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Climate and human stressors on global penguin hotspots: Current assessments for future conservation

Míriam Gimeno[1,2] | Joan Giménez[1,3] | Andre Chiaradia[4] | Lloyd S. Davis[5] | Philip J. Seddon[5] | Yan Ropert-Coudert[6] | Ryan R. Reisinger[7] | Marta Coll[1,8] | Francisco Ramírez[1]

[1]Institut de Ciencies del Mar, Recursos Marins Renovables, Barcelona, Spain

[2]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Barcelona, Spain

[3]Centro Oceanográfico de Málaga (COMA), Instituto Español de Oceanografía (IEO-CSIC), Fuengirola, Spain

[4]Conservation Department, Phillip Island Nature Parks, Cowes, Victoria, Australia

[5]University of Otago, Dunedin, New Zealand

[6]Centre d'Etudes Biologiques de Chizé, Villiers-en-Bois, France

[7]School of Ocean and Earth Science, University of Southampton, Southampton, UK

[8]Ecopath International Initiative (EII), Barcelona, Spain

Correspondence
Míriam Gimeno, Institut de Ciencies del Mar, Recursos Marins Renovables, Passeig Marítim de la Barceloneta 37-49, Barcelona 08003, Spain.
Email: miriam@icm.csic.es

Abstract

As charismatic and iconic species, penguins can act as "ambassadors" or flagship species to promote the conservation of marine habitats in the Southern Hemisphere. Unfortunately, there is a lack of reliable, comprehensive, and systematic analysis aimed at compiling spatially explicit assessments of the multiple impacts that the world's 18 species of penguin are facing. We provide such an assessment by combining the available penguin occurrence information from Global Biodiversity Information Facility (>800,000 occurrences) with three main stressors: climate-driven environmental changes at sea, industrial fisheries, and human disturbances on land. Our analyses provide a quantitative assessment of how these impacts are unevenly distributed spatially within species' distribution ranges. Consequently, contrasting pressures are expected among species, and populations within species. The areas coinciding with the greatest impacts for penguins are the coast of Perú, the Patagonian Shelf, the Benguela upwelling region, and the Australian and New Zealand coasts. When weighting these potential stressors with species-specific vulnerabilities, Humboldt (*Spheniscus humboldti*), African (*Spheniscus demersus*), and Chinstrap penguin (*Pygoscelis antarcticus*) emerge as the species under the most pressure. Our approach explicitly differentiates between climate and human stressors, since the more achievable management of local anthropogenic stressors (e.g., fisheries and land-based threats) may provide a suitable means for facilitating cumulative impacts on penguins, especially where they may remain resilient to global processes such as climate change. Moreover, our study highlights some poorly represented species such as the Northern Rockhopper (*Eudyptes moseleyi*), Snares (*Eudyptes robustus*), and Erect-crested penguin (*Eudyptes sclateri*) that need internationally coordinated efforts for data acquisition and data sharing to understand their spatial distribution properly.

KEYWORDS
environmental trends, fisheries, global change, human pressures, marine systems, sentinels, Southern Hemisphere, threats

1 | INTRODUCTION

Oceans provide societies with significant natural benefits such as food, carbon storage, and climate regulation; marine ecosystem services are vital for maintaining human wellbeing (Barbier, 2017). Oceanic systems are among the most complex, least understood, and likely the most impacted of Earth's biomes (Halpern et al., 2015; Hoegh-Guldberg & Bruno, 2010; IPCC, 2014; Ramírez et al., 2017). Ocean warming, pollution, overexploitation of marine resources and marine habitat degradation (among others) pose severe threats to marine systems and the species that inhabit them (Halpern et al., 2015; O'Hara et al., 2021; Ramírez et al., 2017). Despite the scale of these perturbations, our understanding of how changes in climate and human stressors affect marine ecosystems has lagged far behind our knowledge of their impacts on terrestrial systems (Rosenzweig et al., 2008). There is considerable uncertainty regarding these potential threats' spatial and temporal dimensions in marine environments (Hoegh-Guldberg & Bruno, 2010). This knowledge gap is more significant in the Southern Hemisphere, as studies evaluating the spatial co-occurrence between species and their threats are mainly conducted in the Northern Hemisphere (Ramírez, Shannon, et al., 2022). Identifying areas of ecological significance (Hindell et al., 2020) in the Southern Hemisphere is critical to cost-effective marine conservation and the sustainable exploitation of marine resources (Roberts et al., 2017; Ropert-Coudert et al., 2020).

The challenge for marine conservation is to combine information on the distributions of sentinel species, which are sensitive to threats by climate and human-driven pressures, with data on the distribution and magnitude of known pressures to determine their impact on the structure and function of marine communities. Recent advances in remote sensing have revolutionised how we monitor the oceans, track human pressures, and follow the movements of marine organisms (Hays et al., 2019; Ramírez, Afán, et al., 2022). Spatial environmental and biological data, along with spatial data for at-sea and on-land threats to marine environments and species can now be obtained at high spatial and temporal resolution through arrays of sensors in space, air, on land, and in water (Allan et al., 2018). Concurrently, open-access digital repositories and online information systems now enable the study of patterns of marine biodiversity at high spatial, temporal, and taxonomical resolutions (O'Hara et al., 2021; Ramírez, Sbragaglia, et al., 2022, but see also Beck et al., 2014, for some of the limitations of using these datasets).

Seabirds, including penguins, have been used as sentinel species to monitor the Southern Hemisphere's marine ecosystems (Boersma, 2008; Carpenter-Kling et al., 2019; Ciancio et al., 2021). Currently, 18 species of penguins are distributed from the tropics to Antarctica and across islands and continents in the Southern Hemisphere (Borboroglu & Boersma, 2013). Geographic range varies considerably among species, with some restricted to a single small island such as the Snares penguin (*Eudyptes robustus*), and others covering a large portion of the Antarctic coast such as the Emperor penguin (*Aptenodytes forsteri*) (Borboroglu & Boersma, 2013). As meso predators, penguins integrate and respond to processes occurring throughout the food web (Boersma, 2008). They can act as umbrella species, that is, by protecting penguins, we can also protect their ecosystems and associated services (Giménez et al., 2022). As charismatic species, they can also function as "ambassadors" and play a vital role in education to help explain environmental issues to the public. Their charismatic nature has also resulted in a proliferation of biological observations (e.g., tracking data and direct observations, some of them from citizen projects) over recent years that can help to identify areas of ecological significance (Hindell et al., 2020). Their sensitivity to changes in oceanographic conditions and anthropogenic impacts make them one of the most at-risk groups of seabirds (Dias et al., 2019), with 11 of the 18 penguin species recognized as threatened and 12 of the 18 penguin species' populations decreasing (Boersma et al., 2020).

Climate-driven environmental changes at sea, interaction with fisheries, and marine pollution are the main threats facing the world's 18 penguin species, along with other land-based stressors related to human presence and climate change (Boersma et al., 2020; Ropert-Coudert et al., 2019). However, no previous studies have provided quantitative assessments of how these impacts are distributed within important areas for penguins. Here, we fill some of this knowledge gap by examining how the spatial distribution of different stressors relates to that of penguin assemblages and individual species. We combined occurrence data for penguins globally, extracted from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/), with high spatial resolution assessments of some of their main potential stressors like changes in productivity, temperature, sea ice concentration or fishing effort, and human presence on land (sources in Table S1). We investigated the contrasting pressures among areas/populations within species, and periods within the annual cycle (i.e., breeding vs. non-breeding period). We also explored the cumulative impact on the different penguin species.

2 | MATERIALS AND METHODS

2.1 | Species distribution data

All the occurrences from the order Sphenisciformes were downloaded from GBIF (accessed in September 2021: https://doi.org/10.15468/dl.urxxj2) and filtered by the scientific name of the 18 penguin species (Table 1). We restricted records to those with an observational basis reported as "human observation", "machine observation", or "observation". Within "observation" we kept only the locations associated with "Argos Tracking". We further subset all records from 1980 to 2021 and deleted occurrences outside BirdLife's range maps for each species (BirdLife International and Handbook of the Birds of the World, 2020) to avoid unreliable locations. The filtering proces has been done using R 4.1.1 (R Core Team, 2021). The final database has 821,115 occurrence records for the 18 penguin species (see Table S2 for the number of occurrences by species). Although GBIF provides data on abundance, we used penguin occurrence to avoid bias associated with different sampling procedures, such as colony counts.

TABLE 1 Classification of the main impacts faced by the 18 penguin species.

| Species | Climate change | | Human pressure | | |
	Direct effects	Indirect effects	Fisheries	Land-based impacts	Pollutants[b]
Galápagos penguin *Spheniscus mendiculus*		↓ Productivity (A–) ENSO[b] (–) ↓ SST (+)*	Direct competition (–)	Habitat degradation (–) Behaviour alteration (B≈)	Plastic (–) Oil (–)
Magellanic penguin *Spheniscus magellanicus*	↑ Storms[b] (B–)	↑ SST (–)	Direct competition (–) By-catch (gillnets, trawlers)	Habitat degradation (–) Behaviour alteration (–, ≈) Diseases[b] (–)	Plastic (–) Oil (–)
Humboldt penguin *Spheniscus humboldti*		↓ Productivity (A–) ENSO[b] (–)	Direct competition (–) By-catch (gillnets)	Habitat degradation (–) Behaviour alteration (A–, B–)	
African penguin *Spheniscus demersus*	Heat stress[b] (–)	↓ Productivity (–)	Direct competition (–)	Human settlement (+) Habitat degradation (–) Behaviour alteration (B–) Diseases[b] (–)	Plastic (–) Oil (–) Sediment
Yellow-eyed penguin *Megadyptes antipodes*		↓ Productivity (A–, F–) ENSO[b] (–)	Habitat modification (–) Food web alteration (–) By-catch (gillnets)	Habitat degradation (B–) Behaviour alteration (A–, F–, R–, B–) Diseases[b] (–)	
Northern Rockhopper penguin *Eudyptes moseleyi*	↑ Storms[b] (B–)			Introduced predators (–) Diseases[b] (–)	Plastic Oil (–)
Little penguin *Eudyptula minor*	Bushfires[b] (B–)	↑ SST (–) ENSO[b] (–)		Human settlements (–) Habitat degradation (–)	Hg (–) Oil (–)
Erect-crested penguin *Eudyptes sclateri*[a]					
Royal penguin *Eudyptes schlegeli*		↓ Productivity (–)		Behaviour alteration (–) Diseases[b] (–)	
Snares penguin *Eudyptes robustus*		↓ Productivity (≈) Higher SST (≈) ENSO (B–)			
Fiordland penguin *Eudyptes pachyrhynchus*		↓ Productivity (≈)	Food web alteration (–)	Human settlements (–) Introduced predators (–)	
Macaroni penguin *Eudyptes chrysolophus*	↑ Storms[b] (B–)		Food web alteration (–)	Diseases[b] (–)	Hg (–) POPs (?)
Southern Rockhopper penguin *Eudyptes chrysocome*		↓ Productivity (–, ≈) SST changes	Food web alteration (–)	Diseases[b] (–)	Hg (–) POPs (?)
King penguin *Aptenodytes patagonicus*	↑ Environmental temperature[b] (B–, A–)*	↓ Productivity (B–) ↑ SST (B–, A–) Changes in seafronts ENSO (B–, A–)	Direct competition (–)*	Behaviour alteration (–) Diseases[b] (–)	Hg
Gentoo penguin *Pygoscelis papua*	Early break-out of fast ice (B+) Loss of sea ice (+)	↓ Productivity (–)	Food web alteration (–)	Diseases[b] (–)	Hg (–) POPs (?)

(Continues)

TABLE 1 (Continued)

Species	Climate change		Human pressure		Pollutants[b]
	Direct effects	Indirect effects	Fisheries	Land-based impacts	
Chinstrap penguin *Pygoscelis antarcticus*	↑Storms[b] (B−) Loss of sea ice (−)	↓Productivity (−)	Direct competition krill (−)*	Diseases[b] (−)	Hg POPs (?)
Adélie penguin *Pygoscelis adeliae*	Early break-out of fast ice (B+) ↑Snowfall[b] (−) ↑Environmental temperature[b] (−)* ↑Rainfalls[b] (B−)*	↓Productivity (−)*	Direct competition krill (−)*	Behaviour alteration (R−, B−) Diseases[b] (−)	Hg POPs (?)
Emperor penguin *Aptenodytes forsteri*	Early break-out of fast ice (B−, A+) ↑Environmental temperature[b] (B−, A−)*	↓Productivity (−)		Diseases[b] (−)	Hg POPs (?)

Note: Classification made according to Borboroglu and Boersma (2013), Ropert-Coudert et al. (2019), and Trathan et al. (2015). As different species do not respond to stressors in the same way, we differentiate among positive (+), negative (−), unknown (?) and adaptation (≈). When available, we also distinguish among life stages: breeding success (B), adult survival or alteration in adults' behaviour (A), recruitment success (R), pre-moulting events (P), migration (M), and fledgling survival (F). Predicted responses are denoted with an asterisk (*). Increase (↑), decrease (↓), sea surface temperature (SST), mercury (Hg), persistent organic pollutant (POPs), El Niño Southern Oscilation (ENSO).

[a]Data deficient (Borboroglu & Boersma, 2013).

[b]These stressors have been listed as stressors to penguins but not included in this paper.

2.2 | Penguins' hotspots

We used a kernel density analysis based on occurrence data to assess each penguin species hotspot. This technique calculates the utilization distributions based on a probability density function (Blundell et al., 2001; Powell, 2000; Worton, 1987, 1989). Before calculating kernel distributions, occurrence data were projected using two different spatial reference systems. For penguins with the most southerly distribution (Chinstrap, Adélie, and Emperor penguin) we used NSIDC Sea Ice Polar Stereographic South (EPSG 3412). We used Sphere Mollweide (ESRI 53009) for the other penguin species. Then, we created a fixed kernel density estimator for each penguin species using the heatmap algorithm of QGIS (QGIS Development Team, 2020). To use this algorithm, apart from the occurrence data, we need to select a pixel size and a search radius (i.e., kernel bandwidth). We set the same pixel size (4 km) for all the species. The search radius was calculated for each penguin species using the reference bandwidth (href) (Walter et al., 2011) in the adehabitatHR package (Calenge, 2006) using R 4.1.1 (R Core Team, 2021) and then used in the heatmap algorithm. The outputs from the heatmap algorithm were reclassified according to the 95% isopleth and vectorized to identify species-specific hotspots (i.e., areas that encompass the largest number of presence locations and, therefore, potential Areas of Ecological Significance). These calculations include observations from colonies (on land).

2.2.1 | Migrant species

According to their distributions throughout the year, penguins can be divided into resident and migrant species (Croxall & Davis, 1999; penguin species classification and other biological and ecological characteristics are summarised in Table S2). GBIF information on penguin occurrence is biased towards breeding areas and when individuals are more accessible on land to researchers. It is especially evident for migrant species because they only visit their colonies for breeding and molting and they are usually offshore foragers. We repeated our kernel analyses separating occurrence from breeding and non-breeding period to identify critical marine regions of breeding for migrant species (at-sea hotspots; see Table S2 for the list of migrant species). To distinguish breeding and non-breeding periods, we initially identified species with occurrence data outside typical breeding months (Table S2). For these species, we excluded locations within species-specific maximum foraging distances during breeding (Table S3). This ensures accurate characterization of at-sea, non-breeding hotspots, excluding areas closely linked to breeding colonies. This process resulted in non-breeding observations for only three of the 12 migrant species (Table S3). We used this approach as information on the month associated with GBIF occurrences and breeding stages (breeding vs. non-breeding) is lacking, thus preventing direct inference. This approach is conservative because the maximum foraging distance may differ between colonies. Thus, the resulting areas may underestimate actual non-breeding

hotspots. However, it helps identify those offshore marine areas more likely used by penguins out of the breeding season. The search radius (href) was recalculated for these new data subsets that distinguish breeding and non-breeding distributions.

2.3 | Climate and human stressors data

For climate-driven stressors on penguin species, we evaluated long-term, spatial trends in chlorophyll-*a* concentration (CHL, as a proxy for primary production), sea surface temperature (SST), and sea ice concentration (see Table S1 for product-specific sources, time frames and spatial–temporal resolutions). These trends were explored through per-pixel, least-square linear regressions of yearly average information and using the slopes (significance at α-value = .05) as estimates for the magnitudes of observed changes (see the details in Ramírez et al., 2017).

As a proxy for the industrial fishing potential impact on penguins, we used data on fishing effort (hours of fishing activity by industrial fisheries) from Global Fishing Watch (GFW; http://globalfishingwatch.org/) (Table S1). GFW is a global repository of fishing activity where Automatic Identification System (AIS) data are processed to estimate fishing efforts by main fishing gears (see details in Kroodsma et al., 2018). Our analyses focused on the most up-to-date information on fishing effort, which accounted for the 2013–2020 period, and for those fishing gears likely impacting penguins through resource competition and bycatch: gillnets, long liners, purse seiners, and trawlers (see Table 1 and references therein). Daily fishing AIS messages were summed to spatial totals for 2013 to 2020 to obtain an integrated overview of the spatial distribution of gear-specific fishing pressure.

Satellite imagery of artificial nightlights is a reliable proxy for the spatial distribution of human facilities, settlements, and activities (Ramírez et al., 2020). To evaluate the distribution of human-driven pressure on coastal areas (i.e., direct disturbance of breeding sites or anthropogenic habitat degradation) throughout the Southern Hemisphere (excepting Antarctic breeding species; data available did not cover areas south of −65°S), we calculated the median for the monthly data on nightlight intensity (radiance, in $nW/cm^2/sr$) over the 2004–2021 period (VIIRS sensor datasets publicly available on Google Earth Engine, see details in Table S1). Illuminated areas likely indicating the presence of human settlements/facilities were identified by selecting those pixels with radiance >2 $nW/cm^2/sr$ (see details in Ramírez et al., 2023).

2.4 | Climate and human impact on penguins

We used different approaches to assess the distribution of climate and human impact within species-specific hotspots. We extracted values from species-specific hotspots for climate-driven stressors and fisheries. We summarized them using boxplots (minimum, first quartile, median, third quartile, and maximum; outliers were

removed) to capture their spatial heterogeneity within species distributions. The sea ice concentration was analyzed only for those penguin species that can be affected by sea ice changes according to their geographical distribution. The overall fishing pressure per gear (gillnets, long liners, purse seiners, and trawlers) was evaluated by estimating the number of fishing hours within penguins' hotspots, standardised by their total hotspots' area to make them comparable. Finally, we calculated the percentage of the coastline used by each species that overlaps with the estimated distribution of human settlements/facilities using night lights as a proxy for direct disturbance to breeding colonies and degradation of breeding habitats.

2.5 | Cumulative impact

We created two layers of cumulative impact at sea, one for climate stressors (CHL, SST, and sea ice trends) and another for marine-based human pressure (including fisheries). Before adding all the climate stressors, we calculated the absolute values for the obtained slopes, then normalized them (expressed between 0 and 1) to compare the intensity of impacts. For the human pressure, we summed the hours of all the fishing gears, $\log [X + 1]$ transformed the layer to reduce the effect of extreme outliers, and then we normalized the layer values (Halpern et al., 2015). Next, we calculated the quartiles of each layer and used a bi-scale plot to show the overlap of high values of climate and human impacts (O'Hara, 2022). To calculate the quartiles, we did not consider 0 values. We used R software and a ca. 25×25 km horizontal resolution to estimate and map the results. Before all analysis, we converted all data to the NSIDC Sea Ice Polar Stereographic South (EPSG 3412) projection.

To help guide management to choose where to focus the effort, we summarized the species-specific cumulative impacts weighted by the vulnerability of each species (Figure 5b). To calculate the vulnerability weights, we based our calculations on the vulnerability assessment by Borboroglu and Boersma (2013). This was a qualitative assessment; thus, to use it for weighting the impacts, we transformed it into a quantitative scale (the minimum "none" = 0 and the maximum "major" = 1; see the specific weight values for each species and impact in Table S4). For each species, we averaged per-pixel values extracted for each hotspot, allowing direct comparison among species despite differences in the size of the hotspots.

3 | RESULTS

3.1 | Global species distribution hotspots

We identified 22 hotspots: 15 delimit important areas used year-round by penguins (Figure 1a,b) and 6 separate breeding and non-breeding areas for three migrant penguin species (Figure 1c). The hotspots for Northern rockhopper (*Eudyptes moseleyi*), Little (*Eudyptula minor*), African (*Spheniscus demersus*), and Galápagos
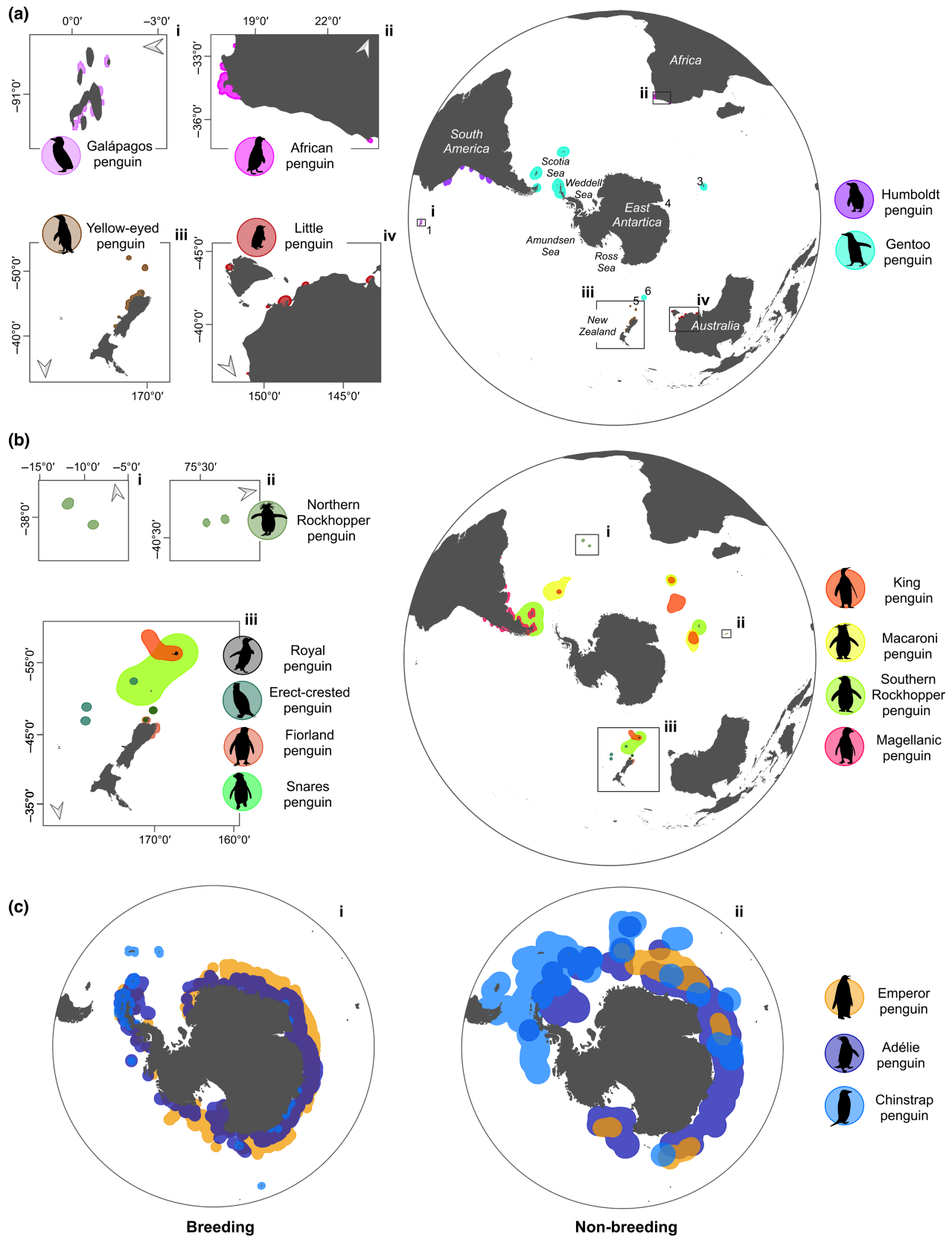
FIGURE 1 Hotspots, according to the 95% isopleth, used by penguin species. (a) Year-round distribution for the six resident penguin species, four areas have been zoomed in (i, ii, iii, iv). (b) Year-round distribution for nine migrant penguin species, three areas have been zoomed in (i, ii, iii). (c) Separating breeding (i) and non-breeding (ii) distribution for three migrant penguin species. 1=Galápagos Islands, 2=Antarctic Peninsula, 3=Kerguelen Islands, 4=Prydz Bay, 5=New Zealand Subantarctic Islands, 6=Macquarie Island. Basemap from: https://www.naturalearthdata.com/downloads/50m-physical-vectors/.

(*Spheniscus mendiculus*) penguins did not overlap with any of other species. All the other penguin species shared part of their hotspots with at least one other penguin species. We found three marine areas with more than four penguin species: the Scotia Sea, the marine region of the Kerguelen Islands, and the marine region of New Zealand's Subantarctic Islands. In the Macquarie Island region, there were up to five different penguin species co-occurring: four breeding species Southern rockhopper, King, Royal, and Gentoo penguin, and Snares penguin that does not breed on this island but uses the surrounding waters as a foraging ground.

3.2 | Spatial overlap between impacts and penguins

3.2.1 | Climate-driven environmental change stressors

Ocean productivity has shown an overall moderate positive trend in the southern hemisphere over the last decades, with the greatest increases in productivity associated with coastal areas and oceanographic fronts (Figure 2a). Following this general trend, the median values of CHL were positive in all penguin hotspots with little variability in most of them (Figure 3a). Nonetheless, some species presented a wider range of values within their hotspots, including Little, Chinstrap, Gentoo (*Pygoscelis papua*), Humboldt (*Spheniscus humboldti*), and Galápagos penguins. Decreasing trends in ocean productivity were also observed in different zones of the southern hemisphere (Figure 2a), some of them overlapping with Adélie and Chinstrap penguin distributions, such as at the western Antarctic Peninsula, or along the coast of Perú and at the Galápagos Islands, where Humboldt and Galápagos penguins occur, respectively (Figures 1a,c and 2a).

We observed a general increase in SST throughout the Southern Hemisphere (Figure 2b). However, there was significant heterogeneity depending on the distributions of penguin species (Figure 3b). Penguin species facing the greatest increasing trends in SST were those distributed around Australia, New Zealand, and the New Zealand Subantarctic Islands: Little, Yellow-eyed (*Megadyptes antipodes*), Fiordland (*Eudyptes pachyrhynchus*), and Erect-crested penguins (*Eudyptes sclateri*). In contrast, marine regions used by several penguin species around the Galápagos Islands, the coast of Chile, and Antarctica, showed negative trends in SST. Yet, these trends were significant only for those areas where Emperor, Adélie, Chinstrap, and Humboldt penguins occur (Figures 1a,c and 3b).

Trends in sea ice concentration showed significant spatial heterogeneity, with some areas showing slightly increasing trends (e.g., the Weddell Sea, the Ross Sea, and the coast of East Antarctica), and others showing drastic and negative trends (e.g., the western Antarctic Peninsula, Amundsen Sea, and Prydz Bay, Figure 2c). This geographic variability in sea ice concentration trends was also observed for all the species analyzed using this proxy (Figure 3c). Positive median values were observed within Emperor and Adélie penguins' hotspots, which are distributed around the Antarctic continent. In contrast, negative median values were observed in penguin species distributed around the Antarctic Peninsula: Chinstrap and Gentoo penguins (Figure 1a,c).

3.2.2 | Human stressors

The fishing effort was mainly distributed above the continental shelf or associated with seamounts (Figure 2d; Figure S1). Areas with 100 or more hours of fishing were distributed on the west coast of Africa and the east coast of South America, where we find African and Magellanic (*Spheniscus magellanicus*) penguins, respectively (Figures 1a,b and 2d).

Different penguin species were exposed to contrasting fishing pressure, by different fishing gears, within their distribution. Five species overlapped with gillnets, including Yellow-eyed and African penguins. These areas face the highest fishing pressure and the greatest variability (Figure 4a[i],b[i]). Royal (*Eudyptes schlegeli*), Little, and Galápagos penguins forage on areas facing the most pressure from longlines (Figure 3b) but were also exposed to the most variable longline fishing pressure inside their hotspots (Figure 4a[ii]). The distribution of only three penguin species, African, Humboldt, and Magellanic penguins, overlapped with that of purse-seiners, with African penguins foraging area facing the greatest fishing pressure (Figure 4a[ii],b[ii]). Magellanic, Yellow-eyed and Snares penguins were the species exposed to the highest pressure by trawlers (Figure 4b[iv]). However, trawling fishing pressure was particularly heterogeneously distributed within the Northern rockhopper penguin hotspot (Figure 4a[iv]).

Night light patterns indicating the distribution of human settlements/facilities were heterogeneously distributed in the Southern Hemisphere, with the greatest aggregations along the coastline. Despite the prevalence in coastal areas, only six species showed spatial evidence of overlap/congruence with this proxy of human presence (Table 2). The greatest percentage of overlap was observed for African penguins (28%) on the South African coast, followed by Humboldt penguins (12%) on the west coast of South America, and Little penguins (6%) on the Australian coast. The other three species had less than 5% of spatial overlap.

3.2.3 | Cumulative impact

While environmental parameter changes (CHL, SST, Sea ice) are distributed throughout the Southern Hemisphere, fishing effort is highly concentrated over the continental shelf. Accordingly, the areas with the greatest cumulative impact (those corresponding to the fourth quartile values of fisheries and climate stressors) broadly lie in coastal areas off the western African coast (e.g., the Benguela upwelling region, Figure 5a[i]), Peruvian coast (Figure 5a[ii]), the Patagonia Shelf (Figure 5a[iii]), the waters surrounding New Zealand, and the south and the eastern Australian coast (Figure 5a[iv]). Within penguins' hotspots, changes in SST contribute most to climatic
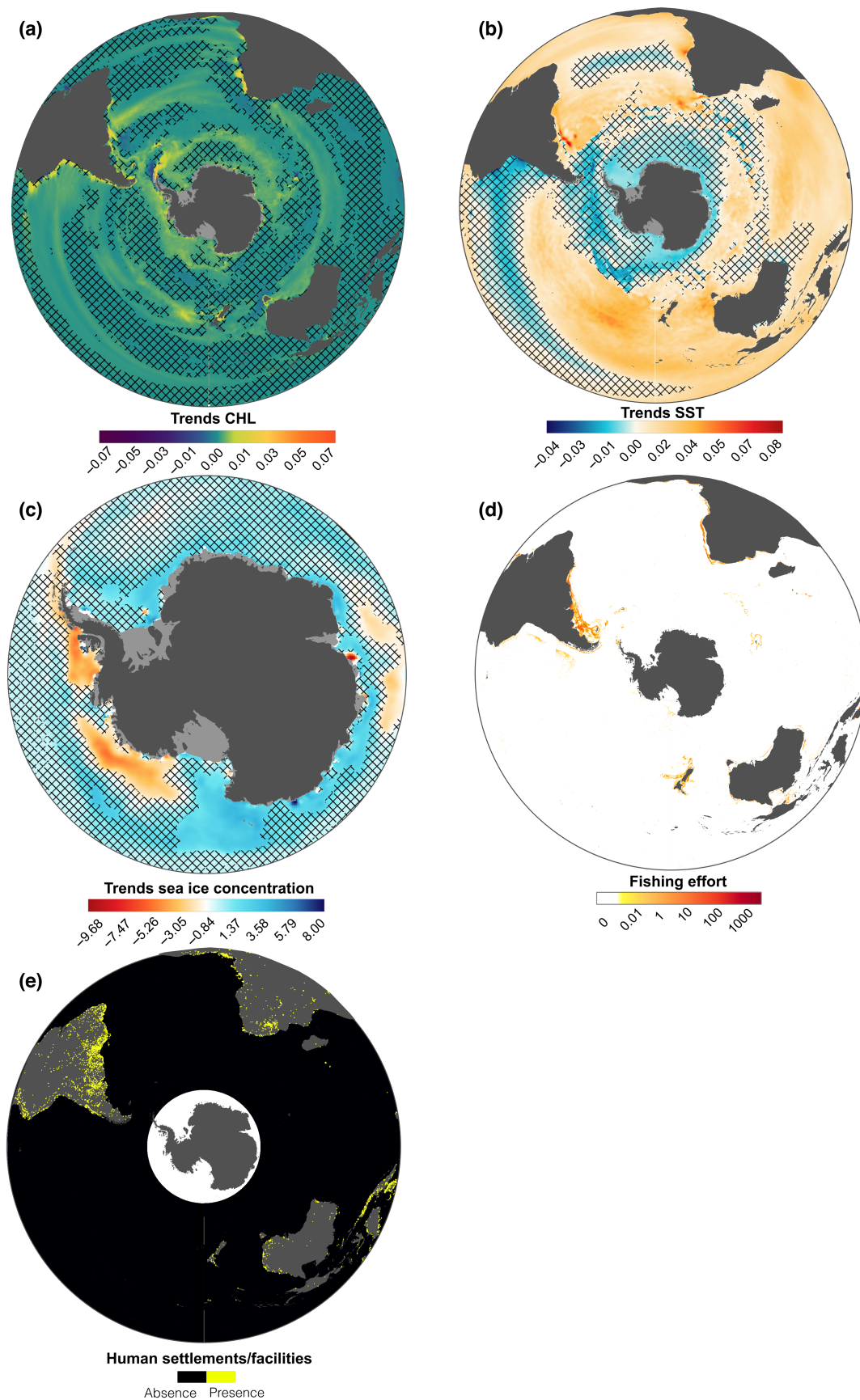
FIGURE 2 Long-term trends in (a) chlorophyll-*a* concentration (CHL-*a*; mg/m³ per year), (b) sea surface temperature (SST; °C per year), and (c) sea ice concentration (per year). Colours in (a–c) represent the slope of per-pixel least-square linear regressions; while gridded areas indicate those water masses in which observed trends were not significant (*p* > .05). Permanent ice is represented in light grey (from: https://doi.org/10.5285/ed0a7b70-5adc-4c1e-8d8a-0bb5ee659d18). (d) Fishing effort sourced from Global Fishing Watch (http://globalfishingwatch.org/). (e) Distribution of human settlements and other facilities in the Southern Hemisphere, as revealed by nightlight radiance >2 nW/cm²/sr (see details in Ramírez et al., 2023). White pixels in (e) indicate no data.

stressors and, hence, to the cumulative impact (Figure 5b). The species showing the highest cumulative impacts (greatest changes) are African, Chinstrap, and Humboldt penguins, whereas the least potentially impacted species are Erect-crested and King penguins (*Aptenodytes patagonicus*).

4 | DISCUSSION

This study evaluated the spatial distribution of environmental and human-driven stressors within penguin hotspots globally, mapping anthropogenic and climatic selected stressors that can affect the different penguin species. The most common stressors for the penguin community were fishing efforts and increasing SST values, which are essential drivers of food availability and accessibility, and, ultimately, penguin population dynamics. Our method for assessing cumulative impacts distinguishes between climate and human-related pressures. Therefore, based on our results, some areas susceptible to applying this conservation framework are the Peruvian coast, the Patagonian Shelf, Benguela upwelling region, and the Australian and New Zealand coasts. We also calculated the potential cumulative impact for all the penguin species, with African penguins as the species facing the greatest changes. Our approach enables the identification of the spatial distribution of the widespread stressors that are likely affecting the world's 18 penguin species.

4.1 | Challenges at studying penguin distribution and stressors: Acknowledging data limitations

Conducting a global study on penguin spatial distribution and stressors is challenging due to diverse datasets with varying completeness and data deficiency at different temporal and spatial scales. Our study provides a comprehensive global perspective on stressors within penguin hotspots, acknowledging data limitations, particularly for certain species like the northern rockhopper, Snares, or erect-crested penguins. This may lead to underestimation of critical areas, hindering the identification of essential zones, especially during non-breeding periods. We also should consider that the use of tracking data, that provide many locations for few individuals, may add some bias due to intraspecific variability.

While focusing on climate-driven changes and human interactions, our study recognizes other impactful factors like pollution, diseases, and land-related climate change (Borboroglu & Boersma, 2013; Ropert-Coudert et al., 2019; Trathan et al., 2015).

However, the absence of spatially resolved data for these stressors excludes them from the analysis. Our approach emphasizes adaptability to include additional drivers of change as more spatially explicit information becomes available.

The holistic overview includes the assessment of different human stressors. However, the lack of available data on global penguin distributions throughout the annual cycle prevents evaluations on temporal co-occurrences, which may be relevant for some fisheries-associated impacts like by-catch. This underscores the need for ongoing research and data refinement to enhance the accuracy and completeness of global penguin impact assessments.

4.2 | Marine-based potential stressors

Changes in the physical properties of the ocean are indirect effects of climate change (Bijma et al., 2013; Rost et al., 2008). Penguins use highly productive foraging areas where prey is abundant and predictable (Forcada & Trathan, 2009), mainly influenced by primary production (CHL concentration) and ocean temperature (SST). Overall, we observed enhanced primary production within all penguins' hotspots (Figure 2a), but we also observed spatial variability. Therefore, those populations that use areas with negative trends in CHL (Figure 3a) might be faring worse than the others (Hennicke & Culik, 2005). The increasing trends in SST in some areas can result in an increased vertical stratification of the water column and a low nutrient supply to the photic zones, affecting productivity and, ultimately, food availability (Behrenfeld et al., 2006; Currie et al., 2013). Previous studies have also shown lower foraging success in penguins associated with increased SST during the breeding period (Carroll et al., 2016). Evaluating the possible combined effects of these two indicators was outside the scope of our global analysis as the covariance of CHL and SST is complex and highly dependent on location (Dunstan et al., 2018). These patterns represent the long-term trends in SST and CHL. The implications are that we were not controlling the effects of short-term events (i.e., marine heatwaves or punctual changes in local productivity) that can hide average changes in some regions (Dunstan et al., 2018; Salinger et al., 2016). Using the longest time series available for both parameters we ensure that the maximum number of phases of the different drivers of climate variability (like ENSO) are included. This would minimise the effect of the changes in the average and extreme values in some variables like CHL or SST associated with the transition of these drivers along the different phases of these modes of climate variability (Salinger et al., 2016).

For penguins breeding in Antarctica, sea ice is another important driver of food availability and accessibility, ultimately affecting
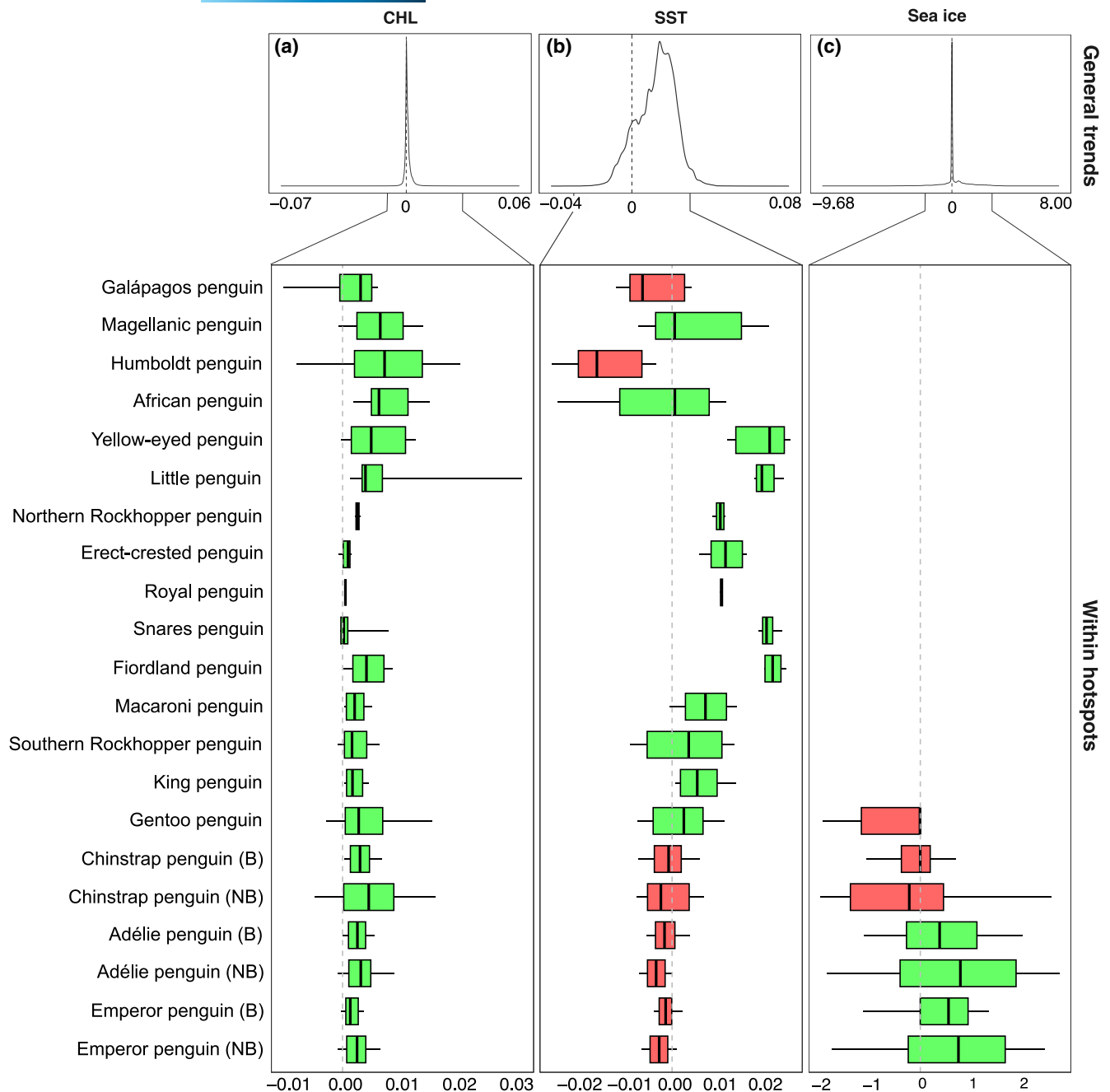
FIGURE 3 Density plots represent the distribution of estimated general trends (slopes for the pixel-basis linear regressions) in climate-driven environmental conditions. Boxplots representing those trends within species-specific penguin hotspots: chlorophyll-*a* concentration—CHL (a), sea surface temperature—SST (b), and sea ice concentration (c). Green boxplots indicate when the median is >0 and red boxplots when the median is ≤0. For Emperor, Adélie and Chinstrap penguins we could differentiate the breeding (B) and the non-breeding (NB) seasons.

breeding success and population dynamics (Barreau et al., 2019; Forcada & Trathan, 2009; Watanabe et al., 2020). Antarctic sea ice concentration varied by region (Figure 2c). However, the observed trends should be taken cautiously as recent assessments suggested that sea ice has drastically decreased since 2016 (Eayrs et al., 2021). Thus, the general increasing trend we observed in sea ice around Antarctica over 1978–2020 may no longer reflect the current trend in all areas. Otherwise, the decreasing trends reported at

the Amundsen and Ross seas are consistent with the general pattern of Antarctic sea ice concentration decrease (Eayrs et al., 2021). Antarctic sea ice coverage has a huge variability occurring on different timescales (Eayrs et al., 2021). In this study, we focus on the trends observed over all the available data because even though punctual events impact breeding failure, prevalent trends have the greatest effects on long-lived species populations (Stahl & Oli, 2006). Not all the species had the same response to changes in
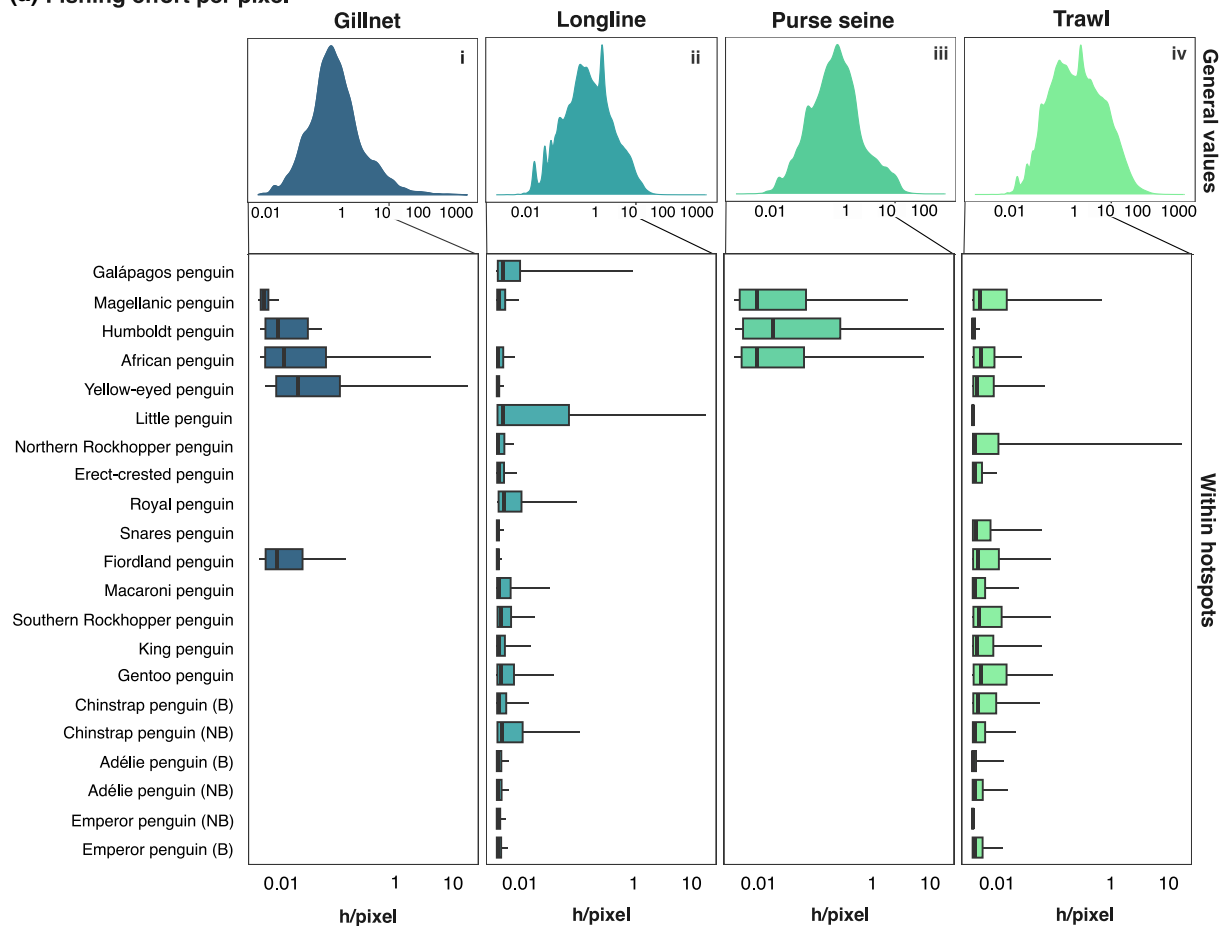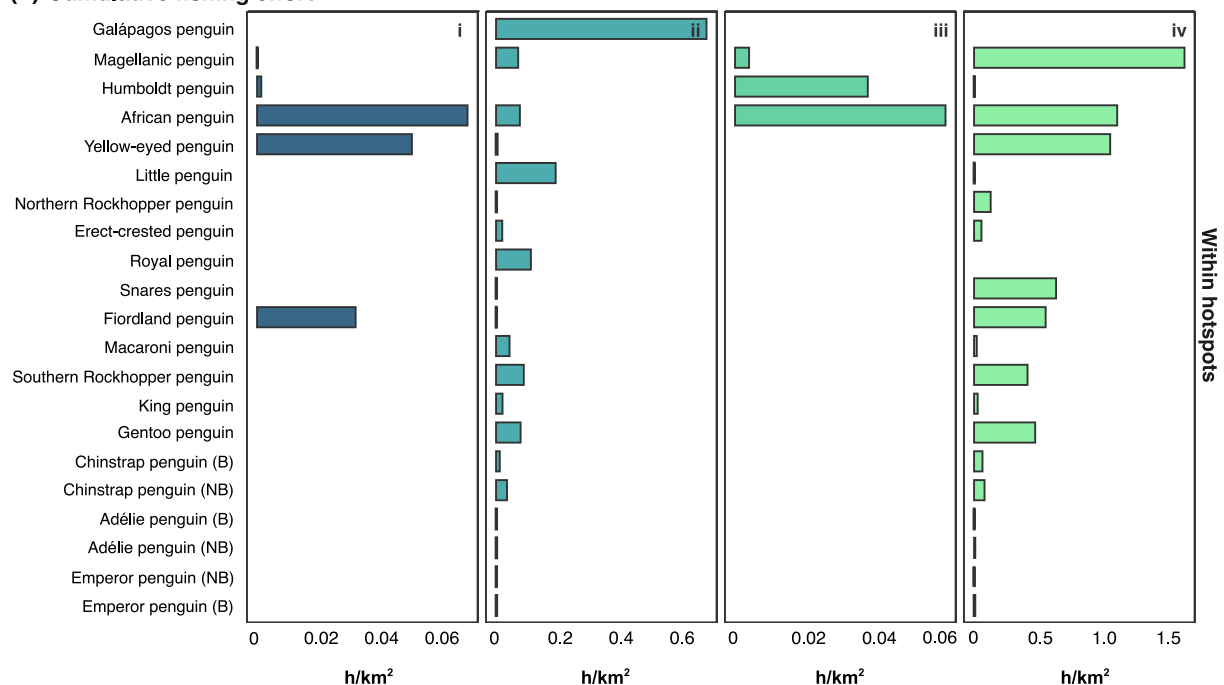
FIGURE 4 (a) Density plots representing the general distribution of fishing effort values (total fishing hours by pixel from 2013 to 2020, values =0 were not represented) for each fishing gear: gillnet (i), longline (ii), purse seine (iii) and trawl (iv). Boxplots represent these values occurring within each penguin's hotspots. (b) Barplots represent the gear-specific total fishing effort within penguin hotspots (h/km²). The total amount of fishing hours by fishing gear for the 2013–2020 period within each hotspot standardised by the area of the hotspot to make them comparable. For Emperor, Adélie and Chinstrap penguins we could differentiate the breeding (B) and the non-breeding (NB) seasons.

TABLE 2 Coastal overlap with human presence.

	Total coastline (km)	Coastline with human presence (km)	% of the coastline with human presence
Magellanic penguin	10,550	381	4
Humboldt penguin	1867	224	12
African penguin	317	88	28
Yellow-eyed penguin	861	9	1
Little penguin	504	31	6
Fiordland penguin	863	9	1

Note: Length of the coastline potentially used by penguins, and part of these potential coastlines occupied by human settlements/facilities (based on night lights). The potential overlap is provided in absolute values and percentages. For the penguin species absent in the table, we observed no spatial overlap between their coastal distributions and our proxy to human presence.

sea ice concentration. Emperor and Adélie penguins are ice-obligate, while Chinstrap and Gentoo penguins are ice-intolerant (Forcada & Trathan, 2009). Hence, the median values of sea ice trends within penguin hotspots were positive for ice-obligate species and negative for ice-intolerant, which might seem like a positive outcome. However, we found variability in regional sea ice trends within penguin hotspots (Figure 3c), which suggests that particular populations/colonies might be at risk. Contrasting trends for different Antarctic penguin colonies have been reported, with some showing decreasing trends or even disappearance (Fretwell & Trathan, 2021; Trathan et al., 2011). Furthermore, the relationship between sea ice and penguins is complex (Watanabe et al., 2020). Bell-shape relationships showing how some ice melting favors the discovery of new foraging areas near the colonies, but significant sea ice melting negatively affects food availability (Jenouvrier et al., 2006).

Fisheries can also alter prey availability (Daskalov, 2002; Jacques, 2015). Intense fishing efforts may substantially reduce fish stocks (Pauly & Zeller, 2016). This may impact penguins when they compete for the same target species or through changes in the structure and functioning of marine food webs (Ainley & Blight, 2009; Hočevar & Kuparinen, 2021). While fisheries may sometimes benefit marine species by providing additional food resources or through resource facilitation (Ouled-Cheikh et al., 2020), in penguins, such positive relationships are not clear, and most of the previously reported penguin-fisheries interactions are negative (see also Table 1 and references therein). All penguin species spatially overlapped with fisheries. However, the intensity of fishing effort contrasts among species and fishing gear, and varied within penguin hotspots. Penguins inhabiting the highly productive areas of the Patagonian Shelf and the Benguela upwelling, where fishing effort is particularly intense, may be more affected by intense interaction with human fisheries (Crawford et al., 2022). Habitat modification by fishing gear such as trawlers can also affect the food web (Preciado et al., 2019). This could be relevant for penguin species that forage on benthic prey and overlap with trawlers (Figure 4a[iii],b[iii], also Browne et al., 2011; Mattern et al., 2007, 2013). Reversing changes in fish stocks due to overfishing or habitat alterations takes time (Hočevar & Kuparinen, 2021). Thus, fishing impacts on penguins due to food web alterations do not necessarily require a temporal

overlap between penguins and fishing vessels. In contrast, temporal overlap is likely more relevant when fisheries and penguins target the same prey species. In this case, fisheries closures might substantially reduce the impact on penguins through food resource depletion (Pichegru et al., 2010). However, as species distribution is dynamic, changes in prey distribution can increase the potential overlap (Ratcliffe et al., 2021).

Fisheries can also cause direct mortality of penguins through bycatch. Given that penguins are pursuit divers, the fishing gears of greatest concern are gillnets (Žydelis et al., 2013), although trawlers may also have a significant impact (Crawford et al., 2017). The effect of bycatch depends on the species foraging ecology and behavior (Cardoso et al., 2011; Mattern et al., 2007). Our spatial assessment of fishing gear distributions found a spatial overlap between gillnets and the distribution of five penguin species. However, penguins and fishing vessels must co-occur both spatially and temporally for bycatch to occur. According to Crawford et al. (2017) Magellanic, Humboldt and Yellow-eyed penguins were categorized as the penguin species with the highest risk of bycatch. For Fiordland and African penguins, the risk of bycatch was classified as moderate and low concern, respectively (Crawford et al., 2017). However, we observed a greater fishing effort in the hotspots of these two species than in Magellanic and Humboldt penguins. That could be partly because penguins and fisheries did not overlap in time. Other reasons could be that we could not correctly delineate wintering areas for these species (Cardoso et al., 2011); also, GFW did not consider artisanal fisheries but we acknowledge that it may have an impact on penguins by-catch (Crawford et al., 2017).

4.3 | Potential land-based stressors

Penguins breeding in areas close to human presence are exposed to several pressures, such as human disturbance, loss of nesting habitat due to infrastructure development, and direct mortality due to predation by invasive species or traffic accidents (Borboroglu & Boersma, 2013; Ropert-Coudert et al., 2019; Trathan et al., 2015). Human facilities along the coastline may also prevent penguins
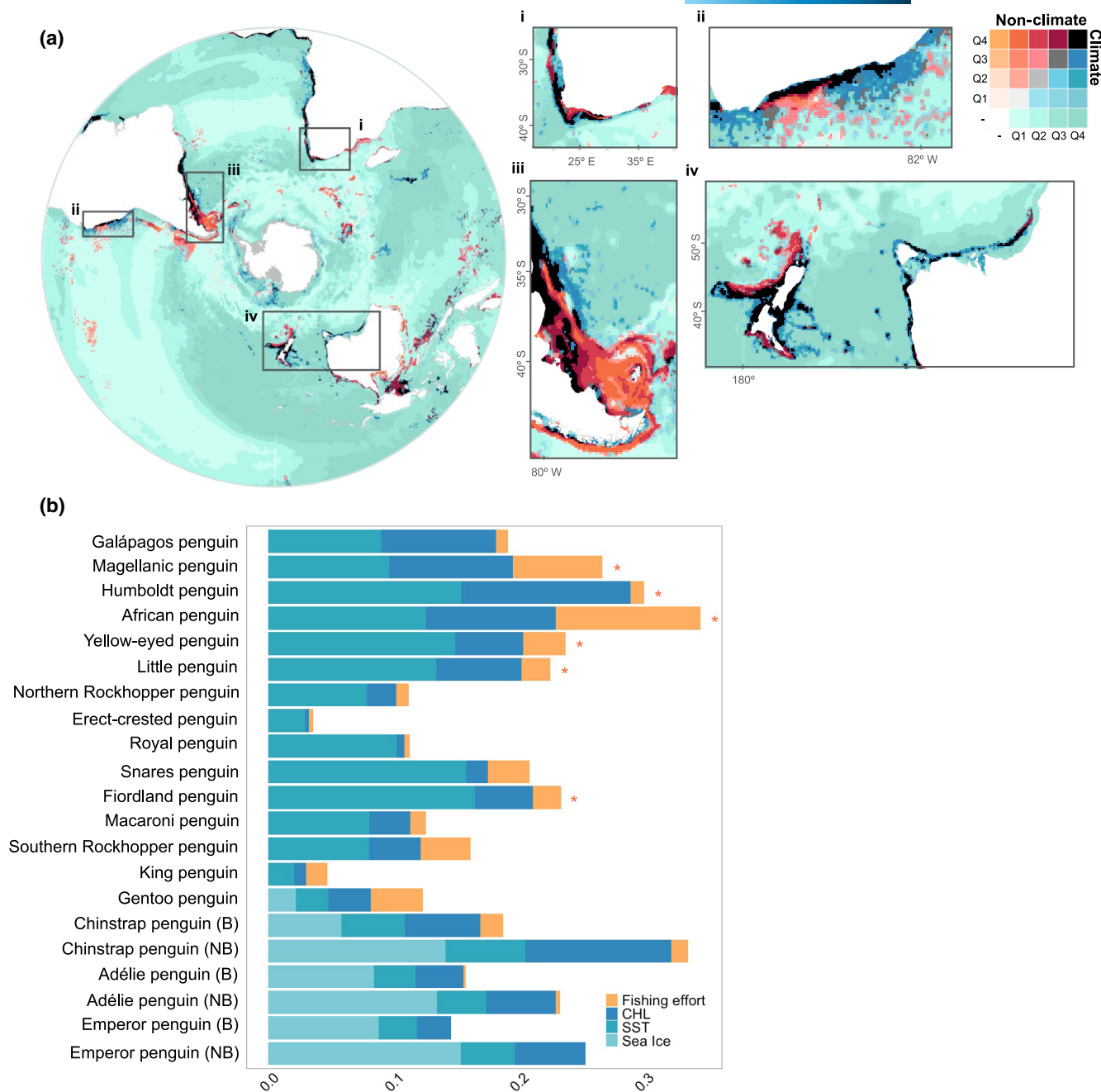
FIGURE 5 (a) Biscale plot shows the distribution of the main potential impacts from climate (blue-green tones) and non-climate stressors (red-orange tones) showing the areas with overlap (black-grey tones) according to their quartile distribution, with insets for the Benguela upwelling (i), Peruvian coast (ii), Patagonia shelf (iii), New Zealand and south-eastern Australian coast (iv). Permanent sea ice is represented in light grey. (b) Stacked barplot showing the cumulative index impact within each penguin hotspot. Asterisks (*) indicate species that have night lights present in their hotspots.

from establishing new colonies (Ropert-Coudert et al., 2019). We used satellite imagery of nightlights as a proxy of human presence (Ramírez et al., 2023). While it does not assess the intensity of the human presence, this proxy revealed the greatest aggregations of human presence along the coastline, in agreement with LandScan-derived products (Halpern et al., 2015). Our proxy also provided a reliable alternative for producing the most up-to-date assessments on the coastal distribution of human settlements/facilities (Halpern et al., 2015, 2019). We found that the on-land (mainly breeding)

distribution of six penguin species partially overlaps with that of human settlements/facilities (Table 2).

There might be other areas where this overlap with human presence occurs, but the light intensity is lower or without spatial information, like Antarctica. According to the International Association of Antarctica Tour Operators (IAATO), there has been an increasing trend of visitors in Antarctica before the worldwide SARS CoV-2 pandemic (IAATO, 2020, 2022). Tourism impact can be reduced when tourists are aware of their presence's effects on the penguins

(Vásquez Lavín et al., 2016). Local economies can coexist with penguin welfare, providing income/resources for penguin management and conservation (Lewis et al., 2012; Wagner et al., 2021). However, as the effect of human presence differs among penguin species (Ropert-Coudert et al., 2019), detailed information on the species site and the site is required to manage any human activity and understand potential signs of resilience and adaptability according to each specific situation.

4.4 | Think globally, act locally

There is no doubt that penguins are threatened by both climate and human stressors (Figure 5a) (Borboroglu & Boersma, 2013; Ropert-Coudert et al., 2019; Trathan et al., 2015) and that interactions between those impacts should be considered to guide international efforts to mitigate widespread threats through effective management strategies (Brown et al., 2014). For instance, ecosystem resilience to climate change effects can increase if synergies between local stressors and climate change are appropriately managed (Raworth, 2017; Rockström et al., 2009). The stressors that are likely related to changes in food availability and accessibility (like fisheries and ocean warming) are the ones that may impact the whole penguin populations. However, while it is difficult to act against climate stressors (but see Clitheroe, 2021), at the local scale it is more feasible to regulate fisheries, which will reduce the total cumulative impact faced by a species (Green et al., 2017; Ramírez et al., 2018; Scheffer et al., 2015). This emphasises the importance of local management of impacts to ease pressures and increase the resilience of penguin species and their underlying ecosystems. According to our results, the Peruvian coast, Patagonian Shelf, Benguela upwelling region, and Australian and New Zealand coasts are the marine areas with penguins most affected by cumulative impact. These are places susceptible to local management for enhancing resilience to climate-driven environmental changes. Local studies should be prioritized to account for the different sources of regional variability (e.g., the temporal dimension of the impact-penguin interactions) that we could not consider in our global assessment.

Our approach is also helpful in identifying those penguin species threatened by the cumulative impact of global processes and local impacts (Figure 5b). When looking at these results, we must remember that we did not differentiate between increasing and decreasing environmental trends. Instead, we just evaluated changes in environmental conditions, so that we cannot directly infer one species' threat level. To do that we must know how the different penguin species respond to any single stressor, and to the combination of them. Information on key demographic parameters of the species/population is for evaluating such responses (Boersma et al., 2020). Fortunately, international initiatives such as MAPPPD (https://www.penguinmap.com), and recent studies that have successfully used satellite imagery to assess some breeding populations in Antarctica (e.g., Fretwell & Trathan, 2021; Strycker

et al., 2020), have proven their value in providing the necessary information on key demographic parameters for addressing the critical question on how global environmental change is impacting the penguin community.

5 | CONCLUSION

Given the comprehensive nature of this study on the global distribution and stressors affecting penguins, several key considerations should guide conservation managers and policymakers in their decision-making processes. Firstly, it is crucial to acknowledge the limitations inherent in the study, particularly the underestimation of hotspot areas for certain penguin species due to limited observational data, especially during non-breeding periods. Additionally, the exclusion of certain stressors, such as pollution and diseases, underscores the need for ongoing data collection and adaptability in incorporating new information as it becomes available. For marine-based stressors, the study emphasises the importance of managing the impacts of climate-driven changes with increasing SST values, fisheries, and sea ice conditions, which are essential drivers of penguins' food availability and accessibility. Localised management actions, especially regulating fisheries in areas with high penguin overlap, can significantly reduce cumulative impacts. The study highlights specific regions, such as the Peruvian coast, Patagonian Shelf, Benguela upwelling region, and Australian and New Zealand coasts, where focused local management efforts could enhance the resilience of penguin species. Furthermore, understanding the complex interactions between global processes and local impacts, including the influence of SST, is essential, as evidenced by the identification of African, Chinstrap, and Humboldt penguins as species facing the greatest pressures. In light of these findings, prioritising and supporting local studies becomes imperative to account for regional variability and guide effective conservation strategies, laying the foundation for the enduring protection of penguins worldwide in the face of evolving challenges and ensuring their resilience for future generations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in DigitalCSIC at https://digital.csic.es/handle/10261/341275. These data were derived from the following resources available in the public domain: GBIF: https://doi.org/10.15468/dl.urxxj2, NOAA: https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html; Copernicus: https://doi.org/10.48670/moi-00019; NSIDC: https://doi.org/10.7265/N5K072F8; GFW: https://globalfishingwatch.org/data-download/datasets/public-fishing-effort; Google Earth Engine: https://developers.google.com/earth-engine/datasets/catalog/NOAA_VIIRS_DNB_MONTHLY_V1_VCMSLCFG?hl=en.

ORCID

Míriam Gimeno https://orcid.org/0000-0002-0325-6576
Joan Giménez https://orcid.org/0000-0001-9207-4792
Andre Chiaradia https://orcid.org/0000-0002-6178-4211
Lloyd S. Davis https://orcid.org/0000-0003-1131-7647
Philip J. Seddon https://orcid.org/0000-0001-9076-9566
Yan Ropert-Coudert https://orcid.org/0000-0001-6494-5300
Ryan R. Reisinger https://orcid.org/0000-0002-8933-6875
Marta Coll https://orcid.org/0000-0001-6235-5868
Francisco Ramírez https://orcid.org/0000-0001-9670-486X

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