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Tracking of marine predators to protect Southern Ocean ecosystems

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Mark A. Hindell[1,2,45]✉, Ryan R. Reisinger[3,4,5,45], Yan Ropert-Coudert[3,45], Luis A. Hückstädt[6], Philip N. Trathan[7], Horst Bornemann[8], Jean-Benoît Charrassin[5], Steven L. Chown[9], Daniel P. Costa[6], Bruno Danis[10], Mary-Anne Lea[1,2], David Thompson[11], Leigh G. Torres[12], Anton P. Van de Putte[13,14], Rachael Alderman[15], Virginia Andrews-Goff[1,16], Ben Arthur[1], Grant Ballard[17], John Bengtson[18], Marthán N. Bester[19], Arnoldus Schytte Blix[20], Lars Boehme[21], Charles-André Bost[3], Peter Boveng[18], Jaimie Cleeland[1], Rochelle Constantine[22], Stuart Corney[1], Robert J. M. Crawford[23], Luciano Dalla Rosa[24], P. J. Nico de Bruyn[19], Karine Delord[3], Sébastien Descamps[25], Mike Double[16], Louise Emmerson[16], Mike Fedak[21], Ari Friedlaender[6,26], Nick Gales[16], Michael E. Goebel[26], Kimberly T. Goetz[11], Christophe Guinet[3], Simon D. Goldsworthy[27], Rob Harcourt[28], Jefferson T. Hinke[29], Kerstin Jerosch[8], Akiko Kato[3], Knowles R. Kerry[16], Roger Kirkwood[16], Gerald L. Kooyman[30], Kit M. Kovacs[25], Kieran Lawton[16], Andrew D. Lowther[25], Christian Lydersen[25], Phil O'B. Lyver[31], Azwianewi B. Makhado[23], Maria E. I. Márquez[32], Birgitte I. McDonald[33], Clive R. McMahon[1,28,34], Monica Muelbert[1,24], Dominik Nachtsheim[8,35], Keith W. Nicholls[7], Erling S. Nordøy[20], Silvia Olmastroni[36,37], Richard A. Phillips[7], Pierre Pistorius[38], Joachim Plötz[8,46], Klemens Pütz[39], Norman Ratcliffe[7], Peter G. Ryan[40], Mercedes Santos[32], Colin Southwell[16], Iain Staniland[7], Akinori Takahashi[41], Arnaud Tarroux[25,42], Wayne Trivelpiece[29], Ewan Wakefield[43], Henri Weimerskirch[3], Barbara Wienecke[16], José C. Xavier[7,44], Simon Wotherspoon[1,16,47], Ian D. Jonsen[28,47] & Ben Raymond[1,2,16,47]

Southern Ocean ecosystems are under pressure from resource exploitation and climate change[1,2]. Mitigation requires the identification and protection of Areas of Ecological Significance (AESs), which have so far not been determined at the ocean-basin scale. Here, using assemblage-level tracking of marine predators, we identify AESs for this globally important region and assess current threats and protection levels. Integration of more than 4,000 tracks from 17 bird and mammal species reveals AESs around sub-Antarctic islands in the Atlantic and Indian Oceans and over the Antarctic continental shelf. Fishing pressure is disproportionately concentrated inside AESs, and climate change over the next century is predicted to impose pressure on these areas, particularly around the Antarctic continent. At present, 7.1% of the ocean south of 40°S is under formal protection, including 29% of the total AESs. The establishment and regular revision of networks of protection that encompass AESs are needed to provide long-term mitigation of growing pressures on Southern Ocean ecosystems.

The Southern Ocean—defined here as the circumpolar waters south of 40°S—is home to a unique fauna and has an important role in biogeochemical cycles and the global climate system[1]. Past industrial sealing, whaling and demersal fishing caused marked perturbations from which some Southern Ocean ecosystems are only now starting to recover[3]. The harvesting of squid and toothfish continues[4,5] and interest is growing in the expansion of Antarctic krill (*Euphausia superba*) fisheries[6]. These target species are crucial prey for upper trophic organisms—krill is a key component of the Southern Ocean food web—and their potential depletion raises substantial concerns about the effects on Southern Ocean ecosystems[2]. Anthropogenic greenhouse gas emissions are simultaneously causing large changes to the Southern Ocean[7]. Strong interest has therefore developed in the long-term conservation of the Southern Ocean, but authorities face the considerable challenge of implementing conservation goals within existing management frameworks[2].

A first step in meeting this challenge is to identify regions that should be considered for protection, for reasons such as their high biodiversity, biological productivity or particular importance for certain life-history stages of species[8,9]. The distribution and demography of marine predators provides a viable basis for this[10]—particularly in the vast and remote Southern Ocean, where integrated ecosystem measures are difficult to obtain at management-relevant, ocean-basin scales[11]. Indeed, on-shore measures of Southern Ocean marine predators have been used as regional indicators of ecosystem status for several decades[12]. Spatial aggregations of predators at sea identify not only areas that are important to the predator species themselves—which depend on lower trophic levels[13]—but also areas of broader ecosystem importance, such as regions of elevated productivity and biomass at lower trophic levels[14]. Combining information across predator species with diverse diets and life histories is essential for an ecosystem-wide approach that is less susceptible to

A list of affiliations appears at the end of the paper.

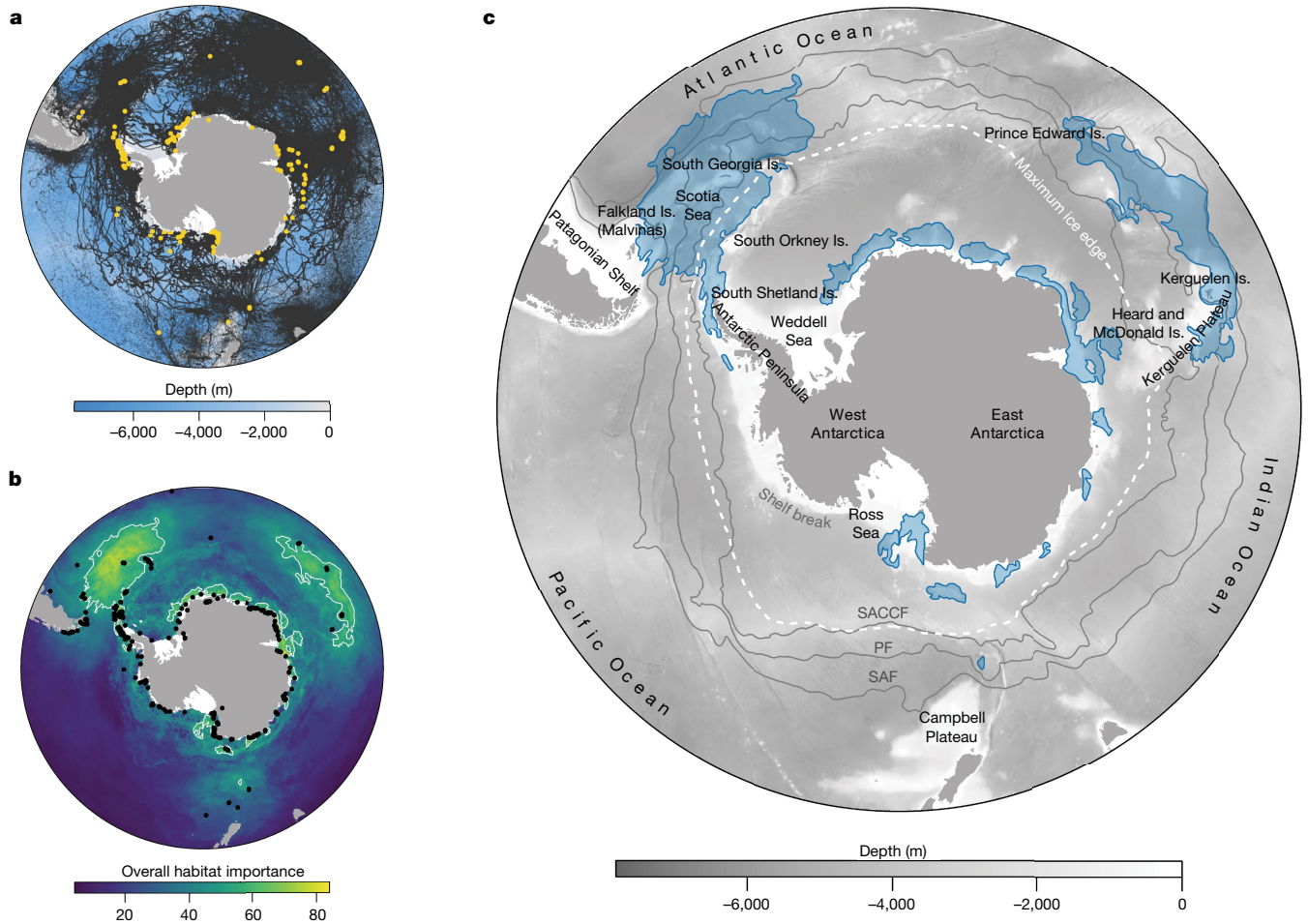

Fig. 1 | AESs in the Southern Ocean. a, Tracking data from 17 predator species were used to model the habitat importance for each species. Black points indicate tracking data and yellow points indicate tagging locations[16]. **b**, Combining these model outputs gives the overall habitat importance, and the upper decile of overall habitat importance delimits AESs (white contours). Black points indicate colony locations for the 14 colony-breeding species. **c**, AESs (blue) shown in context. Major oceanographic fronts are shown with grey lines: SAF, Sub-Antarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Current Front.

factors that affect individual species[12]. There is a growing recognition of the value of tracking data for making decisions about conservation[15].

Using predator tracking data to identify AESs

In the Southern Ocean, many predator species with differing diets and movement patterns have been tracked[16]. We synthesized tracking data from 4,060 individuals of 17 species (Fig. 1a) to provide a circumpolar assessment of regions of ecological importance in the Southern Ocean. We identified regions that were preferred by multiple predator species as indicators of high levels of lower trophic biomass and biodiversity, and refer to these regions as AESs[17]. Our definition of AESs is not the same as Ecologically and Biologically Significant Marine Areas or Key Biodiversity Areas. However, it is consistent with several of the criteria that are used for defining Ecologically and Biologically Significant Marine Areas or Key Biodiversity Areas—particularly biological productivity and diversity[8]—and so provides a similar qualitative, integrated assessment of biodiversity patterns.

We assembled tracking data from 12 species of seabird and 5 species of marine mammal. The data were collected between 1991 and 2016[16]. We used habitat-selection models (Methods, Supplementary Information, Extended Data Figs. 1–3) of individual predator species and then combined their spatial predictions to identify regions that were important to our full suite of species (Fig. 1b). This enabled us to account for incomplete tracking coverage (that is, colonies from which no animals were tracked) and predict habitat importance for each species across the entire Southern Ocean. Combined, these predictions provided an integrated and spatially explicit assessment of areas of high biodiversity and biomass at multiple trophic levels. Sea surface temperature (SST) and wind strength were most often the best predictors of habitat selectivity in these species-specific models (Extended Data Fig. 4). SST has been linked to global patterns of marine biodiversity[18], and in the Southern Ocean it acts as an indicator of water masses with different ecological properties[19]. Wind exerts several influences—including driving ocean currents and mixing; transporting iron; affecting the dynamics of sea ice; and ultimately determining primary production[20]—and has been linked, for example, to the global distribution of albatrosses and petrels[21]. The importance of other predictor variables differed among species (Extended Data Fig. 4). The relationship between habitat selectivity and environmental predictors differed across species, showing how species used their environments in different ways (Extended Data Fig. 5).

Distribution of AESs

Regions with the highest scores for overall habitat importance were identified as AESs (calculated as the upper decile of those scores).

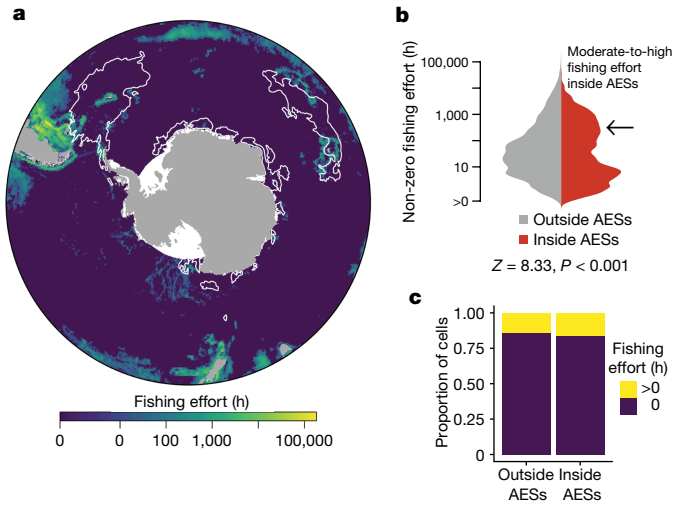

Fig. 2 | Fishing effort in the Southern Ocean. a, Map showing fishing effort (total fishing hours between 2012 and 2016[29]). Contour lines (white) indicate AESs. **b**, Kernel density plot showing the distribution of values of fishing effort (zero values not shown) inside (red) and outside (grey) AESs. Two-tailed permutation tests (n = 1,098,226 grid cells) indicate a significant difference (P < 0.001). **c**, Proportion of cells inside and outside AESs that had some (more than 0 h; yellow) or no (0 h; purple) fishing effort.

These were located over the Antarctic continental shelf (89% of AES pixels south of 60°S were over or within 200 km of the shelf) and in two northerly aggregations: one encompassing much of the Scotia Sea and surrounding waters, and the second covering the chain of sub-Antarctic islands from the Prince Edward Islands through to parts of the Kerguelen Plateau (Fig. 1c). Regions of lower importance were identified in the southern Pacific and Indian Oceans. The distribution of AESs is associated with the availability of suitable habitats for breeding and resting, as well as regional oceanography and sea-ice dynamics that affect biological production (Fig. 1c). The AESs were based on a combination of island-breeding and wholly pelagic species, and therefore reflect broad-scale patterns of importance. These patterns are supported by: (i) broad-scale patterns of primary production (Southern Ocean land masses provide iron fertilization that stimulates downstream production in this otherwise iron-limited ecosystem[22]); (ii) historical whaling catches north of 60°S, which show that relatively few whales were taken in the southern Indian or Pacific Oceans, and that the region identified as an AES in the south Atlantic corresponds with high whaling catches[23]; and (iii) previous estimates of Antarctic krill distribution, which suggest that concentrations are high in the south Atlantic and lower in the south Pacific and southern Indian Ocean[24]. The AES in the south Atlantic corresponds to the area of increased krill biomass, whereas the AES in the Indian Ocean partially corresponds to a region dominated by myctophid fish and other euphausiids[25].

Exposure of AESs to potential stressors

The Southern Ocean is subject to several stressors that influence its ecosystems, including an expansion of resource extraction and rapid climate change[26]. We note that both temperature and wind—which were key parameters in many of our species-specific habitat models—are changing, and are projected to continue to do so[27].

Fishing has both direct effects on Southern Ocean biota through incidental bycatch and indirect effects through resource competition[28]. Many demersal finfish were exploited during the latter part of the 20th century, which led to the decimation of some stocks in the Antarctic and sub-Antarctic[5]. Finfish fishing in the Antarctic is now regulated, and is focused on toothfish species caught with longlines. Fisheries for Antarctic krill began in the 1960s and are now concentrated in the south Atlantic sector, most notably at the Antarctic Peninsula and South Shetland Islands, the South Orkney Islands and South Georgia[6]. Krill is managed with a low, precautionary catch limit that takes account of the key role of krill in the Antarctic food web. By global standards, fishing pressure in the Southern Ocean is low[29], but indications are that pressure on its marine resources will grow[2,5,6]. Fishing effort (Fig. 2a) was significantly different inside and outside of AESs (Fig. 2b), with a disproportionate amount of moderate-to-high effort (100 or more total hours of fishing) occurring inside AESs. Of cells with a moderate-to-high fishing effort, 37.9% were inside AESs, despite AESs only representing 10% of the study area. Areas of conspicuous fishing effort around southern South America, New Zealand and Australia should be treated with caution, as our study does not include temperate predator species that are likely to figure prominently in these ecosystems (Fig. 2a). Nonetheless, relatively high-intensity areas of fishing that are directly relevant to the Southern Ocean occurred around the Falkland Islands (Islas Malvinas), where squid and some finfish are targeted; around South Georgia (ice fish, krill and toothfish); at the West Antarctic Peninsula (krill); and over the Kerguelen (toothfish and ice fish) and Campbell (squid and finfish) plateaux[4–6]. Relatively important fisheries for toothfish also occur within the Ross Sea[30].

The physical attributes of the Southern Ocean are changing. Sea ice is a critical component of high-latitude ecosystems and has central roles in oceanographic, biogeochemical and ecological processes. The biological consequences of sea-ice changes in the Southern Ocean include changes in breeding-site availability or access and prey availability, and changes to the structure and function of ecosystems[31]. The pattern of sea-ice change in the Antarctic displays considerable regional and temporal variation. In the West Antarctic Peninsula, the extent of sea ice has declined markedly in recent decades, but has increased in other areas[32]. Most climate projections indicate that overall sea ice will decline over the next century[27]. Given the broad influence of both SST and wind on ecosystems, these components can also influence aspects of the biology of animals, including their breeding phenology, foraging success, survival and reproductive performance[26]. However, when we contrasted the rates of change of sea-ice duration, SST and wind patterns inside and outside of AESs there were only slight differences, and considerable regional variation (Extended Data Fig. 6). The subtle nature of the differences in environmental change inside versus outside AESs does not negate the fact that the study area overall is undergoing marked changes in physical environmental processes, and that ecologically important areas are not being spared from these changes.

Assessment of spatial management

Management of marine systems is complex, especially in areas that lie beyond national jurisdiction[33] and where international effort is therefore required, particularly for species that move between national and international waters[34]. Relevant management includes traditional process-oriented tools such as individual species protection, stock assessments, decision rules and catch limits, as well as spatial tools such as marine protected areas (MPAs)[35], but also altered fishing practices for mitigating bycatch[36]. In the high-latitude Southern Ocean, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) uses an ecosystem-based management framework that is intended to ensure that there are no long-term effects from fisheries on marine ecosystems[37]. This includes setting precautionary, spatially explicit catch quotas and a call for the establishment of a network of MPAs—the design considerations of which can include the potential to provide climate change refugia and the inclusion of reference areas to help separate the effects of fishing from climate-related environmental change. Both approaches will benefit from better understanding of the locations of AESs. Outside the CCAMLR framework, MPAs have also been established by sovereign management authorities around some sub-Antarctic islands (Fig. 3a). Several other MPAs are currently under

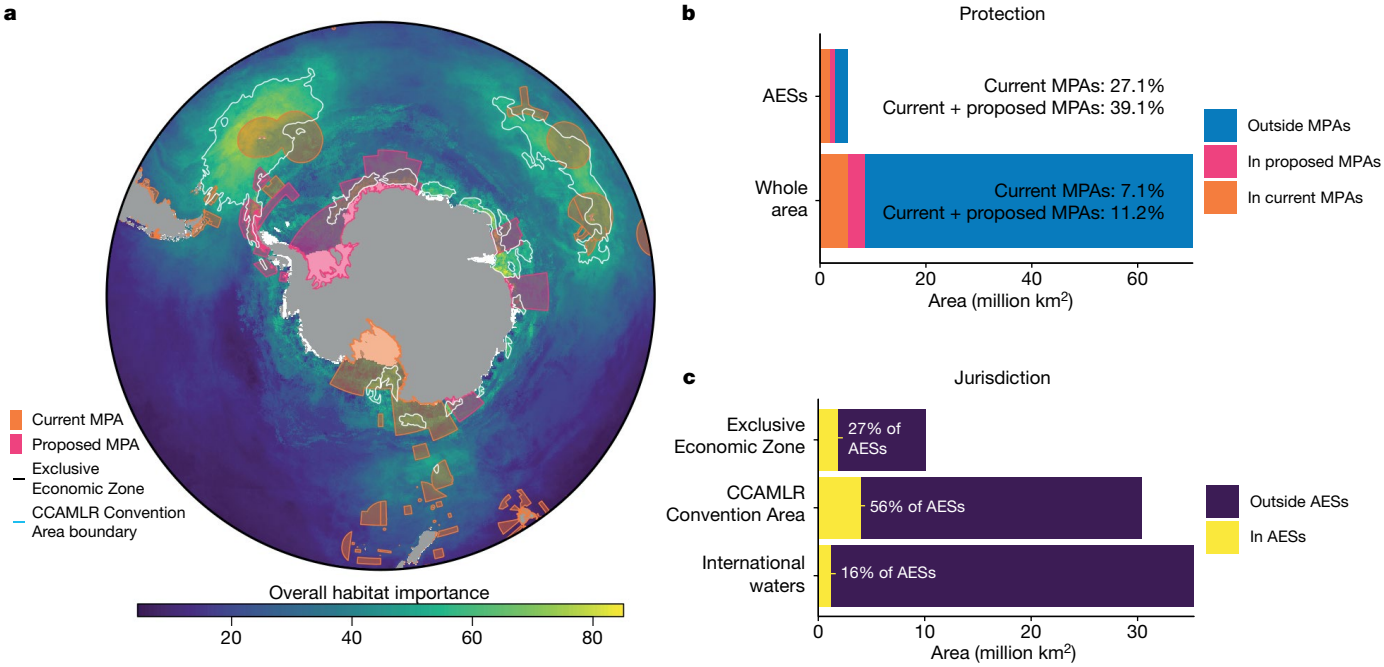

Fig. 3 | Spatial protection of Southern Ocean AESs. a, Current (orange) and proposed (magenta) MPAs superimposed on overall habitat importance. White contours denote AESs, black lines show national Exclusive Economic Zones and the blue line shows the CCAMLR Convention Area. **b**, Area in current (orange) and proposed (magenta) MPAs, and outside MPAs (blue). **c**, Area inside and outside AESs in national Exclusive Economic Zones, the CCAMLR Convention Area and the international waters outside these two areas.

development, including within CCAMLR and by national authorities (Fig. 3a). However, the level of protection afforded by any individual MPA depends on its governance structure and the type and level of permitted activities (for example, fishing)[9,38].

An appropriately designed network of protected areas can help to buffer the effects of climate change and reduce the effect of stressors such as bycatch or competition from fisheries[39]. We therefore quantified the coverage and placement of individual MPAs with reference to identified AESs. Overall, 7.1% of the ocean south of 40°S is currently protected by MPAs, and this would increase to 11.2% if all currently proposed MPAs were implemented (Fig. 3b). This already meets, in a regional setting, the global Aichi Biodiversity Target 11 of 10% by 2020. The level of protection of the Southern Ocean is high by global standards—only 3.6% of the world's oceans has MPA status at present, increasing to 7.3% with the addition of planned and announced MPAs[38]. However, protection needs to be targeted at areas of high conservation value, including those that are important for the persistence of biodiversity[9]. Existing MPAs cover 27% of the AESs identified (Fig. 3b). Southern Ocean MPAs are predominantly in sub-Antarctic regions, and here they show high levels of congruence with AESs (Fig. 3a). Of note is the Davis Bank region, south of the Falkland Islands (Islas Malvinas), where there are high levels of fishing inside AESs (Figs. 1, 2a, b). This area is now part of an MPA that was recently implemented by Argentina (Fig. 3a). Adoption of proposed MPAs for the Antarctic continental margins would raise the MPA coverage of AESs to 39% (Fig. 3b), including areas in East Antarctica, the Weddell Sea and the Antarctic Peninsula. The largest total AESs (4.0 million km^2; 56% of AESs) are under CCAMLR jurisdiction (Fig. 3a, c), followed by 1.9 million km^2 (27% of AESs) in national waters (Exclusive Economic Zones), and only 1.2 million km^2 (16% of AESs) are outside the CCAMLR Convention Area and national waters (Fig. 3c). Implementation of MPA proposals would benefit Southern Ocean ecosystems, especially those in the Antarctic Peninsula, East Antarctic and Weddell Sea.

Likely effects of future climate change

We estimated the likely effects of future climate change on the distribution of AESs under two representative concentration pathway (RCP) simulations: a medium-forcing scenario (RCP4.5) and a more extreme, high-forcing scenario (RCP8.5)[40]. For each scenario, eight global climate models—considered to be most suitable for Southern Ocean studies owing to their reliable reproduction of extant sea-ice conditions—were used to predict the locations of AES-like habitats in 2100. Here we discuss only the RCP8.5 results, as current emissions of carbon dioxide are in line with this scenario[41]. Results for the moderate RCP4.5 scenario are presented in Extended Data Fig. 7. There was an overall reduction in the AES-like area (−3.3%), partitioned into an increase in sub-Antarctic AES-like cells (+5.7%) and a decrease in Antarctic AES-like cells (−10.2%) that outweighed this increase.

In the sub-Antarctic, AES-like areas generally moved south (Fig. 4a), resulting in an overall growth in the area of sub-Antarctic AESs (Fig. 4b). This general southward migration of important habitat is consistent with projections for individual predator species (for example, king penguins (*Aptenodytes patagonicus*))[42], as well as for other species including krill and salps[43,44]. The advantages that predators gain from the overall increase in the area of sub-Antarctic AESs may be offset by the increased cost of travel to more-distant foraging grounds—at least for central-place foragers that dive (penguins and fur seals)—whereas volant species (albatrosses and petrels) or those that are unconstrained by terrestrial breeding sites (whales) may benefit from increased sub-Antarctic foraging opportunities[45]. Changes in the future distribution of AES-like areas along the Antarctic margin are more spatially heterogeneous, with areas where AESs are lost interspersed with areas where they are gained or retained (Fig. 4a). However, there will be a net loss (−10.2%) of AES-like cells in the CCAMLR Convention Area (Fig. 4b). The heterogeneity of this pattern is in part a result of the dynamic nature of the high-latitude Antarctic marine environment and the uncertainty across a number of climate-model variables in this region. This uncertainty is due to the variability in the skill of models in reproducing current climate, and the large range of projected responses from those models. Our projections are based on unchanged future availability (that is, colony locations and sizes) and species–environment relationships. However, as species adapt to future pressures and changes to their available breeding habitat, populations are likely to change both their

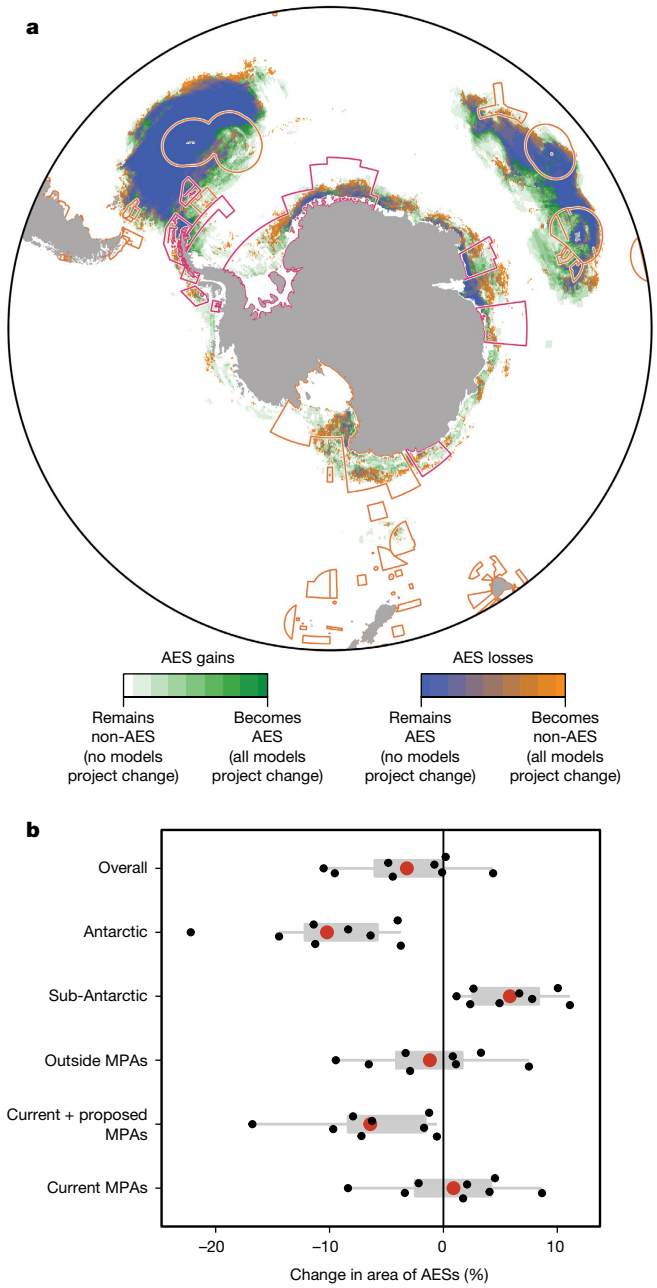

Fig. 4 | Projected change in the distribution of AESs under RCP8.5. a, Cells that were AESs in the original results are shown in blue (remain as AES) or orange (become non-AES in the future). The gradation from orange to blue shows the proportion of climate models that indicate loss (orange) or retention (blue) of AESs. Similarly, the gradation from white to green shows the proportion of models that indicate that non-AES cells will remain as non-AES (white) or become AES (green). Orange and magenta outlines show current and proposed MPAs, respectively. **b**, Percentage change in the area of AESs according to the eight different climate models (black points), and the mean of these (red points). In the box plots, the box indicates the 25th–75th percentiles, and the whiskers extend to the smallest value or largest value that is not further than 1.5 times the interquartile range from the 25th or 75th percentile, respectively.

preferred colony locations and habitat usage. Sub-Antarctic-breeding species have limited availability of alternative breeding sites, but colony sizes might change. Ice-breeding species might be able to relocate, and land-breeding species that require ice-free terrain might be able to occupy previously vacant areas, or some might move to regions that become ice-free owing to changing local conditions[46]. The loss of AES-like habitat on the Antarctic margin that our models project suggests that these populations will be under pressure as the climate continues to change, and therefore continued monitoring of these species and ongoing assessment of the effectiveness of management actions (for example, MPAs) will be important. Monitoring of colonies will need to detect local colonizations, particularly when populations are small[47]. As part of the designation of MPAs within CCAMLR, research and monitoring plans are necessary and required; these plans should—among other factors—consider changes to species–environment relationships and other dynamic processes within and adjacent to the protected area, given the pressures of ongoing climate change.

There was a mixed response across the eight climate models, with changes in the number of AES-like cells that are included in current MPAs ranging from −8.7% to +8.4% (Fig. 4b). When the proposed MPAs were included (current + proposed MPAs in Fig. 4b), all climate models indicated a decrease (between −16.9% and −0.9%) in the number of AES-like cells within MPAs. This suggests that proposed MPAs are in areas that are projected to become less similar to existing AESs by 2100. Any protection afforded by MPAs in such areas could provide better medium-term opportunities for populations to adapt, as they will not have to cope with both climate change and other stressors during that period.

Conclusion

Our work provides strong evidence in support of the ecological importance of existing and proposed Southern Ocean MPAs. By integrating tracking data from a suite of predators, we identified regions that are likely to have high biodiversity and biomass of the prey (and concomitant ecosystems) of the animals that were tracked. Our AESs are clearly candidates for protection, and the implementation of the proposed MPAs within the CCAMLR region would greatly increase the protection of important habitats in the Southern Ocean. Several MPA proposals have failed to reach consensus within the CCAMLR process, and even when adopted result in MPAs with varying degrees of protection. Many sources of input are needed to establish MPAs, but the AESs that we have described here will help to make the scientific case in this multifaceted process[2,48] by providing an ecosystem-level analysis of the areas that most warrant protection. The design of MPAs should also consider future conditions. Pressures on AESs owing to climate change will affect all parts of the Southern Ocean, but their effects are likely to be strongest along the Antarctic margin. The responses of species to these pressures are currently difficult to predict, highlighting the need for continued monitoring as part of ongoing management actions. Because only 16% of all Southern Ocean AESs are outside the CCAMLR Convention Area or national waters, the responsibilities for these future actions lie mostly with CCAMLR members and those nations with sovereign territory in the sub-Antarctic. Adaptive management approaches to conservation measures (including MPAs) will be necessary to deal with these future changes in a timely way. The Southern Ocean can be an exemplar of how science, policy and management can interact to meet the challenges of a changing planet. In the Southern Ocean, these challenges will be considerable, and will include increased fishing pressure as the global demand for marine resources grows[49]. Our results highlight where future science-informed policy efforts might best be directed, including both adaptive spatial protection and improved robust management of fisheries. Similar synthetic approaches should capitalize on the increasing amount of tracking data that are being collected through large-scale initiatives[50] to indicate regions in need of protection globally.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information,

acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-020-2126-y.

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[1]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia. [2]Antarctic Climate and Ecosystems Cooperative Research Centre, University of Tasmania, Hobart, Tasmania, Australia. [3]Centre d'Etudes Biologiques de Chizé, Station d'Écologie de Chizé-La Rochelle Université, CNRS UMR7372, Villiers-en-Bois, France. [4]CESAB-FRB, Institut Bouisson Bertrand, Montpellier, France. [5]LOCEAN/IPSL, Sorbonne Université-CNRS-IRD-MNHN, UMR7159, Paris, France. [6]Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA, USA. [7]British Antarctic Survey, Natural Environment Research Council, Cambridge, UK. [8]Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany. [9]School of Biological Sciences, Monash University, Melbourne, Victoria, Australia. [10]Marine Biology Laboratory, Université Libre de Bruxelles, Brussels, Belgium. [11]National Institute of Water and Atmospheric Research, Wellington, New Zealand. [12]Marine Mammal Institute, Oregon State University, Newport, OR, USA. [13]BEDIC, OD Nature, Royal Belgian Institute for Natural Sciences, Brussels, Belgium. [14]Laboratory of Biodiversity and Evolutionary Genomics, Department of Biology, University of Leuven, Leuven, Belgium. [15]Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania, Australia. [16]Australian Antarctic Division, Department of Agriculture, Water and the Environment, Kingston, Tasmania, Australia. [17]Point Blue Conservation Science, Petaluma, CA, USA. [18]Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, Seattle, WA, USA. [19]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Hatfield, South Africa. [20]UiT-The Arctic University of Norway, Tromsø, Norway. [21]Scottish Oceans Institute, St Andrews, UK. [22]School of Biological Sciences, University of Auckland, Auckland, New Zealand. [23]Oceans and Coasts, Department of Environment, Agriculture and Fisheries, Cape Town, South Africa. [24]Instituto de Oceanografia, Universidade Federal do Rio Grande, Rio Grande, Brazil. [25]Norwegian Polar Institute, Fram Centre, Tromsø, Norway. [26]Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, USA. [27]South Australian Research and Development Institute, West Beach, South Australia, Australia. [28]Department of Biological Sciences, Macquarie University, Sydney, New South Wales, Australia. [29]Antarctic Ecosystems Research Division, Southwest Fisheries Science Center, NOAA Fisheries, La Jolla, CA, USA. [30]Center for Marine Biotechnology and Biomedicine, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, USA. [31]Landcare Research, Lincoln, New Zealand. [32]Instituto Antártico Argentino, Buenos Aires, Argentina. [33]Moss Landing Marine Laboratories, San José State University, Moss Landing, CA, USA. [34]Sydney Institute of Marine Science, Mosman, New South Wales, Australia. [35]Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Büsum, Germany. [36]Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente, Università di Siena, Siena, Italy. [37]Museo Nazionale dell'Antartide, Siena, Italy. [38]DST-NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology, Nelson Mandela University, Port Elizabeth, South Africa. [39]Antarctic Research Trust, Bremervörde, Germany. [40]DST-NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa. [41]National Institute of Polar Research, Tachikawa, Japan. [42]Norwegian Institute for Nature Research, Fram Centre, Tromsø, Norway. [43]Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK. [44]Marine and Environmental Sciences Centre, Department of Life Sciences, University of Coimbra, Coimbra, Portugal. [45]These authors contributed equally: Mark A. Hindell, Ryan R. Reisinger, Yan Ropert-Coudert. [46]Deceased. [47]These authors jointly supervised this work: Simon Wotherspoon, Ian D. Jonsen, Ben Raymond. ✉e-mail: mark.hindell@utas.edu.au

Methods

Data reporting

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Analytical overview

We assembled tracking data from 17 species of seabirds and marine mammals, collected between 1991 and 2016, from across the Antarctic predator research community[16]. Birds and mammals comprise the majority of top predator species in the Southern Ocean, which has few other large, highly mobile marine predator taxa (bony and cartilaginous fishes). These include toothfish, southern bluefin tuna (*Thunnus maccoyii*, which occur in the northernmost part of our study area) and a small number of shark species. Very few of these fish and shark species have been tracked, with very few tracking data available south of 40°S[51]. Although some bias might result from our use of species, this does not detract from the underlying logic of our approach: that by using the at-sea distributions of an ecologically diverse suite of predators we can identify areas of ecological importance. Our dataset represents 4,060 individual tracks and more than 2.9 million location estimates (Fig. 1a). After filtering and quality control, we retained 2,823 tracks comprising 2.3 million locations[16]. The approximately 30% of tracks that were excluded were those with poor-quality location fixes that could not be properly filtered, tracks from individuals that did not actually depart the colony, or tracks with other problems detected during the rigorous quality control process that we implemented. The full process is described in our companion data paper[16], which makes available all of the data for use by the broader community, without providing further analytical investigation to consider the matters raised here. The environmental covariate values along each of these tracks (the 'used' habitat) were compared statistically with the habitat available to each animal, thereby allowing the habitat selection of each species to be determined[52,53] (Extended Data Figs. 1, 2). We fitted habitat-selection models for different life-history stages within a species. Despite the considerable size of the dataset, it is not an exhaustive representation of animals from all known colonies (for central-place foragers) or geographic regions (for non-central-place foragers). To account for incomplete tracking coverage, we used the fitted habitat-selection models to map habitat importance for each life-history stage of each species across the entire Southern Ocean, including areas around colonies without tracking deployments (Extended Data Fig. 3). For each species, we calculated the average habitat importance across life-history stages. For colony-breeding species, colony sizes were used to weight the habitat-importance values, upweighting areas that were of importance to large colonies (Extended Data Fig. 8). Southern Ocean predator species can be clustered into Antarctic and sub-Antarctic species (Extended Data Fig. 9). We mapped assemblage-level habitat importance (Extended Data Fig. 10) for each of these two groups (hereafter 'overall habitat importance' maps) by averaging across species-level maps. To calculate the overall map, we took the maximum of the two assemblage-level importance values in each cell. Areas with high values of overall habitat importance (in the top decile of values) indicate areas that are attractive to many species; these represent AESs[17]. We then compared the overall habitat-importance values inside and outside AESs in the context of fishing effort and changes in physical environmental conditions (duration of sea-ice cover, SST and wind speed). We finally quantified the spatial protection afforded to AESs under current and proposed spatial management plans.

We describe the methods in more detail in the Supplementary Information. We conducted all the analyses in R[54].

Tracking data

The data represent the output from a variety of types of tracking tags, providing location estimates at different spatio-temporal resolution and accuracy. We applied a state-space model[55] to estimate the most-probable locations at regular temporal intervals, while accounting for potential errors in the location estimates with automatic and manual quality control before and after filtering[16]. Although this procedure does not make the track from a light-based tag as accurate as one from a GPS device, it does provide a consistent characterization of the positional accuracy across different tag types, allowing the uncertainty in position to propagate into the uncertainty in the parameters of the fitted movement model and in the track simulation step (see below). We note that the GLS errors are larger than the resolution of the grids used, especially near the poles, which may be problematic for the analyses. However, the light-based tag deployments were made almost exclusively on sub-Antarctic animals (albatrosses and fur seals). The spatial scale of our results (AESs) in the sub-Antarctic zone (around 5 million km^2) is considerably larger than the probable scale of positional error of light-based tags (around 100 km) and so we do not believe that using a mixture of tag types has adversely affected our results.

Life-history stages

Most of the species in the study are central-place foragers (that is, they return periodically to land or sea ice to breed, moult or rest). The constraints faced by these predators at different stages in their life-history cycle mean that their movements differ markedly across these stages. We therefore fitted models separately for up to five predefined life-history stages in the breeding cycle of each species. We automatically assigned tracks to these stages on the basis of calendar date, with manual reassignment where necessary following examination of individual movement patterns. This resulted in 40 data subsets (17 species with 1–4 life-history stages) with sufficient data for habitat-selection modelling (Supplementary Table 1).

Simulating tracks to estimate available space

The observed locations only provide information about where animals occur, not about where they could have gone. To estimate the geographic space potentially available to animals, we simulated sets of tracks for each observed track. For each observed track, we simulated 50 tracks using the movement model described above[55]. This yielded simulated tracks with movement characteristics (distributions of step length and turning angle) that are the same as the observed track, but they are random and independent of environmental effects. Thus, the simulated tracks provide an estimate of the geographic space that each animal could have occupied (given its movement characteristics and track length) if it had no habitat preferences. The environmental differences between the available geographic space and the used geographic space allow the habitat selection of the organisms to be estimated, as detailed below. Locations at the animal's home colony, and locations at known terrestrial resting sites, were fixed at the corresponding time and date in the simulated tracks to accurately simulate central-place foraging behaviour (Supplementary Information).

Environmental data

To characterize the biophysical environment at observed and simulated locations, we compiled a suite of 19 environmental covariates (Extended Data Fig. 2, Supplementary Table 2) and extracted the value of these at each location. The covariates were remotely sensed, measured in situ or model-estimated and represent biophysical features that influence the movement, distribution and density of marine predators[52,53]. It was not computationally feasible to temporally match environmental data to each location estimate. Rather, we created a climatology that spanned each tracking data subset (species by the combination of life-history stages), using the predefined stage dates. We took the mean

(or standard deviation) of the environmental data that fell on these days of the year (stage dates) over the whole study period (November 1991 to June 2016). Some covariates (for example, salinity difference) were only available as monthly climatologies, and we used the months corresponding with the stage dates to calculate the mean (or standard deviation). All covariates were resampled to a 0.1° × 0.1° grid; hereafter we refer to the pixels of this grid as 'cells'. We checked the covariates for each data subset for missing values and if more than 10% of values were missing we excluded the covariate from that model. This influenced mainly the chlorophyll *a* concentration variable, which was excluded from 17 of the 40 habitat models (Supplementary Table 1). This affected life-history stages with a large proportion of winter days, as chlorophyll *a* has poor winter satellite coverage owing to being obscured by extensive cloud cover. However, chlorophyll *a* was rarely an important predictor in the models in which it was included; thus, excluding it from models probably had only a negligible effect.

Habitat-selection models

We used a habitat-selection modelling framework[56] to model and predict the space use of marine birds and mammals of the Southern Ocean. These models use the observed locations of each individual animal and an estimate of the geographic space available to each individual, along with covariates that characterize their environment. The environmental differences between the habitat that was used and the habitat that was available allow the habitat selection of the organisms to be estimated. To fit the models, we used boosted regression trees, a machine-learning algorithm that produces an ensemble of regression trees that have been iteratively fitted in a boosting process to improve accuracy[57]. We tested several other algorithms but boosted regression trees showed the best predictive performance in another study[53] and in our tests. For a given location, the response variable was whether the location was an observed or simulated (available) location, and the explanatory covariates were the associated environmental covariates. Boosted regression trees have four parameters that must be set: the number of trees (boosting iterations), the maximum tree depth, the learning rate (shrinkage) and the minimum number of observations in a node. We chose these values as the combination that minimized the area under the receiver operating characteristic curve (a measure of model predictive performance) during tenfold cross-validation. We also used this metric to evaluate the final fitted models. We used the fitted model to generate spatial predictions for the entire study region and we estimated the uncertainty associated with these predictions using a bootstrap approach (Supplementary Information)

Accessibility model

The modelling procedure described above does not account for the accessibility of a given location to an individual animal (in effect, it estimates the habitat selection of a given location in terms of its environmental characteristics, but without considering whether or not the animal could actually reach that location). For central-place foragers in particular, this is an important consideration. We therefore used a second set of models to account for this[53]. We modelled accessibility in terms of the number of observed plus simulated locations in a given cell as a function of the distance of the cell to the deployment colony. We fitted binomial models with a smooth, monotonic decreasing constraint[58], under the assumption that the accessibility of cells should decrease with geographic distance. To estimate uncertainty, we sampled curves from the posterior distribution of each fitted accessibility model to use in a bootstrap approach (Supplementary Information).

We used these models to predict the accessibility of each cell over the study region to each species during each life-history stage (that is, given the distance of a cell from a colony, the fitted accessibility model provides an estimate of the probability that animals from that colony would be able to visit that cell). For colony-breeding species (those other than humpback whales, crabeater and Weddell seals), colony sizes were used to weight this accessibility estimate: for a given cell, the accessibility from all known colonies of that species was calculated. A weighted mean of these accessibilities was then taken, using colony sizes as weights. Thus, this weighted accessibility represents the probability that a randomly selected individual from the global population would be able to visit that cell, effectively upweighting cells in the vicinity of large colonies.

For the non-colony breeding, ice-associated seals (crabeater and Weddell seals), we modelled accessibility as a function of distance beyond the ice edge (15% ice concentration contour), rather than distance to the colony. For humpback whales, we assumed that the whole study area was equally accessible.

Transforming output and combining models to predict habitat importance

The habitat-selection models predict the value of the habitat at a location given that the animals could access that location. The predictions of the habitat-selection models were therefore multiplied by the predictions of the accessibility models to yield an index that reflects both the habitat selection of each cell and its accessibility to the animals. This is not an estimate of the probability of a species using a given cell, because that probability also depends on the prevalence of the species[59]. As prevalence varies between species, our habitat-selection estimates cannot be compared directly between species. We therefore partitioned the cells into decreasing percentiles based on area[52] to obtain a map of habitat importance expressed in terms of area (for example, cells with values of 90 or higher represent the top 10% most-important habitat by area for that species). We refer to this as habitat importance, and these maps can be compared among species. To create a single habitat-importance layer for each species, we averaged the stage-specific habitat-importance layers.

Species-specific habitat importance

We calculated community-level habitat importance by averaging the species-specific maps of habitat importance. Sub-Antarctic regions are naturally more species-diverse than those of the Antarctic, and so a simple average of all species together tended to strongly favour sub-Antarctic areas simply because of their greater species diversity. To account for the differences in species richness between the Antarctic and sub-Antarctic, we first defined two species groups using an unweighted pair group method with arithmetic mean (UPGMA) hierarchical clustering with Manhattan distance, applied to habitat-importance scores (Extended Data Fig. 9). This produced two clear groups: an Antarctic species group (emperor penguin, crabeater seal, Antarctic petrel, Adélie penguin and Weddell seal) and a sub-Antarctic species group (Antarctic fur seal, black-browed albatross, wandering albatross, sooty albatross, grey-headed albatross, king penguin, macaroni and royal penguin, light-mantled albatross and white-chinned petrel). The wide-ranging humpback whales and southern elephant seals did not clearly fall into either cluster, and so were treated as belonging to both groups. The mean habitat importance was calculated for each of these groups separately and then combined (Extended Data Fig. 10) by taking the maximum of the two values (Antarctic and sub-Antarctic) in each pixel. We refer to this final layer as the overall habitat importance.

AESs

To identify the most-important areas, we calculated the 90th percentile (top decile) of the overall habitat-importance values. Cells with overall habitat-importance values above this threshold together comprised AESs.

Environmental pressures

To assess past environmental stressors on the Southern Ocean ecosystem, we calculated change in SST, wind speed and sea-ice duration. We selected SST and wind because they were frequently the

most-important predictor variables in the habitat models (Extended Data Fig. 4), and sea-ice concentration as this was an important predictor for Antarctic species. Moreover, these variables are considered to be important drivers of ocean and ecosystem dynamics[18,60], and key axes on which environmental change in the Southern Ocean has been detected[26]. For each cell, we calculated the change in SST (°C) or wind speed ($m\ s^{-1}$) as the difference between mean SST or wind speed in 1987–1999 and 2007–2017. For sea-ice duration, we calculated the difference in the mean number of days per year that each pixel had a sea-ice concentration of higher than 15%, for the same periods. These periods represent the decades at the beginning and end of a 30-year period that covers our study period. Thirty years is also the recommended period for climate assessments[61]. We also obtained data on fishing effort—which is considered to be a major environmental stressor in many regions of the Southern Ocean[29,62]—from the Global Fishing Watch dataset, covering the period from 2012 to 2016[29]. We compared the values of these four stressors in the AESs and outside cells using random permutation tests with 10,000 permutations. The null hypothesis is that stressor values inside and outside AESs are from the same distribution.

Future projections of AESs

Our predicted AESs (under current environmental conditions) are determined by both the oceanographic and climatic conditions of an area, as well as the accessibility of that area to each of our species of interest. In principle it would be possible to use future projections of environmental data and accessibility along with our fitted models to obtain future projections of AESs. However, some predictor variables are not available from the climate models used for the future projections, and although other variables might appear to be available, they have different properties owing to factors such as different temporal and spatial resolution in the output, or the ability of the climate model to resolve the relevant processes. For example, sea surface height from satellite altimetry gives information about frontal and mesoscale features. Yet, although sea surface height is available as an output from many CMIP5 models, those models do not explicitly resolve mesoscale features[63] and so the model-output data for sea surface height will not be acting as a proxy for the same oceanographic properties as the data from satellite-derived altimetry.

To assess future distributions of AES-like habitat, we therefore used a *k*-nearest neighbour classifier approach that is conceptually similar to climate analogues[64]. For each grid cell we compiled current (end of 20th century) environmental conditions, as well as projected conditions at the end of the 21st century from climate models (see below). In terms of accessibility, most of our study species breed in colonies, and 'accessibility' for these species is determined both by the geographic distribution of their colonies and by the colony sizes. Future projections of colony location and size do not exist for our study species at present, although initial work has begun for some species, such as king penguins[46]. Colony locations and sizes were therefore assumed to remain constant, and so the accessibility of each grid cell to each species was assumed to remain unchanged. For each grid cell, we compared its projected future environmental and accessibility conditions to every cell in the current (20th century) grid and selected the five cells that were most similar. If the majority of those cells were from current AESs, the projected cell was labelled as 'AES-like'; otherwise, it was labelled as 'not AES-like'. These projections therefore provide an indication of the future distribution of AES-like environmental conditions, under the assumptions that colonies do not move or change in size, and that the animals do not change their habitat preferences. These assumptions are unlikely to hold in reality; however, examining the changes in AES-like habitat under these assumptions allows us to isolate the effects of environmental change from colony or habitat-usage changes. As environmental change occurs, species are likely to adapt by changing their colony distributions and habitat usage. The AES projections offer insights into the likely distribution of environmental pressures, and thus where adaptation by species might be important.

Climate data were compiled from eight global climate models (ACCESS1.0, BCC-CSM1.1, CanESM2, CMCC-CM, EC-EARTH, GISS-E2-H-CC, MIROC-ESM and NorESM-M), which were considered to be most suitable for Southern Ocean studies by virtue of reliably reproducing extant sea-ice conditions[65]. These models were from phase five of the Coupled Model Intercomparison Project (CMIP5) of the World Climate Research Programme. For each model, we extracted data for a 30-year period concomitant with our tracking data (1976–2005), and for a 30-year period at the end of the 21st century (2071–2100). We extracted future (2071–2100) climate data from projections under two RCP simulations: a medium-forcing scenario (RCP4.5, which assumes that society implements changes to limit future CO_2 emissions in the near future, with peak emissions occurring in 2040) and a more-extreme, high-forcing scenario (RCP8.5, which assumes little curbing of emissions and retains a strong reliance on fossil fuels into the foreseeable future)[40]. Reference data (1976–2005) were extracted from hindcast model runs that attempt to simulate historical conditions, and consequently use observed CO_2 concentrations over the past 160 years to guide the models.

A maximum of eight variables were extracted for each model, depending on the available data (not all models provide all variables), at monthly time resolution. The variables used were sea-ice concentration, SST, sea surface salinity, sea surface height, the spatial gradient of sea surface height, near-surface current speed, near-surface wind speed and surface downward heat flux. The 30-year mean and standard deviation of each variable was calculated over summer (December to February) and winter (July to September) months. All variables were normalized to the range 0–1 before further analysis.

The resulting set of up to 48 predictors (mean and standard deviation of up to 8 environmental variables, each for summer and winter, plus accessibility layers for 16 species) naturally showed high correlation between many of the variables. We used a principal component analysis to reduce the dimensionality of this dataset, choosing the lowest number of principal components required to explain at least 95% of the variance in the original data; this number ranged from 14 to 17 components, depending on the model and scenario. For each projected-climate cell, the nearest neighbours in the historical-climate grid were calculated using Euclidean distance on these normalized and dimension-reduced data.

Animal ethics statement

All work was conducted under the appropriate national or institutional ethics approvals. These were: Argentina (Dirección Nacional del Antártico); Australia (Australian Antarctic program; the University of Tasmania); Belgium (Belgian Science Policy Office); Brazil (Brazilian Antarctic Programme; National Council for Scientific and Technological Development (CNPq); Ministry of Science, Technology, Innovation and Communications (MCTIC); Ministry of the Environment; CAPES); France (Terres Australes et Antarctiques Françaises); Germany (Germany Umweltbundesamt (German Environment Agency) and Bundesamt für Naturschutz (Federal Agency for Nature Conservation)); Italy (Programma Nazionale di Ricerche in Antartide (PNRA)); Japan (Japanese Antarctic Research Expedition; National Institute of Polar Research); Monaco (Fondation Prince Albert II de Monaco); New Zealand (Ministry for Primary Industries BRAG); Norway (Norwegian Antarctic Research Expeditions; Norwegian Research Council; Norwegian Animal Research Authority); Portugal (Foundation for Science and Technology); South Africa (Department of Environmental Affairs; National Research Foundation; South African National Antarctic Programme); UK (British Antarctic Survey; Natural Environment Research Council); and USA (NOAA Fisheries Office of Protected Resources; National Science Foundation Office of Polar Programs).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The tracking data are available through our companion paper[16].

Code availability

Computer code is available at https://github.com/SCAR/RAATD.

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Competing interests H.B., J.-B.C., D.P.C., B.D., M.A.H., L.A.H., I.D.J., M.-A.L., M.M., B.R., R.R.R., Y.R.-C., P.G.R., A. Takahashi, D.T., L.G.T., P.N.T., A.P.V. S.W. and J.C.X. are members of the SCAR Expert Group on Birds and Marine Mammals. S.L.C. is President of SCAR.

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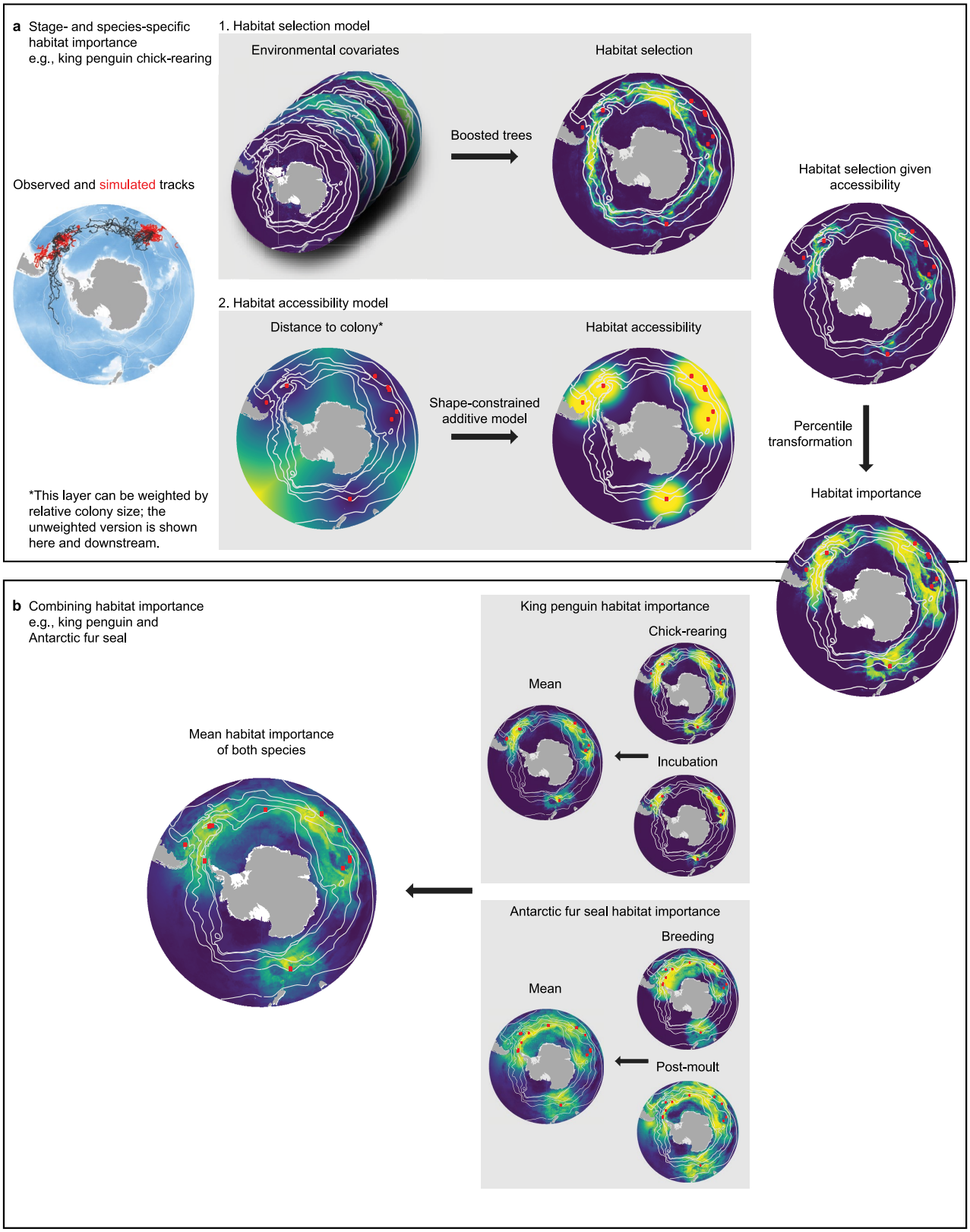
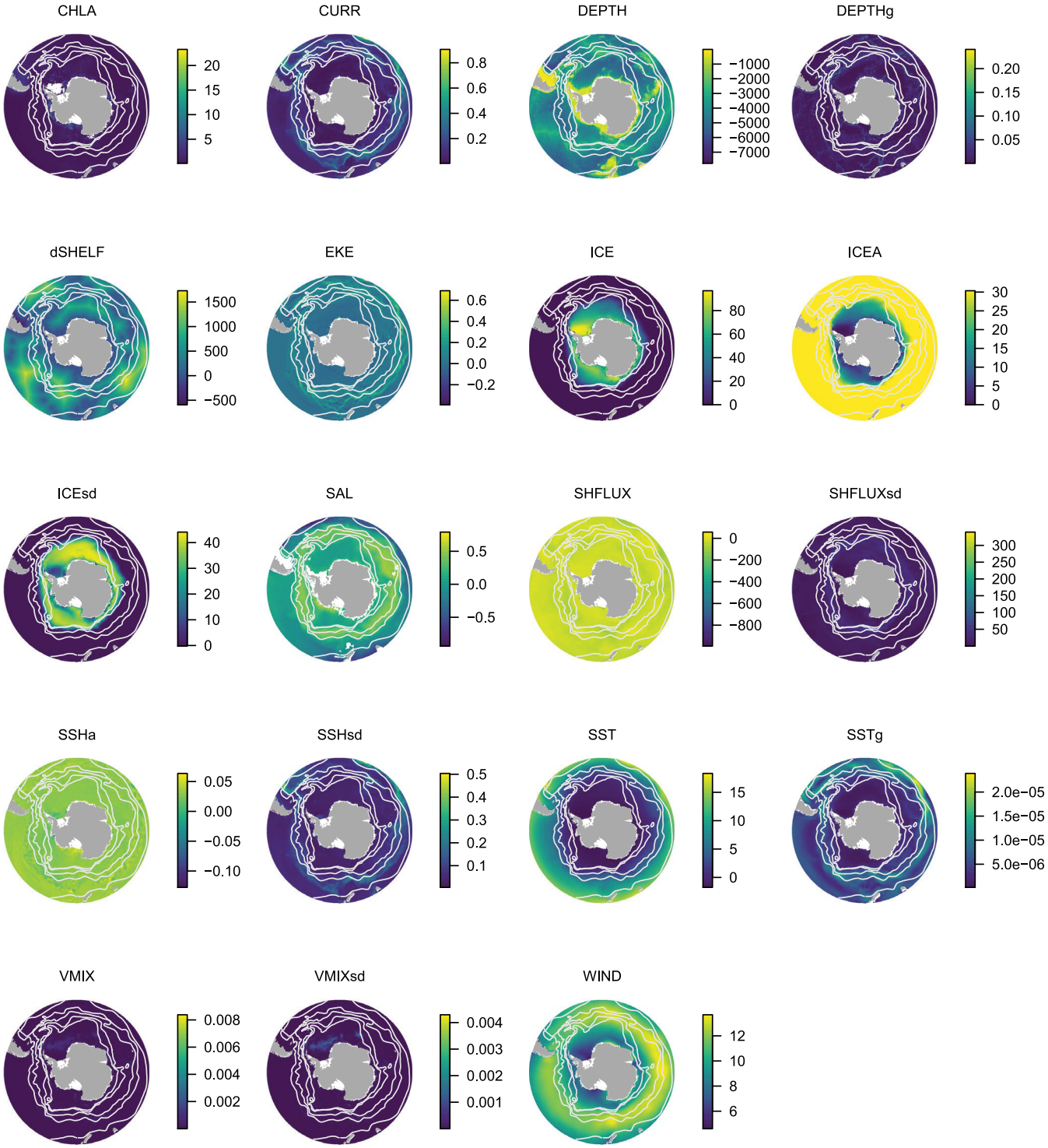
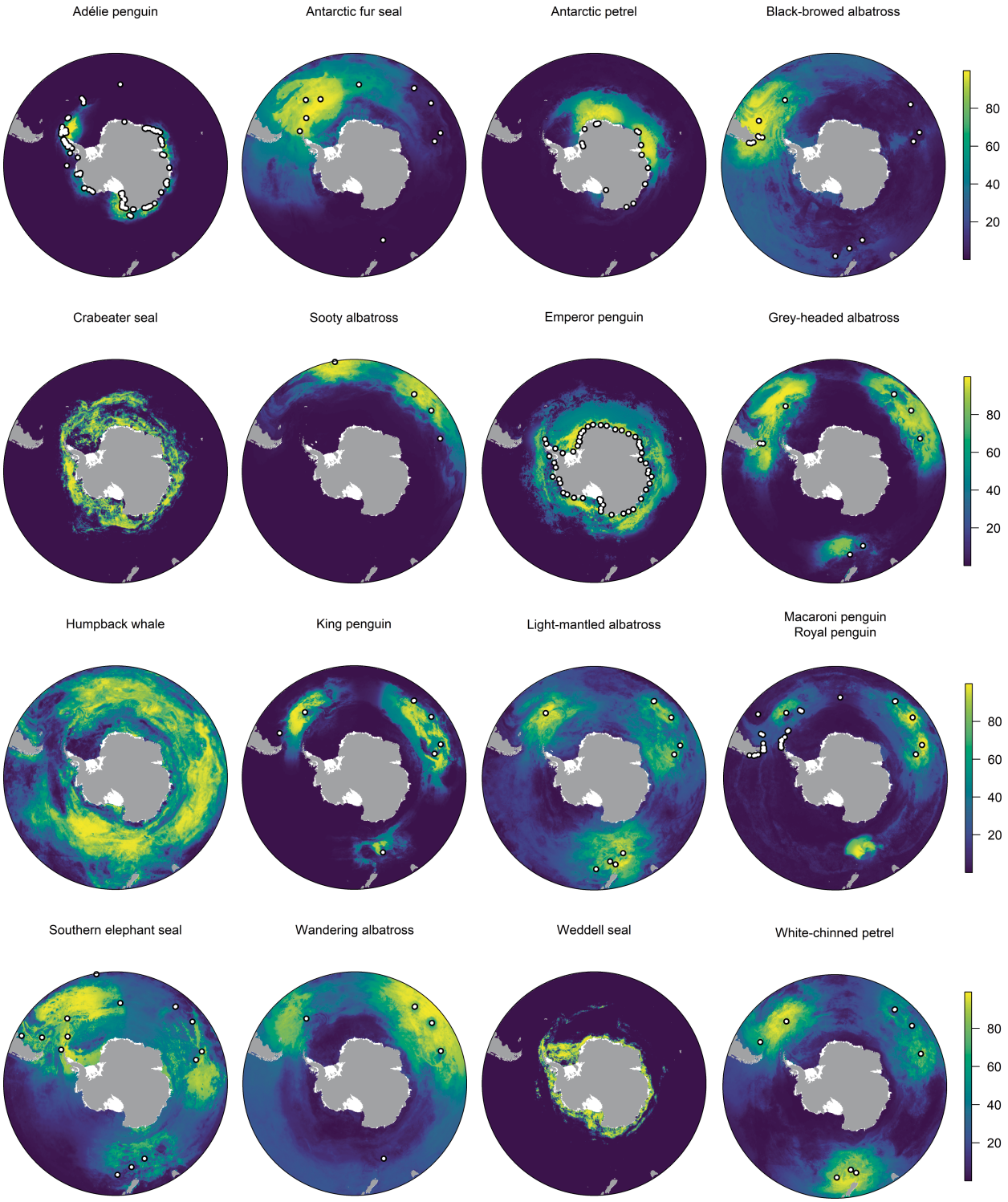


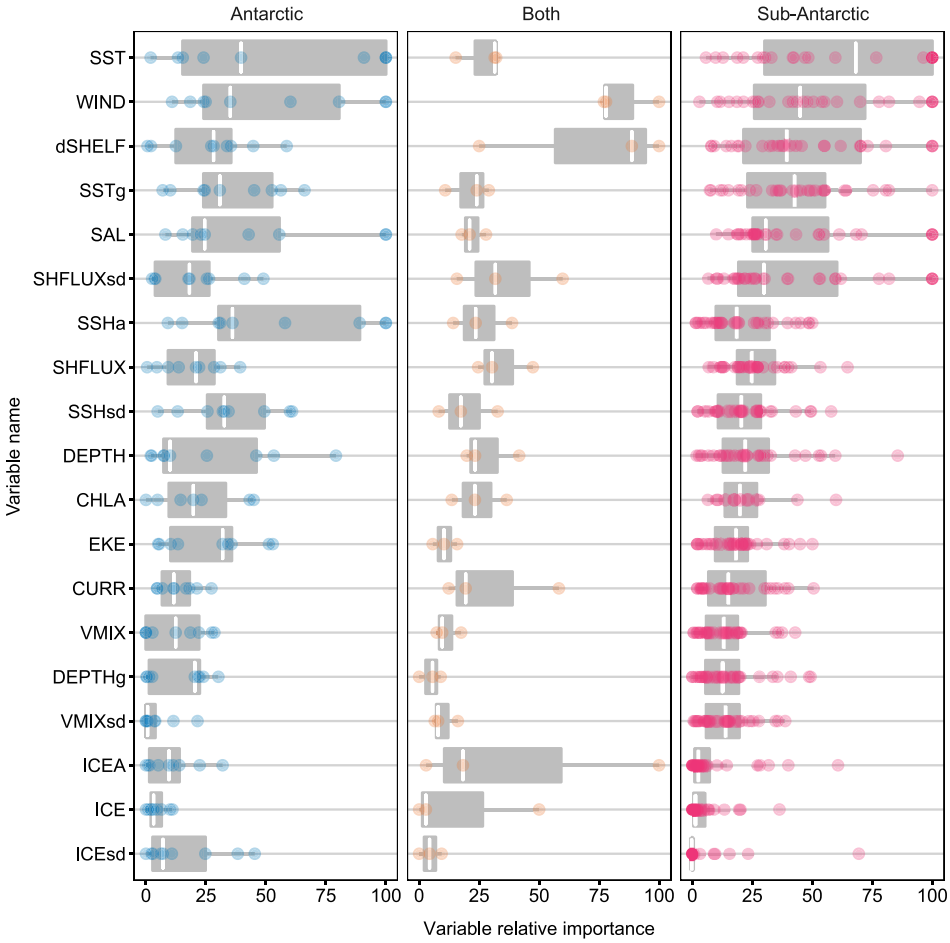
Extended Data Fig. 1 | Overview of the modelling process. a, Habitat importance for a given life-history stage (for example, chick-rearing) of a given species (for example, king penguin (*A. patagonicus*)) is calculated using two models (grey boxes): the habitat-selection model (box 1) and the habitat accessibility model (box 2). **b**, These stage-specific, species-specific predictions of habitat importance are combined to calculate the mean habitat importance for multiple species (for example, king penguin and Antarctic fur seal (*Arctocephalus gazella*)). In the habitat accessibility model (box 2 in **a**) the distance to colony can be weighted by relative colony size or not. The unweighted version is shown here.



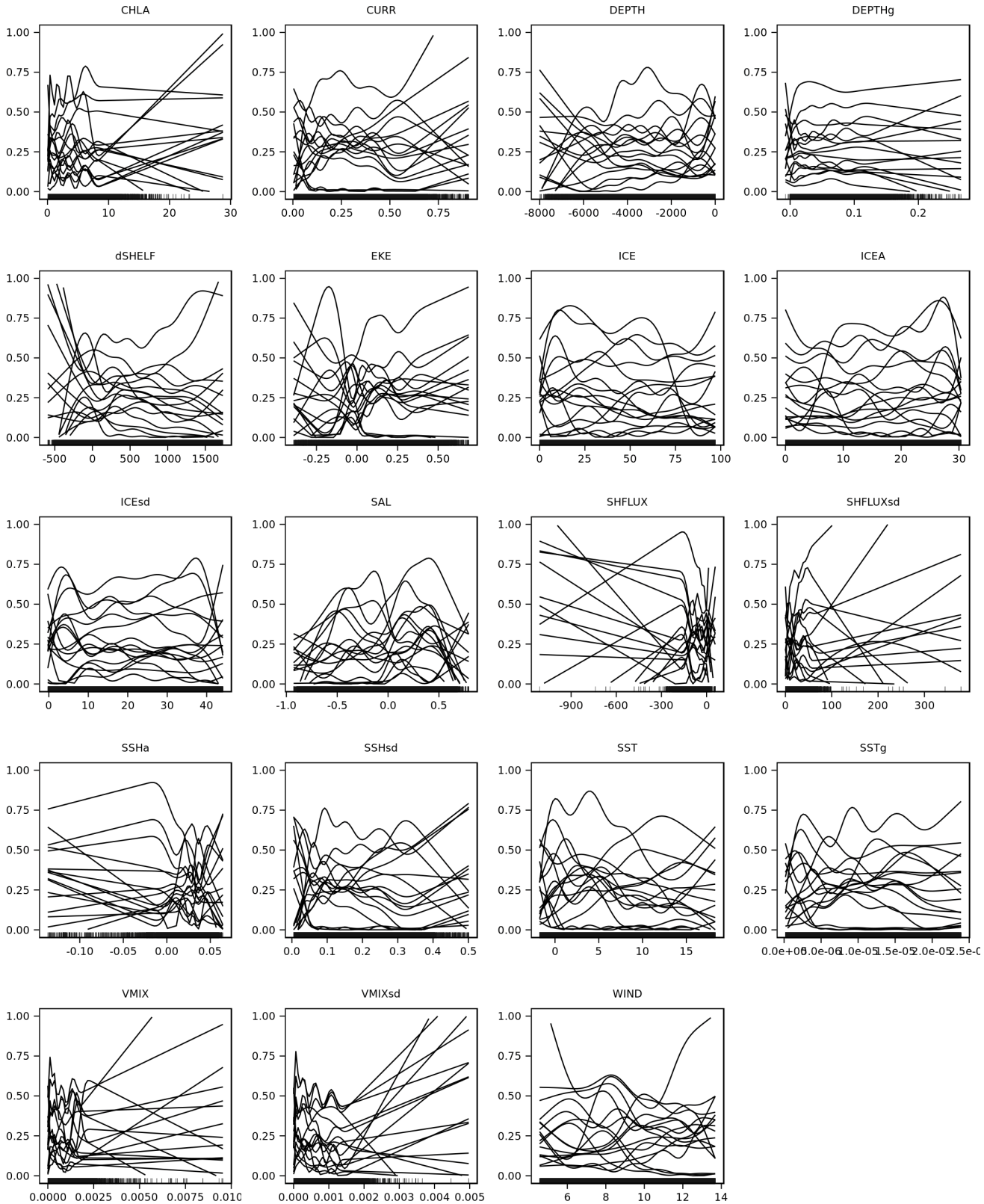
Extended Data Fig. 2 | Maps showing the 19 environmental covariates that were used to model the habitat selection of marine predators in the Southern Ocean. Grey lines indicate major oceanographic fronts. CHLA, chlorophyll *a* concentration; CURR, geostrophic current velocity; DEPTH, depth; DEPTHg, depth gradient; dSHELF, distance to shelf; EKE, eddy kinetic energy; ICE, sea-ice concentration; ICEA, accessibility through sea ice; ICEsd, standard deviation of sea-ice concentration; SAL, salinity difference; SHFLUX, surface heat flux; SHFLUXsd, standard deviation of surface heat flux; SSHa, sea surface height anomaly; SSHsd, sea surface height standard deviation; SST, sea surface temperature; SSTg, sea surface temperature gradient; VMIX, vertical velocity; VMIXsd, standard deviation of vertical velocity; WIND, surface wind speed. Sources and units of measurement are defined in Supplementary Table 2.



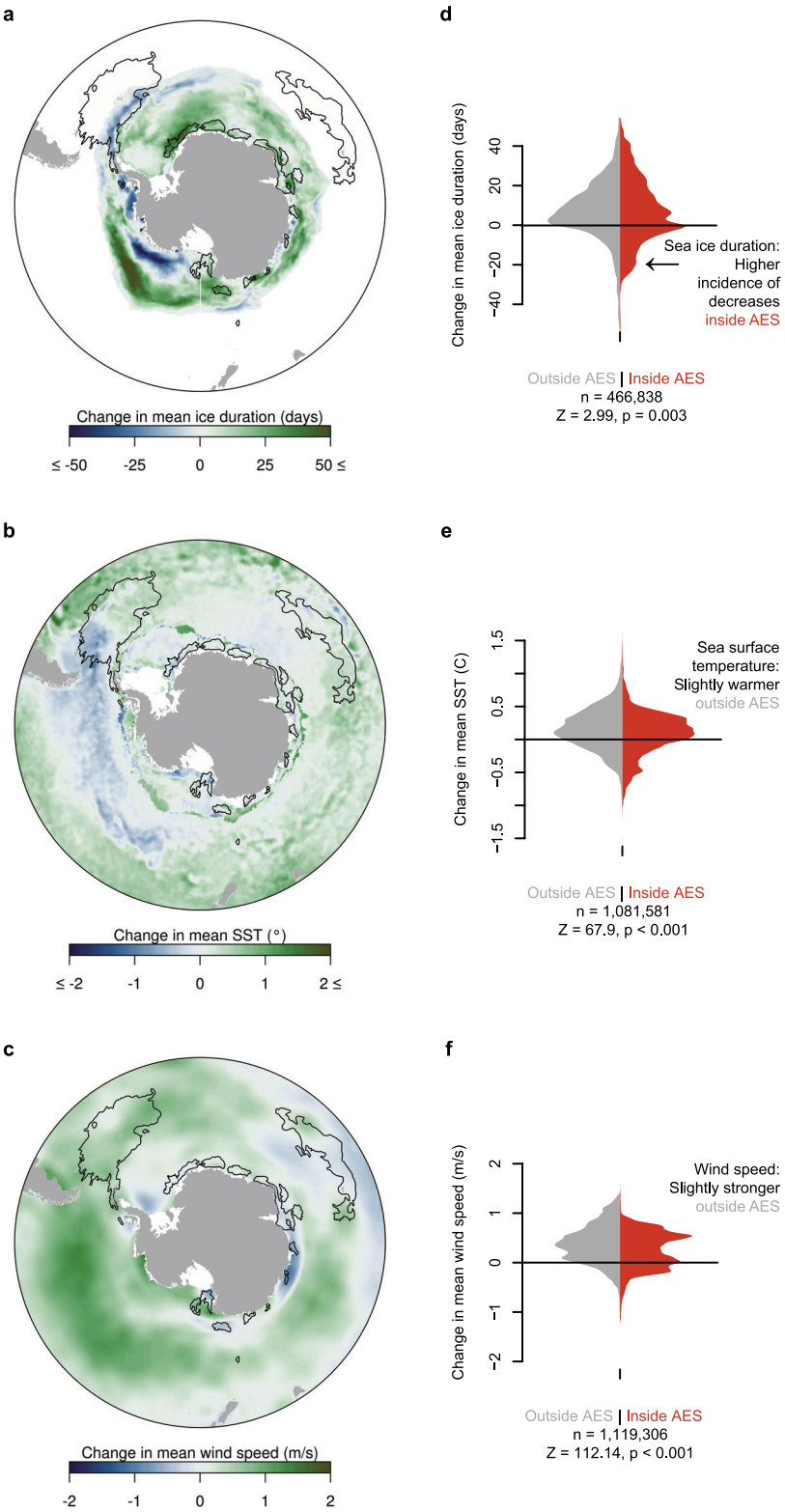
Extended Data Fig. 3 | Habitat-importance scores for 16 marine predator species in the Southern Ocean. The maps show predicted habitat importance for each species. Predictions for macaroni penguins (*Eudyptes chrysocome*) and royal penguins (*Eudyptes schlegeli*) are combined. Black circles show all known colony locations for the 14 colony-breeding species, which we used to predict the models across the whole Southern Ocean.



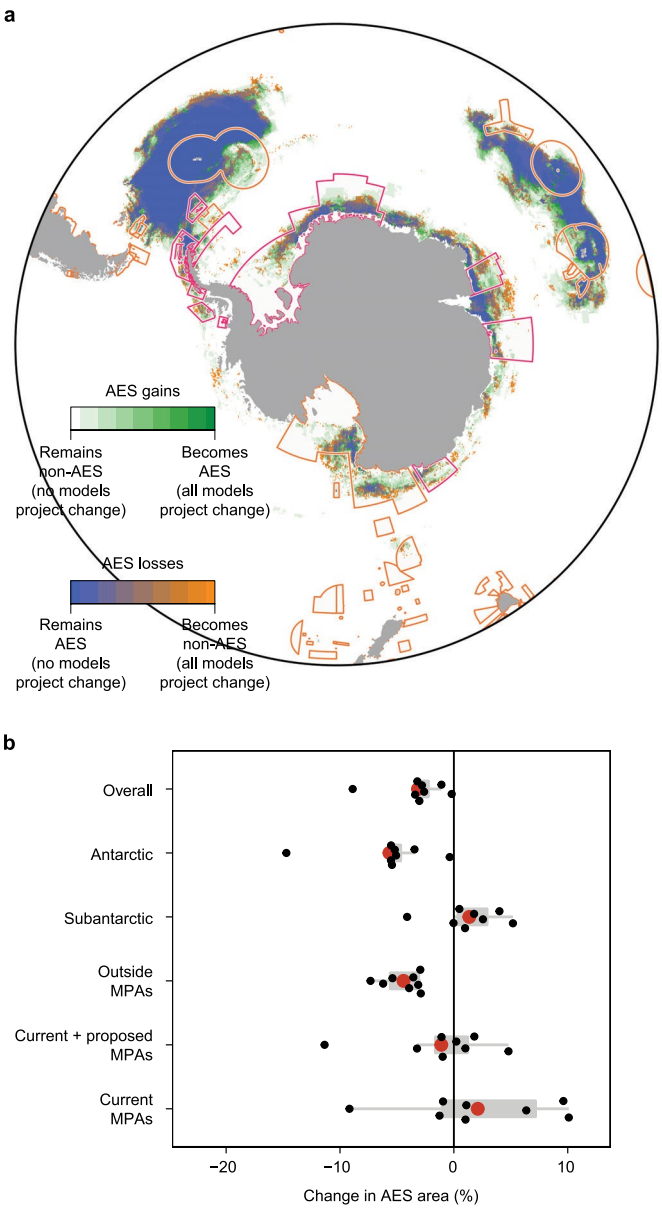
Extended Data Fig. 4 | Covariate importance. Relative importance of 19 environmental variables that were used as predictors in 40 boosted regression tree models of the habitat selection of Southern Ocean marine predators. Higher values of variable relative importance indicate that the variable has higher predictive power. Points show the values for each model and box plots (in grey, behind) show the distribution of values. Variables are ordered (top to bottom) by decreasing median importance. The three panels show the results for three different groups of species that were identified by hierarchical cluster analysis (see 'Species grouping' in Methods, and Extended Data Fig. 7). Full covariate names are provided in Supplementary Table 2. Box plots as in Fig. 4.



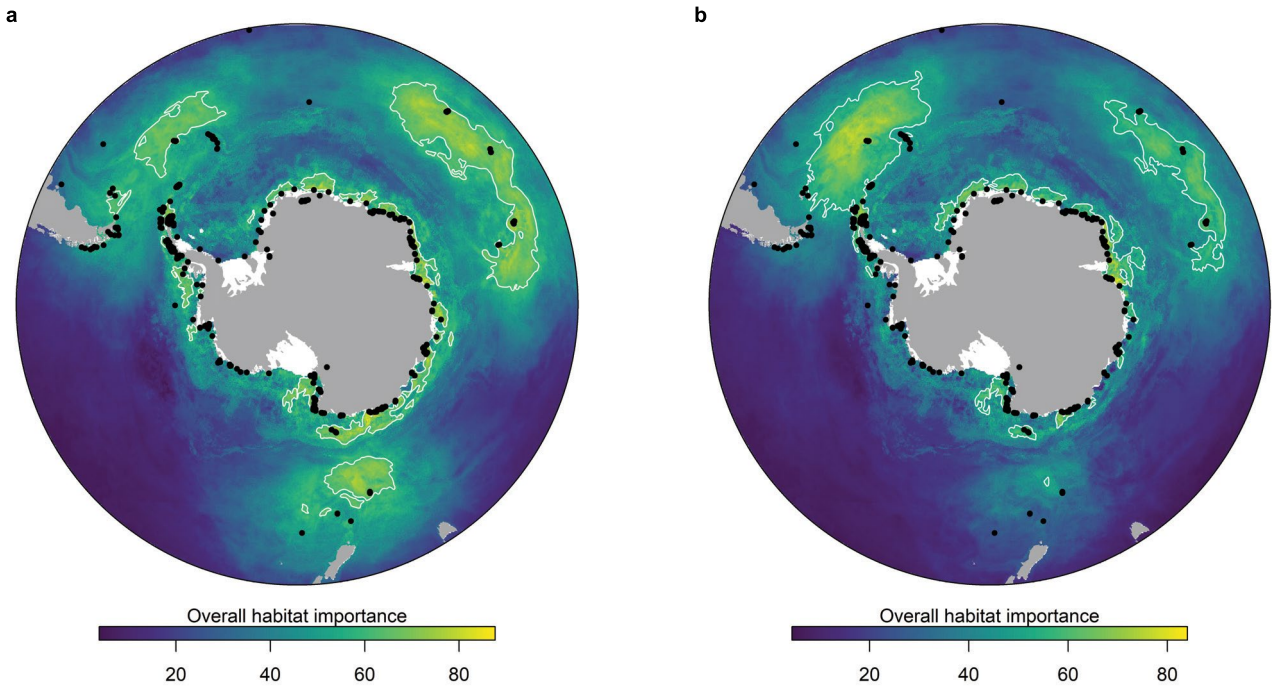
Extended Data Fig. 5 | Varied relationships between covariates and habitat selection across species. Scatter plot smoothed curves (black lines) of the relationship between predictions of the species habitat-selection models (boosted regression trees) (vertical axis) and the values of covariates used as predictors in our boosted regression tree models (horizontal axis). The smoothed curves were drawn by fitting generalized additive models for large datasets with a thin plate regression spline basis, as LOESS (locally estimated scatter plot) smoothing was not computationally feasible. Full covariate names and units are provided in Supplementary Table 2. Higher habitat-selection values indicate higher probabilities of use, irrespective of availability in this case. A smooth curve is shown for each species. Because each species had one to five predictions, for different life-history stages, we took the mean habitat-selection estimate per cell for each species. Rug marks on the horizontal axis indicate the distributions of the data points.



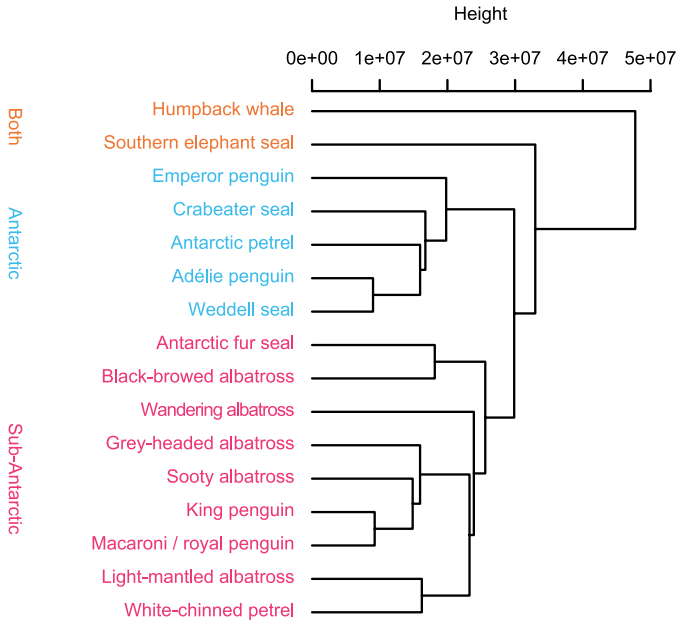
Extended Data Fig. 6 | Potential environmental stressors in the Southern Ocean. a–**c**, Maps showing the change (mean in 1987–1998 compared to mean in 2007–2017) in sea-ice duration (days) (**a**), SST (°C) (**b**) and wind speed (m s^{-1}) (**c**). Contour lines (black) indicate AESs. **d**–**f**, Kernel density plots show the distribution of values of each of **a**–**c** inside (red) and outside (grey) AESs. Horizontal lines represent zero change. Two-tailed permutation tests indicate significant differences in each case, and the number of grid cells included in the test is given in each case (*n*).



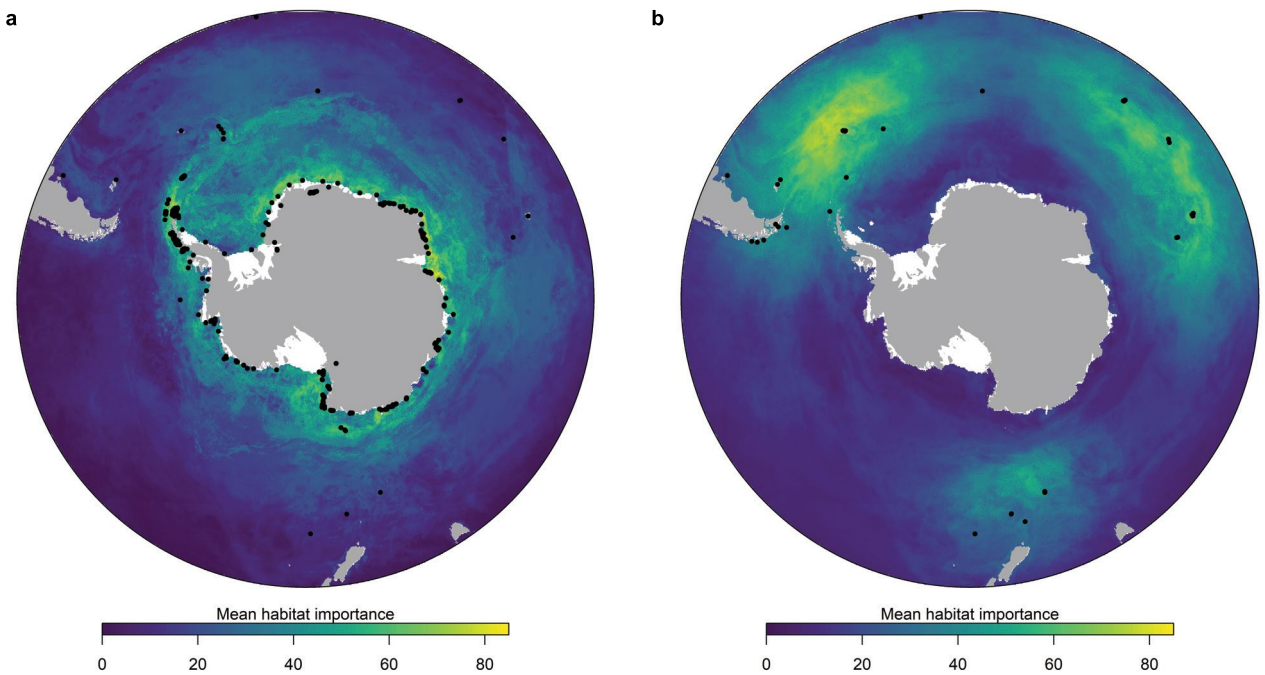
Extended Data Fig. 7 | Change in the distribution of AESs under RCP4.5. **a**, Cells that were AES in the original results are shown in blue (remain as AES) or orange (become non-AES in the future). The gradation from orange to blue shows the proportion of climate models that indicate loss (orange) or retention (blue) of AESs. Similarly, the gradation from white to green shows the proportion of models that indicate that non-AES cells will remain as non-AES (white) or become AES (green). Orange and magenta outlines show current and proposed MPAs, respectively. **b**, Percentage change in the area of AESs according to the eight different climate models (black points), and the mean of these (red points). Box plots as in Fig. 4.



Extended Data Fig. 8 | Comparison of unweighted and weighted overall habitat importance. a, Overall habitat importance, calculated without accounting for colony sizes. **b**, Overall habitat importance if colony sizes are taken into account. Black points indicate colony locations for the 14 colony-breeding species; white contours indicate AESs. See Methods and Supplementary Information for details.



Extended Data Fig. 9 | Dendrogram of hierarchical cluster analysis showing species groups in the dataset. We performed UPGMA hierarchical cluster analysis on the Manhattan distance among species, calculated from the habitat-importance scores. The results show two clear species groups: Antarctic (blue) and sub-Antarctic (magenta). Humpback whales and southern elephant seals (orange) did not fall into either group and we assigned them to both groups for subsequent analyses. The cophenetic correlation coefficient between the distance matrix and the dendrogram was 0.86, which means that the dendrogram is a good representation of the Manhattan distance values among the species. Values can range from 0 (no correlation) to 1 (perfect correlation).



Extended Data Fig. 10 | Mean habitat importance of Antarctic and sub-Antarctic species. a, **b**, To account for regional differences in species richness we defined two species groups (Methods and Extended Data Fig. 5) and calculated the mean habitat importance for these two groups separately. These two mean habitat-importance layers (**a** and **b**) were then combined into a single overall habitat-importance layer by choosing the maximum value in each cell. Black points indicate the colony locations of colony-breeding species in each species group.

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No computer code was used to obtain the data
Data analysis	All analyses were done using R.v3.6 The code are available at https://github.com/SCAR/RAATD

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The data and metadata are available to the public through the Australian Antarctic Data Centre (standardized data, doi:10.4225/15/5afcb927e8162; state-space model-processed (filtered) data, doi:10.4225/15/5afcadad6c130).

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Sample size	Our sample size was determined by the availability of tracking data provided for each species. It is nonetheless the largest data set of this type ever compiled. The number of individuals per species ranged from 35 to 820 which were sufficient to develop a species distribution model for each species
Data exclusions	We excluded some individual tracks that were either too short (i.e. less than 20 locations or were less than 1 days) or for which movement models failed to converge. This reduced our sample size from 4060 to 2823 individual tracks. There exclusion criteria were pre-established in our companion Scientific Data paper
Replication	Experimental replication was not attempted
Randomization	Individuals in the study were randomly selected for wild populations
Blinding	Blinding was not required for this study as it involved random selections of wild animals

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☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
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Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals
Wild animals	This study was a synthesis of existing animal tracking data. it involved 17 species (each with its own particular method of capture) and over 4000 individual animals. In all cases, the animals were released back into the wild at the point of capture after 10-30 minutes of handling. A full breakdown of the data set is provided in our Scientific Data paper: Ropert-Coudert, Y. et al. (In Press) The Retrospective Analysis of Antarctic Tracking Data Project. Sci. Data
Field-collected samples	The study did not involve samples collected in the field
Ethics oversight	All work was conducted under the appropriate National or Institutional Ethics approvals. There were: Argentina (Dirección Nacional del Antártico), Australia (Australian Antarctic program; the University of Tasmania a, Belgium (Belgian Science Policy Office), Brazil (Brazilian Antarctic Programme; National Council for Scientific and Technological Development - CNPq; Ministry of Science, Technology, Innovation and Communications – MCTIC; Ministry of the Environment; CAPES), France (Agence Nationale de la Recherche; Centre National d'Etudes Spatiales; Centre National de la Recherche Scientifique; Fondation Total; Institut Paul-Emile Victor; Programme Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique; Terres Australes et Antarctiques Françaises), Germany (Deutsche Forschungsgemeinschaft, Hanse-Wissenschaftskolleg - Institute for Advanced Study), Italy (Programma Nazionale di Ricerche in Antartide, PNRA), Japan (Japanese Antarctic Research Expedition; JSPS Kakenhi grant), Monaco (Fondation Prince Albert II de Monaco), New Zealand (Ministry for Primary Industries - BRAG; Pew Charitable Trusts), Norway (Norwegian Antarctic Research Expeditions; Norwegian Research Council), Portugal (Foundation for Science and Technology), South Africa (Department of Environmental Affairs; National Research Foundation; South African National Antarctic Programme), UK British Antarctic Survey; Natural Environment Research Council, and USA U.S. AMLR Program of NOAA Fisheries; US Office of Polar Programs.

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