

Global conservation genomics of blue whales calls into question subspecies taxonomy and refines knowledge of population structure

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Abstract

Blue whales (*Balaenoptera musculus*) are the largest living animal and, like other baleen whales, became endangered due to whaling. Here, we used population genomics to infer the number, distribution and other characteristics of subspecies and populations. We used the largest DNA dataset in blue whales, both in terms of genomic markers (16,661 SNPs and mtDNA) and geographic coverage ($n = 276$ for SNPs; $n = 531$ for mtDNA). We found greatest divergence among the eastern Pacific, Indo-western Pacific and Antarctic blue whales. There were indications that natural selection in different environments promoted divergence among these groupings. Within these regions, there was divergence between the eastern North and eastern South Pacific, and among the eastern Indian Ocean, the western South Pacific and the northern Indian Ocean. There was no divergence within the Antarctic. These findings are consistent with the current classification of Antarctic and Indo-western Pacific blue whales in the Southern Hemisphere as different subspecies but call into question the subspecies taxonomy of eastern Pacific blue whales. The study shows that opposite breeding seasons on either side of the equator do not necessarily inhibit connectivity across the equator, and reinforces that population structure needs to be well understood to conserve the diversity within species.

Introduction

Understanding population structure and connectivity is critical for the conservation and management of species. Ecological and evolutionary processes operate on a population level, and so population-based conservation is needed for ecosystems to continue to function and for preserving the evolutionary potential that allows population adaptation to environmental change

(Purvis & Hector, 2000; Stockwell, Hendry, & Kinnison, 2003; Garner, Rachlow, & Hicks, 2005; Pressey *et al.*, 2007). Population-based conservation should consider the natural connectivity of populations to prevent human-induced population isolation, structuring, inbreeding and diversity loss. Genomics is a crucial, modern tool that can determine population structure, connectivity and other population characteristics to assist in conservation (Theissinger *et al.*, 2023).

Baleen whales were killed in the hundreds of thousands during 20th-century whaling. However, the number, distribution and connectivity of baleen whale populations are difficult to determine. The wide-ranging oceanic habitat of many baleen whales makes them particularly costly and logistically difficult to study. Populations typically feed at mid-to-high latitudes during summer and migrate to breed at lower latitudes during winter. Thus, population structure in these animals may be shaped by site fidelity to calving grounds, and to feeding grounds through cultural learning of locations from mothers in the first year of individuals' lives (Hoelzel, 1998).

The recovery of baleen whales is threatened by multiple human sources, including underwater noise (from shipping, oil and gas exploration activities and sonar), changing availability of food driven by human-induced effects on ocean productivity, environmental contaminants, ship collision and entanglement in fishing gear (e.g. Thomas, Reeves, & Brownell, 2015). Localized depletion of blue whales could occur if these threats are concentrated in areas containing populations with limited connectivity to animals in surrounding regions. Thus, describing the spatio-temporal patterns of structure within a species and the geographic boundaries between intraspecific populations will inform management decisions on the timing and location of human activities to minimize impacts on baleen whales.

The blue whale (*Balaenoptera musculus* Linnaeus, 1758) is the largest living animal and is distributed throughout most oceans worldwide. The species became protected from commercial whaling in 1966; 20 years before a global moratorium on whaling implemented through the International Whaling Commission (IWC) in 1986. The Society for Marine Mammalogy's Committee on Taxonomy (www.marinemammalscience.org) currently recognizes four blue whale subspecies: the Antarctic blue whale (*B. m. intermedia* Burmeister, 1871) that feeds in the Antarctic; the pygmy blue whale (*B. m. breviceauda* Ichihara, 1966) that feeds in temperate waters of the Southern Hemisphere; the northern Indian Ocean blue whale (*B. m. indica* Blyth, 1859) in the northern Indian Ocean; and the northern blue whale in the Northern Hemisphere (*B. m. musculus* Linnaeus, 1758). Blue whales that feed in the eastern South Pacific (i.e. off Chile) have been proposed as a separate unnamed subspecies (Branch *et al.*, 2007). Blue whales exhibit morphological, acoustic, genetic or a combination of differences between currently recognized and proposed subspecies (McDonald, Mesnick, & Hildebrand, 2006; LeDuc *et al.*, 2007; Branch *et al.*, 2007; Attard *et al.*, 2012; Torres-Florez *et al.*, 2014; LeDuc *et al.*, 2017). Acoustic differences between areas within the Indo-western Pacific indicate that pygmy blue whales may have at least three populations in the region: eastern Indian, western Indian and western South Pacific populations (McDonald *et al.*, 2006; Samaran *et al.*, 2013; Balcazar *et al.*, 2015; Barlow *et al.*, 2018). It is largely unknown whether these acoustic differences correspond to genetic differences, with a mitochondrial DNA (mtDNA) study showing evidence of a small but significant difference between the eastern Indian and western South Pacific

populations (Barlow *et al.*, 2018). Within the Antarctic subspecies, analyses of microsatellite DNA suggest there may be more than one population (Sremba *et al.*, 2012; Attard, Beheregaray, & Möller, 2016).

Here, we infer the number, distribution and connectivity of blue whale populations (Fig. 1) and their level of genetic diversity and inbreeding (Table 1). We capitalize on 276 samples for reduced representation genomics and 531 mtDNA sequences. This is the most comprehensive DNA dataset of blue whales to date, both in terms of number of markers and geographic coverage. Our methods can be a template for incorporating genomics into population studies of other endangered baleen whales. The genomic-based findings will clarify the number and location of populations and other population-level characteristics. In addition, the dataset will allow the first investigation of loci in the genome that may exhibit ecologically relevant adaptation among blue whales. Our results can inform management decisions to ensure the persistence of multiple, healthy blue whale populations as they recover from intense whaling.

Materials and methods

Full methods for the entire methods are provided in the Supporting Information. In brief, tissue samples were collated from previous and current research efforts from most of the known blue whale populations worldwide (Table 1; Fig. 1). DNA was extracted from the samples. A high-quality SNP dataset was generated from the DNA by sequencing double-digest restriction-site-associated DNA (ddRAD) libraries (Peterson *et al.*, 2012), and aligning sequences to a blue whale reference genome (Table S1).

High-level hierarchical structure was assessed by principal component analysis (PCA), discriminant analysis of principal components (DAPC) (Jombart, Devillard, & Balloux, 2010) and Bayesian clustering analyses using fastSTRUCTURE (Raj, Stephens, & Pritchard, 2014) and ADMIXTURE (Alexander, Novembre, & Lange, 2009). Genetic differentiation (F_{ST}) and rates of recent migration were estimated between the high-level groups. Genetic variation was measured as the percentage of polymorphic loci, observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficient (F_{IS}) and allelic richness (AR).

The potential for sub-structure in blue whales within the high-level groups was explored by extracting the subset of individuals with at least 0.9 ancestry to their assigned cluster in fastSTRUCTURE and assessing each of these cluster subsets separately using PCA, DAPC, fastSTRUCTURE and ADMIXTURE. Pairwise relatedness between individuals and the inbreeding coefficient of individuals were estimated within the lowest level of identified structure. Samples were also stratified *a priori* based on geographic location. Genetic variation was estimated for each *a priori* sampling locality and F_{ST} was calculated between localities.

Candidate loci under natural selection were identified using outlier detection methods in BAYESCAN (Foll & Gaggiotti, 2008) and ARLEQUIN (Excoffier & Lischer, 2010). To be conservative, loci detected as outliers by both

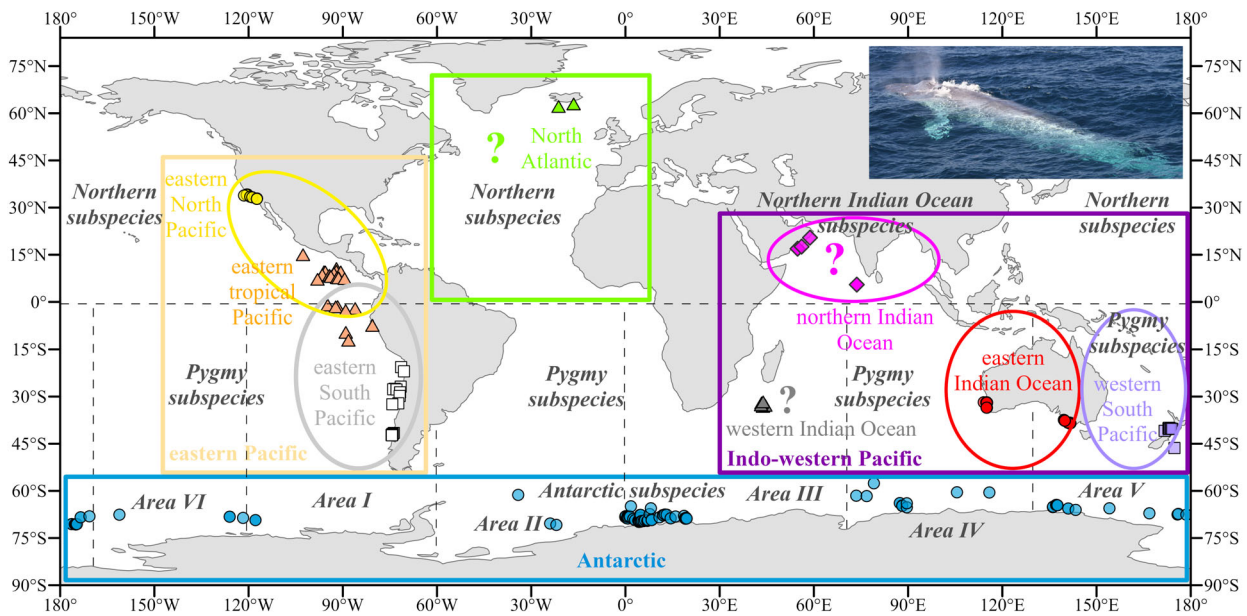


Figure 1 Location of blue whales (*Balaenoptera musculus*) used in this study. The italicized writing is the current subspecies classification by the Society for Marine Mammalogy's Committee on Taxonomy and the IWC Management Areas for blue whales. The highest levels of hierarchical population structure (rectangles) found in this study and substructure within these (ovals) are indicated. The question marks indicate locations with small sample sizes and thus uncertainty in their subspecies or population identity (i.e. northern Indian Ocean blue whales may be a separate or same high-level hierarchical grouping as the other Indo-western Pacific blue whales; western Indian Ocean may be separate or the same population as blue whales in Australia; and North Atlantic blue whales may be a separate subspecies to blue whales elsewhere in the Northern Hemisphere). The locations of the North Atlantic samples are representative only.

BAYESCAN and ARLEQUIN were considered candidate loci under selection. The candidate SNPs were annotated and then tested for enrichment in functional pathways.

MtDNA control region sequences were collated (Table 1) from previous studies and the current study. Pairwise F_{ST} was calculated, and a haplotype network was constructed. The use of mtDNA allowed testing for genetic differentiation between the northern Indian Ocean and other localities because mtDNA but not SNPs for the northern Indian Ocean had a sufficient sample size to test for genetic differentiation. The northern Indian Ocean had a sample size of only one for SNPs because only one sample from the northern Indian Ocean had sufficient DNA quality for ddRAD. Genetic variation for mtDNA was estimated by calculating haplotype diversity (h), nucleotide diversity (π) and haplotype richness (HR).

Results

The final nuclear dataset was 16,661 SNPs genotyped in 276 individuals. The average missing data per individual was 1.8%. We identified the Antarctic, eastern Pacific and Indo-western Pacific (i.e. Indian Ocean and western South Pacific) as high-level hierarchical groupings in blue whales based on all population structure methods (Fig. 1): PCA (Fig. 2), DAPC (Figs S1 and S2) and Bayesian clustering (Fig. 3). Significant genetic differentiation was identified between these groups (Fig. 4; Tables S2 and S3). Genomic variation in decreasing order was the Antarctic, the eastern

Pacific and the Indo-western Pacific blue whales, and was similar among localities within the high-level hierarchical groupings (Table 1). Migration rate estimates (Table S4) were highest from the Indo-western Pacific to the Antarctic (4%), followed by from the Antarctic to the eastern Pacific (2–3%). There were similar migration rates among the remaining pairs of regions (1–2%). The single North Atlantic sample fell outside of the clusters representing the high-level hierarchical groupings in the PCA (Fig. 2).

Within the high-level hierarchical groupings, there was low ($F_{ST} = 0.01$) but significant structure between the eastern North and eastern South Pacific, and between the eastern Indian Ocean (i.e. off Australia) and western South Pacific (i.e. off New Zealand) (Fig. 4; Table S2). The eastern tropical Pacific was a transition zone between the eastern North and South Pacific populations (Fig. 5). There were 52 pairs of individuals with relatedness above 0.10 within the Antarctic region (Fig. 6), and only 4 within the eastern Indian Ocean, 2 within the eastern South Pacific, 1 within the eastern North Pacific and none within the western South Pacific. The inbreeding coefficients of individuals averaged -0.03 for the Antarctic, -0.04 for the eastern South Pacific, -0.04 for the eastern Indian Ocean, -0.05 for the eastern North Pacific and -0.06 for the western South Pacific.

Blue whales from the western Indian Ocean (i.e. off Madagascar) and the northern Indian Ocean, which along with the North Atlantic had the smallest sample sizes (so findings are only suggestive), were genetically most similar to the Indo-western Pacific blue whales sampled in the eastern

Table 1 Genomic variation of blue whales (*Balaenoptera musculus*) for oceanic regions and localities within regions at 16,661 SNPs and the mtDNA control region

Oceanic region and localities within regions	SNPs										mtDNA						
	Sampling date		n	% missing data	AR		% Poly-morphic loci	H_0 (\pm SD)	H_e (\pm SD)	F_{IS} (P value)	n	No. haplotypes	h (\pm SD)	π (\pm SD)	HR		
	Months	Years			n = 5	n = 18									n = 6	n = 7	n = 44
Eastern Pacific	Jul–Mar	1995–2013	84	1.7	1.66	1.87	97.5	0.248 (0.175)	0.237 (0.158)	−0.065 (0.998)	192	25	0.867 (0.015)	0.008 (0.005)	3.5	4.0	13.2
Eastern North Pacific	Jul–Sep	1995–1999	19	3.5	1.63	1.84	84.5	0.235 (0.190)	0.228 (0.171)	−0.065 (0.916)	50	13	0.738 (0.064)	0.006 (0.004)	2.7	3.2	11.4
Eastern Tropical Pacific	Sep–Nov	1998–2006	30	1.8	1.65	1.86	90.9	0.242 (0.181)	0.235 (0.165)	−0.050 (0.922)	44	11	0.810 (0.040)	0.006 (0.004)	3.0	3.3	10.0
Eastern South Pacific	Dec–Mar	1997–2013	35	0.7	1.66	1.88	93.7	0.260 (0.192)	0.240 (0.164)	−0.088 (0.990)	98	17	0.894 (0.012)	0.010 (0.005)	3.7	4.2	11.9
Indo-western Pacific	Jan–Apr	1996–2017	74	2.5	1.53	1.72	87.2	0.205 (0.191)	0.195 (0.175)	−0.077 (0.999)	187	17	0.651 (0.039)	0.003 (0.002)	2.3	2.6	9.6
Eastern Indian Ocean (i.e. Australia)	Nov–Apr	2009–2015	50	2.4	1.53	1.71	82.1	0.207 (0.196)	0.194 (0.177)	−0.089 (0.999)	125	14	0.697 (0.042)	0.003 (0.002)	2.5	2.8	8.7
Western South Pacific (i.e. New Zealand)	Jan–Feb	2014–2017	18	2.6	1.51	1.68	68.4	0.197 (0.205)	0.188 (0.185)	−0.070 (0.943)	49	7	0.365 (0.087)	0.001 (0.001)	1.2	1.3	5.6
Western Indian Ocean (i.e. Madagascar)	Dec	1996	5	2.7	1.58	–	58.4	0.233 (0.257)	0.212 (0.207)	−0.144 (0.871)	6	4	0.867 (0.129)	0.004 (0.003)	3.0	–	–
Northern Indian Ocean	Apr	1998	1 ^a	0.2	–	–	–	–	–	–	7 ^b	3	0.667 (0.160)	0.004 (0.003)	1.9	2.0	–
Antarctic	Dec–Feb	1993–2009	117 ^c	1.6	1.70	1.92	99.6	0.256 (0.168)	0.250 (0.148)	−0.081 (1.000)	150	50	0.971 (0.004)	0.014 (0.007)	4.6	5.4	26.2
North Atlantic	–	1969–1974	1	0.0	–	–	–	–	–	–	2	2	–	–	–	–	–

In parentheses are standard deviations (SD) for the heterozygosity measures and the P value from permutation tests for F_{IS} . n, sample size; AR, allelic richness; H_0 , mean observed heterozygosity; H_e , mean unbiased expected heterozygosity; F_{IS} , inbreeding coefficient; h, haplotype diversity; π , nucleotide diversity; HR, haplotype richness.

^a One from the Maldives.

^b Two from the Maldives and five from Oman.

^c Three from IWC Management Area I, 5 from Area II, 68 from Area III, 11 from Area IV, 25 from Area V and 5 from Area VI.

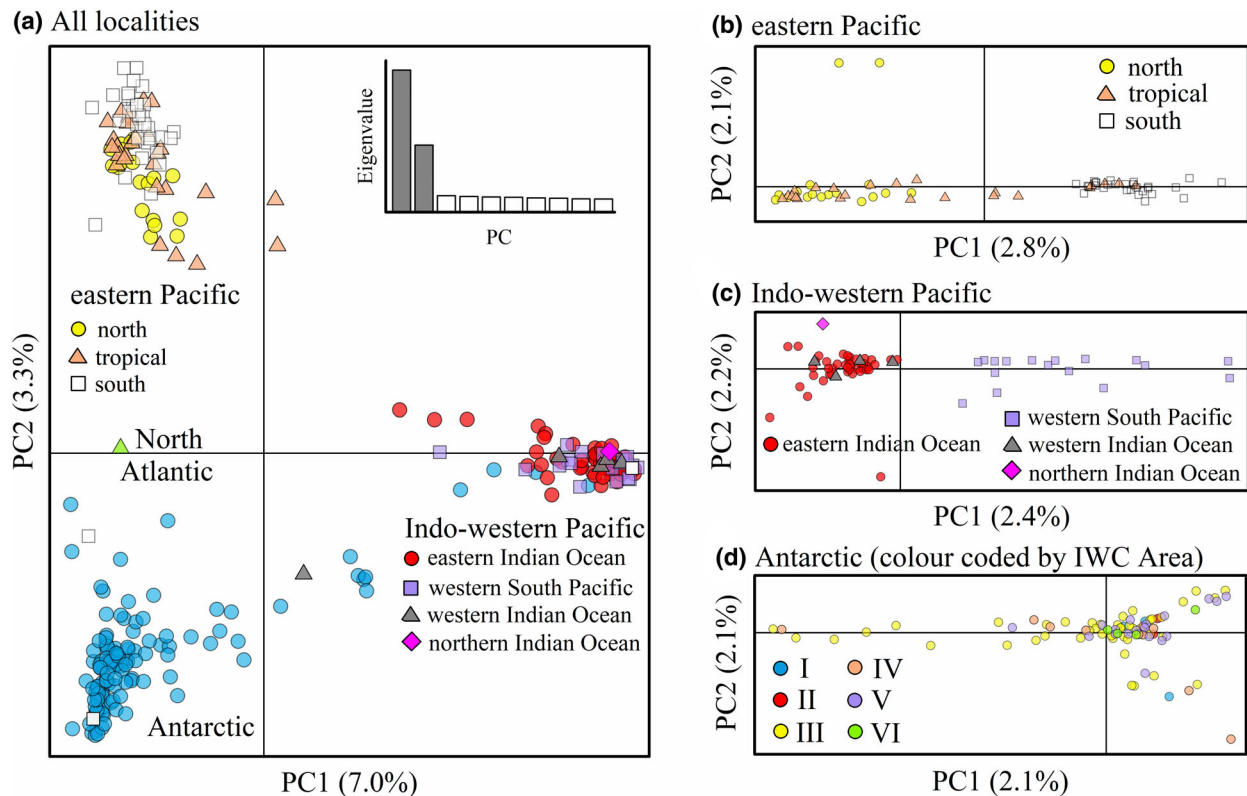


Figure 2 PCAs of blue whales (*Balaenoptera musculus*) at 16,661 SNPs for (a) all localities, and (b–d) each of the three clusters where individuals have at least 0.9 ancestry to a cluster in fastSTRUCTURE (see Fig. 3a). There were 16 samples from the eastern Pacific, 8 from the Indo-western Pacific and 33 from the Antarctic with less than 0.9 ancestry to a cluster. In (d), the samples outside the central cluster are related individuals (Fig. 6). Color coding and shape in (a–c) are the same as Fig. 1, and color coding in (d) is the same as Fig. 6.

Indian Ocean and western South Pacific Ocean. Of the Indo-western Pacific comparisons, the five samples from the western Indian Ocean had the lowest ($F_{ST} = 0.002$; Table S2), but still significant, genetic differentiation at SNPs to the eastern Indian Ocean. The one sample from the northern Indian Ocean for which SNP data were generated was located outside the main cluster of eastern Indian Ocean samples in the PCA for the Indo-western Pacific blue whales (Fig. 2).

The genetic differentiation findings largely aligned between the SNPs and the mtDNA (Tables S2 and S3). In mtDNA (Fig. S3), the greater sample size of eight for the northern Indian Ocean allowed testing for genetic differentiation and showed significant evidence of divergence from the eastern Indian Ocean ($F_{ST} = 0.26$; Table S2) and western South Pacific Ocean ($F_{ST} = 0.49$; Table S2).

We identified 18 loci among the 16,661 SNPs as candidates for divergent selection among blue whale localities. Most of the 18 candidates for natural selection were in intergenic regions or introns (Table S5). The genes associated with the candidates were enriched for two functional pathways – abnormal glucose tolerance and lipid binding (Table S6) – and the candidates more broadly were involved in a range of biological functions (Fig. S4). The allele frequencies of the candidates differed mostly among the high-

level hierarchical groups, usually with a similar allele frequency in two of the high-level groups and a different allele frequency in the remaining high-level group (Fig. 7; Table S7).

Discussion

Our study provides evolutionarily relevant measures to understand the number, distribution and other characteristics of blue whale subspecies and populations (Fig. 1). We found three major groupings of blue whales: the eastern Pacific; the pygmy subspecies of the Indo-western Pacific, which may include the northern Indian Ocean blue whales; and the Antarctic subspecies. There were indications that natural selection in different environments contributed to driving divergence between the high-level groups. Each of these groups needs to be conserved to maintain biodiversity in the species. The estimated migration rates were 1–4% among each of the high-level groups, with both migrant individuals (i.e. movement without necessarily interbreeding) and hybrids (i.e. interbreeding) among the high-level groups. Within groupings, there was lower but significant divergence between the eastern North and eastern South Pacific, and within the pygmy subspecies in the Indo-western Pacific. There was no evidence of divergence within the Antarctic

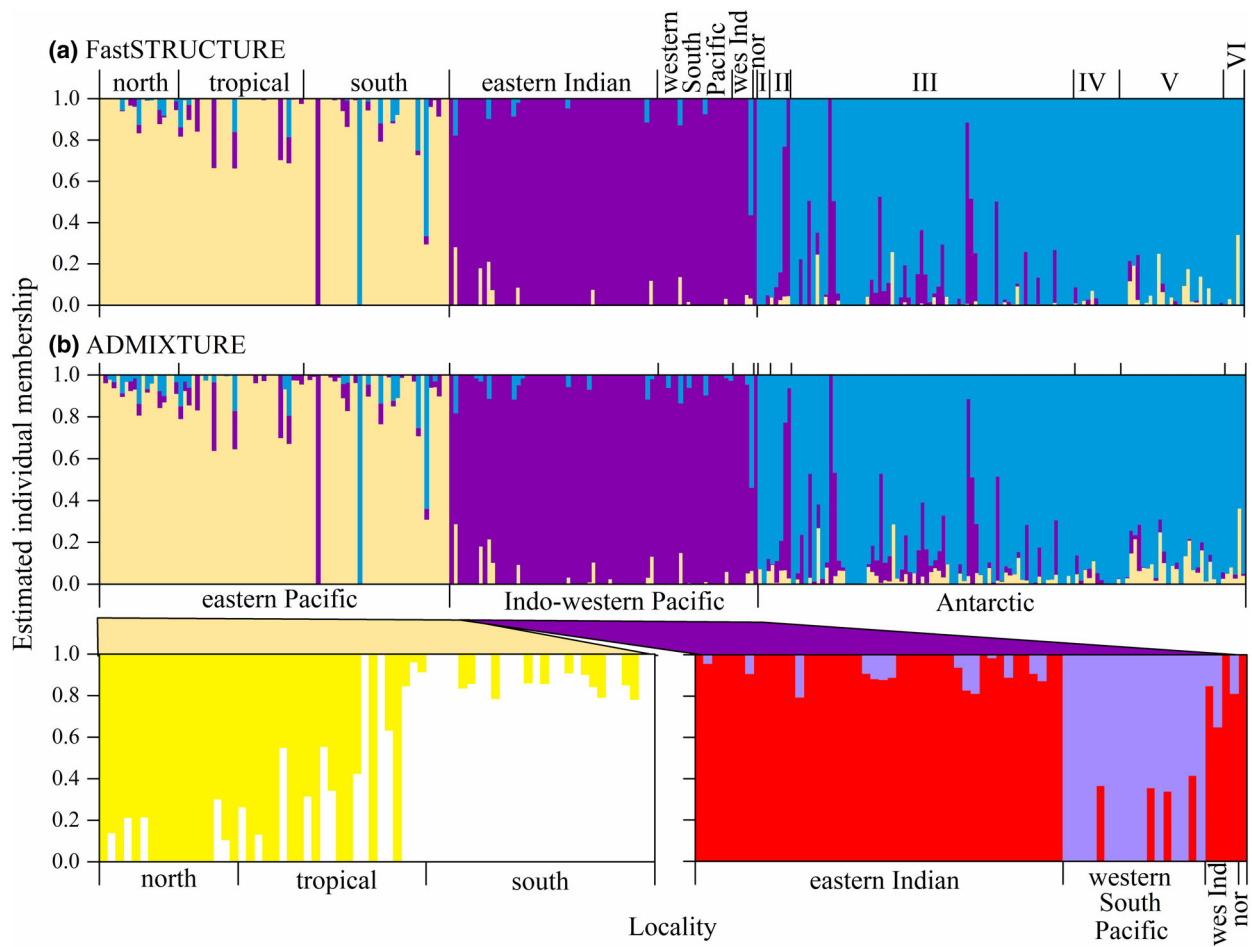


Figure 3 Clustering results of blue whales (*Balaenoptera musculus*) at 16,661 SNPs for (a) fastSTRUCTURE and (b) ADMIXTURE, when structure was detected. Structure was detected among the highest hierarchy in both software and within the eastern Pacific and Indo-western Pacific only using ADMIXTURE. The substructure analyses were run on individuals that had at least 0.9 ancestry to the eastern Pacific, Indo-western Pacific or Antarctic clusters (see Fig. 2 caption for the number of individuals removed). The eastern Pacific individuals are ordered by latitude (also see Fig. 5). Color coding of the clusters aligns with the color coding in Fig. 1. On the x-axis, ‘wes Ind’ means western Indian Ocean and ‘nor’ means northern Indian Ocean.

subspecies. There was no evidence of inbreeding, which is good news for the potential recovery of subspecies and populations.

The similarity between the eastern South Pacific and eastern North Pacific blue whales ($F_{ST} = 0.01$) suggests they are part of the same subspecies, rather than their current classification as separate subspecies. This finding was unexpected given that populations are thought to have opposite breeding seasons when those populations exist on either side of the equator. We know of no other instances of high population connectivity across the equator in a baleen whale species, except perhaps in Bryde’s whales due to that species preferring to inhabit tropical waters. Tracking of migratory movements using satellite tagging (e.g. Irvine *et al.*, 2014), acoustics (e.g. Paniagua-Mendoza *et al.*, 2017) and stable isotopes (Busquets-Vass *et al.*, 2021) indicates that most blue whale populations do adhere to typical migratory and breeding patterns. The eastern South Pacific and eastern North

Pacific populations have phenotypic differences, but not to the extent that they are clearly different subspecies. The populations are acoustically divergent, which is common among blue whale populations as well as blue whale subspecies (McDonald *et al.*, 2006). The populations are perhaps slightly morphologically divergent: there is a small and significant difference in length between eastern South Pacific blue whales and Indo-Western Pacific pygmy blue whales (Branch *et al.*, 2007), but there seems to be morphological similarity between the eastern North Pacific blue whales and Indo-western Pacific pygmy blue whales (Gilpatrick Jr. & Perryman, 2008). The low genetic divergence detected here across the equator could be mediated by overlap at the tails of each hemisphere’s breeding season; the year-round occurrence of each population in the eastern tropical Pacific as evident from stable isotopes (Busquets-Vass *et al.*, 2021) and acoustics (Stafford, Nieu Kirk, & Fox, 1999; Buchan, Stafford, & Hucke-Gaete, 2015); and the eastern tropical Pacific

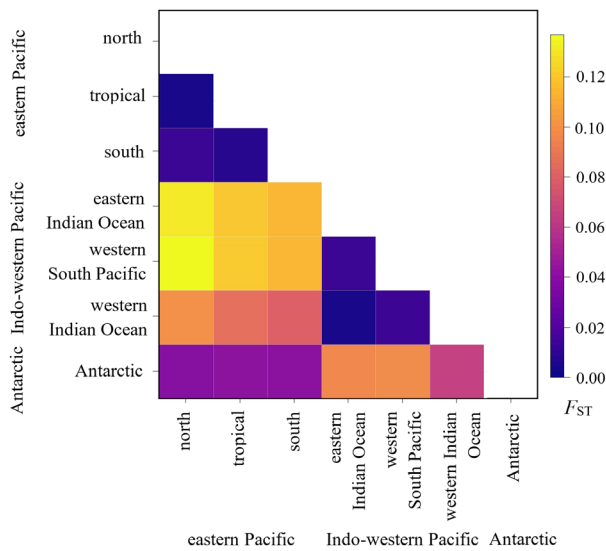


Figure 4 Genetic differentiation (F_{ST}) of blue whales (*Balaenoptera musculus*) at 16,661 SNPs (also see Table S2).

acting as a transition zone between the populations, as evident in the genomic data and a traditional genetic dataset (LeDuc *et al.*, 2017). An alternative explanation to the low divergence across the equator is that one of the populations was extirpated during whaling and has since been recolonized by the population in the other hemisphere. This hypothesis, however, seems improbable because blue whales from the eastern North Pacific and the eastern South Pacific exhibit similar levels of genetic diversity, which suggests no founding event (although no evidence of a founding event could be confounded by other factors). Also, only one to

three generations (Taylor *et al.*, 2007) have passed since the end of 20th-century whaling (Branch *et al.*, 2007), which would likely be insufficient to evolve the low level of divergence found here. There has also likely not been recolonization since whaling because blue whale calls have been divergent between the eastern North and eastern South Pacific since at least the end of whaling (McDonald *et al.*, 2006). If there was a recent founder event, the calls would likely be the same on either side of the equator.

Another unexpected finding of the genomic data is no evidence of multiple populations within the Antarctic subspecies. This result contradicts previous suggestions of multiple populations based on traditional genetic datasets (Sremba *et al.*, 2012; Attard *et al.*, 2016). The finding from genomic data is supported by the results of ‘Discovery’ marks, as the Discovery marks showed Antarctic blue whales can travel more than 100 degrees of longitude in the Antarctic between the location of tagging and eventual capture by whalers (Brown, 1962; Branch *et al.*, 2007). The number and distribution of Antarctic blue whale populations have been difficult to determine as there are no apparent geographic barriers in their feeding ground and samples are only available from the Antarctic. There is no acoustic divergence within the Antarctic, and Antarctic blue whales appear to migrate to lower latitudes during the breeding season based on acoustic detections (Stafford *et al.*, 2004). The previous inference of multiple Antarctic populations was possibly driven by some limited movements, gene flow or a combination from other blue whale subspecies, as the previous studies had no (Sremba *et al.*, 2012) or limited (only eastern Indian Ocean blue whales (Attard *et al.*, 2016)) baseline samples from other subspecies to detect such patterns. The signal of multiple populations could also have been

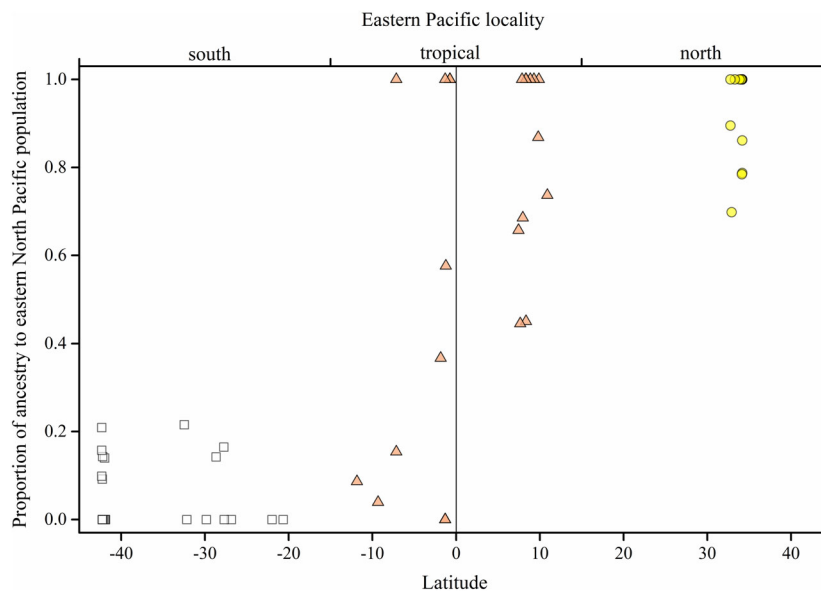


Figure 5 Relationship between latitude and ancestry of blue whales (*Balaenoptera musculus*) sampled in the eastern Pacific. Ancestry was estimated using 16,661 SNPs in ADMIXTURE on the subset of individuals that had at least 0.9 ancestry to the eastern Pacific in fastSTRUCTURE (see Fig. 3). Color coding and shape are the same as in Fig. 1.

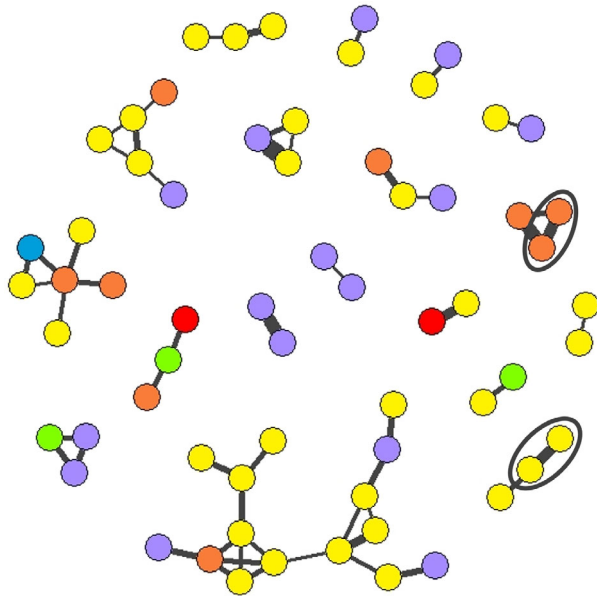


Figure 6 Pairwise relatedness network of individuals with at least 0.9 ancestry to Antarctic blue whales (*Balaenoptera musculus intermedia*) in fastSTRUCTURE (see Fig. 3a). Nodes represent individuals, and the color of the nodes represents the IWC Management Area (see Fig. 1) where the individual was sampled (color coding same as Fig. 2d: I, blue; II, red; III, yellow; IV, orange; V, purple; and VI, green). Edge widths are proportional to Ritland's estimator of relatedness, and are only displayed when the pairwise relatedness is at least 0.1. The ovals indicate known mother–calf pairs based on field observations. The calves were included in this relatedness analysis for reference, and are in no other data analyses of this study. Individuals that clustered on the left of the PCA of Antarctic samples (Fig. 2d) are some of the relatedness group of 15 individuals, and those that clustered on the bottom right of the PCA are the relatedness group of 5 individuals.

influenced by the relatively high number of related individuals within the Antarctic, as detected here. The high number is likely because Antarctic blue whales were the most exploited blue whale subspecies from 20th-century whaling, having been reduced from 239,000 to 360 individuals and are now recovering in numbers (Branch, Matsuoka, & Miyashita, 2004; Branch, 2007). This means individuals born post-whaling would inevitably include related individuals. Fortunately, we found negligible evidence of inbreeding. There is no clear evidence of site fidelity to feeding localities in the Antarctic because the related individuals are between both nearby and distant localities in the Antarctic. Also, there do not seem to be more related individuals in a given area than in other areas, as the proportion of related individuals from different localities aligns with the proportion of samples from different localities in the Antarctic. The difference in population structure findings between studies is unlikely due to differences in samples, as all the Antarctic samples were from the same collection held at the Southwest Fisheries Science Center in the USA, the number of Antarctic samples was large and similar across studies (117, current

study; 142 (Attard *et al.*, 2016); and 166 (Sremba *et al.*, 2012)) and the geographic coverage is the same across the Antarctic among the studies. Our findings for Antarctic blue whales emphasize the need to take care in interpreting genetic data when there could be conflating factors, such as connectivity from unsampled adjacent localities.

The current study found evidence of both adaptive (i.e. ecologically relevant) and neutral divergence among the high-level blue whale groups, suggesting those groups should be considered evolutionarily significant units (ESUs) for management and conservation – regardless of their subspecies status. An ESU is essentially a population or group of populations that are evolving independently, and so should be conserved to ensure the maintenance of evolutionary potential (Funk *et al.*, 2012; Hoelzel, 2023). The maintenance of evolutionary potential is paramount for populations to adapt to contemporary environmental change. The current study identified 18 significant SNPs that are potentially under adaptive selection and divergence between the high-level groups. Each of these SNPs usually had a highly divergent allele frequency in one of the high-level groups compared with the remaining high-level groups (Fig. 7). The adaptive divergences between the high-level groups are perhaps related to physiological and behavioural adaptations to different migratory routes, oceanographic conditions at the destinations and prey resources (e.g. Santora *et al.*, 2010; Gill *et al.*, 2011; Olson *et al.*, 2015; Barlow *et al.*, 2020). Blue whales also exhibit morphological differences among the high-level groups (Branch *et al.*, 2007; Gilpatrick Jr. & Perryman, 2008; Ortega-Ortiz, Gómez-Muñoz, & Gendron, 2018; Leslie *et al.*, 2020; Pastene, Acevedo, & Branch, 2020). The morphological differences are potentially reflective of adaptations to the environment, phenotypic plasticity or a combination. Most of the candidates for adaptive divergence were in introns or intragenic regions, so may control the expression of a gene or be physically linked to a gene under selection. A candidate was associated with the PLCZ1 gene, which is a metabolic gene that appears to have been selected during the evolution of marine mammals to increase blubber thickness (Wang *et al.*, 2015). The extent of energy storage and thermal insulation needed from blubber conceivably diverges for blue whales in different localities and migratory routes, depending on food availability and water temperatures. The current study is limited in its ability to detect putatively adaptive loci because the SNPs are only a reduced representation of the genome. Whole-genome population studies and comparisons with environmental conditions are needed to better understand adaptive divergences within blue whales and potentially in other baleen whales.

Our study helps refine knowledge of blue whale population structure in the Indo-western Pacific. The genomic data at the highest hierarchical level grouped together the blue whales in the Indo-western Pacific. The grouping together of Indo-western Pacific blue whales aligns with the current classification of populations throughout this range in the Southern Hemisphere as pygmy blue whales. The Indo-western Pacific blue whales had the lowest genetic diversity of the high-level hierarchical groups, which is likely due to

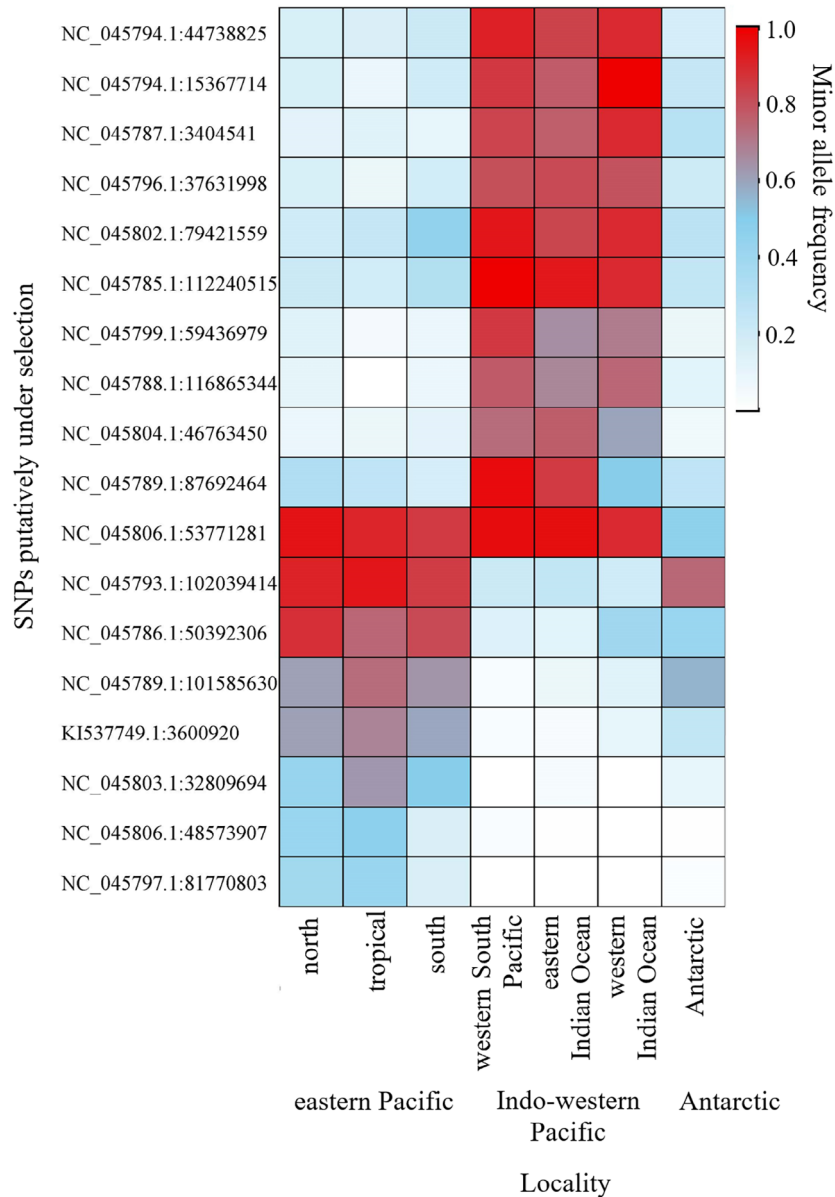


Figure 7 Heatmap of minor allele frequencies in the 18 SNPs putatively under selection among blue whale (*Balaenoptera musculus*) groups (also see Table S7). The name of the SNP is the SNP's scaffold: position on the reference blue whale genome (Table S5).

climate-induced diversification rather than anthropogenic impacts (Attard *et al.*, 2015). Our study identified the eastern Indian Ocean (i.e. off Australia), western South Pacific Ocean (i.e. off New Zealand) and potentially western Indian Ocean (i.e. off Madagascar) as different populations within the Indo-western Pacific. Blue whales in this range have negligible morphological divergence (Branch & Mikhalev, 2008), but show acoustic divergence among these three localities (McDonald *et al.*, 2006; Samaran *et al.*, 2013; Balcazar *et al.*, 2015; Torterotot *et al.*, 2020). The low ($F_{ST} = 0.01$) but significant genomic divergence between the eastern Indian Ocean and western South Pacific complements previous evidence of divergence based on mtDNA (Barlow

et al., 2018). More DNA samples from the western Indian Ocean (here only $n = 5$) are needed to determine if the very low but significant divergence ($F_{ST} = 0.002$) from the eastern Indian Ocean is biologically meaningful. The genomic data also confirmed that the blue whales transiting through Geographe Bay in south-west Australia are part of the eastern Indian Ocean population (Attard *et al.*, 2010; Attard *et al.*, 2018). The current study is the first DNA study to include blue whales sampled in Geographe Bay. The genomic population identity of blue whales transiting through Geographe Bay aligns with acoustic (Salgado Kent *et al.*, 2012), photo-identification (Gill *et al.*, 2011) and satellite track (Möller *et al.*, 2020) data.

The mtDNA and nuclear data presented here suggest that northern Indian Ocean blue whales are at least a separate population from other blue whales. The northern Indian Ocean blue whales were genetically most similar, but with evidence of divergence, to the other blue whales sampled in the Indo-western Pacific. This aligns with acoustic (McDonald *et al.*, 2006) and morphological (Branch & Mikhalev, 2008) data. Northern Indian Ocean blue whales are currently classified as a separate subspecies, suggested by the expectation of opposite breeding seasons and negligible movement across the equator. However, this assumption has fallen short for blue whales in the eastern Pacific based on the genomic data. Also, the calls of northern Indian Ocean blue whales have been detected south of the equator (Samaran *et al.*, 2013; Cerchio *et al.*, 2020; Leroy *et al.*, 2021). Based on acoustic differences, the northern Indian Ocean may include divergent western, central and eastern blue whale populations (Cerchio *et al.*, 2020; Leroy *et al.*, 2021). More DNA samples are needed from the northern Indian Ocean to clarify the number of populations and whether they are pygmy blue whales or a separate subspecies (Anderson *et al.*, 2012; Ilangakoon & Sathasivam, 2012).

Our findings build on decades of work to improve the management of endangered blue whales under the IWC. We expect the IWC to use these findings to refine the stock delineations of blue whales. We recommend the ESUs for conservation and management purposes are the three major groupings identified: the eastern Pacific blue whales, the pygmy subspecies of the Indo-western Pacific and the Antarctic subspecies. The lower-level conservation units we identified within the eastern Pacific are the eastern North Pacific and the eastern South Pacific (i.e. off Chile), and within the Indo-western Pacific are the eastern Indian Ocean (i.e. off Australia), the western South Pacific (i.e. off New Zealand) and the northern Indian Ocean. No lower-level conservation units were identified within the Antarctic. We recommend that national management bodies minimize human activities that can impact these management groups when the blue whales are within their jurisdiction. Our genomic data complement phenotypic evidence from acoustics, morphology, photo-identification, sighting records, satellite tracks and stable isotopes. In the future, the geographic range of the current study could be expanded to include blue whales from the central and western North Pacific and additional samples from the North Atlantic. While no published studies incorporate genetic comparisons of blue whales from these regions, these whales are acoustically divergent (McDonald *et al.*, 2006) and there are morphological differences between the central-western North Pacific blue whales and the eastern North Pacific blue whales (Gilpatrick Jr. & Perryman, 2008).

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Author contributions

C.R.M.A., L.M.M. and L.B.B. conceived and designed the study. C.R.M.A., J.S.-C., A.R.L., B.G.V., L.G.T., R.B., K.C.S.J., P.C.G., C.L.K.B., M.S., M.-N.M.J., M.G.M. and L.M.M. collected the data. C.R.M.A. and J.S.-C. analysed the data. C.R.M.A., J.S.-C., A.B., L.M.M. and L.B.B. interpreted the data. C.R.M.A. led the writing of the paper, with input from J.S.-C., A.B., L.M.M. and L.B.B. All authors reviewed a draft of the paper and gave final approval for publication.

Data availability statement

Genomic data are available from FigShare at <https://doi.org/10.6084/m9.figshare.25241827>.

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Supporting information

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

Appendix S1. Supporting information.