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Cradles and museums of Antarctic teleost biodiversity

Alex Dornburg^{1*}, Sarah Federman², April D. Lamb^{1,3}, Christopher D. Jones⁴ and Thomas J. Near^{2,5}

Isolated in one of the most extreme marine environments on Earth, teleost fish diversity in Antarctica's Southern Ocean is dominated by one lineage: the notothenioids. Throughout the past century, the long-term persistence of this unique marine fauna has become increasingly threatened by regional atmospheric and, to a lesser extent oceanic, warming. Developing an understanding of how historical temperature shifts have shaped source-sink dynamics for Antarctica's teleost lineages provides critical insight for predicting future demographic responses to climate change. We use a combination of phylogenetic and biogeographic modelling to show that high-latitude Antarctic nearshore habitats have been an evolutionary sink for notothenioid species diversity. Contrary to expectations from island biogeographic theory, lower latitude regions of the Southern Ocean that include the northern Antarctic Peninsula and peripheral island archipelagos act as source areas to continental diversity. These peripheral areas facilitate both the generation of new species and repeated colonization of nearshore Antarctic continental regions. Our results provide historical context to contemporary trends of global climate change that threaten to invert these evolutionary dynamics.

Since the onset of glacial conditions in the Oligocene epoch, Antarctica's climate has been characterized by periods of global warming and cooling that have had a pronounced impact on its marine biodiversity^{1–3}. Recurring glacial cycles associated with climatic oscillations are hypothesized as providing key ecological opportunities for the diversification of the highly endemic fauna of the Southern Ocean¹. However, during times of glacial maxima the Southern Ocean is also hypothesized to be characterized by high levels of local extirpation and lineage extinction^{1,4}. This raises the question of whether there are general biogeographic pathways facilitating the persistence and subsequent re-colonization of lineages following glacial maxima in the Southern Ocean. Specifically, understanding colonization patterns and the biogeographic source-sink dynamics of diversification in Antarctic marine organisms is important for contextualizing contemporary changes in community diversity, as well as the pathways of species invasion in a rapidly warming Southern Ocean.

Three mechanisms are generally proposed to explain the persistence of the Southern Ocean's marine fauna during periods of glacial maxima: (1) isolation in small refugia high-latitude Antarctic (HLA) nearshore habitats; (2) movement to deeper waters; and (3) range shifting to peri- and sub-Antarctic islands^{5,6}. These three biogeographic hypotheses each illustrate fundamentally different modes of persistence and radiation of the Southern Ocean marine fauna. Exploring whether one mechanism is more broadly relevant than the others is important for understanding the maintenance of Southern Ocean biodiversity and for predicting responses to climate change. For example, assuming new ecological opportunities follow glacial maxima, Antarctica would act predominantly as a cradle of biodiversity under the small refugia hypothesis (Fig. 1a). In contrast, movement to deeper water habitats as a result of higher extinction in HLA habitats would yield lineages colonizing areas both within and outside the HLA (Fig. 1b). Under this scenario, the

HLA would facilitate a higher rate of immigration into sub-Antarctic areas, essentially acting as a centre of lineage export. Range shifting presents a third set of expectations, limiting the accumulation of in situ diversity and instead requiring pulses of colonization to populate the HLA following glacial maxima. In its extreme case, asymmetric immigration rates into the HLA coupled with high rates of local extinction would yield an Antarctic continent that acts as an evolutionary sink of polar biodiversity⁷ (Fig. 1c). Understanding to what extent these broad expectations characterize the generation and maintenance of biodiversity is key to understanding the evolution of this endemic and unique fauna, and is integral for effective stewardship of the living resources in the Southern Ocean.

The teleost fauna of the nearshore continental shelf regions of the Southern Ocean is unusual in that the bulk of diversity and abundance is dominated by one clade: the notothenioids¹. These fishes are ecologically and economically important; they form the basis of several international marine fisheries⁸, are studied as a model of adaptive radiation^{1,9,10}, and contain several species that are critical links in the Antarctic marine food web between lower-trophic-level consumers and higher-level predators such as whales, seals and penguins^{8,11}. The persistence and success of notothenioids in the Southern Ocean has been correlated with the evolution of anti-freeze glycoproteins in the Oligocene (~25 Myr ago; Ma)^{9,12}, but extant notothenioid species diversity corresponds to a period of secondary Antarctic cooling beginning in the late Miocene (14 Ma)^{9,13}. This more recent evolutionary radiation is correlated with glacial oscillations that acted to periodically reset the ecological stage of Antarctic marine habitats between periods of pronounced warming and relatively rapid periods of cooling¹. However, the biogeographic pathways allowing species to persist through these climatic transitions remain largely unknown. Owing to the collapse of primary productivity and obliteration of nearshore habitats by grounded ice sheets during periods of glacial maxima, regions of HLA

¹North Carolina Museum of Natural Sciences, Raleigh, NC 27601, USA. ²Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA. ³Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695, USA. ⁴Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, USA. ⁵Peabody Museum of Natural History, Yale University, New Haven, CT 06520, USA.

*e-mail: alex.dornburg@naturalsciences.org

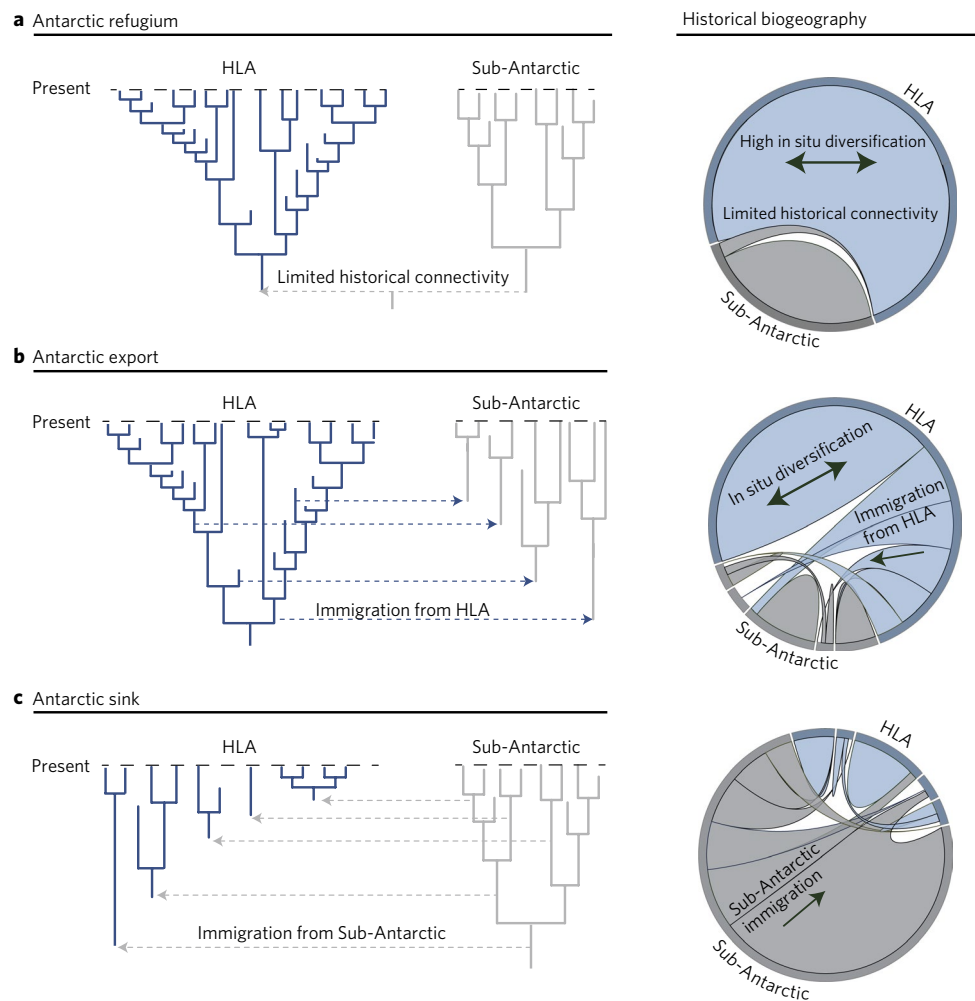


Fig. 1 | Expectations of dominant biogeographic patterns¹¹ under three models of origination and persistence. **a, Isolation in small refugia depicts a signature of Antarctica acting primarily as a cradle for biodiversity. In this model, lineages are largely restricted to continental refugia during times of glacial maxima and then take advantage of new ecological opportunities that promote diversification as glaciers recede and nearshore communities reassemble. This model generates a tree topology with high levels of in situ diversification in the HLA nearshore marine habitats, while the biogeographic connectivity (illustrated through a chord diagram depicting connectivity patterns) between the HLA and peripheral areas is limited. **b**, Movement to deeper waters facilitates biogeographic connectivity, making Antarctica an important source of peripheral area biodiversity. Following glacial maxima, lineages within the HLA experience ecological opportunity and diversification as in **a**, while more widespread biogeographic connectivity in deeper waters also allows for colonization of nearshore peripheral areas and creates a phylogenetic pattern with numerous peripheral lineages that possess HLA origins, leaving a strong signature of the HLA acting as a source for one or numerous peripheral areas. **c**, Range shifting to peripheral areas produces a phylogenetic pattern similar to those exhibited by sinks of biodiversity. Given the same expectations of ecological opportunity as **b** and **c**, changes in suitable habitat during times of glacial maxima and the presence of lineages already in peripheral areas impose constraints on the number of lineages able to transition out of Antarctica⁶⁵. Colonization rates would be asymmetric, with more immigration from peripheral areas into the HLA than in situ lineage accumulation and export (that is, favouring higher values of immigration into the high Antarctic following glacial maxima over immigration into peripheral areas during periods of sea-ice scouring). A similar pattern could also result when speciation primarily occurs in the sub-Antarctic and range shifts are promoted through biotic interactions⁶⁶.**

refugia were probably limited¹⁴. This limitation raises the possibility that peripheral or lower latitude regions that might otherwise be hypothesized to act as sinks played critical roles in the diversification and maintenance of HLA notothenioids.

Results and discussion

To explicitly test the role of peripheral areas in notothenioid evolution, we integrated a time-calibrated molecular phylogeny with maximum-likelihood-based biogeographic modelling¹⁵. Our time-calibrated phylogeny sampled 89 species that represent all major evolutionary lineages of notothenioids¹ (Fig. 2a). Geographic ranges of each species were based on distribution data from museum collections and

the primary literature (Fig. 2a). We simultaneously accounted for phylogenetic and biogeographic model uncertainty by conducting analyses across the phylogenetic Bayesian posterior distribution, and additionally across a series of biogeographic model parameterizations. All analyses consistently demonstrated the importance of one peripheral zone, the Antarctic Peninsula–South Shetland Islands region (APSS), as a source area of HLA notothenioid species diversity (Fig. 2). The estimated role of the HLA as a biogeographic sink through evolutionary time was emphasized by the relatively recent divergence times of most HLA endemic lineages, as well as the finding that peripheral areas were estimated as ancestral to all of the deeper nodes in the notothenioid phylogeny (Figs. 2 and 3a,b).

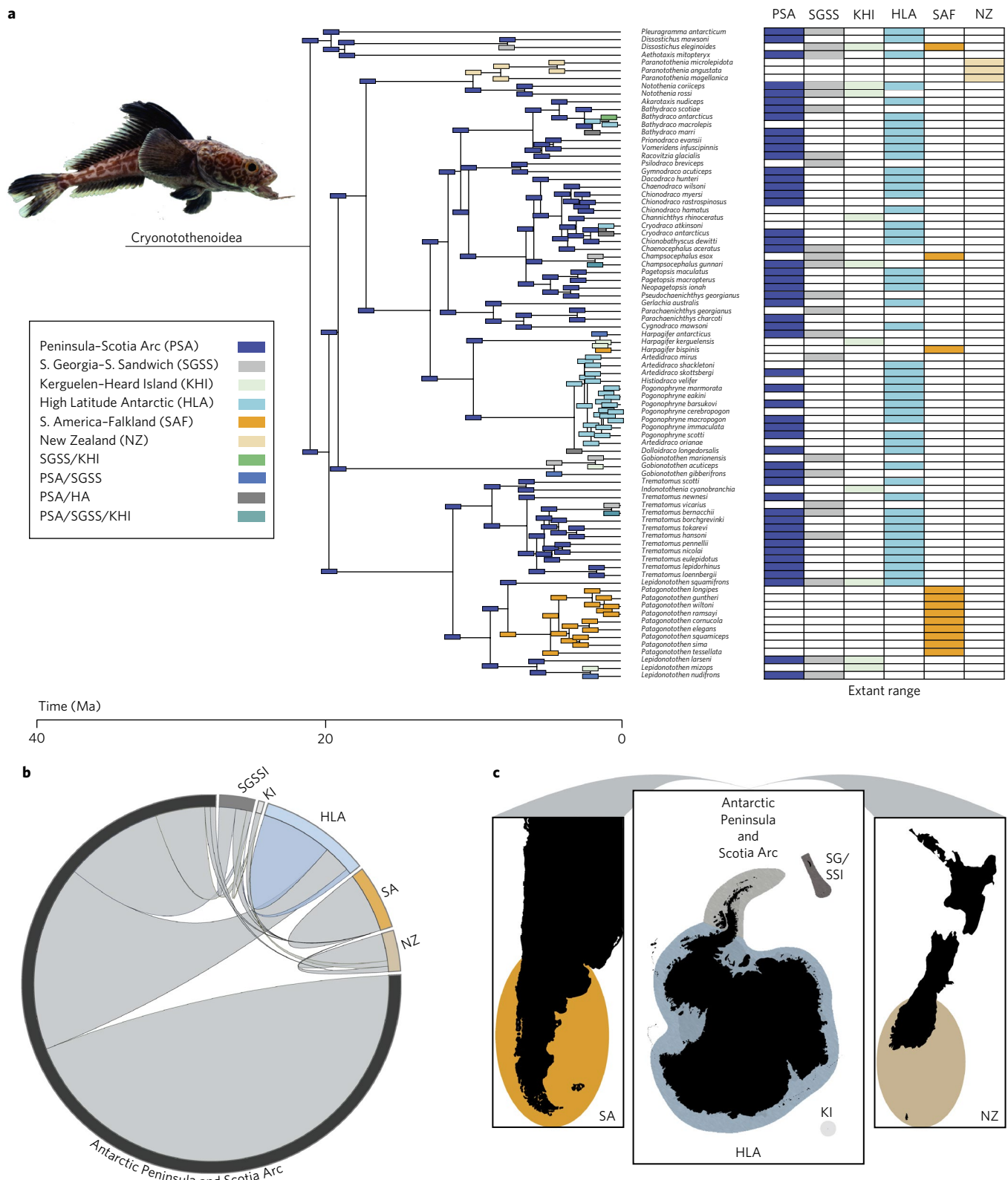


Fig. 2 | Biogeographic transitions in the Southern Ocean. a, Distribution and ancestral areas of notothenioids estimated using BioGeoBEARS, where tips represent present-day species distributions. Colours correspond to six primary biogeographical areas: Peninsula-Scotia Arc (PSA), South Georgia and South Sandwich Islands (SGSS), Kerguelen-Heard Island (KHI), HLA, southern South America and Falkland Islands (SAF), and New Zealand (NZ). Nodes where species distributions were reconstructed across multiple areas are indicated by additional colours. **b**, Chord diagram showing lineage transitions among biogeographic regions (SGSSI, South Georgia South Sandwich Islands; KI, Kerguelen Island; SA, South America), each of which is coloured and labelled on the periphery of the diagram. **c**, Illustration of considered areas, with colours corresponding the areas illustrated in **b**. Lineage transitions are illustrated in light grey, with the frequency of transition proportional to the size of the chord.

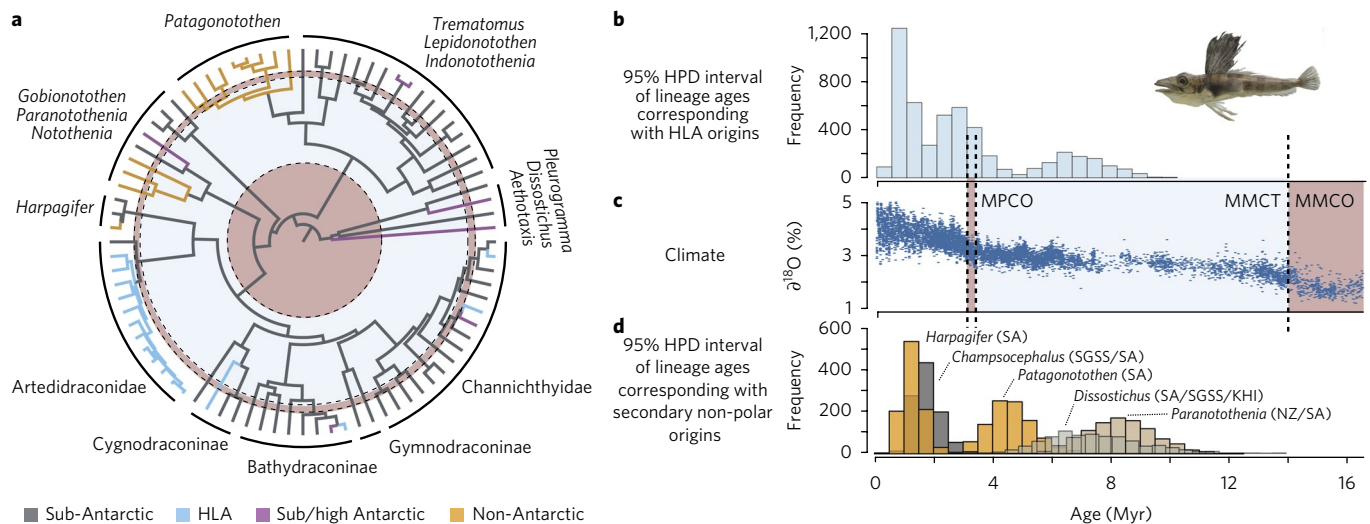


Fig. 3 | Patterns of HLA endemism and biogeographic transitions to non-polar areas. **a**, Time-calibrated phylogeny of the Cryonotothenioidea. Major clades are labelled at the tips, which are coloured according to contemporary lineage geographic distributions. **b**, The 95% highest posterior density (HPD) intervals of age estimates for lineages endemic to HLA nearshore areas. **c**, Climatic transitions depicted by oxygen isotopes. Coloured bars that represent periods of warming and cooling are also highlighted in **a**. MPCO, Middle Pliocene Climatic Optimum; MMCT, Middle Miocene Climatic Transition; MMCO: Middle Miocene Climatic Optimum. **d**, The 95% HPD interval of age estimates for the origins of secondarily non-polar notothenioids^{57–60}.

Expectations concerning the role of peripheral areas and islands in the maintenance of continental biodiversity are changing¹⁶. Rather than acting as evolutionary dead ends, islands have the potential to reseed continental biodiversity following periods of climatic instability¹⁶. During times of glacial maxima, Antarctica's continental marine habitats may be disproportionately affected by ice scouring relative to habitats that are geographically peripheral to nearshore Antarctica¹⁴. By considering these large-scale glaciation cycles it is expected that nearshore marine habitats around the Antarctic continent will experience pulses of extinction at different rates to those in lower latitude peripheral areas. Such a scenario would invert typical source–sink dynamics between islands and continental regions¹², and allow colonization of continent habitats from island populations (Fig. 1c). While colonization to the HLA can facilitate rapid lineage diversification, such as observed in the Artedidraconidae¹, the ages of origination for HLA endemic species are consistently young, with most being less than 4 Myr old. Despite the presence of lineages that exhibit bursts of diversification, increased rates of turnover largely render the HLA a biogeographic sink and not an area of substantial lineage origination over macroevolutionary timescales. This source–sink relationship begs the question of how diversity is maintained in the peripheral areas of the Southern Ocean. Our results support widespread biogeographic connectivity among Antarctic peripheral areas¹⁷ and between the Antarctic peripheral areas and cold-temperate non-Antarctic regions (Fig. 2b), and identify the APSS as the primary gateway out of the HLA (Fig. 3). We found evidence of multiple transitions through the APSS gateway into cold-temperate non-Antarctic regions over the past 12 Myr (Fig. 3d), providing additional inference for the central role of the APSS in maintaining both HLA and non-HLA notothenioid species diversity (Fig. 2; Supplementary Fig. 2)¹³.

In a reversal of these historical biogeographic patterns that helped to mediate the long evolutionary history and success of Southern Ocean fishes, the Antarctic Peninsula is currently emerging as the primary pathway for continental species invasions^{13,18}. These potential colonization pathways include a steady increase of human-made floating islands (flotsam) and increased ship traffic, the ballast waters of which often contain larval forms of non-Antarctic organisms^{3,13}. It is unclear whether these new arrivals will establish and change the Antarctic marine biota, nor is it clear to what

extent colonizers from outside the polar front have reshaped the benthic community over evolutionary timescales. Invasions by new predators¹⁹ or the presumed range expansion and colonization by durophagous crushing predators such as king crabs, which are primarily restricted to deeper warmer waters just off of the Antarctic shelf, have the potential to disrupt the structure of the Southern Ocean marine benthic faunal communities^{20–22}. The threat posed by newly colonizing or invasive species to Antarctica corresponds to a larger Anthropocene phenomenon of the flattening of species–area relationships and shifting of the natural distributions of animals that are increasing the frequency of exotic introductions worldwide^{23,24}.

Our study provides an evolutionary context for the role of the APSS as the primary geographic area of origination and colonization for the dominant component of the contemporary Antarctic teleost fish fauna, and highlights the potential for a rapid biogeographic reversal as a consequence of climate change. Although not as extensive as atmospheric temperature rises^{19,25}, rising oceanic temperatures in the waters surrounding regions of Antarctica and its peripheral islands have been repeatedly forecast to change both in terms of chemistry and temperature in our lifetimes^{26–28}, with the area around the APSS among the most impacted. Many notothenioid species have a low level of tolerance to changes in water temperature²⁹, including several lineages that have lost the genetic variability necessary to cope with temperature shifts³⁰. It is possible that notothenioids, like many other organisms, may shift their ranges in response to changing conditions in a manner consistent with global patterns of biodiversity range shifts forecast for the next century^{24,26}. These findings imply a future with limited dispersal opportunities across the region for notothenioids and could ultimately lead to a breakdown of population connectivity for many of these species. Additionally, Antarctica is no longer as isolated as it was even a few hundred years ago, and species invasions are a concern for both terrestrial and marine habitats¹⁸. In an almost elegant twist of fate, the area that once facilitated connectivity between peripheral areas of the Southern Ocean and the HLA is now the area most threatened with a new wave of colonizers from temperate regions^{20,21}. These new colonists have the potential to fundamentally alter Antarctica's marine ecosystems to the detriment of their unique biota^{20,21}. Assessing the ecological impact of colonizing cold-temperate marine species on the endemic Southern Ocean biota

is an urgent priority for effective conservation management of the unique living resources of Antarctica.

Methods

Estimating notothenioid divergence times. DNA alignments were generated using a combination of previously published data¹ and sequences generated for this study (Supplementary Table 1). For sequencing, DNA was isolated using Qiagen DNeasy kits, and previously published polymerase chain reaction primers^{31–33} were used to amplify and sequence two mitochondrial DNA genes: *nd2* and *16S* rRNA; and five nuclear gene regions consisting of four unlinked exons and a single intron: *RPS71*, *myh6*, *sh3px3*, *tbr1* and *zic1*. All gene regions were aligned using the computer software MUSCLE³⁴ and protein coding gene regions were checked against frame mutations or DNA substitutions that resulted in stop codons in the aligned sequences. The combined seven-gene dataset spans 89 species and contains 6,431 base pairs, with 98.5% of the data matrix (taxa and genes) complete.

Phylogenetic relationships and divergence times were simultaneously estimated using the BEAST version 1.8.2 software package^{35,36} under an uncorrelated model of molecular rates with a lognormal distribution. The dataset was partitioned by gene following refs^{1,37} with divergence times calibrated following protocols from previous studies of notothenioid divergence times^{1,10,37,38}. Following ref.¹, we placed prior age constraints on four nodes of the notothenioid phylogeny: (1) the most recent common ancestor (MRCA) of all notothenioids was calibrated using a normal distribution with a mean of 71.4 Myr and a standard deviation (s.d.) of 11.0 Myr, based on previous age estimates^{1,10}; (2) the MRCA of *Pseudaphritus urvillii* and all other notothenioids (mean, 63.0 Myr; s.d., 10.4 Myr); (3) the MRCA of *Eleginops maclovinus* and Cryonotothenioidea (mean, 42.9 Myr; s.d., 8.0 Myr); and (4) the MRCA of Cryonotothenioidea (mean, 23.8 Myr; s.d., 1.5 Myr). All these calibrations stem from ages estimated previously³⁹ and have been used repeatedly in divergence time studies of notothenioids^{1,37}. Although we did not use the fossil *Proeleginops grandestmanorum*, previous studies using this alternative prior produced age estimates consistent with those generated in this study. Using these external age estimates as calibrations offers an advantage to the use of a single fossil whose taxonomic affinity is debated⁴⁰, as they reflect the use of numerous non-notothenioid fossils and broader expectations of lineage divergence times of notothenioids within the diversity of acanthomorph fishes^{39,41}.

Analyses were run five times, with each run consisting of 3.0×10^7 generations that were sampled every 1,000 generations. Effective sample size (ESS) values for each parameter were calculated to quantify adequate sampling of the posterior distribution for each parameter within each run (ESS > 200). Convergence of model parameter values between runs was assessed by plotting the marginal posterior probabilities versus the generation state in the computer program Tracer version 1.6 (<http://beast.bio.ed.ac.uk/Tracer>). To ensure that that priors were updated by information from the sequence data, median tree heights and tree topologies were compared between runs that included or omitted all data⁴². The posterior probability density of the combined tree and log files was summarized as a maximum clade credibility tree using TreeAnnotator version 1.8.2 (<http://beast.bio.ed.ac.uk/TreeAnnotator>).

Estimates of colonization pathways. We assigned each species sampled in the phylogeny to one or more of the following seven biogeographic areas that broadly delimit ranges between high Antarctic and all other major peri-, sub- and non-Antarctic regions that are within the range of living notothenioid taxa: (1) high Antarctic, here defined as the area of marine habitats with latitudes higher than the polar circle (66° S); (2) Antarctic Peninsula and nearby islands including the South Shetland and South Orkney Islands; (3) South Georgia, Bouvet and the South Sandwich Islands; (4) Kerguelen Island; (5) South America and the Falkland Islands; (6) New Zealand including Macquarie Island; and (7) Australia (Supplementary Fig. 3). Although there are biogeographic divisions within the high Antarctic⁴³, geographic biases in survey locations along the continent may artificially inflate or deflate the biodiversity of a given region. Therefore this delimitation of ranges provides a conservative measure of transitions in and out of any portion of the high Antarctic. Distributions of extant species were taken from the primary literature^{37,44,45}. We used the R package BioGeoBEARS¹⁵ to test the fit of four biogeographic models to our data: (1) the maximum likelihood dispersal extinction cladogenesis model (DEC)⁴⁶; (2) a DEC model that allowed for a founder event parameter, *J*, which describes a speciation event common to island systems where a 'jump dispersal' event quickly results in an evolutionarily independent lineage¹⁵; (3) a DEC model that allowed for a range switching parameter, *A*, that allows lineages to quickly change ranges along a branch; and (4) a DEC model that allowed for a combination of range switching and founder event speciation. Model comparisons were evaluated using Akaike's information criterion (AIC) scores calculated from each model's log likelihood, with a difference in AIC greater than 4 indicating the best-fit model⁴⁷.

Modelling biogeographic transitions. To infer dominant dispersal and colonization pathways in the Southern Ocean, we tracked the cumulative number of transitions between biogeographic areas for each of our biogeographic models. Resulting transitions were visualized using chord diagrams in the D3 web

visualization software⁴⁸. The numbers of estimated transitions were compared between all models to assess the impact of model choice on the inference of major biogeographic pathways (Supplementary Fig. 1).

To mitigate against potential for the use of a single tree topology to generate false confidence in the fit of the best-fit biogeographic model used in generating ancestral area estimates⁴⁹, we compared the model fit conditioned on a single topology to the distribution of AIC weights for each model across 1,000 trees randomly sampled from the posterior distribution of tree topologies after the burn-in. This approach allows us to incorporate both topological and branch length uncertainty into assessments of model fit. To further accommodate model uncertainty as well as phylogenetic uncertainty, we repeated our analyses of ancestral area estimates across the posterior distribution of tree topologies with a model-averaging approach⁵⁰.

Model averaging has been used for a variety of purposes in phylogenetics^{51–53}; however, this approach has not been extended into a biogeographic framework. For each topology from the posterior, we conducted a series of BioGeoBEARS runs that included all of the candidate models outlined above. For each run we calculated the AIC weight⁴⁷ of each model fit based on the log likelihood score, and multiplied the probability of each area estimate at each node for a given run by the conditioned model's AIC weight. These probabilities were then summed to provide a model-averaged probability for each estimated area at each node. These analyses were conducted across the posterior distribution of trees and summarized using both the median of each model-averaged ancestral area probability at each node and the relative model-averaged ancestral area probability at each node.

This approach specifically allowed us to examine how uncertainty in model choice and phylogeny influenced the probability of transitions among peripheral areas and the high Antarctic. To examine these major pathways within a meaningful geologic context, we binned ancestral area estimates on the topology into intervals of 1 Myr and created heatmaps of three sets of ancestral area estimates: (1) high Antarctic endemic; (2) high Antarctic and peninsular region endemic; and (3) occurring in any non-high Antarctic region and the high Antarctic (the inverse of which would represent sub-polar-only lineages). We also plotted the posterior relative model-averaged probabilities on the maximum clade credibility tree using the R package phytools⁵⁴, allowing for a visualization of node state changes across the tree that account for both biogeographic model and phylogenetic uncertainty. Combined, these visualizations allowed us to infer when the highest connectivity between peripheral and high Antarctic areas occurred across the posterior distribution for trees, thereby also assessing the robustness of results conditioned on a single tree and model.

Data availability. Phylogenetic alignments, xml files and biogeographic datasets used in this study, along with any associated R scripts and the time calibrated phylogeny, are available in the Zenodo repository 801836 (DOI: 105281/zenodo.801836; <https://zenodo.org/record/801836>).

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Author contributions

A.D. and T.J.N. designed the study. C.D.J. and T.J.N. collected data. A.D., A.D.L. and T.J.N. performed analyses. A.D., A.D.L., S.F. and T.J.N. wrote the initial manuscript. C.D.J. contributed to the subsequent writing and development of the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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Correspondence and requests for materials should be addressed to A.D.

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