% of *B. gaini*'s distribution (Supporting Information S10).

In SSA, the model suggests *B. gaini* may occur between 51° S and 53° S in areas north of Torres del Paine National Park, west of Punta Arenas, in Yendegaia National Park (within the RBCH), east of Hoste Island and at ~54 to 55° S on South Georgia. In Antarctica, suitable habitats were projected at multiple locations

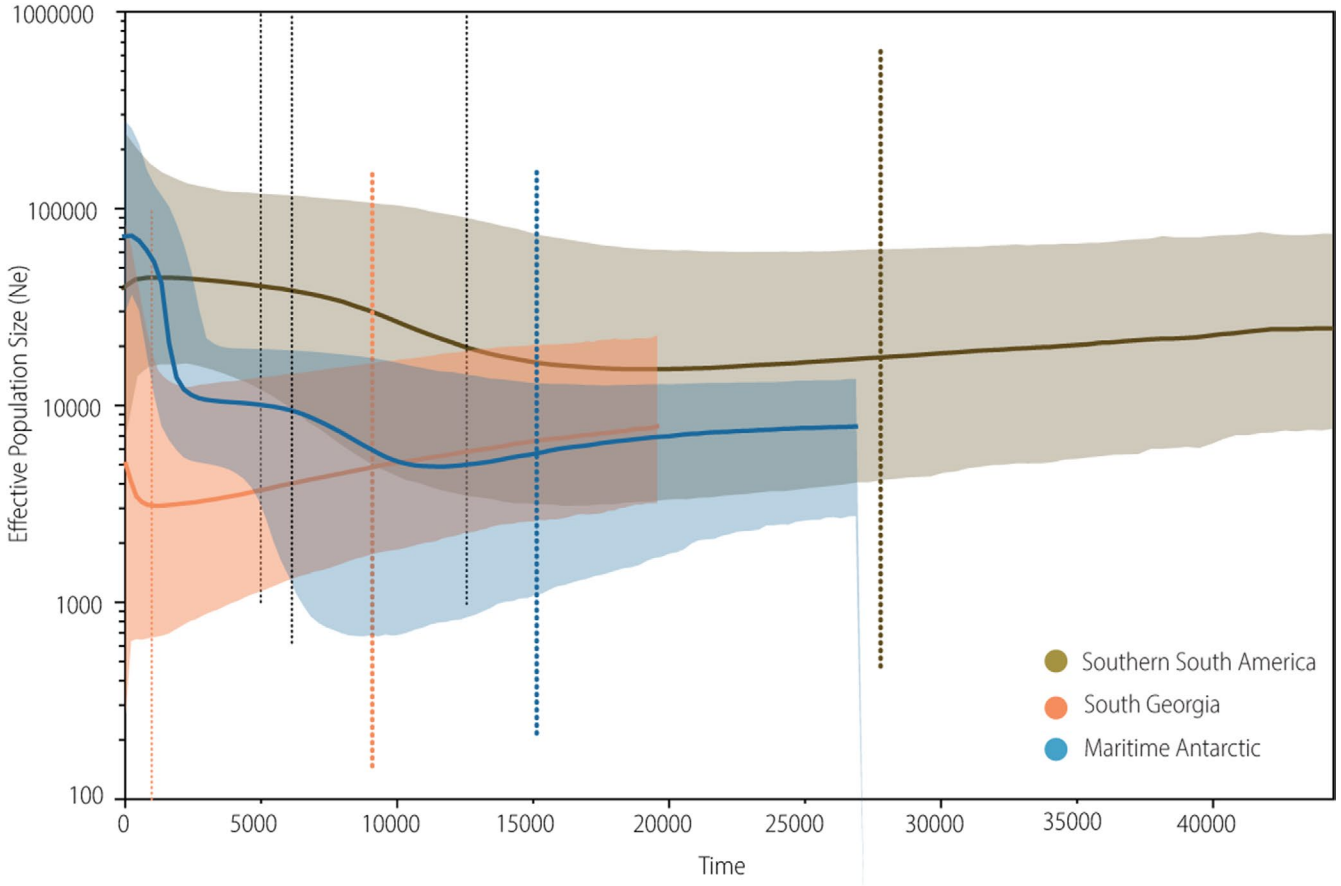

FIGURE 3 | Historical demographic trends of the effective population size (Ne) were constructed using a Bayesian skyline plot approach based on Cytochrome oxidase subunit I (*cox*1) haplotypes of *Branchinecta gaini*. The *y*-axis is the product of effective population size (Ne) and generation length on a log scale, while the *x*-axis is the time before the present. The median estimate and 95% highest probability density (HPD) limits. The thin dashed line represents the time for the expansion in the population.

TABLE 2 | Genetic Diversity for SNP-GBS of *Branchinecta gaini*.

Biogeographic Regions	Code	Pop	*N*	Al	H_o	He	G_{is}
Sub-Antarctic islands	SGI	SGB	24	1.335	0.177	0.205	0.14
Antarctica	SOI	Heywood Lake (HEY)	8	1.348	0.211	0.222	0.049
		Spyrogira Lake (SPR)	16	1.256	0.15	0.155	0.028
		Emerald Lake (EMR)	15	1.299	0.165	0.181	0.086
		Twisted Lake (TWS)	6	1.298	0.183	0.194	0.058
	SSI	Wukja Lake (WUJ)	7	1.267	0.173	0.169	−0.021
		Fildes (FLD)	10	1.318	0.13	0.204	0.362
		Coppermine (CPP)	12	1.416	0.224	0.257	0.128
		Somer Lake (LVG)	24	1.323	0.188	0.199	0.052
	NEAP	James Ross Island (RSS)	26	1.235	0.147	0.145	−0.01
	WAP	Rothera Lake (RTR)	14	1.271	0.161	0.167	0.031
		Lagotellerie (LGT)	8	1.188	0.126	0.122	−0.039
		Avian (AVN)	16	1.291	0.172	0.184	0.063

Note: This table shows the acronyms for each location, the number of alleles corrected after rarefaction (Ar), expected heterozygosity (H_e), observed heterozygosity (H_o) and inbreeding coefficient (Gis).

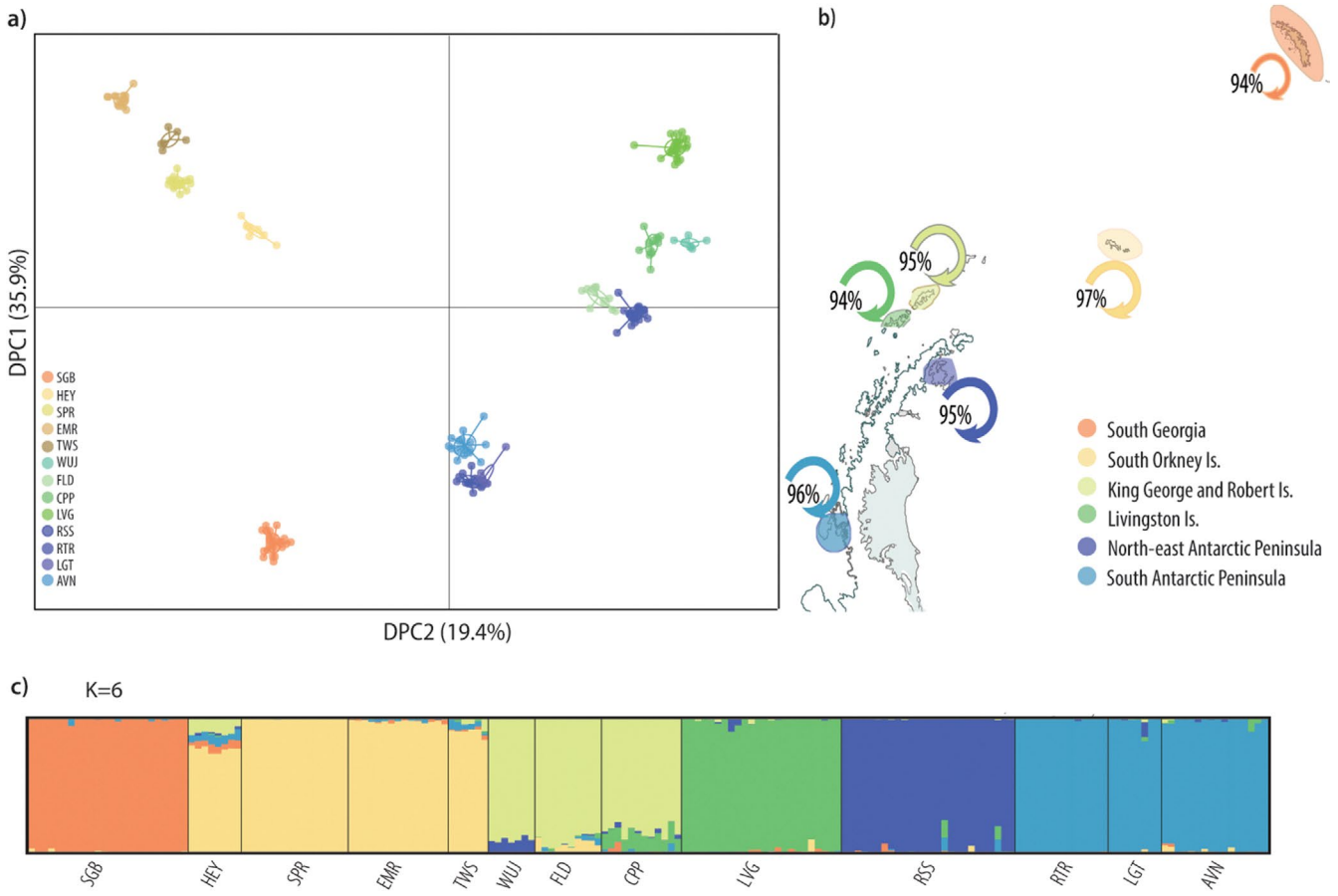

FIGURE 4 | Genetic structure of neutral SNP loci of *Branchinecta gaini* along the Scotia Arc (sub-Antarctic South Georgia and Maritime Antarctica). (a) The scatter plot of DAPC showing the first two axes, (b) gene flow estimations from BayeAss, considering six clusters (values below 4% are not shown). Arrow directions indicate the proportion of local recruitment, and (c) the structure bar plots represent population structure with optima $k = 6$. Colours in each panel represent the assignment of individuals to each genetic cluster. Single bars with < 1 colour indicate an admixture of that particular individual (i.e., sharing of genetic ancestry across more than one genetic cluster).

from 61.0° S to 71.0° S, including on Elephant Island, various parts of the South Shetland Islands, D'Urville and Joinville Islands and in ice-free areas east of the Trinity Peninsula (Oscar and Foin coasts). In the western Antarctic Peninsula, potential occurrence locations include ice-free parts of Davis, Brabant and Anvers Islands and farther south, on Renaud, Mitre and Adelaide Islands, the Fallieres Coast and Alexander Island (see Figure 6). Notably, *B. gaini* is currently positively confirmed to occur in only 8% of the total modelled suitable area.

For both time intervals (2040–2070 and 2070–2100), in SSA the models predicted contrasting scenarios for suitable habitats compared to the current potential distribution. Habitat loss was projected east of Tierra del Fuego, in Yendegaia National Park, on Hoste Island and north of South Georgia Island under both SSP scenarios (Figure 6). While the sub-Antarctic shows a decrease in suitable habitat for *B. gaini* across both periods and SSP scenarios, with an approximate 50% loss in the 2040–2070 period and a 75%–83% loss in the 2070–2100 period for SSP3-7.0 and SSP5-8.5 scenarios, respectively (Supporting Information S11, and more detail see Table 3). Conversely, in MA, both SSP scenarios predicted a slight increase across all areas currently inhabited by *B. gaini*, with emphasis on the eastern Antarctic Peninsula (Figure 6). In particular, suitable habitat areas for *B. gaini* increase under both SSP scenarios for MA with an increase of 27%–30% in the first period and 36%–39% in the second (Supporting Information S11, and for more detail see Table 3).

4 | Discussion

Freshwater landscapes include considerable variation in habitat complexity and physical connectivity that distinguishes them from terrestrial ecosystems (Grummer et al. 2019). Understanding the intrinsic migratory capacities of organisms across different timescales, along with the environmental variables influencing this process, is required to understand how connectivity is shaped in aquatic species. These intrinsic and external factors are essential for predicting how environmental changes will impact freshwater invertebrates and their evolutionary potential. In this study, we used indirect approaches to evaluate past and current population connectivity, including historical models and landscape genomics, together with projections of biological colonisation of new ice-free areas. This comprehensive framework provides novel insights into the complexity of potential range shifts triggered by contemporary climate change in the anostracan fairy shrimp *B. gaini* across its southern South American to the southern maritime Antarctic range.

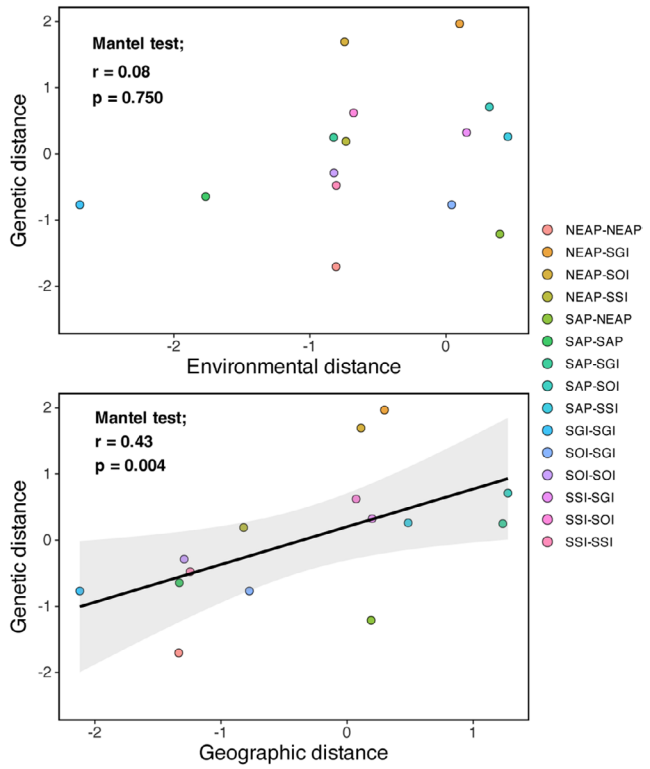

FIGURE 5 | Scatter plots showing the relationships between environmental or geographic distances and genetic distance (F_{ST}) of *B. gaini* populations based on Mantel test results.

4.1 | Historical Biogeography and Population Dynamics

Overall, our analyses demonstrate that the historical connection among the three biogeographic provinces considered—the maritime Antarctic, core sub-Antarctic South Georgia and SSA—was restricted, supporting their being discrete evolutionary units. Even within the Antarctic provinces, we observed a very structured genetic diversity, with only a very limited number of haplotypes shared among the different sampling locations. Moreover, based on past demographic changes, haplotype networks and nucleotidic diversity, our data consistently demonstrated that SSA harbours the oldest population of *B. gaini* across its sampling distribution. These results support the recently published article of Pokorný et al. (2024), in which they dated the separation of *B. gaini* from its sister species *B. granulosa* from northern Argentinean Patagonia between 17 and 50 ka BP. Overall, gathering all the available evidence and previously hypothesised colonisation routes and origins (Hawes 2009; Hodgson et al. 2013), our study strongly supports a South American origin of Antarctic populations of *B. gaini*, during the onset of the last deglaciation process at ca 7000–3000 BYP. Additionally, past demographic changes and the evaluation of possible colonisation scenarios supported the hypothesis that any previous Antarctic populations may have become extinct during the LGM (Baird et al. 2021), with current genetic diversity resulting from postglacial (re)colonisation from a less impacted region of SSA. Alternatively, a third scenario that we did not test and cannot rule out is that the Antarctic populations of *Branchinecta gaini* originated from colonisation(s) event(s) from South America from the outset, without a prior presence in Antarctic regions. To test this third hypothesis, it would require fossil record evidence dated prior to the LGM, at least from the Pleistocene. Currently, there are only published records of *Branchinecta* eggs in the stratigraphic record in maritime Antarctica from the Holocene at ~5000 years ago (Björck et al. 1996; Jones et al. 2000). The lack of an older fossil record does not allow us to distinguish between the scenario of extinction and recolonisation proposed here and this third alternative hypothesis.

Patterns of strong genetic structure, even at a small scale within MA, is consistent with previous analyses in *B. gaini* (Pokorný et al. 2024), and have also been reported within freshwater ecosystems for the copepod *Boeckella poppei* (Centropagidae), the winged Antarctic midge *Parochlus steinenii* (Chironomidae) (Maturana et al. 2022, 2024) and diatoms (Verleyen et al. 2021). Furthermore, evidence of local extinction of most Antarctic populations during LGM and subsequent population expansion following rare colonisation event(s) from SSA was also suggested for freshwater copepods (Maturana et al. 2022).

4.2 | Contrasting Potential Colonisation and Contemporary Gene Flow

Spatial genetic differentiation remains the rule at a small geographic scale and a more recent temporal scale. The landscape genomic analyses showed the differentiation of at least six regional groups of *B. gaini* in SGI and MA. The limited recent rates of effective gene flow across the species' distribution, supported by minimal observed admixture, have shaped this high level of genetic differentiation. These results have implications for understanding the consequences of dispersal limitations in Antarctic freshwater species, suggesting they may face difficulties adapting to and dispersing in a constantly fluctuating landscape with rapid environmental changes, potentially leading to local extinctions.

4.3 | Isolation by Distance Drives Genetic Structure in *B. gaini*

Our results indicate that IBD is the primary driver of genetic structure in *B. gaini* across its distributional range, indicating that geographic constraints on dispersal could shape genetic differentiation more strongly than climatic variables. Dispersal in *Branchinecta* is primarily passive, occurring through wind, waterfowl and animals (Hawes 2009). While long-range dispersal events have been suggested in congeneric species (Rodríguez-Flores et al. 2017), their frequency appears to be low, leading to a pattern where gene flow predominantly occurs among geographically proximate populations, reinforcing IBD. Additionally, the species' diapause strategy, in which cysts remain dormant in sediment until favourable conditions return, likely enhances population persistence while limiting the influence of environmental factors on genetic structure (Philippi et al. 2001). Although the broad-scale climatic variables integrated into our study did not explain genetic structure, we cannot discard that local physicochemical conditions such as photoperiod, temperature, or conductivity might

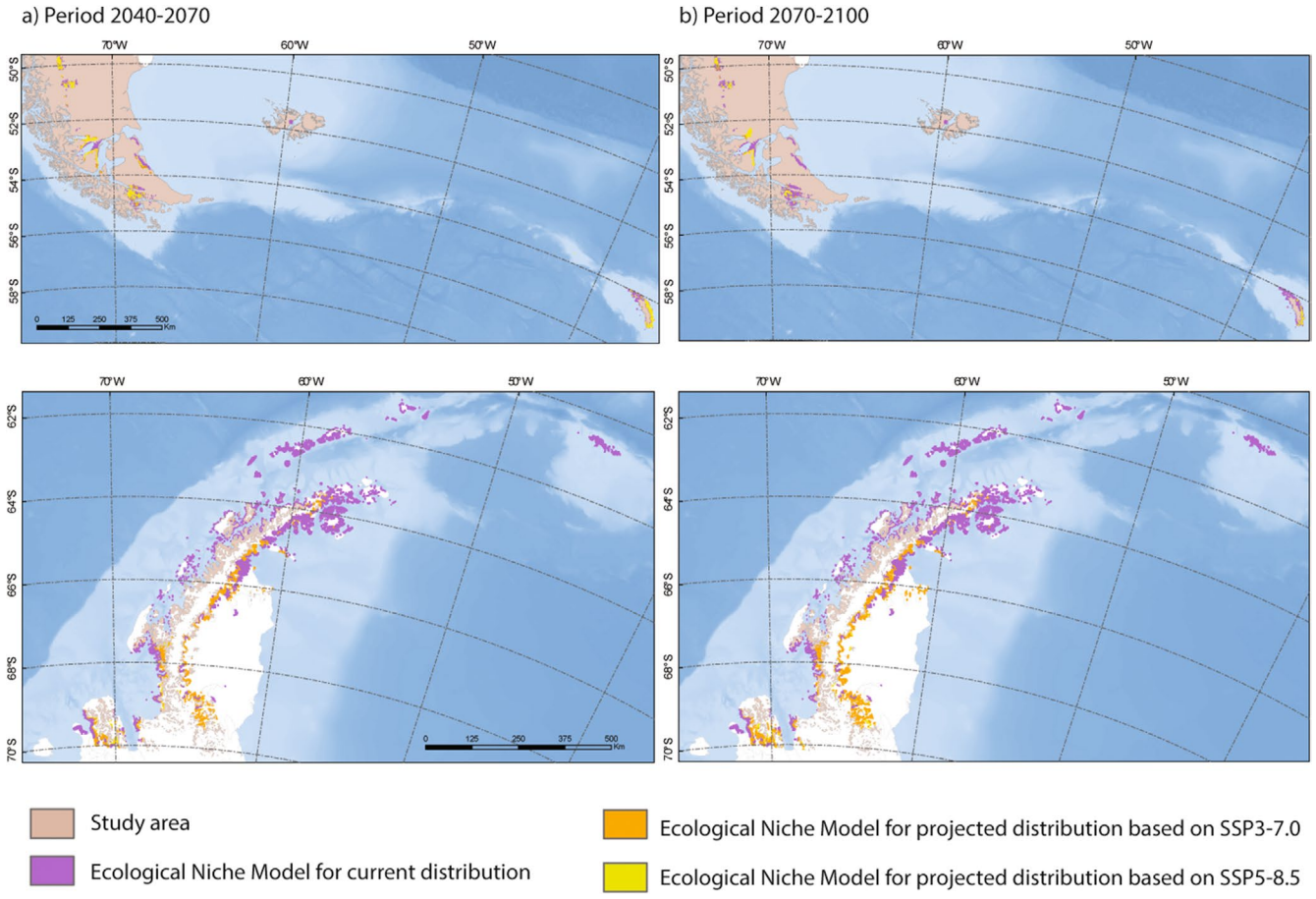

FIGURE 6 | *Branchinecta gaini* Ecological Niche Model for current and projected distribution for Maritime Antarctic and sub-Antarctic provinces for 2040–2070 (panel a) and 2070–2100 (panel b) based on SSP3-7.0 (orange) and SSP5-8.5 (yellow). Different projected scenarios would occupy the current area (purple) and expand to the places marked with the corresponding colour. This map was created following the same protocol as Figure 1.

influence population density and gene flow at a finer spatial scale (Brendonck 1996; Farhadi et al. 2021). Alternatively, the genetic structure in *B. gaini* may also be shaped by stochastic processes, density-dependent biotic interactions and microbiome assemblage rather than deterministic environmental filtering. For instance, for *B. gaini* populations within MA, we detected robust correlations between genetic structure and its microbiomes' composition (Schwob et al. 2024). This new evidence of phylosymbiosis in an unexplored taxonomic group opens promising avenues of research to further understand the roles of biotic variables in shaping the Antarctic freshwater biodiversity.

4.4 | Knowing the Past to Predict the Future

The close relationship between climate oscillations and species distribution makes the use of ENM a powerful tool; however, the spatial resolution employed in this study might not capture environmental gradients and landscape complexity that are especially important for small organisms such as *B. gaini* (Bazzato et al. 2021). In light of future predicted warming under both 'moderate/mid/partial—mitigation' (SSP3-7.5) and 'no mitigation' (SSP5-8.5) greenhouse gas emissions, both scenarios predict a significant reduction of suitable habitat in lower latitude SSA and core sub-Antarctic regions, including South Georgia and parts of Tierra del Fuego, with up to 83% habitat loss by 2100. Our demographic and phylogeographic analyses detected an ancient genetic diversity in the SSA population, suggesting that this population should have survived in glacial and interglacial refugia through successive and historical climate oscillations. Therefore, we hypothesised that this population may present some degree of resilience to current and predicted climatic changes even in the case of unfavourable scenarios of habitat contraction. In the case of the SGI population, this displayed the lowest genetic diversity with two high-frequency haplotypes, and – considering the significant sampling effort on the island in areas with no current records—this population of *B. gaini* could have a fragile ability for the maintenance of genetic diversity. In contrast, suitable habitats in the MA are projected to increase. These model results suggest that climate change may facilitate leading-edge expansion into newly ice-free areas but also threaten trailing-edge populations in lower-latitude regions.

4.5 | Conservation Implications and Future Directions

Aquatic invertebrates are often severely underrepresented in conservation status assessments and are often overlooked in aquatic conservation efforts, particularly in the Southern Hemisphere and SSA (Collier et al. 2016; Contador et al. 2012). Likewise, of the invertebrate groups that have been analysed in the world, the most

TABLE 3 | Suitable habitat area for *B. gaini* in the present and under different climate change scenarios (SSP3-7.0 and SSP5-8.5) projected for the periods 2040–2070 and 2070–2100.

	Area (km²)	Area (km ²)	%
Study area	292,137.9		
Present (Ant + SubAnt)	23,439.9		8
Antarctica		Area gained	
2040–2070 SSP3-7.0		5852.4	30.8
2040–2070 SSP5-8.5		5280.4	27.8
2070–2100 SSP3-7.0		7446.6	39.2
2070–2100 SSP5-8.5		6857.3	36.1
Sub-Antarctica		Area lost (km²)	
2040–2070 SSP3-7.0		−2273.6	−50.9
2040–2070 SSP5-8.5		−2569.2	−57.6
2070–2100 SSP3-7.0		−3710	−83.1
2070–2100 SSP5-8.5		−3364.6	−75.4
Total			
2040–2070 SSP3-7.0	27,018.7	3578.8	15.3
2040–2070 SSP5-8.5	26,151.0	2711.2	11.6
2070–2100 SSP3-7.0	27,176.4	3736.6	15.9
2070–2100 SSP5-8.5	26,932.6	3492.7	14.9

Note: A positive result indicates an expansion of suitable habitat, while a negative result indicates a reduction in the availability of suitable habitat for *B. gaini*.

threatened are those with low dispersal capacity and high local endemism (Collier et al. 2016). Our integration of historical and contemporary connectivity potentially provides a solid foundation for the development of conservation strategies, especially in fragile areas with dramatic changes projected, such as Signy Island (SOI) and the northern parts of the Antarctic Peninsula (Lee et al. 2017). The strong genetic structure and low contemporary gene flow highlight the need for region-specific conservation strategies for *B. gaini*. This becomes particularly relevant since no current conservation strategies for freshwater ecosystems or specific zonation exist in the MA that consider the increasing data available for the existence of structured populations of Antarctic freshwater species. Our analyses suggest that lower latitude trailing edge populations from SSA and SGI will face higher risks due to habitat loss. Therefore, conservation and management efforts should prioritise protecting these populations and monitoring potential climate-driven range shifts. Future research is required that focuses on (1) whole-genome sequencing and studying genes under selection to assess adaptive genetic variation and (2) experimental studies addressing the contribution of the microbiome to evaluate the species' tolerance to changing environmental conditions and (3) descriptive studies on changes in phenological patterns in this species under different climate change scenarios to assess adaptive responses or phenotypic plasticity.

Author Contributions

C.S.M.: research development and leadership, sampling, molecular analysis, software, writing, and review. V.B.-D.: molecular analysis, R and software, writing and reviewing. M.G.: ecological niche modelling analyses, figures, and review. C.E.: ecological niche modelling analyses. S.R.: sampling, analysis, reviewing. G.S.: sampling, mantel analysis, software, writing, and review. M.P.: sampling, molecular analysis, writing, and review. P.C.: sampling, writing, and review. P.C.G.: ecological niche modelling analyses, writing, and review. E.P.: conceived the original idea, molecular infrastructure and analysis, and review. T.C.: sampling, funding, and ecological niche modelling infrastructure.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All Supporting Information cited in this manuscript, including occurrences and genetic protocols used in this study, is available at DataDryad (https://doi.org/10.5061/dryad.hqbzkh1v5). New sequences were deposited in GenBank under the following accession numbers: cox1 (PV821534 - PV821747), 16S rRNA (PV822333-PV822400).

Peer Review

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References

Allouche, O., A. Tsoar, and R. Kadmon. 2006. "Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS)." *Journal of Applied Ecology* 43: 1223–1232.

Baird, H. P., S. Shin, R. G. Oberprieler, et al. 2021. "Fifty Million Years of Beetle Evolution Along the Antarctic Polar Front." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2017384118.

Bazzato, E., L. Rosati, S. Canu, M. Fiori, E. Farris, and M. Marignani. 2021. "High Spatial Resolution Bioclimatic Variables to Support Ecological Modelling in a Mediterranean Biodiversity Hotspot." *Ecological Modelling* 441: 109354.

Benjamini, Y., A. M. Krieger, and D. Yekutieli. 2005. "Adaptive Linear Step-Up Procedures That Control the False Discovery Rate." *Biometrika* 93: 491–507.

Biersma, E. M., C. Torres-Díaz, M. A. Molina-Montenegro, et al. 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: 1–11.

Björck, S., S. Olsson, C. Ellis-Evans, et al. 1996. "Late Holocene Paleoclimatic Records From Lake Sediments on James Ross Island, Antarctica." *Palaeogeography, Palaeoclimatology, Palaeoecology* 121: 195–220.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. "Evaluating Resource Selection Functions." *Ecological Modelling* 157: 281–300.

Brendonck, L. 1996. "Diapause, Quiescence, Hatching Requirements: What We Can Learn From Large Freshwater Branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca)." *Hydrobiologia* 320: 85–97.

Burton-Johnson, A., M. Black, P. T. Fretwell, and J. Kaluza-Gilbert. 2016. "An Automated Methodology for Differentiating Rock From Snow, Clouds and Sea in Antarctica From Landsat 8 Imagery: A New Rock Outcrop Map and Area Estimation for the Entire Antarctic Continent." *Cryosphere* 10: 1665–1677.

Butler, H. G. 1999. "Temporal Plankton Dynamics in a Maritime Antarctic Lake." *Archiv für Hydrobiologie* 148: 311–339.

Cattell, R. B. 1966. "The Scree Test for the Number of Factors." *Multivariate Behavioral Research* 1: 245–276.

Chhatre, V. E., and K. J. Emerson. 2017. "StrAuto: Automation and Parallelization of STRUCTURE Analysis." *BMC Bioinformatics* 18: 192.

Cobben, M. M. P., J. Verboom, P. F. M. Opdam, et al. 2011. "Projected Climate Change Causes Loss and Redistribution of Genetic Diversity in a Model Metapopulation of a Medium-Good Disperser." *Ecography* 34: 920–932.

Cohen, R. G. 1992. "Redescription of *Branchinecta granulosa* Daday, 1902 From Argentina (Crustacea: Branchiopoda)." *Hydrobiologia* 228: 195–202.

Collier, K. J., P. K. Probert, and M. Jeffries. 2016. "Conservation of Aquatic Invertebrates: Concerns, Challenges and Conundrums." *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 817–837.

Collin, F. D., G. Durif, L. Raynal, et al. 2021. "Extending Approximate Bayesian Computation With Supervised Machine Learning to Infer Demographic History From Genetic Polymorphisms Using DIYABC Random Forest." *Molecular Ecology Resources* 21: 2598–2613.

Collins, G. E., I. D. Hogg, P. Convey, et al. 2020. "Genetic Diversity of Soil Invertebrates Corroborates Timing Estimates for Past Collapses of the West Antarctic Ice Sheet." *Proceedings of the National Academy of Sciences of the United States of America* 117: 22293–22302.

Collins, G. E., M. R. Young, P. Convey, et al. 2023. "Biogeography and Genetic Diversity of Terrestrial Mites in the Ross Sea Region, Antarctica." *Genes* 14: 606.

Contador, T. A., J. H. Kennedy, and R. Rozzi. 2012. "The Conservation Status of Southern South American Aquatic Insects in the Literature." *Biodiversity and Conservation* 21: 2095–2107.

Convey, P. 1996. "The Influence of Environmental Characteristics on Life History Attributes of Antarctic Terrestrial Biota." *Biological Reviews* 71: 191–225.

Convey, P. 2011. "Antarctic Terrestrial Biodiversity in a Changing World." *Polar Biology* 34: 1629–1641.

Convey, P., and E. M. Biersma. 2024. "Antarctic Ecosystems." In *Encyclopedia of Biodiversity*, edited by S. M. Scheiner, 133–148. Elsevier.

Convey, P., E. M. Biersma, A. Casanova-Katny, and C. S. Maturana. 2020. "Refuges of Antarctic Diversity." In *Past Antarctica*, edited by M. Oliva. Elsevier.

Cornuet, J. M., V. Ravigné, and A. Estoup. 2010. "Inference on Population History and Model Checking Using DNA Sequence and Microsatellite Data With the Software DIYABC (v1.0)." *BMC Bioinformatics* 11: 401.

Dartnall, H. J. G. 2017. "The Freshwater Fauna of the South Polar Region: A 140-Year Review." *Papers and Proceedings of the Royal Society of Tasmania* 151: 19–58.

Delekto, C. L. 2003. "Anostracan Adaptations to Harsh Environments."

Díaz, A., C. S. Maturana, L. Boyero, P. de Los Ríos Escalante, A. M. Tonin, and F. Correa-Araneda. 2019. "Spatial Distribution of Freshwater Crustaceans in Antarctic and Subantarctic Lakes." *Scientific Reports* 9: 7928.

Edgar, R. C. 2004. "MUSCLE: A Multiple Sequence Alignment Method With Reduced Time and Space Complexity." *BMC Bioinformatics* 5: 1–19.

Evanno, G., S. Regnaut, and J. Goudet. 2005. "Detecting the Number of Clusters of Individuals Using the Software Structure: A Simulation Study." *Molecular Ecology* 14: 2611–2620.

Excoffier, L., and H. E. Lischer. 2010. "Arlequin Suite ver 3.5: A New Series of Programs to Perform Population Genetics Analyses Under Linux and Windows." *Molecular Ecology Resources* 10: 564–567.

Farhadi, S., B. Atashbar Kangarloei, A. Imani, and K. Sarvi Moghanlou. 2021. "Biological Impact of Photoperiod on Fairy Shrimp (*Branchinecta orientalis*): Life History and Biochemical Composition." *Biology* 10: 695.

Foll, M., and O. Gaggiotti. 2008. "A Genome-Scan Method to Identify Selected Loci Appropriate for Both Dominant and Codominant Markers: A Bayesian Perspective." *Genetics* 180: 977–993.

Gañán, M. 2023. *Occurrences of Aquatic Invertebrates in the Antarctic and Subantarctic Regions*. Instituto de Biodiversidad de Ecosistemas Antárticos y Subantárticos (BASE).

Grummer, J. A., L. B. Beheregaray, L. Bernatchez, et al. 2019. "Aquatic Landscape Genomics and Environmental Effects on Genetic Variation." *Trends in Ecology & Evolution* 34: 641–654.

Hampe, A., and R. J. Petit. 2005. "Conserving Biodiversity Under Climate Change: The Rear Edge Matters." *Ecology Letters* 8: 461–467.

Hawes, T. C. 2009. "Origins and Dispersal of the Antarctic Fairy Shrimp." *Antarctic Science* 21: 477–482.

Hewitt, G. M. 1996. "Some Genetic Consequences of Ice Ages, and Their Role, in Divergence and Speciation." *Biological Journal of the Linnean Society* 58: 247–276.

Hewitt, G. M. 2000. "The Genetic Legacy of the Quaternary Ice Ages." *Nature* 405: 907–913.

Ho, S. Y., S. Y. W. Ho, U. Saarma, R. Barnett, J. Haile, and B. Shapiro. 2008. "The Effect of Inappropriate Calibration: Three Case Studies in Molecular Ecology." *PLoS One* 3: e1615.

Ho, S. Y., R. Lanfear, L. Bromham, et al. 2011. "Time-Dependent Rates of Molecular Evolution." *Molecular Ecology* 20: 3087–3101.

Hodgson, D. A., S. J. Roberts, J. A. Smith, et al. 2013. "Late Quaternary Environmental Changes in Marguerite Bay, Antarctic Peninsula,

Inferred From Lake Sediments and Raised Beaches." *Quaternary Science Reviews* 68: 216–236.

Hoffmann, A. A., and C. M. Sgro. 2011. "Climate Change and Evolutionary Adaptation." *Nature* 470: 479–485.

Hogg, I. D., S. Craig Cary, P. Convey, et al. 2006. "Biotic Interactions in Antarctic Terrestrial Ecosystems: Are They a Factor?" *Soil Biology & Biochemistry* 38: 3035–3040.

IPCC. 2021. "Summary for Policymakers." In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by V. Masson-Delmotte. Cambridge University Press.

Jombart, T., S. Devillard, and F. Balloux. 2010. "Discriminant Analysis of Principal Components: A New Method for the Analysis of Genetically Structured Populations." *BMC Genetics* 11: 1–15.

Jones, V. J., D. A. Hodgson, and A. Chepstow-Lusty. 2000. "Palaeolimnological Evidence for Marked Holocene Environmental Changes on Signy Island, Antarctica." *Holocene* 10: 43–60.

Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the Earth's Land Surface Areas." *Scientific Data* 4: 170122.

Lahr, J. 1997. "Ecotoxicology of Organisms Adapted to Life in Temporary Freshwater Ponds in Arid and Semi-Arid Regions." *Archives of Environmental Contamination and Toxicology* 32: 50–57.

Laybourn-Parry, J., and J.-L. Wadham. 2014. "Freshwater Lakes." In *Antarctic Lakes*, edited by J. Laybourn-Parry and J.-L. Wadham, 56–58. Oxford University Press.

Lee, J. R., B. Raymond, T. J. Bracegirdle, et al. 2017. "Climate Change Drives Expansion of Antarctic Ice-Free Habitat." *Nature* 547: 49–54.

Librado, P., and J. Rozas. 2009. "DnaSP v5: A Software for Comprehensive Analysis of DNA Polymorphism Data." *Bioinformatics* 25: 1451–1452.

Lu, F., A. E. Lipka, J. Glaubitz, et al. 2013. "Switchgrass Genomic Diversity, Ploidy, and Evolution: Novel Insights From a Network-Based SNP Discovery Protocol." *PLoS Genetics* 9: e1003215.

Luu, K., E. Bazin, and M. G. B. Blum. 2017. "Pcadapt: An R Package to Perform Genome Scans for Selection Based on Principal Component Analysis." *Molecular Ecology Resources* 17: 67–77.

Maturana, C. S., E. M. Biersma, A. Díaz, et al. 2022. "Survivors and Colonizers: Contrasting Biogeographic Histories Reconciled in the Antarctic Freshwater Copepod *Boeckella poppei*." *Frontiers in Ecology and Evolution* 10: 1012852.

Maturana, C. S., T. Contador Mejias, F. L. Simões, et al. 2024. "Ancient Diversification in Extreme Environments: Exploring the Historical Biogeography of the Antarctic Winged Midge *Parochlus steinenii* (Diptera: Chironomidae)." *Frontiers in Ecology and Evolution* 12: 1393376.

Maturana, C. S., S. Rosenfeld, E. M. Biersma, et al. 2021. "Historical Biogeography of the Gondwanan Freshwater Genus *Boeckella* (Crustacea): Timing and Modes of Speciation in the Southern Hemisphere." *Diversity and Distributions* 27: 2330–2343.

Meirmans, P. G. 2015. "Seven Common Mistakes in Population Genetics and How to Avoid Them." *Molecular Ecology* 24: 3223–3231.

Meirmans, P. G. 2020. "Genodive Version 3.0: Easy-To-Use Software for the Analysis of Genetic Data of Diploids and Polyploids." *Molecular Ecology Resources* 20: 1126–1131.

Mussmann, S. M., M. R. Douglas, T. K. Chafin, and M. E. Douglas. 2019. "BA3-SNPs: Contemporary Migration Reconfigured in BayesAss for Next-Generation Sequence Data." *Methods in Ecology and Evolution* 10: 1808–1813.

Norris, R. D., S. K. Turner, P. M. Hull, and A. Ridgwell. 2013. "Marine Ecosystem Responses to Cenozoic Global Change." *Science* 341: 492–498.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, et al. 2001. "Terrestrial Ecoregions of the Worlds: A New Map of Life on Earth." *Bioscience* 51: 933–938.

Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts Across Natural Systems." *Nature* 421: 37–42.

Pauls, S. U., C. Nowak, M. Bálint, and M. Pfenninger. 2013. "The Impact of Global Climate Change on Genetic Diversity Within Populations and Species." *Molecular Ecology* 22: 925–946.

Pearman, W. S., L. Urban, and A. Alexander. 2022. "Commonly Used Hardy-Weinberg Equilibrium Filtering Schemes Impact Population Structure Inferences Using RADseq Data." *Molecular Ecology Resources* 22: 2599–2613.

Peck, L. S. 2004. "Physiological Flexibility: The Key to Success and Survival for Antarctic Fairy Shrimps in Highly Fluctuating Extreme Environments." *Freshwater Biology* 49: 1195–1205.

Peck, L. S. 2005. "Prospects for Surviving Climate Change in Antarctic Aquatic Species." *Frontiers in Zoology* 2: 9.

Philippi, T. E., M. A. Simovich, E. T. Bauder, et al. 2001. "Habitat Ephemerality and Hatching Fractions of a Diapausing Anostracan (Crustacea: Branchiopoda)." *Israel Journal of Zoology* 47: 387–396.

Pointing, S. B., B. Büdel, P. Convey, et al. 2015. "Biogeography of Photoautotrophs in the High Polar Biome." *Frontiers in Plant Science* 6: 692.

Pokorný, M., R. G. Cohen, L. Nedbalová, J. M. Lirio, and V. Sacherová. 2024. "South! Phylogeography of the Antarctic Fairy Shrimp Branchinecta Gaini and Its Closest Patagonian Congener *Branchinecta granulosa* Reveals a Long-Term Association of Freshwater Fauna With the Southern Continent." *Organisms Diversity & Evolution* 24: 489–506.

Porras-Hurtado, L., Y. Ruiz, C. Santos, et al. 2013. "An Overview of STRUCTURE: Applications, Parameter Settings, and Supporting Software." *Frontiers in Genetics* 4: 98.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. "Inference of Population Structure Using Multilocus Genotype Data." *Genetics* 155: 945–959.

Pugh, P. J. A., H. J. G. Dartnall, and S. J. McInnes. 2002. "The Non-Marine Crustacea of Antarctica and the Islands of the Southern Ocean: Biodiversity and Biogeography." *Journal of Natural History* 36: 1047–1103.

Quayle, W. C., L. S. Peck, H. Peat, et al. 2002. "Extreme Responses to Climate Change in Antarctic Lakes." *Science* 295, no. 5555: 645.

Quayle, W. C., P. Convey, L. S. Peck, et al. 2003. "Ecological Response of Maritime Antarctic Lakes to Regional Climate Change." *Paleobiology and Paleoenvironments of Eocene Rocks and Antarctic Research Series* 76: 335–347.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rodríguez-Flores, P. C., Y. Jiménez-Ruiz, L. Forró, J. Vörös, and M. García-París. 2017. "Non-Congruent Geographic Patterns of Genetic Divergence Across European Species of Branchinecta (Anostraca: Branchinectidae)." *Hydrobiologia* 801: 47–57.

Rogers, D. C., F. Severo-Neto, M. V. Volcan, et al. 2021. "Comments and Records on the Large Branchiopod Crustacea (Anostraca, Notostraca, Laevicaudata, Spinicaudata, Cyclestherida) of the Neotropical and Antarctic Bioregions." *Studies on Neotropical Fauna and Environment* 56: 53–77.

Rosenfeld, S., C. Maturana, M. Gañan, et al. 2023. "Revealing the Hidden Biodiversity of Antarctic and the Magellanic Sub-Antarctic Ecoregion: A Comprehensive Study of Aquatic Invertebrates From the BASE Project." *Biodiversity Data Journal* 11: e108566.

Rozzi, R., J. J. Armesto, J. R. Gutiérrez, et al. 2012. "Integrating Ecology and Environmental Ethics: Earth Stewardship in the Southern End of the Americas." *Bioscience* 62: 226–236.

Schwob, G., L. Cabrol, P. M. Vidal, et al. 2024. "Which Microbiome Are We Talking About? Contrasted Diversity Patterns and Eco-Evolutionary Processes Between Gill and Intestinal Microbiomes of Antarctic Fairy Shrimps." *Frontiers in Ecology and Evolution* 12: 1438057.

Spaulding, S. A., B. Van de Vijver, D. A. Hodgson, et al. 2010. "Diatoms as Indicators of Environmental Change in Antarctic and Subantarctic Freshwaters." In *The Diatoms*, 267–284. Cambridge University Press.

Terauds, A., and J. R. Lee. 2016. "Antarctic Biogeography Revisited: Updating the Antarctic Conservation Biogeographic Regions." *Diversity and Distributions* 22: 836–840.

Terauds, A., J. R. Lee, H. S. Wauchope, et al. 2025. "The Biodiversity of Ice-Free Antarctica Database." *Ecology* 106: e70000.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. "BIOMOD – A Platform for Ensemble Forecasting of Species Distributions." *Ecography* 32: 369–373.

Turner, J. 2013. "Antarctic Climate Change and the Environment: An Update."

Tytgat, B., E. Verleyen, M. Sweetlove, et al. 2023. "Polar Lake Microbiome Have Distinct Evolutionary Histories." *Science Advances* 9: 1–14.

van de Wouw, M., M. van de Wouw, P. van Dijk, and A. H. L. Huiskes. 2008. "Regional Genetic Diversity Patterns in Antarctic Hairgrass (*Deschampsia antarctica* Desv.)." *Journal of Biogeography* 35: 365–376.

Verleyen, E., B. van de Vijver, B. Tytgat, et al. 2021. "Diatoms Define a Novel Freshwater Biogeography of the Antarctic." *Ecography* 44: 548–560.

Walton, D. W. H. 2008. *Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator*, edited by D. M. Bergstrom, P. Convey, and A. H. L. Huiskes, vol. 20, 611. Springer.

Wang, I. J. 2013. "Examining the Full Effects of Landscape Heterogeneity on Spatial Genetic Variation: A Multiple Matrix Regression Approach for Quantifying Geographic and Ecological Isolation." *Evolution* 67: 3403–3411.

Wharton, D. A. 2002. *Life at the Limits: Organisms in Extreme Environments*. Cambridge University Press.

Wilson, A. G., and B. Rannala. 2003. "Bayesiand Inference of Recent Migration Rates Using Multilocus Genotypes." *Genetics* 163: 1177–1191.

Supporting Information

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