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ORIGINAL PAPER

Penguindex: a Living Planet Index for *Pygoscelis* species penguins identifies key eras of population change

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Abstract

As one of the best studied components of the Southern Ocean food web, *Pygoscelis* penguins serve as an important window into the larger marine ecosystem, but the patchiness and heterogeneity of the census data available have made it difficult to assess trends in a policy-accessible way. Here we introduce a *Pygoscelis* penguin-specific biodiversity index, the 'Penguindex,' using the framework of the Living Planet Index (LPI), distilling 40 year population trends of pygoscelid penguins for the first time into a single pan-Antarctic indicator for use by policymakers. We also calculate species- and region-specific indices from which discrete eras of population dynamics can be identified. These indices, similar to the LPI itself, do not provide estimates of changes in absolute abundance of species but, instead, reflect comparable population trends and the relative magnitude of these changes. We find that the Adélie Penguin (*Pygoscelis adeliae*) index was relatively stable across the Antarctic since 1980, with declines in regional indices across the Antarctic Peninsula region being contrasted by increases in regional indices for the Ross Sea and East Antarctica. The Chinstrap Penguin (*Pygoscelis antarctica*) index across the Antarctic declined by 61%. In stark contrast, the index for Gentoo Penguin (*Pygoscelis papua*) has increased seven-fold. Our analysis also identifies several marked eras of regional pygoscelid population change that may help identify key mechanistic drivers. We expect that the Penguindex will act as a useful reference tool for policymakers and hope that, by following this example, other taxonomic groups in the Antarctic might be tracked using the Living Planet Index framework. Importantly, our development of the Penguindex should facilitate the much-needed integration of Antarctic data into global biodiversity monitoring.

Keywords Antarctic · Biodiversity · Convention on Biological Diversity · Living Planet Index · Population change · Pygoscelis penguin

Introduction

As summarized in the most recent Global Biodiversity Outlook from the Convention on Biological Diversity, none of the 20 Aichi Biodiversity targets set for 2011–2020 were fully met (Convention on Biological Diversity 2020), and the Antarctic, often considered unburdened by anthropogenic disturbance, is not fairing any better (Chown et al. 2017). The Kunming-Montreal Global Biodiversity Framework agreed to in 2022 includes a new set of goals and targets for which progress must be measured (Convention on Biological Diversity 2022), so quantifying the changes in global biodiversity remains one of the most important ecological endeavors today. Understanding ecological change is especially urgent for systems in which changes are occurring more rapidly. Among these is the Antarctic and its Southern Ocean ecosystem, which is experiencing significant

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warming and the resulting changes in sea ice distribution, shifting winds, and increased ocean acidification (Parkinson 2002; Kwok and Comiso 2002; Zwally et al. 2002; Turner et al. 2005; Russell et al. 2006; Turner et al. 2014). These changes have influenced the intricately connected Southern Ocean food webs in countless ways, affecting the success, abundance, and distribution of many species (Fowbert and Smith 1994; Ainley et al. 2010; Weimerskirch et al. 2012). It is particularly difficult, however, to assess ecological change in the Antarctic; complications include separating natural variability from shifting regional trends, inadequate historical and current data on both terrestrial and marine diversity, and logistical challenges to science in remote regions.

As important marine predators in the Southern Ocean ecosystem, penguins of the genus *Pygoscelis* (Adélie Penguins, *Pygoscelis adeliae*; Chinstrap Penguins, *Pygoscelis antarctica*; and Gentoo Penguins, *Pygoscelis papua*) are critical bellwethers of climate change and, as a result, serve as an ideal focus for investigations into ecological change in the Antarctic. Over the last decade, there has been a concerted effort to catalog the distribution and abundance of each of the three *Pygoscelis* species penguins in the Antarctic (south of 60°S), including several efforts to use satellite imagery to complete pan-Antarctic population censuses for each species (Lynch and LaRue 2014; Strycker et al. 2020; Herman et al. 2020). In addition, the completion of the mapping application for penguin populations and projected dynamics (MAPPPD; Humphries et al. (2017)) now provides easy access to all publicly available census data dating back to 1979 (Che-Castaldo et al 2023). MAPPPD's release has facilitated a renewed interest in continental scale penguin dynamics that has uncovered differing trends across pygoscelids in response to climate change (Che-Castaldo et al. 2017; Şen et al. 2023). However, until now, population trends of pygoscelid penguins have not been synthesized into a single pan-Antarctic indicator for use by policymakers. The need for easy-to-interpret metrics of penguin trends has never been more critical, as the Antarctic Treaty Parties address threats of the changing climate and increased human activities, and the convention on the conservation of antarctic marine living resources (CCAMLR) wrestles with the design (and eventual evaluation) of Marine Protected Areas (Berkman et al. 2011; Miller and Slicer 2014). In an effort to meet this urgent need, we introduce here a pygoscelid penguin-specific biodiversity index, the 'Penguindex,' using the framework of the Living Planet Index (LPI).

The LPI, a global biodiversity index produced by the World Wildlife Fund and the Zoological Society of London, is a major collaborative effort to track trends in vertebrate abundance around the globe (Almond et al. 2022). The index aggregates individual time series of vertebrate population measures to track average changes in abundance of species over time (Loh et al. 2005; Collen et al. 2009; McRae et al. 2017). The biennial Living Planet Report (LPR) uses the LPI to distill global biodiversity trends into a singular message on the health of our planet. The 2022 LPR describes a 69% average decrease in global biodiversity since 1970 (Almond et al. 2022). It is important to note, however, that the LPI should not be interpreted as summarizing changes in abundance across populations or species (Puurtinen et al. 2022). Instead, the LPI provides estimates of population trends and a way to compare the relative magnitude of these changes (Leung et al. 2022; Westveer et al. 2022). In addition to the biennial global LPR, the LPI has also been used to identify trends across many taxa, and several country- (van Strien et al. 2016; Marconi et al. 2021), biome- (Galewski et al. 2011; McRae et al. 2012), and taxa-specific (Saha et al. 2018; He et al. 2019; Pacoureau et al. 2021) sub-indices have been developed to allow for easy-to-understand monitoring of biodiversity. Our Penguindex leverages this methodology for pygoscelid penguins, and fills a critical gap in the monitoring of biodiversity change in the Antarctic.

While penguin population data have been collected and analyzed for decades, the Antarctic community has not made a concerted effort to integrate those data into global biodiversity efforts such as the LPI. As a result, the Antarctic is vastly underrepresented in the database underlying the global LPI (LPI 2022), and little attention has been drawn to how this might influence global patterns. The 2022 LPR acknowledges that "polar regions...showed the highest impact probabilities for climate change, driven in particular by impacts on birds" (page 41, Almond et al. (2022)), but there is no specific mention of the Antarctic in the report. Though the rate of new Antarctic time series added to the LPI database has accelerated in recent years (Ledger et al. 2022), the data within MAPPPD has not been integrated into the LPI database and the LPI's coverage of Antarctica remains inadequate.

We present the Penguindex as a pygoscelid-specific LPI and an easily-interpreted measure of penguin trends in the Antarctic. Including almost every known pygoscelid breeding site, we first use a Bayesian state-space framework (Che-Castaldo et al. 2017) to estimate trends in the relative abundance for all three pygoscelid species, allowing us to leverage experience modeling penguin abundance to more accurately interpolate gaps in observed time series. Using these trends, we calculated the pan-Antarctic Penguindex for pygoscelid penguins by aggregating over each of eight Antarctic regions for each species, calculating both species-specific indices and region-specific indices for each species along the way. In evaluating these trends we also estimate change points—that is, points in time where an index curve shifts significantly—in an effort to understand the mechanisms of these changes. We anticipate that this Penguindex will represent the latest significant development in the monitoring of these important sentinel species of climate change.

Methods

Population time series

Data on nests and chicks for the three pygoscelid species were collected and organized under the auspices of MAPPPD (Humphries et al. 2017). We included data from all known breeding colonies with at least one observed abundance count between the 1970/1971 season (hereafter referred to as the 1970 season) and the 2019 season, totaling 271 Adélie, 358 Chinstrap, and 109 Gentoo Penguin colonies with a total of 3884 observed counts. These data were used to fit a Bayesian state-space model (SSM) to estimate annual pygoscelid nest abundances for each breeding colony from 1970 to 2020. This hierarchical model, adapted from Che-Castaldo et al. (2017), included observation error (uncertainty in the number of true nests counted in each year) and process error (stochastic variability in the population growth rate); we modeled the intrinsic rate of growth $r_{i,t}$, for the i_{th} colony in the t_{th} season as a function of site and season effects. Notably, the Penguindex does not yet include the Emperor penguin because the data available are currently too patchy. While our analysis is complete with regards to the known penguin colonies south of 60° S, Gentoo and Chinstrap Penguins both breed in sub-Antarctic islands found further north than this cut-off for the Antarctic region. As noted in our Discussion, expanding this index to all penguin species throughout the Southern Hemisphere is a high priority.

Calculating the penguindex

Data subsetting and Antarctic regions

In calculating the Penguindex, since few abundance counts are available prior to 1979 or for the year 2020, we restrict our calculation to the 1980–2019 seasons. While the Bayesian state space model provides estimates for all years for all breeding colonies, here we follow the criteria for inclusion of time series in the global LPI (Collen et al. 2009) and discard from consideration those time series with fewer than two observed abundance counts from 1980 to 2019. This filtering results in 118 Adélie Penguin, 94 Chinstrap Penguin, and 58 Gentoo Penguin colonies with fully interpolated time series from which to calculate the Penguindex. Following the LPI framework (Collen et al. 2009), one percent of the mean population for the whole time series was added to years in time series for which the Bayesian state space model assigned a population value of zero (as was the case for change with confirmed absence for that species) in any year.

Each breeding colony is assigned a geographical region of the Antarctic: (1) Central-west Antarctic Peninsula (AP) and Northwest AP; (2) Southwest AP; (3) Elephant Island, South Orkney Islands, and South Shetland Islands; (4) Northeast AP; (5) Ross Sea (CCAMLR Subareas 88.1 and 88.2); (6) Bellingshausen Sea (CCAMLR Subarea 88.3); (7) Adélie/Wilkes Land (CCAMLR Division 58.4.1); and (8) Mac. Robertson to Queen Maud Land (CCAMLR Division 58.4.2). The locations of the breeding colonies for each species are shown, differentiated by region, in Online Resource 1: Figs. S1–S3. Adélie Penguins are found in all eight regions but Chinstraps breed only in Regions 1–3 and 5, and Gentoos in Regions 1, 3, and 4.

Calculation of index values

The Penguindex is calculated following the general format of the LPI (Collen et al. 2009; McRae et al. 2017) (see Online Resource 1: Fig. S4). The pan-Antarctic pygoscelid index is calculated by aggregating over all three species, each of which is first aggregated over each region. For each breeding colony, the annual rate of change d_t is the logarithm of the growth rate in a given year t, $d_t = \log_{10}(N_t/N_{t-1})$, where N_t denotes a draw from the posterior for nest abundance in year t as estimated from the SSM. Drawing from the posterior allows us to propagate the uncertainty regarding abundance in years t and $t-1$ to the estimate of d_t. For each year t, the values of d_t for each breeding colony in a region is then averaged within each species × region combination, with each breeding colony weighted equally regardless of size, yielding a region-and-species-specific estimate of d_t for each year. These region-specific interannual changes were then aggregated to obtain a single annual rate of change for each species, with each region's interannual change weighted by the proportion of the total number of that species' breeding colonies that occur in that region. Annual trends for each species were then aggregated to obtain a single pan-Antarctic annual rate of change for all pygoscelid species, $\bar{d}_t$. All three pygoscelid species were weighted equally for this aggregation. Each of these regional, species, and global trends were then converted to index values, $I_t = I_{t-1} \times 10^{\bar{d}_t}$, with $I_{t=1} = 1$ for the reference year 1980. Indices are calculated for each of 1000 draws from the posterior distributions of nest abundance estimates from the Bayesian SSM. These analyses were performed using R v4.1.2 (R Core Team R 2021).

Penguindex null models

Random fluctuations in time series, even when overall population trends are stable, can disproportionately affect the LPI relative to actual trends (Buschke 2021). Additionally, the population dynamics of *Pygoscelis* penguins are characterized by large interannual fluctuations (Che-Castaldo et al. 2017; Youngflesh et al. 2017). To account for this potential bias in the Penguindex, we used a null model that maintained the starting populations in each time series (as estimated by the Bayesian SSM) and simulated stable dynamics with random fluctuations. For each species, the posterior mean for the species-specific process error σ was used and the abundance of breeding colony i in year t, $N_{sim_{i,t}}$ was simulated as:

$$\log(N_{sim_{i,t}}) \sim \text{normal}(\mu_{i,t} = \log(N_{sim_{i,t-1}}), \sigma^2_{spp}) \quad (1)$$

where $N_{sim_{i,t=0}}$ is drawn from the posterior distribution for nest abundance for colony i in year $t = 1980$ as estimated from the Bayesian SSM (see Online Resource 1). For Adélie Penguins, the process error σ depends on the region. These null model time series are then used to calculate the Penguindex as described above. We iterate this null model 1000 times and average the index over all iterations, obtaining a null index for each region, species, pan-Antarctic index as above. This index can then be used as a null expectation of the Penguindex rather than the static baseline of $I_{1980} = 1$.

Era identification

Change points in the Penguindex were identified via segmented regression (Muggeo 2003) to find years at which the linear trend of the index changed significantly. This change point analysis allowed us to establish eras of pygoscelid population dynamics between 1980 and 2019. Change points were identified for the pan-Antarctic *Pygoscelis* Penguindex as well as for each species- and region-level indices. These analyses were performed using R v4.1.2 (R Core Team R 2021) and the package 'segmented' (Muggeo 2017). The Bayesian information criterion (BIC) was used to select the number change points between 0 and 10 (Tiwari et al. 2005). The maximum number of change points allowed in this procedure was set to 10 since the optimal number of change points never reached the limit of 10 for any index.

Results

Pan-Antarctic *Pygoscelis* trends

The average change in *Pygoscelis* penguin breeding colonies between 1980 and 2019 was an increase of 46.6% (95% credible interval, 28.2–66.9%) (Fig. 1a). Our data suggest an initial surge of growth prior to 1986 (1986 index 1.500, 95% CI 1.327–1.684), followed by a period of stability until 1994 (1994 index 1.384, 95% CI 1.226–1.556); pan-Antarctic *Pygoscelis* penguin colonies steadily grew between 1994 and 2015 (2015 index 1.668, 95%

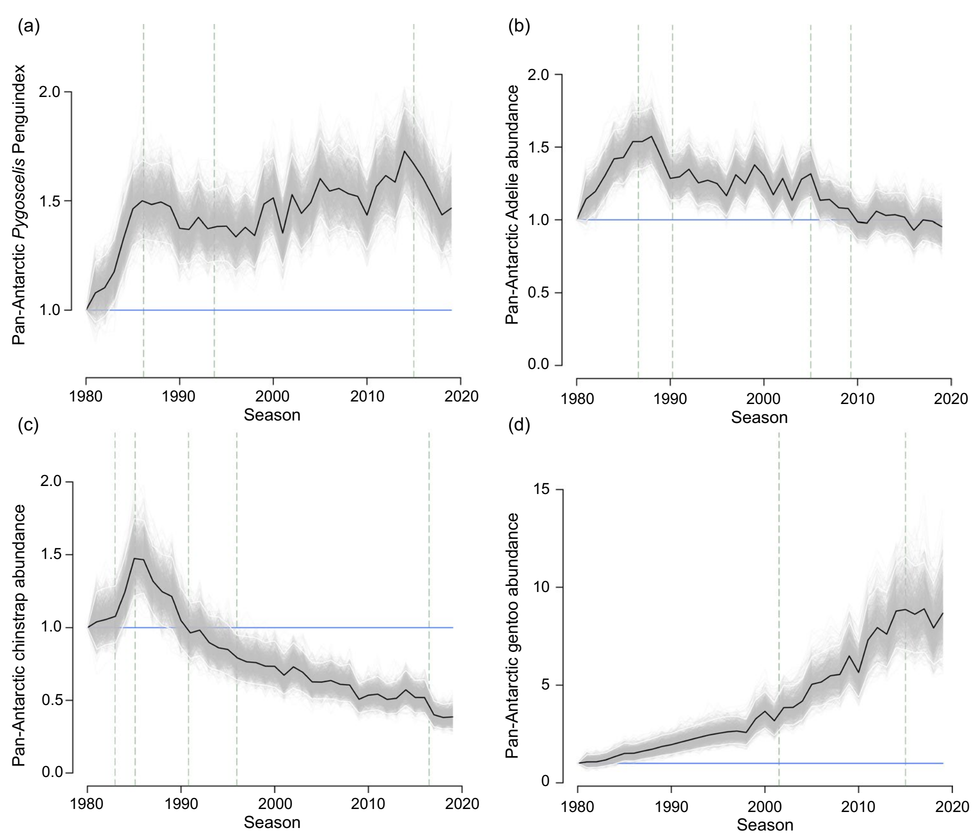


Fig. 1 Pan-Antarctic **a** *Pygoscelis* and **b–d** species-level Penguindex for **b** Adélie (*Pygoscelis adeliae*), **c** Chinstrap (*Pygoscelis antarctica*), and **d** Gentoo (*Pygoscelis papua*) Penguin colonies from 1980 to 2019; each black line denotes the mean, the white lines the 95% credible intervals, and the gray lines each iteration, each blue line denotes the null model index; identified change points are reported in Online Resource 2: Table S1

CI 1.473–1.890), after which the average breeding colony declined suddenly. The null model for the pan-Antarctic *Pygoscelis* Penguindex stayed steady at 1.0.

Pan-Antarctic species-level trends

The pan-Antarctic *Pygoscelis* Penguindex can be disaggregated by species to identify species-specific trends. On average, Adélie Penguin colonies were mostly stable across the Antarctic between 1980 and 2019 (Fig. 1b). Following the pan-Antarctic trend for all pygoscelid species, Adélie Penguin colonies increased between 1980 and 1986, with the index maximum around this time representing a 57.3% increase in the average colony (95% CI 38.3–77.4%). Between 1986 and 1990, however, the pan-Antarctic Adélie index declined quickly (1990 index 1.385, 95% CI 1.136–1.455), followed by a period of relative stability until 2005 (2005 index 1.316, 95% CI 1.16–1.48). This was followed by another period of rapid decline until 2009 during which the average Adélie Penguin colony returned to the 1980 baseline (2009 index 1.077, 95% CI 0.949–1.231). Between 2009 and 2019, the pan-Antarctic Adélie Penguindex remained approximately stable (2019 index 0.955, 95% CI 0.810–1.129).

Chinstrap Penguin colonies south of 60° S decreased on average by 61.4% (95% CI 51.7–69.6%) between 1980 and 2019 (Fig. 1c). While Chinstrap Penguin colonies declined the most on average across the Antarctic, declines were not constant, with trends in the pan-Antarctic Chinstrap Penguindex displaying the largest number of distinct eras of change compared with the other two *Pygoscelis* species. An initial period of minor growth between 1980 and 1983 (1983 index 1.078, 95% CI 0.895–1.285) was followed by one of sharper growth until 1985 (1985 index 1.473, 95% CI 1.217–1.748). Between 1985 and 1991, the pan-Antarctic Chinstrap index declined back to baseline (1991 index 0.963, 95% CI 0.788–1.166). Two eras of slower decline were identified between 1991 and 2017 (2017 index 0.401, 95% CI 0.317–0.496).

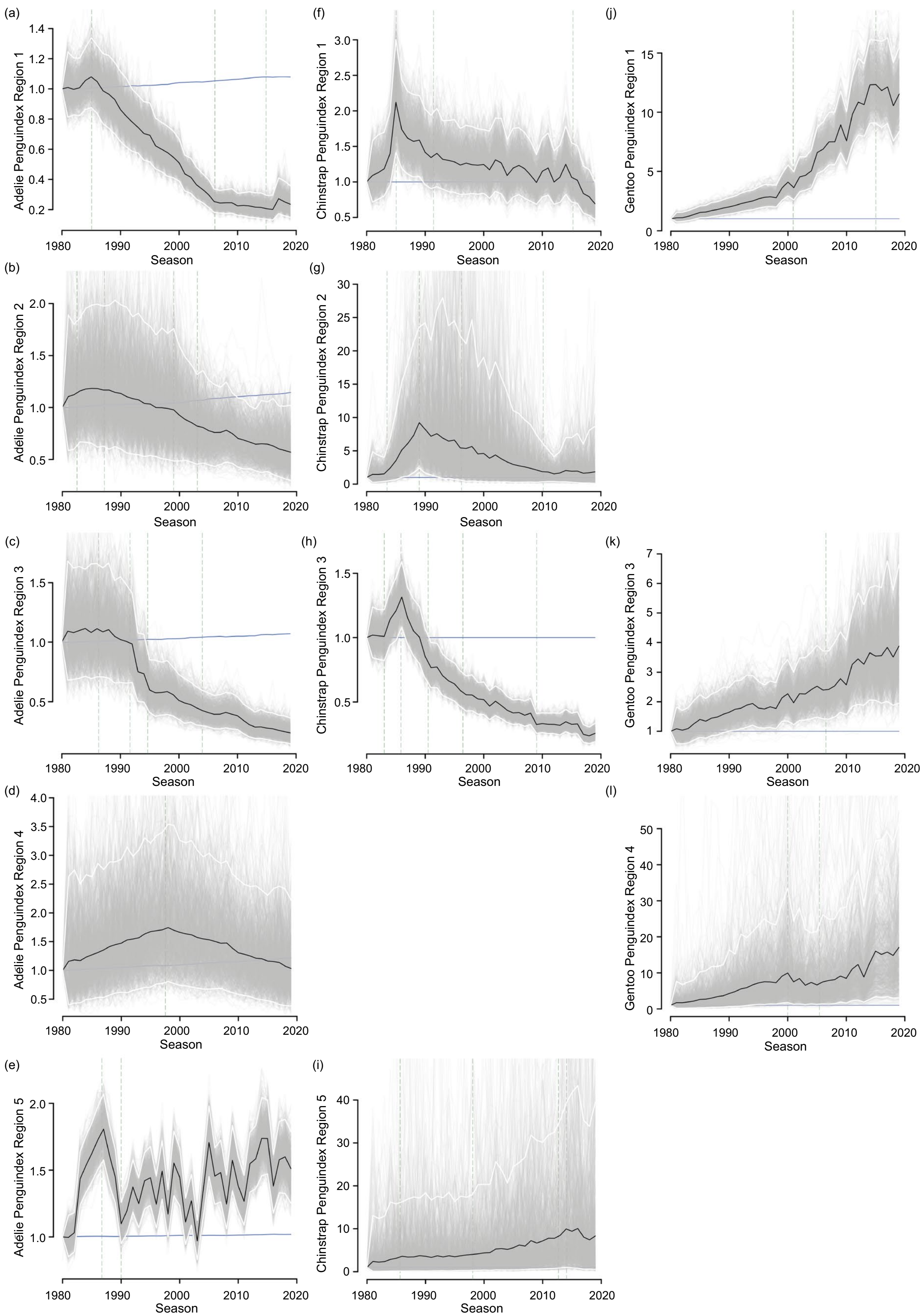
Conversely, Gentoo Penguin breeding colonies increased by 768.3% (95% CI 540.8–1057.6%) across the Antarctic between 1980 and 2019 (Fig. 1d). Prior to 2002, the average Gentoo Penguin colony increased by 285.0% (95% CI 198.1–398.6%). This period of growth was followed by a shorter period of even more rapid growth between 2001 and 2015 (2015 index 8.876, 95% CI 6.799–11.540). Notably, however, the average Gentoo Penguin colony was almost completely stagnant between 2015 and 2019 (2019 index 8.683, 95% CI 6.408–11.576). Null models for all species-level indices remained stable at 1.0 through 2019.

Species-specific regional trends

Regional Adélie trends

Species trends disaggregated by region show differing patterns across the Antarctic (Figs. 2 and 3). Note in Figs. 2 and 3 we choose a layout to emphasize differences between species; a geographic comparison for each species is presented in Online Resource 2: Figs. S1–S3. The Ross Sea (Region 5) contains the largest number of Adélie Penguin breeding colonies (37 breeding colonies; Fig. 2e). Change point analysis identified three major eras of change for these colonies, with an initial surge of growth between 1980 and 1987 leading to an average increase in abundance of 80.8% (95% CI 57.7–107.0%) of the 1980 baseline. This was followed by a shorter period of rapid decline until 1990 (1990 index 1.098, 95% CI 0.951–1.259). The period from 1990 to 2019 displayed large fluctuations, with the overall trend being positive (2019 index 1.510, 95% CI 1.252–1.789; null model index 1.019). Adélie Penguin colonies in East Antarctica also increased on average between 1980 and 2019. In Adélie/Wilkes Land (12 breeding colonies; Region 7, Fig. 3b), Adélie colonies increased by 291.9% (95% CI 106.3–576.4%; the null model increased by 4.9%) on average between 1980 and 2019, though a period of rapid decline was observed between 2004 and 2010 (2004 index 4.276, 95% CI 2.532–6.464; 2010 index 2.676, 95% CI 1.624–4.151). Adélie Penguin colonies in Mac. Robertson to Queen Maud Land (19 breeding colonies; Region 8, Fig. 3c) increased on average by 164.8% (95% CI 70.7–296.9%; the null model increased by 2.6%) over the 40-year time series, though the average colony peaked at 472.1% (95% CI 308.1–678.2%) of the 1980 baseline in 2004 before declining rapidly between 2004 and 2009 (2009 index 2.67, 95% CI 1.876–3.670). Between 2009 and 2019, Adélie colonies in Mac. Robertson to Queen Maud Land remained approximately stable on average.

Adélie breeding colonies on Elephant Island, South Orkney Islands, and South Shetland Islands (19 breeding colonies; Region 3, Fig. 2c) declined on average 76.2% between 1980 and 2019 (95% CI 63.7–85.5%; the null model increased by 7.1%) after an initial period of growth. Most of this decline occurred between 1992 and 1995 (1992 index 0.985, 95% CI 0.662–1.413; 1995 index 0.598, 95% CI 0.409–0.853), while recent declines have been slower. The average Adélie colony on the Central- and Northwest AP (14 breeding colonies; Region 1, Fig. 2a) declined by 75.7% (95% CI 67.3–82.3%) of baseline by 2007 following a small amount of initial growth. In later years, Adélie colonies on the Central- and Northwest AP were more stable on average (2019 index 0.235, 95% CI 0.149–0.358; null model index 1.079).


(a)
Adélie Penguindex Region 1
(b)
Adélie Penguindex Region 2
(c)
Adélie Penguindex Region 3
(d)
Adélie Penguindex Region 4
(e)
Adélie Penguindex Region 5
(f)
Chinstrap Penguindex Region 1
(g)
Chinstrap Penguindex Region 2
(h)
Chinstrap Penguindex Region 3
(i)
Chinstrap Penguindex Region 5
(j)
Gentoo Penguindex Region 1
(k)
Gentoo Penguindex Region 3
(l)
Gentoo Penguindex Region 4
Season
1980
1990
2000
2010
2020

◂**Fig. 2** Region-level Penguindex for Regions 1–5 for **a**–**e** Adélie (*Pygoscelis adeliae*), **f**–**i** Chinstrap (*Pygoscelis antarctica*), and **j**–**l** Gentoo (*Pygoscelis papua*) Penguin colonies from 1980 to 2019; each black line denotes the mean, the white lines the 95% credible intervals, and the gray lines each iteration, each blue line denotes the null model index; identified change points are reported in Online Resource 2: Table S1

For Adélie colonies on the Southwestern AP (9 breeding colonies; Region 2, Fig. 2b), two short periods of initial growth—first rapid until 1983 (1983 index 1.159, 95% CI 0.670–01.861) and then slow between 1983 and 1987 (1987 index 1.170, 95% CI 0.628–1.976)—were followed by three longer periods of slow decline—1987–1999 (1999 index 0.978, 95% CI 0.485–1.759), 1999–2003 (2003 index 0.822, 95% CI 0.455–1.320), and 2003–2019 (2019 index 0.570, 95% CI 0.299–1.023; null model index 1.145). On the Northeastern AP (7 breeding colonies; Region 4, Fig. 2d), Adélie colonies increased steadily until 1998, by 74.4% (95% CI 19.3% decrease – 254.2% increase) on average. Between 1998 and 2019, however, these Adélie Penguin colonies decreased just as steadily (2019 index 1.034, 95% CI 0.382–2.219; null model index 1.064). The Bellingshausen Sea (Region 6, Fig. 3a) had only one Adélie Penguin colony and contributed little to the pan-Antarctic Adélie Penguindex.

Regional Chinstrap trends

The majority of Chinstrap breeding colonies included were located in Elephant Island, the South Orkney Islands, and the South Shetland Islands (60 breeding colonies; Region 3, Fig. 2h). On average, these colonies declined by 74.4% (95% CI 81.0–66.7%) between 1980 and 2019. Prior to 1986, however, these colonies increased on average by 31.5% (95% CI 7.8–59.1%). After 1986, these colonies declined at various rates until 2009 (2009 index 0.324, 95% CI 0.256–0.411), after which colonies remained relatively stable until 2019 (2019 index 0.256, 95% CI 0.256–0.411). On average, Chinstrap colonies on the Central- and Northwestern AP (31 breeding colonies; Region 1, Fig. 2f) declined by only 30.9% (95% CI 0.6–52.8%). Compared to Elephant Island, the South Orkney Islands, and the South Shetland Islands, Chinstrap colonies on the Central- and Northwestern AP displayed a much steeper period of growth prior to 1985, more than doubling the 1980 baseline on average (1985 index 2.12, 95% CI 1.41–3.00). Chinstrap breeding colonies in this region declined after this initial period of growth, first quickly until 1991 (1991 index 0.768, 95% CI 0.612–0.961) and then slowly from 1991 to 2005 (2005 index 1.193, 95% CI 0.786–1.754). The Southwestern AP (Region 2, Fig. 2g) and Ross Sea (Region 5, Fig. 2i) each had two or fewer Chinstrap Penguin breeding colonies and contributed little to the pan-Antarctic Chinstrap Penguindex. Null models for all regional-level Chinstrap indices were stable at 1.0.

Regional Gentoo trends

Gentoo Penguin colonies on the Central- and Northwestern AP (39 breeding colonies; Region 1, Fig. 2j) increased on average over ten-fold (2019 index 11.529, 95% CI 8.362–15.482). Initial growth was slow until 2001 (2001 index 3.622, 95% CI 2.584–4.983), then steeper between 2001 and 2015 (2015 index 12.343, 95% CI 9.090–16.094). The growth of these colonies, however, stalled between 2015 and 2019. Growth was relatively steady for Gentoo breeding colonies on Elephant, South Orkney, and South Shetland Islands (Region 3, Fig. 2k), with the average colony increasing by 287.6% (95% CI 195.2–664.2%) by 2019. On the Northeastern AP (Region 4, Fig. 2l), Gentoo Penguin colonies increased 17-fold on average (2019 index 17.050, 95% CI 3.094–51.692). With only 4 Gentoo Penguin breeding colonies, this region contributed relatively little to the pan-Antarctic Gentoo Penguindex. Null models for all three regional-level Gentoo Penguin indices were stable at 1.0.

Discussion

To our knowledge, this is the first comprehensive examination of genus-wide trends for *Pygoscelis* penguins across the whole of the Antarctic. Our results identify key eras of change for the average pygoscelid breeding colony. While the dominant approach to Antarctic monitoring strategies has been to model overall population abundance (Croxall et al. 2002; Che-Castaldo et al. 2017), the LPI framework used here instead aims to measure average trends in populations (Leung et al. 2022; Puurtinen et al. 2022; Westveer et al. 2022). Since region-level Penguindex calculations equally weight all breeding colonies within a region regardless of their size, our index is different from one calculated by aggregating populations at larger scales. Thus the trends described here by a region-level Penguindex are not commensurate with the trends observed for the total abundance of that species across the region (i.e., as in Che-Castaldo et al. (2017), Fig. 2). For example, a region-level Penguindex for a species can be interpreted as describing the relative percentage increase or decrease in any given colony's abundance within that region, enabling trends in all breeding colonies to be reflected in the index rather than being dominated by the largest breeding colony. Notably, the integration of data from all breeding colonies avoids having to base our understanding of broad trends on a small number of long-term study sites that, by virtue of size or location, may not necessarily reflect broader dynamics; the Penguindex's equal weighting of all colonies also prevents the very largest

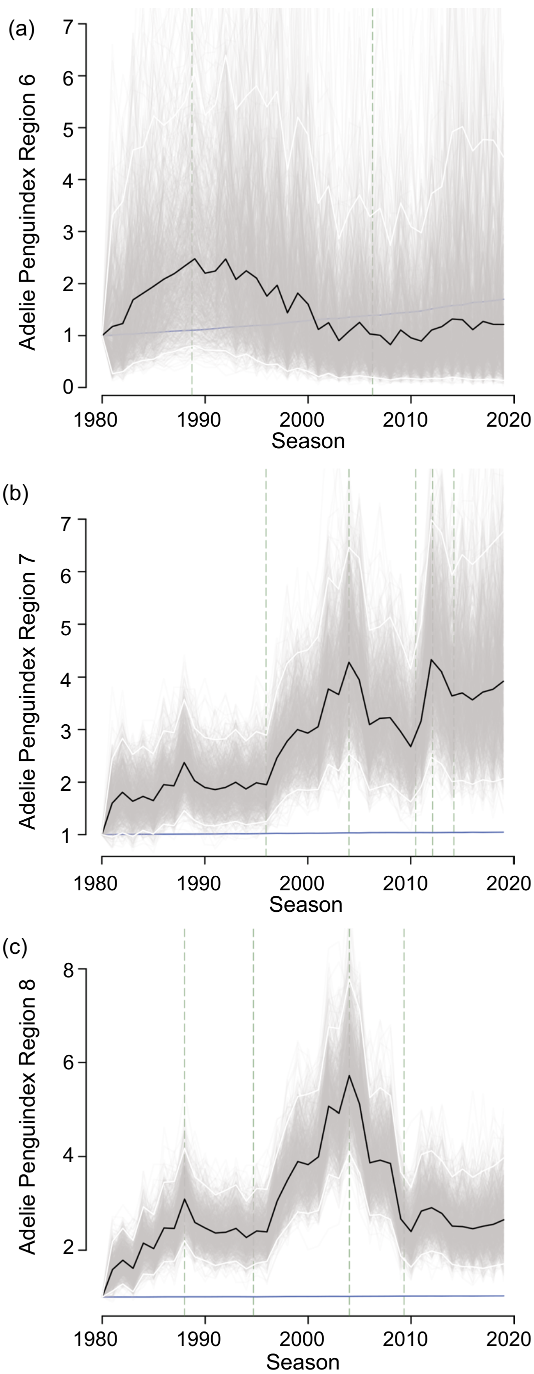


Fig. 3 Region-level Penguindex for Regions 6–8 for Adélie Penguin (*Pygoscelis adeliae*) colonies from 1980 to 2019 (Chinstrap and Gentoo Penguin colonies were not present in Regions 6–8); each black line denotes the mean, the white lines the 95% credible intervals, and the gray lines each iteration, each blue line denotes the null model index; identified change points are reported in Online Resource 2: Table S1

colonies from obscuring the information provided by the large numbers of smaller colonies throughout a region. As such, we see the Penguindex and the LPI framework as a complement to ongoing efforts to model aggregated abundance across the Antarctic.

Stark differences in individual species trends

Over the last four decades, our time series suggest an average decline of 21% within Chinstrap Penguin breeding colonies across the Antarctic. While data are sparse, studies up to the 1990s found many Chinstrap colonies to be increasing (Jabłoński 1984; Fraser et al. 1992), with evidence of this growth dating back to the mid 1950s. For example, Croxall and Kirkwood (1979) note a five-fold increase at North Point (S. Orkney Islands) between 1958 and 1978. However, more recent studies have established global declines in Chinstrap colonies (Sander et al. 2007; Lynch et al. 2012; Naveen et al. 2012; Dunn et al. 2016; Strycker et al. 2020). Our pan-Antarctic Chinstrap Penguindex quantifies both this initial period of Chinstrap population growth and its subsequent crash.

In stark contrast to the grim trend of Chinstrap colonies, however, Gentoo Penguin breeding colonies have skyrocketed (an increase of 768.3%). In fact, an analysis of the public LPR database (LPI 2022) reveals that the growth observed for Gentoo Penguin breeding colonies below 60° S is in the 89th percentile for species undergoing population growth (see Online Resource 1: Sect. S3). It is worth noting, however, that outside of the Antarctic there is evidence that Gentoo Penguin colonies are in decline (Lescroël and Bost 2006; Barbraud et al. 2020). The regional trends observed here also align with previous studies showing that Gentoo breeding colonies along the Western AP have experienced the most rapid growth (Herman et al. 2020). Compared to the overwhelming decline of Chinstrap Penguin colonies and staggering growth of Gentoo breeding colonies, Adélie Penguin colonies across the Antarctic have experienced little change on average over the 40 years considered here. Regional Adélie trends differ markedly, with relative declines in Adélie breeding colonies across the AP and sub-Antarctic islands being contrasted with increases in colonies in the Ross Sea and East Antarctica. These trends are similar in relative magnitude, resulting in the relatively stable species-wide index, and correspond to those identified by the first (and only) pan-Antarctic Adélie Penguin census, conducted in 2014 (Lynch and LaRue 2014).

Notable eras of population change may be linked to warming

While Adélie breeding colonies on the Western AP and Elephant, South Orkney, and South Shetland Islands decreased drastically between 1980 and 2019, each constituent region was identified as having a recent distinct era of change in which declines slowed significantly. These eras each started roughly between 2003 and 2006 and extended until the end of our study period (2019). This recent leveling of decline among Adélie colonies is perhaps related to the shift between a long period of steady warming to a recent period of cooling (beginning circa 1999) identified by Turner et al. (Turner et al. 2016, 2020), with a lag roughly consistent with the time necessary for a shift in either reproductive success or juvenile survival to affect breeding abundance (Talis et al. 2022). Adélie Penguins have a tight-knit coupling to Antarctic sea ice (Fraser et al. 1992; Wilson et al. 2001; Ballerini et al. 2009) that has been the subject of considerable research over the last 40 years, though the relative roles of climate and Antarctic krill fishing as drivers of Adélie trends on the Peninsula remain subject to debate. Our findings are consistent with, though not conclusive of, climatically-driven forcings playing a key role in the observed and much discussed declines of Adélie Penguins in this region.

While, on average, the 2019 abundance of Adélie breeding colonies on the Northeastern AP was nearly identical to the 1980 abundance, our data suggest that these colonies were not stable over the 40 year time series considered here (Borowicz et al. 2018). We identified a clear era of growth between 1980 and 1998 followed by an era of decline (1998–2019). Thus the period of warming across the AP prior to 1999 (Turner et al. 2016, 2020) was correlated with growth of Adélie colonies on the Northeastern AP, in contrast to the decline seen on the Western AP and sub-Antarctic islands. Additionally, the period of cooling observed across the AP after 1999 was met with declines in these Northeastern AP colonies. These trends may indicate that the sea ice concentration in the Weddell Sea was unfavorably high at the start of our time series in 1980, and that the warming period prior to 1999 benefited Adélies until the region began to cool again. Our species-level index for Gentoo Penguins also suggests a recent period of relative stagnation in the growth of the average breeding colony, with a distinct period of stability identified between 2015–2019. While we have been unable to identify any promising potential environmental drivers for this halt in growth of Gentoo breeding colonies, it is clear that recent years have marked a new era for this species.

Pan-Antarctic *Pygoscelis* trends are dominated by different species over time

Species-level pygoscelid penguin trends were equally weighted to obtain the pan-Antarctic *Pygoscelis* Penguindex. Four distinct eras of pan-Antarctic pygoscelid trends were identified, beginning with a period of growth across Antarctica for all species (1980–1986). Between 1986 and 1994, growth in the average Gentoo breeding colonies was balanced with the decline in the average Adélie and Chinstrap breeding colonies, resulting in virtually complete stagnation in the pan-Antarctic *Pygoscelis* Penguindex across this era. For the next two decades, from 1994–2015, growth in Gentoo colonies outweighed the declines in Adélie and Chinstrap colonies, as illustrated by a steadily rising pan-Antarctic *Pygoscelis* Penguindex. As discussed above, recent years have seen a halt of growth in Gentoo Penguin colonies. This change point was identified in the pan-Antarctic pygoscelid index as well, with the recent era between 2015–2019 demonstrating a pan-Antarctic decline in the Penguindex as stable Gentoo breeding colonies were eclipsed by continuing, albeit gradual, declines in Adélie and Chinstrap colonies.

While changes in the pan-Antarctic Penguindex are driven by different species through time, it is important to note that both Adélie and Chinstrap Penguins outnumber Gentoo Penguins almost ten-fold across the Antarctic (Lynch and LaRue 2014; Strycker et al. 2020; Herman et al. 2020). Thus the Penguindex provides information that is complementary, but not equivalent, to changes in overall penguin abundance. Instead, the Penguindex reflects the relative changes in colonies on a percentage basis by treating species trends equally regardless of the species colony size, as described above. While Antarctic policymakers may prefer the more granular species- and region-level indices to understand *Pygoscelis* trends, this genus-wide pan-Antarctic Penguindex is intended primarily for those working outside the Antarctic and serves as a comparable analog to other taxa-specific LPI (Saha et al. 2018; Pacoureau et al. 2021).

Benefits of state-space models and the Penguindex approach

SSMs similar to the one employed here are valuable in their ability to synthesize data collected by different methods or with different precision by incorporating observation error into their estimation of trends (Che-Castaldo et al. 2017; Kindsvater et al. 2018; Pacoureau et al. 2021). Here, the use of our hierarchical Bayesian SSMs also allowed for a more informed modeling approach than is provided by a generalized additive model (GAM) like the one employed by the LPI for interpolation (Collen et al. 2009; McRae et al. 2017). In the traditional LPI framework, a GAM not only interpolates missing data but also smooths time series, reducing interannual variation and affecting the resulting index. As *Pygoscelis* penguin time series display considerable interannual fluctuations (Che-Castaldo et al. 2017; Youngflesh et al. 2017; Talis et al. 2022), preserving this variability is important to understanding their dynamics and producing an accurate index of pygoscelid biodiversity. As an aggregation of species population trends, the traditional LPI can mask variation in the underlying data. By maintaining empirical interannual variation with the use of our SSMs and including species-specific indices to aid interpretation, the reflection of different species trends in the Penguindex can help to illustrate underlying environmental changes happening in the Antarctic. SSMs also allow for the incorporation of covariates or spatial autocorrelation to improve interpolation of missing data, which stand as future improvements to the Penguindex and the underlying SSMs.

The traditional LPI framework has several other shortcomings that we mitigate in the formulation of the Penguindex. First, the LPI is sensitive to random fluctuations in underlying population time series (Buschke et al. 2021), leading to shifting a counterfactual rather than a fixed baseline set at 1980. The null models utilized in the Penguindex address this issue by allowing for a null expectation of the index that is robust to large population fluctuations. While most null model indices are fairly static, some (particularly for Adélies in Regions 1–3, see Fig. 2) demonstrate an increasing counterfactual rather than a constant standard equal to the 1980 index. Additionally, the use of the geometric mean in the standard LPI means it is often sensitive to extremes. While the aggregation of the Penguindex does not weight breeding colony time series based on their size, and thus may still be sensitive to the influence of small colonies, our region-level indices, showing underlying regional trends, and use of credible intervals, illustrating the variation in each index, aid in the determination of pan-Antarctic and species-wide trends.

Updating the Living Planet Index for Antarctica and expanding the Penguindex

Pygoscelis penguins and the Southern Ocean ecosystem are extremely underrepresented in the database underlying the LPI and the biennial LPR. Though MAPPPD has identified 271 Adélie, 358 Chinstrap, and 109 Gentoo Penguin breeding colonies across the Antarctic, the Living Planet database currently includes only 76 Adélie, 18 Chinstrap, and 66 Gentoo time series. Addressing this gap was the primary motivation for our analysis. Through our analysis we have aggregated and adapted all MAPPPD pygoscelid penguin abundance observations into the format required for integration into the LPI (see Online Resource 1: Sect. S4) (McRae et al. 2017). While the inclusion of these time series will drastically increase the Antarctica's representation in global assessments using the LPI, this is only the start of what is required for Antarctica as a region and for penguins as a taxonomic group. First, it is important to recognize that our Antarctic Penguindex includes only the three species with the greatest data coverage and includes only those populations south of 60° S. Both Chinstrap and Gentoo penguins have significant breeding populations further north that are not included in our Antarctic Penguindex and, as such, our evaluation of their changes through time may not be representative of changes over their entire range. In addition, there are several species that were not included due to extreme data scarcity. Ongoing efforts to track Emperor penguins using satellite imagery will greatly expand data availability for this species of conservation concern, and we consider the incorporation of these data into the Penguindex—and, further, the LPI—as a top priority. In addition, King and Macaroni Penguins were recently added to MAPPPD. While these two species have relatively few breeding colonies in this region and the time series are particularly short and/or sparse, we expect that the Penguindex can be expanded to include them in the near future. Finally, penguins are only one small component of Antarctic biodiversity. As time series are collated for other species of long-standing research interest (e.g., pack-ice seals, petrels, fur seals, whales; Boveng et al. (1998); Schwaller et al. (2018); Borowicz et al. (2019); Gonçalves et al. (2022)), their full incorporation into the LPI will allow for a straight-forward assessment of biodiversity trends by a wide range of stakeholders. Though the LPI alone cannot reverse the biodiversity crisis, its broad adoption for global assessments creates an imperative to integrate what we know to be rapid and only partially understood changes in the distribution and abundance of Antarctic biota.

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Author Contributions HJL, LM, and TH initially conceived of the Penguindex (along with Ben Collen). HJL, along with CCC developed the underlying penguin database used for analysis and developed the state-space model. ET designed and completed the LPI analyses presented in the manuscript. ET and HJL led the manuscript writing. All authors read and approved the manuscript.

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Data availability All data, R scripts, and results supporting this study are available at Zenodo, https://doi.org/10.5281/zenodo.7884501.

Declarations

Competing interest The authors have no financial or proprietary interests in any material discussed in this article.

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