



Short communication



Living with uncertainty: Using multi-model large ensembles to assess emperor penguin extinction risk for the IUCN Red List

Stéphanie Jenouvrier^a, Alice Eparvier^{b,1}, Bilgecan Şen^{a,c}, Francesco Ventura^{a,2}, Christian Che-Castaldo^d, Marika Holland^e, Laura Landrum^e, Kristen Krumhardt^e, Jimmy Garnier^f, Karine Delord^g, Christophe Barbraud^g, Philip Trathan^{h,i}

^a Biology, Woods Hole Oceanographic Institution, 86 Water St, Woods Hole, 02543, MA, USA

^b Master de Biologie, École Normale Supérieure de Lyon, Université Claude Bernard Lyon 1, Lyon, 69007, France

^c Institute for Advanced Computational Science, Stony Brook University, Stony Brook, New York, 11790, NY, USA

^d U.S. Geological Survey, Wisconsin Cooperative Wildlife Research Unit, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

^e Climate and Global Dynamics, NSF National Center for Atmospheric Research, Boulder, CO, USA

^f LAMA, CNRS-Université Grenoble Alpes, Université de Savoie Mont Blanc, UMR-5127, Chambéry, 39 384, France

^g Centre d'Études Biologiques de Chizé, UMR7372 CNRS-La Rochelle Université, Villiers en Bois, 79360, France

^h School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton, SO14 3ZH, UK

ⁱ British Antarctic Survey, Madingley Road, Cambridge, CB3 0ET, UK

ARTICLE INFO

Dataset link: https://github.com/fledge-whoie/empereur_penguin_IUCN

Keywords:

Natural climate uncertainties
Structural model uncertainties
Ecological forecasts
Eco-ensemble
Conservation
Seabirds

ABSTRACT

Improved methods for identifying species at risk are needed to strengthen climate change vulnerability assessments, as current estimates indicate that up to one million species face extinction due to environmental changes. Integrating multiple sources of uncertainty enhances the robustness of Red List of Threatened Species assessments, providing a more comprehensive understanding of species' risks. We present a comprehensive framework that incorporates uncertainties, including measurement error, structural uncertainty, natural variability, future climate emissions scenario, and extreme events of sea ice loss, to evaluate the extinction risk of the emperor penguin (*Aptenodytes forsteri*), currently classified as Near-Threatened. We apply three ecological models, one bioclimatic and two metapopulation models, combined with a multi-model large ensemble (MMLE) of climate projections from general circulation models, to conduct a Red List evaluation at both global, regional and colony levels. Our results show that emperor penguins could be classified under a range of Red List categories depending on the ecological model, Intergovernmental Panel on Climate Change (IPCC) climate emissions scenario, and extreme event frequency. Under Criterion A, global classifications vary from Vulnerable to Critically Endangered. Severe declines are projected in the Indian and East Pacific sectors, Dronning Maud Land and the Amundsen-Bellinghousen Sea, with Criterion E indicating that 24% to 100% of colonies meet *Endangered* status thresholds, depending on huddling thresholds and ecological models. This study represents the first application of an MMLE coupled with an ecological ensemble approach to project climate change impacts on a species, capturing a comprehensive range of uncertainties and offering a framework for improving forecasting and decision-making under climate change.

1. Introduction

Species are affected by anthropogenic climate change (Hoegh-Guldberg and Bruno, 2010; Urban, 2015). Preliminary estimates forecast climate-related extinctions of 14%–32% of macroscopic species by 2074, potentially including 3–6 million animal and plant

taxa, even under intermediate climate change scenarios (Wiens and Zelinka, 2024). This contrasts with only 10,967 species identified on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species that have an increased risk of extinction from

* Corresponding author.

E-mail address: sjenouvrier@whoie.edu (S. Jenouvrier).

¹ Stéphanie Jenouvrier and Alice Eparvier share first co-authorship.

² Bilgecan Şen and Francesco Ventura share second authorship.

<https://doi.org/10.1016/j.biocon.2025.111037>

Received 16 December 2024; Received in revised form 7 February 2025; Accepted 14 February 2025

Available online 25 March 2025

0006-3207/© 2025 The US Geological Survey and The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

climate change (IUCN, 2019; Akçakaya et al., 2014). Improved methods for identifying species at risk are necessary to strengthen climate change vulnerability assessments, as current extinction risk evaluations indicate that approximately one million species face potential extinction due to climate-related and anthropogenic pressures (Trull et al., 2018; Foden et al., 2019; Mancini et al., 2024; Pacifici et al., 2015; IPBES, 2019). Integrating multiple sources of uncertainty can improve the robustness of threat category assignment for Red List assessments and provide a more comprehensive understanding of species risk (Akçakaya et al., 2006; Rueda-Cediel et al., 2018).

The IUCN Red List recognizes various sources of uncertainty, including measurement error, natural variability in ecological and climatic processes, structural uncertainties related to model choice and techniques, and future climate scenarios (IUCN, 2024) (Fig. 1 boxes 5 and 9). For species threatened by climate change, the IUCN guidelines emphasize the importance of accounting for uncertainties in general circulation models (Fig. 1 box 9b), Intergovernmental Panel on Climate Change (IPCC) climate emissions scenarios (Box 6 on Fig. 1) and ecological modeling approaches (Fig. 1 box 5b). They specifically recommend incorporating projections from multiple general circulation models, across both high and low emission scenarios, and using results from at least two or three different ecological models to ensure robustness in projections (Araújo and New, 2007; Pearson et al., 2006; Buisson et al., 2010).

Natural variability, as defined by the IUCN, refers to inherent fluctuations in species' life histories and environmental conditions over time and space (IUCN, 2024). This variability reflects the dynamic nature of ecological systems and their interactions with changing environmental conditions. In ecological modeling, natural variability encompasses fluctuations intrinsic to population and community dynamics, driven by stochastic processes, life-history traits, and internal feedbacks. Natural variability aligns closely with the concepts of endogenous variability, stochasticity in biological processes, parameter variability, and process error, all of which help determine the predictive variance of a system (Lande et al., 2003; Dietze, 2017). In climate science, natural variability is defined as unforced variability arising internally within the climate system, such as chaotic atmospheric processes or decadal oscillations (e.g. El Niño–Southern Oscillation), and is often captured through Single Model Large Ensembles (Kay et al., 2015). Although climate variability also impacts the predictability of ecological systems, few ecological studies have systematically integrated this variability as derived from Single Model Large Ensembles (Trisos et al., 2020; Jenouvrier et al., 2021).

Natural variability is an important source of uncertainty, but it is just one component. Equally important is structural model uncertainty, which arises from the assumptions and formulations inherent in any given model. Unlike natural variability, structural uncertainties have only recently begun to be systematically addressed in ecology through ecological ensembles (Clare et al., 2024; Tittensor et al., 2021; Spence et al., 2018; Cheung et al., 2016; Bagchi et al., 2013), whereas climate science has been incorporating them for decades with Multi-Model Ensembles (Tebaldi and Knutti, 2007). More recently, climate science has developed the Multi-Model Large Ensemble (MMLE), which captures natural variability through single model large ensembles while simultaneously addressing structural uncertainties (Deser et al., 2020).

Eco-climatic modeling, which links ecological models with general circulation models, is particularly relevant for the emperor penguin (*Aptenodytes forsteri*), currently categorized by the IUCN Red List as *Near-Threatened*. The life cycle of emperor penguins is closely tied to sea ice conditions, affecting both their population dynamics and their distribution (Ainley et al., 2010; Trathan et al., 2020; Labrousse et al., 2023). On a global scale, a recent comprehensive assessment reveals that the abundance of emperor penguins declined by 9.6% between 2009 and 2018 (LaRue et al., 2024). Projections indicate that by 2100, almost all emperor penguin colonies will become quasi-extinct under high greenhouse gas emission scenarios, with the global

population expected to decline by approximately 99% compared to current levels (Jenouvrier et al., 2021). Even under moderate emission scenarios, more than two-thirds of colonies are projected to disappear by midcentury (Jenouvrier et al., 2020). These findings have supported the listing of emperor penguin as a threatened species under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2022), but they were based on a single large ensemble of climate projections (Kay et al., 2015) and only one ecological model (Jenouvrier et al., 2010, 2012, 2017).

These past approaches to anticipatory projections of emperor penguin futures have used the latest outputs from the Intergovernmental Panel on Climate Change (IPCC) assessments and the Coupled Model Intercomparison Project (CMIP), which provides standardized climate model simulations. However, climate models have struggled to capture some aspects of observed Antarctic sea ice variations (Roach et al., 2020), such as the small increases that occurred between 1979 and 2014 (Comiso et al., 2017; Parkinson, 2019) and the abrupt reductions in recent years (Diamond et al., 2024; Fogt et al., 2022; Hobbs et al., 2024; Purich and Doddridge, 2023; Raphael and Handcock, 2022). This observational-model discrepancy may in part be due to internal variability (Singh et al., 2019) as well as to the relatively short satellite record. Nonetheless, on longer timescales (1979–2023), observed sea ice trends fall within the range simulated by climate models (Hobbs et al., 2024), suggesting that the models can simulate a reasonable long-term response to anthropogenic forcing.

While appearing deficient in some aspects related to simulating Antarctic climate, eco-climatic modeling remains the best tool available for projecting the abundance and distribution of emperor penguins under multiple scenarios. Additionally, eco-climatic models enable both long-term hindcasting of penguin populations and projections of future trends, allowing us to validate ecological models against historical data (IUCN, 2024). Here we present a multi-model framework aligned with IUCN guidelines to address key uncertainties, including natural variability, structural uncertainties, and scenario-based factors, such as IPCC climate emissions and extreme event scenarios, to deliver anticipatory projections and a comprehensive Red List evaluation for the emperor penguin.

This study marks the first application of MMLEs in ecological forecasting for species risk assessment. To do this, we incorporated projections from multiple climate models, each with different sea ice structural biases, into three ecological models, including both bioclimatic and process-oriented metapopulation models. Each ecological model is based on different ecological data and has a distinct structure and set of assumptions (Table A.1), resulting in different projection outcomes. This approach enabled us to capture a range of climate futures and assess the influence of these critical sources of variability on emperor penguin population dynamics and extinction risks (Table A.2). Despite the large uncertainties identified, our findings suggest that the emperor penguin warrants a listing status within the range of *Vulnerable* to *Critically Endangered* under the IUCN guidelines on risk and uncertainty (IUCN, 2024), representing an important change from its current classification as *Near Threatened*.

2. Methods

2.1. Emperor penguin life cycle

The emperor penguin has a highly specialized life cycle that is intricately linked to Antarctic sea ice (Ainley et al., 2010; Trathan et al., 2020). Penguins rely on sea ice for breeding, resting, moulting, feeding, and evading predators (Stonehouse, 1953; Prevost, 1961). The extent of sea ice is crucial; insufficient ice can disrupt marine food webs and make breeding habitats unstable, while excessive ice increases the distance between nesting and feeding areas, limiting the penguins' ability to nourish their chicks adequately (Jenouvrier et al., 2012). Adults arrive at their breeding sites in March or April, with

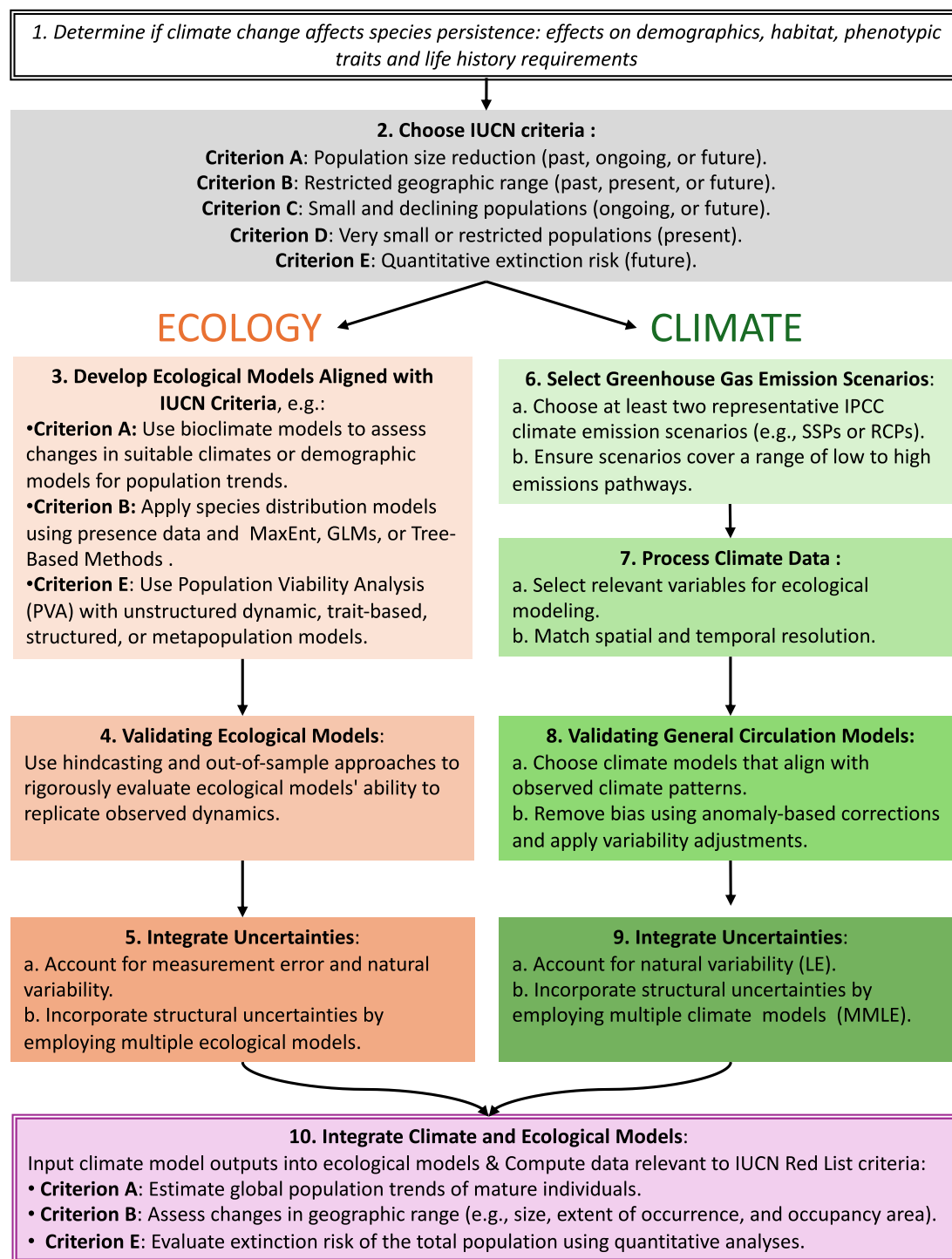


Fig. 1. Framework for assessing climate change impacts on species for the International Union for Conservation of Nature (IUCN) Red List. The process starts by identifying the impacts of climate change on species persistence, considering demographics, habitat suitability, phenotypic traits, and life history requirements (Box 1), which informs the selection of appropriate IUCN criteria (Gray Box 2). Ecological models tailored to these criteria are developed (Light Orange Box 3) and validated (Orange Box 4). Climate projections are built using at least two greenhouse gas emissions scenarios, such as Shared Socioeconomic Pathways (SSPs) or Representative Concentration Pathways (RCPs), to represent a range of emissions pathways (Light Green Box 6). These data are processed by selecting relevant variables, aligning resolutions (Green Box 7), choosing climate models that agree well with observed climate patterns, and applying corrections for biases and variability (Green Box 8). Uncertainties are integrated through ecological and climate model ensembles, addressing natural variability and structural differences (Dark Orange Box 5 and Dark Green Box 9). The final step combines processed climate outputs with ecological models to compute metrics relevant to the selected criteria, enabling a robust and uncertainty-informed evaluation of extinction risks (Purple Box 10). (Interpretation of the references to color in this figure legend is available in the web version of this article. The boxes are also numbered, ensuring clarity even in grayscale print.)

females laying a single egg by mid-May. The males then incubate the egg for 65 to 75 days without feeding, enduring the harsh Antarctic winter by huddling together for warmth. In August, after the chicks hatch, the females return, and both parents alternate between foraging and caring for the chick. By December, the chicks and adults leave the colony, returning to the ocean. Their diet consists primarily of Antarctic silverfish, krill, and squid, with sea ice conditions affecting the availability of these prey species (Offredo and Ridoux, 1986).

2.2. IUCN criteria

Emperor penguins are currently classified as *Near Threatened* (NT) on the IUCN Red List, which indicates the species is on the verge of meeting the criteria for a threatened category (*Vulnerable*, *Endangered*, or *Critically Endangered*) but do not fully meet the requirements. The IUCN Red List (IUCN, 2024) uses a set of criteria to assess the risk of extinction of species both globally and regionally. Five main criteria (A-E) are used to determine the threat level for a species. In this analysis, we focus on criteria A and E (Fig. 1 box 2).

Criterion A: Population Reduction examines the rate of population decline of a species. A species can be considered threatened if it has undergone a reduction in the number of mature individuals of at least the amount (%) stated under the criterion over a given time frame (generally 10 years or three generations, whichever is longer). Sub-criteria under Criterion A detail whether the population reduction is derived from actual counts, inferred in the past, or projected into the future. Our analysis is based on future projections over three generations (Criterion A3), specifically targeting the year 2073 for the emperor penguin, based on three generations from 2024 and a generation time of 16.4 years (Bird et al., 2020).

Criterion E: Quantitative Analysis involves a quantitative risk analysis to estimate the probability of extinction. Here, extinction for each penguin colony was defined as the colony population size falling below a huddling threshold, rather than reaching zero, to account for the species' unique behavior of huddling during winter to survive both wind and extreme cold. Huddling represents a form of Allee effect, enabling individuals to conserve heat and survive the harsh winter conditions. Huddling efficiency depends upon the number of penguins in a group; smaller groups are less effective at heat conservation, resulting in higher mortality rates (Gilbert et al., 2006). Without huddling, emperor penguins would reach the metabolic status that would trigger refeeding three weeks earlier; the egg would then be abandoned before the return of the female (Ancel et al., 1997).

Various studies suggest that colonies which form larger huddles have positive thermoregulatory benefits (Gilbert et al., 2006), with smaller huddles likely present only in the smallest and most isolated colonies (Trathan et al., 2011). These findings suggest that a larger huddle threshold is likely more representative of typical huddling behavior, especially in established and stable colonies. In warmer (more northerly) regions such as at the Antarctic Peninsula, huddles as small as 10 breeding individuals may occur, whereas in colder regions typical thresholds are closer to 100, as supported by photographic evidence (Daniel Zitterbart, Woods Hole Oceanographic Institution, and Tom Hart, University of Oxford, email personal communications, July 2024). To address uncertainty, we analyzed two thresholds: 10 and 100 individuals. The primary analysis adopts the 100-individual threshold, reflecting observed colony behavior and the thermal benefits of larger huddles. Results for the 10-individual threshold are included in the Appendix to explore a more conservative scenario, where extinction risks are reduced by assuming resilience at smaller huddling thresholds (Figure B.1, Table A.3).

According to IUCN guidelines (IUCN, 2024), extinction risk assessments should be conducted over three time periods: 10 years or three generations (whichever is longer), 20 years or five generations (whichever is longer), and 100 years. However, given the generation time of emperor penguins of 16.4 years (Bird et al., 2020) and the

availability of climate data only up to 2100 (Kay et al., 2015; Deser et al., 2020; Rodgers et al., 2021), we performed extinction risk assessments for two key time periods: the year 2073 and the year 2100. We calculated and report the probability of extinction for each known colony across Antarctica following methods outlined in Jenouvrier et al. (2014).

2.3. Climate models and their projections under different scenarios

IUCN guidelines (IUCN, 2024) state assessments must use projections from a minimum of two scenarios and at least two General Circulation Models to account for the uncertainties involved in climate projections (Fig. 1 Boxes 6 and 9). To account for natural variability and structural model and IPCC climate emissions scenario uncertainty, we used different combinations of large ensembles or MMLEs of climate projections from three general circulation models (CanESM, CESM, and CSIRO) under three IPCC climate emissions scenarios (RCP 8.5, SSP3.7-0, and the Paris Agreement) as inputs to our three ecological models (Kay et al., 2015; Deser et al., 2020). Table A.2 details the full names and combinations of these models and scenarios, as we were unable to include all sources of uncertainty in a single eco-climatic model, given constraints on how these climate projections are created and the way our ecological models are formulated.

While the availability of such large ensembles is limited, we employed the most comprehensive set currently available by using simulations from the Multi-Model Large Ensemble Archive. These simulations were conducted using six distinct CMIP5-class climate models under a high-emission scenario (RCP 8.5), the only scenario for which large ensemble experiments were performed for all six models (Deser et al., 2020). Three of the models under this scenario (GFDL-CM3, GFDL-ESM2M, and MPI-ESM) have low Antarctic sea ice cover, with near-zero ice area during the summer months even in the historical period (Figure B.2). Given this discrepancy with actual observations, projections from these climate models were not suitable for use with our ecological models, and we excluded them from our analysis (Fig. 1 Box 8.a). Restricting our MMLE to the CanESM, CESM1, and CSIRO large ensembles, we were able to explore differences in penguin population projections due to both natural variability and structural model uncertainty associated with climate modeling (Table A.2).

To address emissions scenario uncertainty in climate models, we used output from three IPCC scenario forcings of either the CESM1 or CESM2 general circulation model. The CESM performs well at capturing the seasonal and annual hemispheric and regional mean and variability of Antarctic Sea Ice compared with other CMIP5 and CMIP6-class models (Roach et al., 2020; Singh et al., 2019, 2021). To investigate the latest emissions scenarios under CMIP6, we used the CESM2 Large Ensemble Community Project under the SSP3-7.0 future radiative forcing scenario (Rodgers et al., 2021) (Table A.2). To examine a low-emission scenario, we used climate projections from CESM1, that offer long-term climate data that reach stabilization pathways at 2 °C levels (Sanderson et al., 2017) (Table A.2).

2.4. Ecological models

Our emperor penguin population projections are based on an extensive and diverse array of data (LaRue et al., 2024; Jenouvrier et al., 2012; Garnier et al., 2023), which we used to develop three ecological models (Appendix C), each with distinct strengths tailored to capture different facets of emperor penguin ecology (Fig. 1 Box 3, Table A.1, Appendix C). These models provide a state-of-the-art quantitative analysis of population declines and extinction risks at the global, regional, and colony levels, with results directly relevant for IUCN assessments. Population projections from these models (Section 2.5) were driven by climate inputs from climate model large ensembles or an MMLE of three climate models (Section 2.3), and included three IPCC climate emissions scenarios as well as extreme sea ice loss event scenarios

not directly simulated by these general circulation models (Table A.2, Section 2.7). This approach allowed us to integrate sources of climate and ecological uncertainty needed to meet IUCN guidelines, as well as measurement or observation error (Fig. 1 Box 5).

Two of these ecological models are structured metapopulation models, one based on a multi-event capture-recapture model (SPCMR) and the other an integrated population model (SPIPM). Both rely on a unique long-term time series of individual-based mark-recapture data spanning 30–40 years at the Pointe Géologie breeding colony, while the SPIPM model also uses population counts and breeding success data collected over 60 years at the same site (Barbraud and Weimerskirch, 2001; Jenouvrier et al., 2009, Table A.1) These two models, which include age and breeding stages, assess how environmental variables affect vital rates, such as mortality and reproduction. In contrast, the bioclimatic abundance species distribution model (or Scalar (unstructured) Count-based Dynamic model: SCDSAT), relies on 10 years of satellite-derived adult population counts across 50 colonies (LaRue et al., 2024). While less process-oriented than the other two models, SCDSAT offers broad spatial coverage, partitioning variability in penguin abundance from 2009–2018 across 50 breeding colonies distributed around Antarctica conditional on decadal sea ice estimates (Table A.4, Table A.1).

Both metapopulation models use a mechanistic-statistical model that incorporates novel genetic and demographic information (Garnier et al., 2023). This enabled us to examine how different dispersal behaviors and climate scenarios affect population projections to assess how dispersal influences global population responses to climate change relative to mitigation efforts, updating the analysis of Jenouvrier et al. (2017). Emperor penguins are most likely to disperse through semi-informed dispersal, characterized by a relatively small mean dispersal distance of 414 km and low emigration rates (Garnier et al., 2023). Under high emission climate scenarios that lead to population declines, semi-informed dispersal is estimated to increase the global population size by up to 7% compared to projections without dispersal (Figure D.1). However, under a low emission climate scenario, dispersal processes do not enhance the global population size and may even result in a slight reduction compared to a scenario without dispersal (Figure D.1). Overall, while dispersal behaviors remain important, their impact on future global population sizes is relatively small compared to the influence of climate change mitigation efforts (Jenouvrier et al., 2017, 2021).

The two metapopulation models incorporate density dependence using the Ricker model (Appendix C.1.1), which accounts for negative density dependence in population growth rates. We did not introduce structural uncertainties specific to negative density dependence effects on reproduction and survival, as there is insufficient evidence to support these effects in emperor penguins and previous studies provide justification for minimal density effects in the Pointe Géologie population (Gimenez and Barbraud, 2009; Jenouvrier et al., 2012). Earlier analyses of density dependence demonstrated a positive relationship between population size and adult survival, likely driven by huddling behavior during the harsh Antarctic winter (Barbraud and Weimerskirch, 2001; Jenouvrier et al., 2005). We opted for evidence-based modeling by employing a Ricker model to represent negative density-dependent effects on population growth rates, rather than hypothesizing about these effects on survival and reproduction. Moreover, our extinction risk analysis incorporated the Allee effects associated with positive density-dependence from huddling behavior (Section 2.2).

2.5. Ecological model projections

The three ecological models estimate population dynamics over varying scales: SPCMR produces annual counts of mature and immature individuals of both sexes for a single colony; SPIPM does the same, but solely for females; and SCDSAT generates annual counts of adults in spring across all 66 colonies. Given this, each of these models relies

on different spatial and temporal substitutions to project global and regional population dynamics.

Our metapopulation models (SPIPM and SPCMR) employed a time-for-space substitution to project population dynamics for other colonies by assuming that the functional relationships between environmental factors and vital rates estimated at Point Géologie are consistent across space, despite potential local adaptive differences or other site-level effects. In contrast, the SCDSAT model uses a space-for-time substitution to project the average expected adult abundance of colonies in a given year based on the average decadal sea ice concentration (SIC) (Sen et al., 2023). Built using data from 50 colonies across a spatial environmental gradient, the SCDSAT model transfers the spatial relationship between average environmental conditions and penguin abundance across time to predict a time series of abundance at each colony. It should be noted that this approach comes at the expense of not fully capturing year-to-year dependencies, fast processes such as birth and death rates, and transitional dynamics driven by initial conditions.

We used these functional relationships between environmental conditions and either abundance (SCDSAT) or vital rates (SPCMR and SPIPM) to compute future (beyond 2018) and past (prior to 2009) population projections. We did this in such a way as to include structural uncertainty, natural variability, and scenario-based uncertainty found in both these ecological models (Table A.1) and the general circulation models (Table A.2) used to supply the necessary climate projections (Appendix C). These population projections were then aggregated to create regional or global penguin abundance time series for each ecological model, which were subsequently used to calculate annual percent changes in abundance needed for the eco-ensemble (Section 2.6) and for model validation Appendix E.

2.6. Multi-model ecological eco-ensemble

To account for structural uncertainty in our ecological models, we employed a Bayesian model-averaging approach, using model weights to combine projections from the three ecological models into a multi-model ecological ensemble (Fig. 1 Box 5.b). We estimated model weights at the global population level, aligning with the requirements of the IUCN Red List criteria, which prioritize global population assessments for evaluating extinction risk. While satellite data offer valuable insights into colony-specific dynamics, their ability to reliably detect colony trends over a 10-year period is limited by substantial observation error and intrinsic variability (Labrousse et al., 2022). Factors such as weather conditions, huddling behavior, and satellite resolution introduce noise into population indices derived from very high-resolution imagery (Fretwell et al., 2012; Labrousse et al., 2022). These limitations undermine the reliability of short-term trend detection at the colony level, necessitating either extended monitoring periods or the aggregation of data across multiple colonies to improve precision (Che-Castaldo et al., 2017; Labrousse et al., 2022). Focusing on global trends and integrating data from multiple colonies provides a robust way to use these model weights to develop an eco-ensemble that supports conservation assessments.

Model averaging in this framework consists of two key steps (McElreath, 2016): (1) determining model weights and (2) resampling from the posterior distributions with the respective weight of each model to generate an ensemble posterior. Model weights are typically derived through actual out-of-sample performance via leave-one-out cross-validation (e.g., stacking) or methods that approximate out-of-sample performance using the full dataset (e.g., Widely Applicable Information Criterion WAIC or pseudo-Bayesian Model Averaging, see Yao et al., 2018). In our case, metrics such as WAIC were not applicable because the response variables used to build the three predictive models differed, rendering their posterior likelihoods incomparable. Similarly, leave-one-out cross-validation was not sufficiently rigorous for determining model weights, as we employed both space-for-time

and time-for-space substitutions to project global penguin population abundances.

Instead, to assess substitution performance, we predicted the trend of global abundance between 2009–2018 for each model ($\beta_{\text{predicted}}$) and then contrasted these projections with the trend in the observed global abundance time series (β_{observed}) from LaRue et al. (2024). These trends were calculated as the slope of annual abundance regressed against year. We computed model weights using the posterior averages of the slopes as:

$$\frac{1}{|\beta_{\text{observed}} - \beta_{\text{predicted}}|},$$

where the resulting weights for SPIPM, SCDSAT, and SPCMR were 0.29, 0.31, and 0.40, respectively. We adopted a similar approach for annual variations in abundance, where the resulting weights for SPIPM, SCDSAT, and SPCMR, were 0.33, 0.30, and 0.37, respectively. In this way, we were able to directly compare the time-for-space substitution ability of the SPIPM and SPCMR metapopulation models with the space-for-time substitution ability of the SCDSAT bioclimatic model.

Since each model produces different model outputs (Table A.1), we built a model ensemble using the percent rate of change, rather than the direct model outputs themselves. The percent rate of change for each model was calculated relative to the average abundance of mature individuals between 2009 and 2018 ($\overline{N}_{2009-2018}$), as:

$$\text{Percent Rate of Change} = \frac{N_t - \overline{N}_{2009-2018}}{\overline{N}_{2009-2018}},$$

where N_t is the abundance in year t taken from the global population projections computed in Section 2.5. For each year, we resampled the percent rate of change from the posterior of each model, with the model weights serving as the probability of sampling from the posterior of the respective models. The combined posterior of these samples for each year were used to produce the eco-ensemble percent change projections across the three models.

2.7. Extreme event scenario

Extreme events, such as sea ice loss and glacial calving, directly impact vital rates and colony dynamics (Fretwell et al., 2014; Fretwell and Trathan, 2019; Fretwell et al., 2023), amplifying global population declines (Jenouvrier et al., 2021). Specifically, satellite data reveal that early sea ice breakup and glacial calving events frequently lead to breeding failures and colony relocations, underscoring the species' vulnerability to extreme events (Fretwell et al., 2014; Fretwell and Trathan, 2019; Fretwell et al., 2023). We developed three scenarios to assess the impact of extreme events on emperor penguin population dynamics, updated from Jenouvrier et al. (2021): (1) **No Extreme Events**, where reproduction is unaffected by extreme conditions; (2) **Fixed Frequency of Extreme Events**, where the historical frequency (3.6%) is held constant, and extreme events cause complete reproductive failure; and (3) **Increasing Frequency of Extreme Events**, where the frequency increases proportionally to sea ice decline. For scenarios 2 and 3, an extreme event occurs when sea ice falls below a sea ice threshold T_{S_I} , based on the observed historical data of massive breeding failures. When an extreme event occurs, reproductive success may be reduced to zero during those years, modeled using a binomial distribution.

The third scenario accounts for the projected decrease in sea ice concentration under future climate conditions. Because climate models do not explicitly project the frequency of glacier or ice shelf calving, we combined recent observational data on breeding failures from 2018 to 2022 with sea ice projections (Antarctic Treaty Consultative Meeting, 2023). For each climate model, we calculated a SIC threshold corresponding to the number of extreme events historically observed. Years in which SIC fell below this threshold were considered extreme. For these extreme years, we sampled a proportion p to simulate a fraction

of these colonies experiencing total breeding failure. The value of p was calibrated for each climate model to ensure that the number of colonies experiencing at least one total breeding failure between 2018 and 2022 matched the observed rate of 42% (Antarctic Treaty Consultative Meeting, 2023).

3. Results

3.1. IUCN criterion A: Global population reduction

Despite differences in the timing and magnitude of predicted declines, all three ecological models individually project global emperor penguin population declines throughout the 21st century (Fig. 2). Our SPCMR model projects a stable, slightly increasing population from 1950 until 2000, followed by a sharp decline (Fig. 2a). The SPIPM model projects a growing population from 1950–1970, before a very steep decline beginning in the 1980s and culminating in global population extinction by 2100 (Fig. 2b). Lastly, the SCDSAT model projects a slightly decreasing population, with the rate of decline accelerating from 1980 onwards (Fig. 2c). Taken together, the eco-ensemble projects a population decline of 59% (95% credible interval: –98%, –30%) over the next three generations. This decline is consistent with an IUCN Red List *Endangered* (EN) assignment.

To further explore the details of climate and scenarios uncertainties, we use the SPCMR model, which provided the best out-of-sample predictive performance relative to other models based on the reported weights and produced mid-range projections. In terms of climate, the greatest uncertainties arise from the range of future projected emission scenarios (Figs. 3a, 4a). In our ecological models, we use environmental data as anomalies relative to a historical period (Table A.1). This approach helps reduce biases from different climate models because it focuses on relative changes rather than absolute values, allowing for a more standardized comparison (Box 8.b on Fig. 1). This standardization minimizes differences amongst climate models by accounting for their varying baseline states (Fig. 3a, B.2). As a result, the projected environmental variable anomalies do not differ as much compared with the raw projections (Figure B.2). Moreover, even though natural climate variability can lead to uncertainty in projections, especially for intricate non-linear demographic models such as the SPCMR model (Figs. 3 b,c,d, F.1), the difference in trajectories with or without natural variability is less than the difference between low and high emissions scenarios (Fig. 4).

In addition, extreme climate events add uncertainty to our projections. An increase in the frequency of extreme events will considerably exacerbate the decline in population (Fig. 4 b,c,d). In high emissions scenarios, a rise in the number of extreme events, proportional to the anticipated declines in sea ice concentration, could result in the extinction of emperor penguins by 2100 (scenario 3 on Fig. 4 b,c).

Table 1 presents the probability of classifying the emperor penguin at three different levels of threat according to criteria A3 (b). The IUCN recommends a precautionary approach: a threat status is designated if the probability of decline exceeds 40%. Table 1 highlights the range of uncertainties in assignment, based on different models. Projections from the SCDSAT model categorize the species as *Vulnerable*, while the SPIPM model classifies it as *Critically Endangered*. Under a high-emission scenario, all three climate models consistently project an *Endangered* status, whereas a low-emission scenario suggests a listing of *Vulnerable*. Projections that account for historical extreme events or exclude them both indicate an *Endangered* status. However, an increased frequency of extreme events is expected to raise the status to *Critically Endangered*.

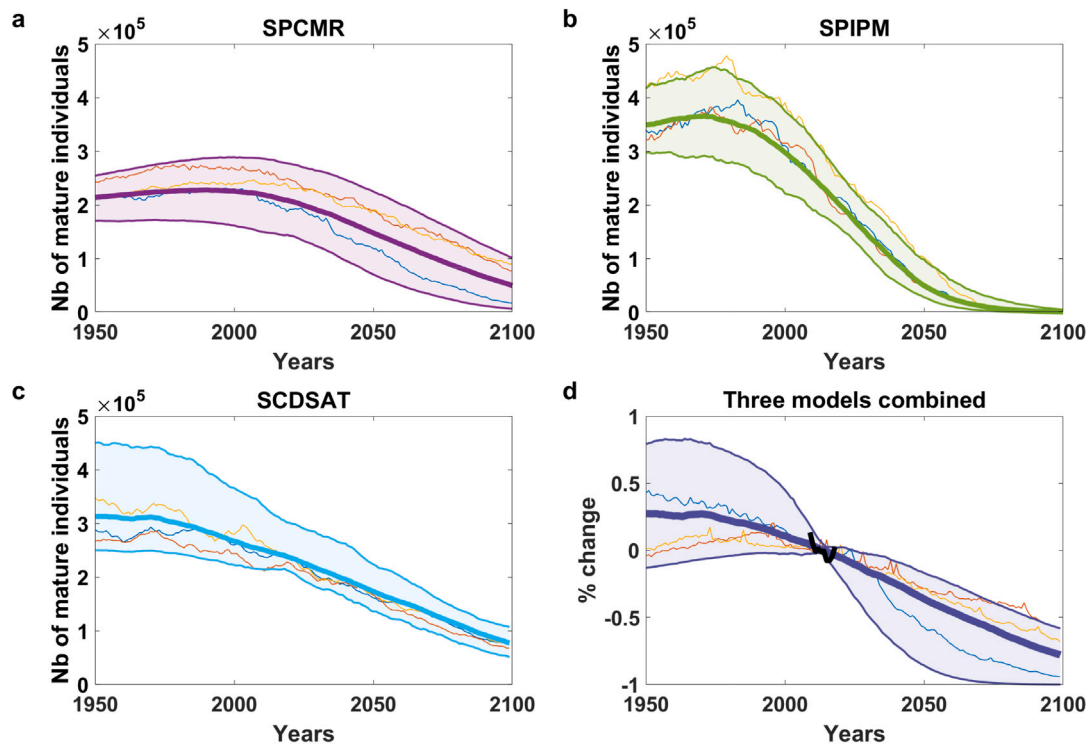


Fig. 2. Projections of emperor penguin (*Aptenodytes forsteri*) global population based on three different ecological models from 1950 to 2100. (a,b) The metapopulation models (SPCMR and SPIPM) both project year-to-year variations of the number of mature individuals. (c) The space-for-time substitution model (SCDSAT) projects the number of adults in spring. (d) Estimates of the percentage change in population size compared to the observed number averaged from 2009 to 2018, for the three models combined. The black thick line shows the observations of the global adult population size in spring, estimated from satellite data collected between 2009 and 2018 (LaRue et al., 2024). Thick lines show medians, colored area show the 95% confidence intervals. Thin lines are 3 random projections. The projections were derived using climate projections from the Community Earth System Model version 2 (CESM2) Large Ensemble Community Project (LENS2) model, applying the Shared Socioeconomic Pathway 3 (SSP3.7-0) high emission climate scenario spanning the years 1900 to 2100. The first fifty years have been excluded to eliminate the transient effects of the initial conditions.

3.2. IUCN criterion E: Quantitative analysis to estimate the probability of extinction

Sea ice concentration is projected to decrease around Antarctica (Fig. 5), but with some areas such as the Weddell Sea and the Ross Sea remaining comparatively unaffected. These areas continue to support the largest colonies, which show the lowest probabilities of extinction (Table A.3). In contrast, the Indian and East Pacific sectors are expected to undergo the most substantial declines in sea ice concentration, with the highest risks of extinction.

Extinction for each penguin colony was defined as the population size falling below a huddling threshold, rather than reaching zero, to account for the species' reliance on huddling to survive harsh winter conditions. According to the SCDSAT model, 6% of the colonies are projected to reach a *Critically Endangered* status with a huddling threshold of 10, while this percent increases to 20% when the threshold is 100 (Figs. 5, B.1, Table A.3). In contrast, the SPIPM model projects a risk of extinction greater than 50% for most colonies within three generations, resulting in a *Critically Endangered* status for 64% of colonies with a huddling threshold of 10 and 94% with a threshold of 100. According to the SPCMR model, 20% of colonies are expected to attain the status of *Critically Endangered* when the huddling threshold is 10, rising to 74% if the threshold increases to 100. Furthermore, the SPCMR model projects that 77% (huddling threshold of 10) and 89% (huddling threshold of 100) of colonies will be classified as *Endangered*. These large differences in patterns between huddling thresholds arise because many emperor penguin colonies are small (Table A.4), making them more susceptible to falling below the higher huddling threshold.

4. Discussion

Our study presents a comprehensive framework for integrating ecological models with climate projections to assess extinction risks for

species under climate change (Fig. 1). This framework represents the first application of a Multi-Model Large Ensemble (MMLE) approach to project the impacts of climate change on a species, effectively capturing a more complete spectrum of anticipated future environmental conditions while accounting for structural differences between models. Results under Criterion A show that Red List classifications for the emperor penguin global population range from *Vulnerable* to *Critically Endangered*, depending upon the ecological model used, and the emissions and extreme events scenario (Table 1). Results under Criterion E indicate that up to 100% of colonies could be listed as *Endangered*, depending on the huddling threshold for extinction probability and the ecological models used under a high-emissions scenario (Figs. 5, B.1).

Uncertainty in assessments necessitates outlining the range of potential classifications, but a single category must finally be selected based on a documented, precautionary rationale (IUCN, 2024; Akçakaya et al., 2000). The IUCN emphasizes that assessors should adopt a precautionary yet realistic position on uncertainty. Given the range of projections, the emperor penguin is likely to be classified as *Endangered*, balancing the risks across climate and extreme scenarios (Table 1).

4.1. Accounting for ecological model structural uncertainty in projections

Our analyses include three distinct demographic models (Table A.1) that encompass natural variability to represent annual natural fluctuations in population and measurement errors. All three models project a decline in penguin populations, but differ in the magnitude of that decline (Fig. 2). Estimates of population decline are greatest with SPIPM, intermediate with SPCMR and least with SCDSAT (Table 1, Table A.3). The different model structures introduce uncertainty leading to differences in Red List assessment. The SPIPM model projects a global decline of over 90% in the population of mature individuals

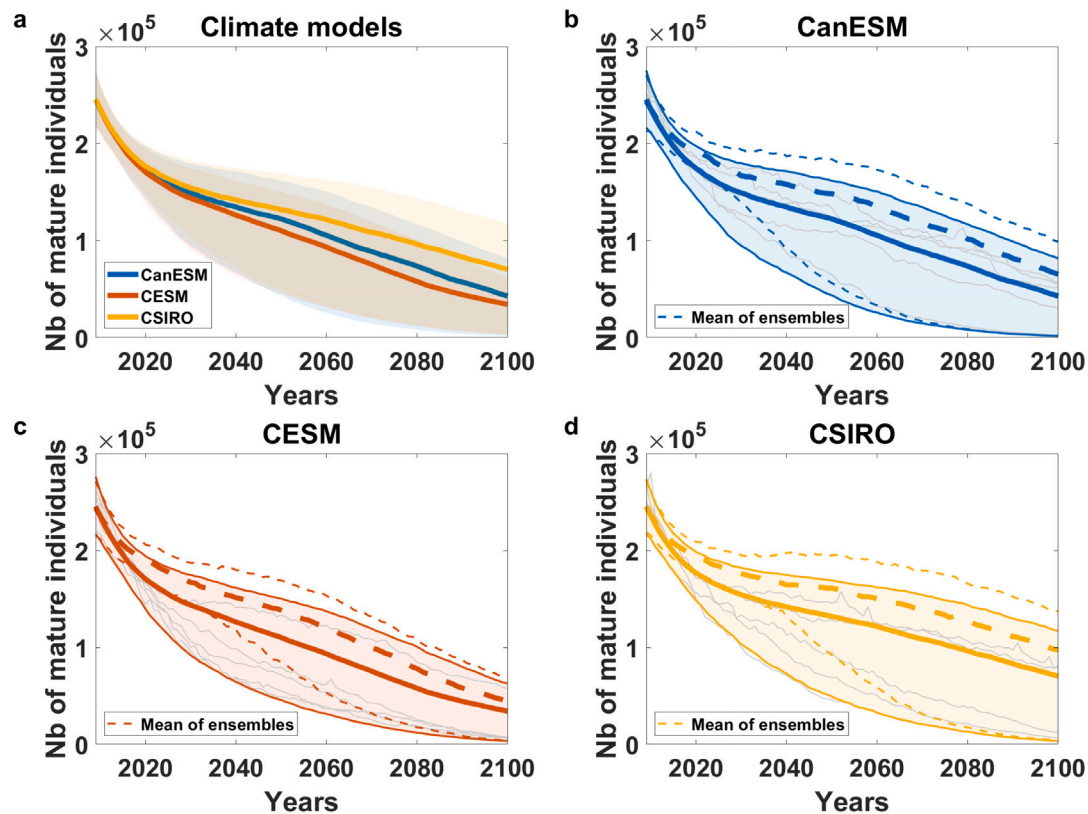


Fig. 3. Projections of emperor penguin (*Aptenodytes forsteri*) global population abundances from 2009 to 2100 based on three different general circulation climate models with or without natural climate uncertainty using the SPCMR metapopulation model. (a) Climate model comparison where large ensemble climate projections from the Canadian Earth System Model (CanESM), Commonwealth Scientific and Industrial Research Organisation model (CSIRO) and the Community Earth System Model Community Atmosphere Model version 1 (CESM1) were executed using the Representative Concentration Pathway (RCP8.5) high emission climate scenario integrated with the SPCMR metapopulation model. For each general circulation climate model, solid lines show the median and 95% confidence interval of abundance projections using all ensemble members to represent natural climatic variability. Panels (b) CanESM: 50 members, (c) CESM1: 40 members, and (d) CSIRO: 30 members detail those projections for each model where gray lines are 5 random projections depicting natural climate variability. In addition, dashed lines show the median abundances and 95% confidence interval of abundance projections based on the mean of the climate ensembles for each model, which ignores natural climate variability. All projections include the three extreme event scenarios (Fig. 4).

within three generations, with a 100% probability, which meets the criteria for listing the species as *Critically Endangered*. In contrast, the SCDSAT model projects a decrease of more than 30%, corresponding to a classification of *Vulnerable* (Table 1). Hindcasts from all models match observed data closely, supporting their dependability (Figure B.3). Using a Bayesian model-averaging approach, the probability that the global population decline projected by the ecological ensemble is greater than 50% by 2073 is 45%, supporting an IUCN status of *Endangered*.

4.2. Accounting for climate uncertainty in projections

While the ecological ensemble provides robust global projections, to explore uncertainties related to climate and extreme events we focus on SPCMR, the model with moderate projections and the strongest alignment with observed data in our analysis relative to other models (i.e. highest weight). SPCMR indicates that a range of threat categories is plausible under different climate scenarios (Fig. 4, Table 1).

We considered two high-emission scenarios (RCP8.5 and SSP3-7.0) and a low-emission scenario aligned with the Paris Agreement's goal. There is ongoing debate about the plausibility of high-emission scenarios. Schwalm et al. (2020b, 2020a) argue RCP8.5 remains valuable for near- to mid-term risk quantification due to alignment with historical emissions. Pielke et al. (2022), however, suggest the world may be on a lower emissions trajectory, though still off track from limiting warming to below 2 °C. This uncertainty highlights the need to consider both high and low emissions scenarios (IUCN, 2024, Box 6a on Fig. 1).

Under the high-emission scenarios, the emperor penguin is projected to fall into the *Endangered* category. In contrast, with strong international constraints on emissions, consistent with the Paris Agreement, the species would be classified as *Vulnerable*. A conservative approach might classify the species as *Vulnerable*, while a more precautionary stance could suggest *Endangered*.

While climate scenarios are the primary drivers of variation in our classifications, model structure and internal natural variability also influence projections. However, all models converge on an *Endangered* status under high emissions. This convergence occurs because we have minimized climate biases in the mean state by using climate anomalies, which standardizes the differences amongst models (Figure B.2).

Including internal natural climate variability affects projections, which if omitted could lead to underestimation of extinction risk (Fig. 3). Internal climate variability will lead to effects on population dynamics that depend upon the functional relationship between population growth rate and the environment (Appendix F, Jenouvrier et al., 2012; Barraquand and Yoccoz, 2013).

Extreme events are a critical source of uncertainty that can influence the Red List status of the emperor penguin. Events such as exceptionally low sea ice concentration, early breakup of fast ice, and iceberg calving have been shown to severely impact emperor penguin colonies, sometimes resulting in entire colonies forgoing breeding or experiencing nearly complete chick mortality, leading to total breeding failure in certain years (Fretwell and Trathan, 2019; Fretwell et al., 2023). The frequency and intensity of such extreme events are difficult to predict, and future projections remain highly uncertain (Siebert et al., 2023). However, recent trends show an increase in such occurrences, with four

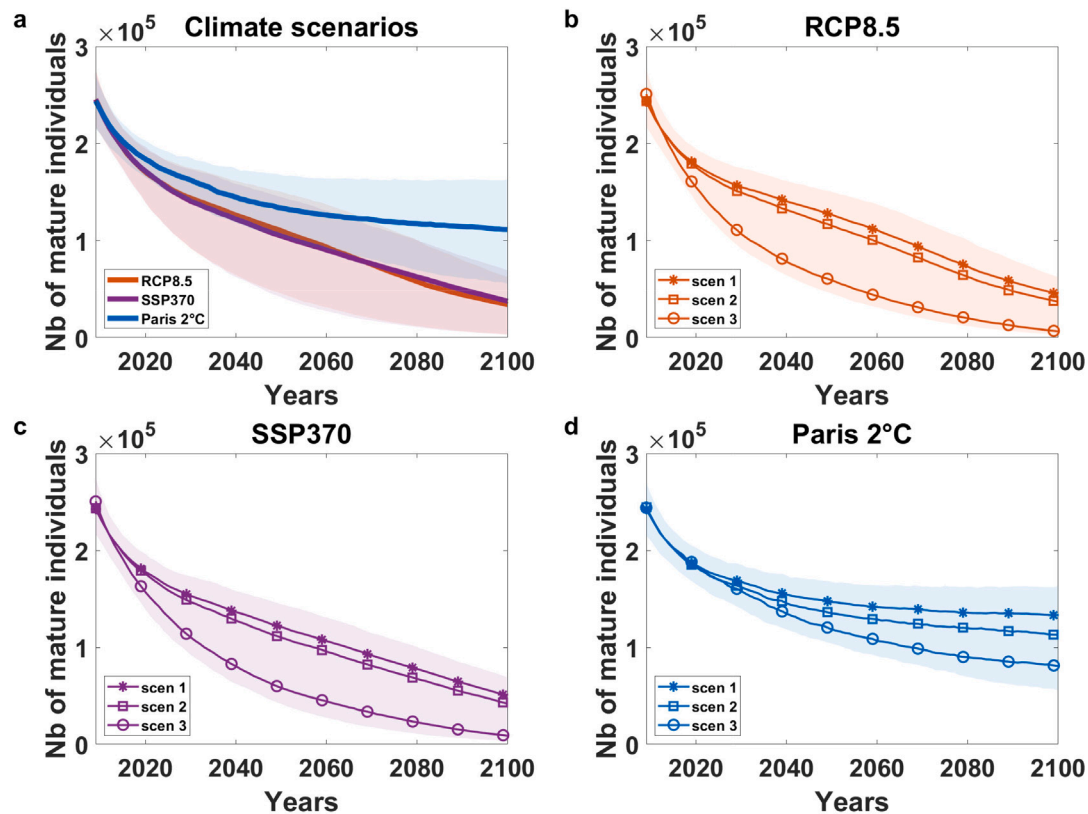


Fig. 4. Projections of emperor penguin (*Aptenodytes forsteri*) global population abundances using the SPCMR metapopulation model under different combinations of extreme event and climate scenarios from 2009 to 2100. (a) Abundance projections under the Representative Concentration Pathway (RCP 8.5), Shared Socioeconomic Pathway 3 (SSP3.7-0), and Paris Agreement (Paris 2 °C) climate scenarios, including all extreme event scenarios for each climate scenario. Thick lines represent median abundances and shaded envelopes show 95% confidence intervals of abundance projections. (b,c,d) For each climate scenario, results for different extreme event scenario are shown, where scen 1 refers to a scenario without extreme events, where reproduction is not affected by extreme conditions; scen 2 has a fixed frequency of extreme events, where the historical frequency of extreme events is held constant and these events cause complete reproductive failure; and scen 3 simulates an increasing frequency of extreme events, where the frequency of extreme events increases proportionally to sea ice decline, affecting reproduction. Each line represents the median projected abundance for one extreme event scenario and the envelope shows the 95% confidence interval for the three extreme event scenarios combined.

of the lowest sea ice minima recorded since 2016 (National Snow and Ice Data Center, 2024) and a rising number of colonies affected by early fast ice disintegration between 2018 and 2022 (Fretwell et al., 2023). Excluding these events results in an *Endangered* status, but increased frequency could shift the classification to *Critically Endangered*. Improved forecasting of extreme events (Frölicher et al., 2018) is essential for guiding conservation strategies.

4.3. Extinction risks across antarctic regions

Over the 21st century, Antarctic sea ice is projected to decline, but the extent and rate of this decline will vary across different regions due to complex interactions between atmospheric, oceanic, and cryospheric processes (Lefebvre and Goosse, 2008) (Appendix G, Fig. 5). For example, the Weddell Sea and Ross Sea regions, which currently hold the largest emperor penguin populations (Fretwell et al., 2012), are expected to experience slower rates of decline compared to other areas (e.g. the Amundsen and Bellingshausen Seas), where sea ice loss may be more rapid (Appendix G) (Parkinson, 2019; Lefebvre and Goosse, 2008). Such variation is evident in the regional assessments using criteria A (Appendix G), and the extinction risks under criteria E (Fig. 5, Figure B.1). Areas experiencing faster sea ice loss show more rapid declines in emperor penguin populations and higher extinction risks, whereas regions with slower sea ice reduction exhibit more gradual population declines and lower extinction risks.

Applying IUCN Criterion E at the colony level, rather than at the global level, is essential for emperor penguins due to their unique reliance on huddling behavior for survival. Our results show that

extinction risks vary with huddling thresholds: at the more conservative 10-individual threshold, up to 64% of colonies are projected to reach Critically Endangered status. This rises to 94% with the more precautionary 100-individual threshold, highlighting the range of uncertainties in extinction risk estimates.

4.4. Limitations and opportunities in species adaptation

To persist under climate change, species must either disperse to more favorable conditions or adapt to the changing conditions within their current habitats. Indeed, dispersal is a key ecological response to climate change, enabling species to shift their ranges to track suitable habitats and avoid extinction (Travis et al., 2013). Dispersal capacity can reduce extinction risks through range expansion, whereas limited dispersal exacerbates habitat loss, placing species in higher extinction risk categories (Mancini et al., 2024). For emperor penguins, our results suggest that dispersal alone does not sufficiently mitigate climate-induced population declines. While semi-informed dispersal with low emigration rates and a mean distance of 414 km provides a modest population increase under high-emission scenarios, it offers little benefit and may even reduce population size under low-emission scenarios (Appendix D, Jenouvrier et al., 2017). This suggests that dispersal is insufficient to offset the severe impacts of climate change on emperor penguin populations. Therefore, our findings underscore that effective climate change mitigation remains critical for conserving this species.

An important property of species, but one not included in our models, is that they have the potential to adapt (Bonnet et al., 2022), switching behavior or diet in novel ways (Divoky et al., 2015). One plausible

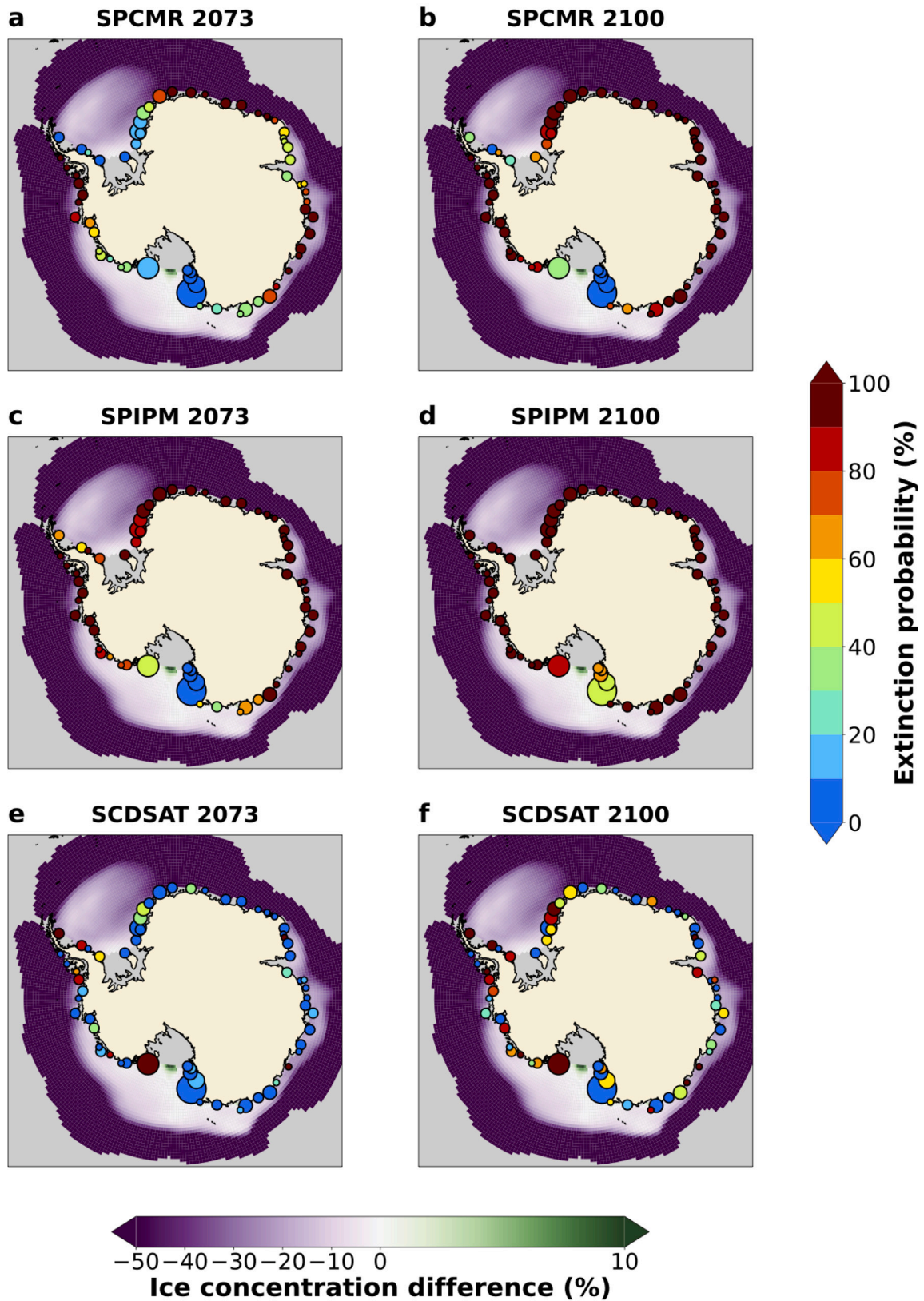


Fig. 5. Map of extinction risks under International Union for Conservation of Nature (IUCN) Criteria E. Extinction probabilities for emperor penguin (*Aptenodytes forsteri*) colonies are shown for 2073 and 2100, along with the annual mean change in sea ice concentration between 2024–2073 and 2024–2100. Extinction probabilities are defined for a huddling threshold of 100 individuals. Panels show the SPCMR and SPIPM metapopulation models or the SCDSAT bioclimatic model, where sea ice concentration projections were obtained from the Community Earth System Model Large Ensemble version 2 (CESM2) under the Shared Socioeconomic Pathway 3 (SSP 3.7-0) climate scenario. Dots show the location of colonies (Table A.4), dot colors show the projected extinction risk (Table A.3), and dot size represents the average colony size from 2009–2018 (Table A.4).

Table 1
Likelihood of emperor penguin population declines under the International Union for Conservation of Nature (IUCN) Red List Criterion A. The probabilities of decline for emperor penguins were assessed across the SPIPM (Structured Population model parametrized with Integrated Population Model), SPCMR (Structured Population model parametrized with Capture-Mark-Recapture), and SCDSAT ecological models (Scalar Count-based Dynamic model parametrized with SATellite data), the Canadian Earth System Model (CanESM), Community Earth System Model (CESM), and Commonwealth Scientific and the Industrial Research Organisation Model (CSIRO) general circulation models, the Representative Concentration Pathway (RCP 8.5), Shared Socioeconomic Pathway 3 (SSP3.7-0), and Paris Agreement (Paris 2 °C) climate scenarios, as well as different extreme events scenarios, and with and without natural climate variability. These probabilities are reported as the proportion of simulations that fall below the decline IUCN threshold over three generations (i.e., 2073). The IUCN thresholds correspond to population declines of 30%, 50%, and 80% of mature individuals relative to the average between 2009 and 2018. See Tables A.1 and A.2 more details on ecological models and climate projections used.

Ecological Models			
	Vulnerable	Endangered	Critically Endangered
SPCMR	100	97	30
SPIPM	100	100	100
SCDSAT	68	6	0
Climate Models			
	Vulnerable	Endangered	Critically Endangered
CanESM	100	85	32
CESM	100	96	33
CSIRO	98	56	26
Climate Scenarios			
	Vulnerable	Endangered	Critically Endangered
RCP8.5	100	96	33
SSP 3.7-0	100	97	30
Paris 2 °C	95	38	0
Extreme Events (EE) Scenarios			
	Vulnerable	Endangered	Critically Endangered
No EE	100	93	0
Historical EE	100	98	0
Increase EE	100	100	90
Natural Climate Variability			
	Vulnerable	Endangered	Critically Endangered
With	100	97	30
Without	100	85	33

adaptation is the possibility of breeding on ice shelves (Fretwell et al., 2014), something which could facilitate breeding success in the absence of reliable sea ice. Even though this adaptation is unlikely to change our projections since breeding success is reduced with decreasing sea ice, other adaptations could potentially have an impact. Speculation about such futures is challenging, and outside the realms of evidence-based assessment. Importantly, all our population projections are conditional upon a set of estimated parameters, which incorporate a set of hypothetical assumptions (Table A.1).

While recognizing that all models are simplifications of reality and come with inherent uncertainties, our climate and population models are grounded in robust scientific frameworks and have demonstrated skill in capturing observed changes and trends in both environmental and population dynamics. Given the increasing rates of climate change and biodiversity loss, employing these tools is essential to provide scientists, managers, and decision-makers with data on future extinction risks and to guide conservation strategies (IPBES, 2019).

4.5. Future directions

To provide the most comprehensive analysis possible, we have incorporated key elements of emperor penguin habitat in our environmental models (SST, SIC, winds). However, we acknowledge that some critical factors — such as fast ice and polynyas (Labrousse et al., 2021, 2023) — are not yet predicted by climate models and are therefore not included. For emperor penguins, future work could prioritize integrating fast ice dynamics and polynya formation into climate models, as these factors play critical roles in colony persistence but are currently underrepresented in projections.

4.6. A framework to assess risks for other species

While our study focuses on the emperor penguin, the framework developed here (Fig. 1) has broad applicability for assessing extinction risks in other species. The flowchart provides a structured framework for assessing species extinction risks under climate change by integrating ecological and climate modeling with IUCN Red List criteria (Fig. 1). This framework aligns primarily with an evidence-based decision-making model, where ecological predictions serve as an external input to inform policy and conservation actions (Maris et al., 2018). By systematically addressing uncertainties — such as structural model differences, natural variability, and measurement errors — we aim to improve the robustness of anticipatory projections.

The process begins with determining whether climate change impacts species persistence by analyzing demographic, habitat, and phenotypic traits (Step 1). Next, the appropriate IUCN Red List criteria (A–E) are selected based on the type of risk being evaluated, such as population size reduction or quantitative extinction risk (Step 2, Akçakaya et al., 2000). Ecological models tailored to these criteria are then developed (Step 3), employing a range of approaches, such as population viability analysis or species distribution modeling, to capture the complexities of ecological dynamics (IUCN, 2024; Mace et al., 2008). These models are rigorously validated using hindcasting and/or out-of-sample methods to ensure their transferability and reliability in replicating observed trends (Step 4) (Wenger and Olden, 2012; Şen et al., 2023; Willis et al., 2007). Simultaneously, climate models are selected (Step 6, Tebaldi and Knutti, 2007; Stock et al., 2011) and processed (Step 7) to provide relevant data for ecological analyses (Snover et al., 2013), ensuring alignment with observed climate patterns and addressing biases. Uncertainties are systematically addressed at multiple stages: structural differences between models (Araújo and New,

2007; Pearson et al., 2006; Buisson et al., 2010; Tittensor et al., 2021), measurement error and natural variability (Rueda-Cediel et al., 2018), are incorporated through advanced techniques like MMLE (Deser et al., 2020) (Steps 5 and 9). Finally, climate and ecological models are integrated (Step 10, Jenouvrier, 2013) to generate outputs relevant to IUCN Red List assessments, allowing for a comprehensive evaluation of species status and informing evidence-based conservation actions.

4.7. Conclusion

Building on the demonstrable success of the IUCN Red List, our framework enhances its utility by systematically addressing uncertainties and promoting a precautionary yet pragmatic approach to decision-making. This integration strengthens the link between ecological forecasting and conservation practice.

CRedit authorship contribution statement

Stéphanie Jenouvrier: Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Alice Eparvier:** Writing – original draft, Visualization, Formal analysis. **Bilgecan Şen:** Writing – original draft, Methodology, Formal analysis. **Francesco Ventura:** Writing – original draft, Methodology, Formal analysis. **Christian Che-Castaldo:** Writing – review & editing, Methodology. **Marika Holland:** Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis. **Laura Landrum:** Writing – review & editing, Methodology. **Kristen Krumhardt:** Writing – review & editing, Methodology, Formal analysis. **Jimmy Garnier:** Writing – review & editing, Methodology, Data curation. **Karine Delord:** Writing – review & editing, Data curation. **Philip Trathan:** Writing – original draft, Conceptualization.

Declaration of generative AI in scientific writing

During the preparation of this work, we used WRITEFULL and ChatGPT for spelling and grammatical assistance. After using these tools/services, the authors reviewed and edited the content as needed and take full responsibility for the final content of the published article.

Funding

We gratefully acknowledge the support of the National Science Foundation (NSF), USA OPP under grant number 2037561 and the National Aeronautics and Space Administration (NASA), USA grants 80NSSC20K1289 and 80NSSC21K1132.

Declaration of competing interest

The authors declare that they have no competing interests.

Acknowledgments

We thank Dan Zitterbart and Tom Hart for sharing unpublished data on huddling sizes at emperor penguin colonies, as well as Andy Solow for insightful discussions on the ensemble modeling approach. We acknowledge the Institut Polaire Français Paul Emile Victor (Project IPEV 109 Ornitho2E), the Zone Atelier Antarctique et Terres Australes and Terres Australes et Antarctiques Françaises for providing support and access to collect the Pointe Géologie penguin data. Special thanks to D. Joubert for the management of Pointe Géologie penguin data. We also acknowledge the US CLIVAR Working Group on Large Ensembles and CESM2 Large Ensemble Community Project with supercomputing resources provided by the IBS Center for Climate Physics in South Korea for their contributions to the use of climate data.

Code availability

Analysis code is available at <https://github.com/fledge-who/>.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111037>.

Data availability

The data supporting this study are available at https://github.com/fledge-who/emperor_penguin_IUCN.

References

- Ainley, D., Russell, J., Jenouvrier, S., Woehler, E., Lyver, P.O., Fraser, W.R., Kooyman, G.L., 2010. Antarctic penguin response to habitat change as Earth's troposphere reaches 2 C above preindustrial levels. *Ecol. Monograph.* 80 (1), 49–66.
- Akçakaya, H.R., Butchart, S.H., Watson, J.E., Pearson, R.G., 2014. Preventing species extinctions resulting from climate change. *Nat. Clim. Chang.* 4 (12), 1048–1049.
- Akçakaya, H.R., Person, S., Burgman, M.A., Keith, D.A., Mace, G.M., Todd, C.R., 2000. Making consistent IUCN classifications under uncertainty. *Conserv. Biol.* 14 (4), 1001–1013.
- Akçakaya, H.R., Kennedy, E., Hilton-Taylor, C., 2006. Biodiversity indicators based on trends in conservation status: strengths of the IUCN Red List Index. *Conserv. Biol.* 20 (2), 579–581.
- Ancel, A., Visser, H., Handrich, Y., Masman, D., Le Maho, Y., 1997. Energy saving in huddling penguins. *Nature* 385 (6614), 304–305.
- Antarctic Treaty Consultative Meeting, 2023. A five-year assessment of the impacts on emperor penguins of low sea-ice extent. Working Paper submitted by the United Kingdom, France, Germany, United States for the Antarctic Treaty Consultative Meeting. Report, Working Paper presented at the Antarctic Treaty Consultative Meeting.
- Araújo, M., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evolut.* 22, 42–47.
- Bagchi, R., Crosby, M., Huntley, B., Hole, D.G., Butchart, S.H., Collingham, Y., Kalra, M., Rajkumar, J., Rahmani, A., Pandey, M., et al., 2013. Evaluating the effectiveness of conservation site networks under climate change: accounting for uncertainty. *Global Change Biol.* 19 (4), 1236–1248.
- Barbraud, C., Weimerskirch, H., 2001. Emperor penguins and climate change. *Nature* 411 (6834), 183–186.
- Barraquand, F., Yoccoz, N.G., 2013. When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. *Theor. Popul. Biol.* 89, 1–11.
- Bird, J.P., Martin, R., Akçakaya, H.R., Gilroy, J., Burfield, L.J., Garnett, S.T., Symes, A., Taylor, J., Şekerciöğlü, Ç.H., Butchart, S.H., 2020. Generation lengths of the world's birds and their implications for extinction risk. *Conserv. Biol.* 34 (5), 1252–1261.
- Bonnet, T., Morrissey, M.B., De Villemereuil, P., Alberts, S.C., Arcese, P., Bailey, L.D., Boutin, S., Brekke, P., Brent, L.J., Camenisch, G., et al., 2022. Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. *Science* 376 (6596), 1012–1016.
- Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. *Global Change Biol.* 16, 1145–1157.
- Che-Castaldo, C., Jenouvrier, S., Youngflesh, C., Shoemaker, K.T., Humphries, G., McDowall, P., Landrum, L., Holland, M.M., Li, Y., Ji, R., et al., 2017. Pan-Antarctic analysis aggregating spatial estimates of Adélie penguin abundance reveals robust dynamics despite stochastic noise. *Nat. Commun.* 8 (1), 832.
- Cheung, W.W., Jones, M.C., Reygondeau, G., Stock, C.A., Lam, V.W., Frölicher, T.L., 2016. Structural uncertainty in projecting global fisheries catches under climate change. *Ecol. Model.* 325, 57–66.
- Clare, J.D., de Valpine, P., Moanga, D.A., Tingley, M.W., Beissinger, S.R., 2024. A cloudy forecast for species distribution models: Predictive uncertainties abound for California birds after a century of climate and land-use change. *Global Change Biol.* 30 (1), e17019.
- Comiso, J.C., Gersten, R.A., Stock, L.V., Turner, J., Perez, G.J., Cho, K., 2017. Positive trend in the antarctic sea ice cover and associated changes in surface temperature. *J. Clim.* 30 (6), 2251–2267. <http://dx.doi.org/10.1175/JCLI-D-16-0408.1>, URL <https://journals.ametsoc.org/view/journals/clim/30/6/jcli-d-16-0408.1.xml>.
- Deser, C., Lehner, F., Rodgers, K.B., Ault, T., Delworth, T.L., DiNezio, P.N., Fiore, A., Frankignoul, C., Fyfe, J.C., Horton, D.E., et al., 2020. Insights from Earth system model initial-condition large ensembles and future prospects. *Nat. Clim. Chang.* 10 (4), 277–286.

- Diamond, R., Sime, L.C., Holmes, C.R., Schroeder, D., 2024. CMIP6 models rarely simulate antarctic winter sea-ice anomalies as large as observed in 2023. *Geophys. Res. Lett.* 51 (10), <http://dx.doi.org/10.1029/2024GL109265>, e2024GL109265.
- Dietze, M., 2017. Ecological forecasting. In: *Ecological Forecasting*. Princeton University Press.
- Divoky, G.J., Lukacs, P.M., Druckenmiller, M.L., 2015. Effects of recent decreases in arctic sea ice on an ice-associated marine bird. *Prog. Oceanogr.* 136, 151–161.
- Foden, W.B., Young, B.E., Akçakaya, H.R., Garcia, R.A., Hoffmann, A.A., Stein, B.A., Thomas, C.D., Wheatley, C.J., Bickford, D., Carr, J.A., et al., 2019. Climate change vulnerability assessment of species. *Wiley Interdiscip. Reviews: Clim. Chang.* 10 (1), e551.
- Fogt, R.L., Sleinkofer, A.M., Raphael, M.N., Handcock, M.S., 2022. A regime shift in seasonal total antarctic sea ice extent in the twentieth century. *Nat. Clim. Chang.* 12, 54–62. <http://dx.doi.org/10.1038/s41558-021-01254-9>.
- Fretwell, P.T., Boutet, A., Ratcliffe, N., 2023. Record low 2022 Antarctic sea ice led to catastrophic breeding failure of emperor penguins. *Commun. Earth & Environ.* 4 (1), 273.
- Fretwell, P.T., LaRue, M.A., Morin, P., Kooyman, G.L., Wienecke, B., Ratcliffe, N., Fox, A.J., Fleming, A.H., Porter, C., Trathan, P.N., 2012. An emperor penguin population estimate: the first global, synoptic survey of a species from space. *PLoS One* 7 (4), e33751.
- Fretwell, P.T., Trathan, P.N., 2019. Emperors on thin ice: three years of breeding failure at Halley Bay. *Antarct. Sci.* 31 (3), 133–138.
- Fretwell, P.T., Trathan, P.N., Wienecke, B., Kooyman, G.L., 2014. Emperor penguins breeding on iceshelves. *PLOS ONE* 9 (1), e85285.
- Frölicher, T.L., Fischer, E.M., Gruber, N., 2018. Marine heatwaves under global warming. *Nature* 560 (7718), 360–364.
- Garnier, J., Lucas, G., Younger, J., Sen, B., Barbraud, C., Larue, M., Fraser, A.D., Labrousse, S., Jenouvrier, S., 2023. Massive and infrequent informed emigration events in a species threatened by climate change: the emperor penguins. *Hal-0382288v2*.
- Gilbert, C., Robertson, G., Le Maho, Y., Naito, Y., Ancel, A., 2006. Huddling behavior in emperor penguins: dynamics of huddling. *Physiol. Behav.* 88 (4–5), 479–488.
- Gimenez, O., Barbraud, C., 2009. The efficient semiparametric regression modeling of capture-recapture data: assessing the impact of climate on survival of two Antarctic seabird species. *Model. Demogr. Process. Mark. Popul.* 43–58.
- Hobbs, W., Spence, P., Meyer, A., Schroeter, S., Fraser, A.D., Reid, P., Tian, T.R., Wang, Z., Liniger, G., Doddridge, E.W., Boyd, P.W., 2024. Observational evidence for a regime shift in summer antarctic sea ice. *J. Clim.* 37 (7), 2263–2275. <http://dx.doi.org/10.1175/JCLI-D-23-0479.1>, URL <https://journals.ametsoc.org/view/journals/clim/37/7/JCLI-D-23-0479.1.xml>.
- Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. *Science* 328 (5985), 1523–1528.
- IPBES, 2019. Global Assessment Report on Biodiversity and Ecosystem Services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services Secretariat, Bonn, Germany, URL <https://ipbes.net/global-assessment>.
- IUCN, 2019. Species and climate change. Downloadable from: <https://www.iucn.org>.
- IUCN, 2024. Guidelines for using the IUCN red list categories and criteria. Version 16. Prepared by the standards and petitions committee. Downloadable from: <https://www.iucnredlist.org/documents/RedListGuidelines.pdf>.
- Jenouvrier, S., 2013. Impacts of climate change on avian populations. *Global Change Biol.* 19 (7), 2036–2057.
- Jenouvrier, S., Barbraud, C., Weimerskirch, H., 2005. Long-term contrasted responses to climate of two Antarctic seabird species. *Ecology* 86 (11), 2889–2903.
- Jenouvrier, S., Caswell, H., Barbraud, C., Holland, M., Stroeve, J., Weimerskirch, H., 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proc. Natl. Acad. Sci.* 106 (6), 1844–1847.
- Jenouvrier, S., Caswell, H., Barbraud, C., Weimerskirch, H., 2010. Mating behavior, population growth, and the operational sex ratio: A periodic two-sex model approach. *Amer. Nat.* 175 (6), 739–752.
- Jenouvrier, S., Che-Castaldo, J., Wolf, S., Holland, M., Labrousse, S., LaRue, M., Wienecke, B., Fretwell, P., Barbraud, C., Greenwald, N., Stroeve, J., Trathan, P.N., 2021. The call of the emperor penguin: Legal responses to species threatened by climate change. *Global Change Biol.* 27 (20), 5008–5029.
- Jenouvrier, S., Garnier, J., Patout, F., Desvillettes, L., 2017. Influence of dispersal processes on the global dynamics of Emperor penguin, a species threatened by climate change. *Biol. Cons.* 212, 63–73.
- Jenouvrier, S., Holland, M., Iles, D., Labrousse, S., Landrum, L., Garnier, J., Caswell, H., Weimerskirch, H., LaRue, M., Ji, R., Barbraud, C., 2020. The Paris Agreement objectives will likely halt future declines of emperor penguins. *Global Change Biol.* 26 (3), 1170–1184.
- Jenouvrier, S., Holland, M., Stroeve, J., Barbraud, C., Weimerskirch, H., Serreze, M., Caswell, H., 2012. Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. *Global Change Biol.* 18 (9), 2756–2770.
- Jenouvrier, S., Holland, M., Stroeve, J., Serreze, M., Barbraud, C., Weimerskirch, H., Caswell, H., 2014. Projected continent-wide declines of the emperor penguin under climate change. *Nat. Clim. Chang.* 4 (8), 715–718.
- Kay, J.E., Deser, C., Phillips, A., Mai, A., Hannay, C., Strand, G., Arblaster, J.M., Bates, S., Danabasoglu, G., Edwards, J., et al., 2015. The Community Earth System Model (CESM) large ensemble project: A community resource for studying climate change in the presence of internal climate variability. *Bull. Am. Meteorol. Soc.* 96 (8), 1333–1349.
- Labrousse, S., Fraser, A.D., Sumner, M., Le Manach, F., Sauser, C., Horstmann, I., Devane, E., Delord, K., Jenouvrier, S., Barbraud, C., 2021. Landfast ice: A major driver of reproductive success in a polar seabird. *Biology Lett.* 17 (6), 20210097.
- Labrousse, S., Iles, D., Violat, L., Fretwell, P., Trathan, P.N., Zitterbart, D.P., Jenouvrier, S., LaRue, M., 2022. Quantifying the causes and consequences of variation in satellite-derived population indices: a case study of emperor penguins. *Remote. Sens. Ecol. Conserv.* 8 (2), 151–165.
- Labrousse, S., Nerini, D., Fraser, A.D., Salas, L., Sumner, M., Le Manach, F., Jenouvrier, S., Iles, D., LaRue, M., 2023. Where to live? Landfast sea ice shapes emperor penguin habitat around Antarctica. *Sci. Adv.* 9 (39), eadg8340.
- Lande, R., Engen, S., Saether, B.-E., 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, USA.
- LaRue, M., Iles, D., Labrousse, S., Fretwell, P., Ortega, D., Devane, E., Horstman, B., Violat, L., Foster-Dyer, R., Le Bohec, C., Zitterbart, D., Houstin, A., Richter, S., Winter, A., Wienecke, B., Salas, L., Nixon, M., Barbraud, C., Kooyman, G., Ponganis, P., Ainley, D., Trathan, P., Jenouvrier, S., 2024. Advances in remote sensing of emperor penguins: first multi-year time series documenting trends in the global population. *Proc. R. Soc. B* 291 (2018), 20232067.
- Lefebvre, W., Gooose, H., 2008. Analysis of the projected regional sea-ice changes in the southern ocean during the twenty-first century. *Clim. Dyn.* 30, 59–76. <http://dx.doi.org/10.1007/s00382-007-0273-6>.
- Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J., Stuart, S.N., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* 22 (6), 1424–1442.
- Mancini, G., Santini, L., Cazalis, V., Akçakaya, H.R., Lucas, P.M., Brooks, T.M., Foden, W., Di Marco, M., 2024. A standard approach for including climate change responses in IUCN Red List assessments. *Conserv. Biol.* 38 (3), e14227.
- Maris, V., Huneman, P., Coreau, A., Kéfi, S., Pradel, R., Devictor, V., 2018. Prediction in ecology: promises, obstacles and clarifications. *Oikos* 127 (2), 171–183.
- McElreath, R., 2016. *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. CRC Press Taylor & Francis, Boca Raton.
- National Snow and Ice Data Center, 2024. Sea ice index. Downloadable from <https://nsidc.org>.
- Offredo, C., Ridoux, V., 1986. The diet of emperor penguins *Aptenodytes forsteri* in Adélie Land, Antarctica. *Ibis* 128 (3), 409–413.
- Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E., Butchart, S.H., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., et al., 2015. Assessing species vulnerability to climate change. *Nat. Clim. Chang.* 5 (3), 215–224.
- Parkinson, C.L., 2019. A 40-y record reveals gradual Antarctic sea ice increases followed by decreases at rates far exceeding the rates seen in the Arctic. *Proc. Natl. Acad. Sci.* 116 (29), 14414–14423.
- Pearson, R., Thuiller, W., Araújo, M., Martinez, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T., Lees, D., 2006. Model-based uncertainty in species' range prediction. *J. Biogeogr.* 33, 1704–1711.
- Pielke Jr., R., Burgess, M.G., Ritchie, J., 2022. Plausible 2005–2050 emissions scenarios project between 2 and 3 degrees C of warming by 2100. *Environ. Res. Lett.* 17 (2), 024027.
- Prevost, J., 1961. In: J., P. (Ed.), *Expéditions polaires françaises*. 222, Hermann Press, Paris, France, pp. 1–204.
- Purich, A., Doddridge, E.W., 2023. Record low Antarctic sea ice coverage indicates a new sea ice state. *Commun. Earth & Environ.* 4, 314. <http://dx.doi.org/10.1038/s43247-023-00961-9>.
- Raphael, M.N., Handcock, M.S., 2022. A new record minimum for Antarctic sea ice. *Nat. Rev. Earth & Environ.* 3, 215–216. <http://dx.doi.org/10.1038/s43017-022-00281-0>.
- Roach, L.A., Dörr, J., Holmes, C.R., Massonnet, F., Blockley, E.W., Notz, D., Rackow, T., Raphael, M.N., O'Farrell, S.P., Bailey, D.A., Bitz, C.M., 2020. Antarctic Sea Ice Area in CMIP6. *Geophys. Res. Lett.* 47 (9), <http://dx.doi.org/10.1029/2019GL086729>, e2019GL086729, URL <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2019GL086729>.
- Rodgers, K.B., Lee, S.-S., Rosenbloom, N., Timmermann, A., Danabasoglu, G., Deser, C., Edwards, J., Kim, J.-E., Simpson, I.R., Stein, K., et al., 2021. Ubiquity of human-induced changes in climate variability. *Earth Syst. Dyn.* 12 (4), 1393–1411.
- Rueda-Cediel, P., Anderson, K.E., Regan, T.J., Regan, H.M., 2018. Effects of uncertainty and variability on population declines and IUCN Red List classifications. *Conserv. Biol.* 32 (4), 916–925.
- Sanderson, B.M., Xu, Y., Tebaldi, C., Wehner, M., O'Neill, B., Jahn, A., Pendergrass, A.G., Lehner, F., Strand, W.G., Lin, L., et al., 2017. Community climate simulations to assess avoided impacts in 1.5 and 2 C futures. *Earth Syst. Dyn.* 8 (3), 827–847.
- Schwalm, C.R., Glendon, S., Duffy, P.B., 2020a. RCP8.5 tracks cumulative CO2 emissions. *Proc. Natl. Acad. Sci.* 117 (33), 19656–19657.
- Schwalm, C.R., Glendon, S., Duffy, P.B., 2020b. Reply to Hausfather and Peters: RCP8.5 is neither problematic nor misleading. *Proc. Natl. Acad. Sci.* 117 (45), 27793–27794.

- Şen, B., Che-Castaldo, C., Krumhardt, K.M., Landrum, L., Holland, M.M., LaRue, M.A., Long, M.C., Jenouvrier, S., Lynch, H.J., 2023. Spatio-temporal transferability of environmentally-dependent population models: insights from the intrinsic predictabilities of Adélie penguin abundance time series. *Ecol. Indic.* 150, 110239.
- Siegert, M.J., Bentley, M.J., Atkinson, A., Bracegirdle, T.J., Convey, P., Davies, B., Downie, R., Hogg, A.E., Holmes, C., Hughes, K.A., et al., 2023. Antarctic extreme events. *Front. Environ. Sci.* 11, 1229283.
- Singh, H.K.A., Landrum, L., Holland, M.M., Bailey, D.A., DuVivier, A.K., 2021. An overview of antarctic sea ice in the community earth system model version 2, part I: Analysis of the seasonal cycle in the context of sea ice thermodynamics and coupled atmosphere-ocean-ice processes. *J. Adv. Model. Earth Syst.* 13 (3), <http://dx.doi.org/10.1029/2020MS002143>, e2020MS002143, URL <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2020MS002143>.
- Singh, H.A., Polvani, L.M., Rasch, P.J., 2019. Antarctic sea ice expansion, driven by internal variability, in the presence of increasing atmospheric CO₂. *Geophys. Res. Lett.* 46 (24), 14762–14771. <http://dx.doi.org/10.1029/2019GL083758>, URL <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2019GL083758>.
- Snover, A.K., Mantua, N.J., Littell, J.S., Alexander, M.A., McClure, M.M., Nye, J., 2013. Choosing and using climate-change scenarios for ecological-impact assessments and conservation decisions. *Conserv. Biol.* 27 (6), 1147–1157.
- Spence, M.A., Blanchard, J.L., Rossberg, A.G., Heath, M.R., Heymans, J.J., Mackinson, S., Serpetti, N., Speirs, D.C., Thorpe, R.B., Blackwell, P.G., 2018. A general framework for combining ecosystem models. *Fish Fish.* 19 (6), 1031–1042.
- Stock, C.A., Alexander, M.A., Bond, N.A., Brander, K.M., Cheung, W.W., Curchitser, E.N., Delworth, T.L., Dunne, J.P., Griffies, S.M., Haltuch, M.A., et al., 2011. On the use of IPCC-class models to assess the impact of climate on living marine resources. *Prog. Oceanogr.* 88 (1–4), 1–27.
- Stonehouse, B., 1953. The emperor penguin (*Aptenodytes forsteri*): Breeding behaviour and development. *Sci. Rep. Falkland Isl. Depend. Surv.*
- Tebaldi, C., Knutti, R., 2007. The use of the multi-model ensemble in probabilistic climate projections. *Philos. Trans. R. Soc. A: Math. Phys. Eng. Sci.* 365 (1857), 2053–2075.
- Tittensor, D.P., Novaglio, C., Harrison, C.S., Heneghan, R.F., Barrier, N., Bianchi, D., Bopp, L., Bryndum-Buchholz, A., Britten, G.L., Büchner, M., et al., 2021. Next-generation ensemble projections reveal higher climate risks for marine ecosystems. *Nat. Clim. Chang.* 11 (11), 973–981.
- Trathan, P.N., Fretwell, P.T., Stonehouse, B., 2011. First recorded loss of an emperor penguin colony in the recent period of antarctic regional warming: implications for other colonies. *PLoS One* 6 (2), e14738.
- Trathan, P.N., Wienecke, B., Barbraud, C., Jenouvrier, S., Kooyman, G., Le Bohec, C., Ainley, D.G., Ancel, A., Zitterbart, D.P., Chown, S.L., et al., 2020. The emperor penguin-Vulnerable to projected rates of warming and sea ice loss. *Biol. Cons.* 241, 108216.
- Travis, J.M., Delgado, M., Bocedi, G., Bague, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J.A., Kubisch, A., Penteriani, V., et al., 2013. Dispersal and species' responses to climate change. *Oikos* 122 (11), 1532–1540.
- Trisos, C.H., Merow, C., Pigot, A.L., 2020. The projected timing of abrupt ecological disruption from climate change. *Nature* 580 (7804), 496–501.
- Trull, N., Böhm, M., Carr, J., 2018. Patterns and biases of climate change threats in the IUCN Red List. *Conserv. Biol.* 32 (1), 135–147.
- Urban, M.C., 2015. Accelerating extinction risk from climate change. *Science* 348 (6234), 571–573.
- U.S. Fish and Wildlife Service, 2022. Endangered and threatened wildlife and plants; threatened species status for emperor penguin with section 4(d) rule. *Fed. Regist.* 87 (206), 64700–64724, URL <https://www.federalregister.gov/documents/2022/10/26/2022-23164/endangered-and-threatened-wildlife-and-plants-threatened-species-status-for-emperor-penguin-with>.
- Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods Ecol. Evol.* 3 (2), 260–267.
- Wiens, J.J., Zelinka, J., 2024. How many species will earth lose to climate change? *Global Change Biol.* 30 (1), e17125.
- Willis, K.J., Araujo, M.B., Bennett, K.D., Figueroa-Rangel, B., Froyd, C.A., Myers, N., 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Phil. Trans. R. Soc. B* 362 (1478), 175–187.
- Yao, Y., Vehtari, A., Simpson, D., Gelman, A., 2018. Using stacking to average Bayesian predictive distributions (with discussion). *Bayesian Anal.* 13.