Detecting climate signals in populations across life histories

Stéphanie Jenouvrier[1], Matthew C. Long[2], Christophe F. D. Coste[3],

Marika Holland[2], Marlène Gamelon[3,4], Nigel G. Yoccoz[5] and Bernt-Erik Sæther[3]

Affiliations:

1. Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA

2. National Center for Atmospheric Research, Boulder, CO, USA

3. Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway

4. Laboratoire de Biométrie et Biologie Évolutive, CNRS, Unité Mixte de Recherche (UMR) 5558, Université Lyon 1, Université de Lyon, Villeurbanne, France

5. Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway.

E-mail addresses: Stéphanie Jenouvrier: `sjenouvrier@whoi.edu`;

Matthew C. Long: `mclong@ucar.edu`;

Christophe F. D. Coste: `christophe.f.d.coste@ntnu.no`;

Marika Holland: `mholland@ucar.edu`;

Marlène Gamelon: `marlene.gamelon@univ-lyon1.fr`,

Nigel Yoccoz: `nigel.yoccoz@uit.no`;

Bernt-Erik Sæther: `bernt-erik.sather@ntnu.no`.

Statement of authorship: SJ and ML developed the research ideas, conceptualized and designed the study. SJ performed modeling work and analyzed theoretical and empirical data. CC derived the mathematical equations. MH computed the sea ice forecasts. SJ wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Running title: Time of emergence in populations

Keywords: Time of emergence, signal to noise, climate change, life histories, population variability, population trend, emperor penguin.

Type of article: Reports

Length: The number of words in the abstract is 264. The number of words in the main text is ~ 9000. The number of references is 111. There are 8 figures, 3 tables.

Corresponding author: Stéphanie Jenouvrier

E-mail: sjenouvrier@whoi.edu

Telephone: (508) 289-3245

Fax: (508) 457-2169

Woods Hole Oceanographic Institution

266 Woods Hole Road,

Woods Hole, MA 02543-1050

U.S.A

Abstract

Climate impacts are not always easily discerned in wild populations as detecting climate change signals in populations is challenged by stochastic noise associated with natural climate variability, variability in biotic and abiotic processes, and observation error in demographic rates. Detection of the impact of climate change on populations requires making a formal distinction between signals in the population associated with long-term climate trends from those generated by stochastic noise. The time of emergence (ToE) identifies when the signal of anthropogenic climate change can be quantitatively distinguished from natural climate variability. This concept has been applied extensively in the climate sciences, but has not been explored in the context of population dynamics. Here, we outline an approach to detecting climate-driven signals in populations based on an assessment of when climate change drives population dynamics beyond the envelope characteristic of stochastic variations in an unperturbed state. Specifically, we present a theoretical assessment of the time of emergence of climate-driven signals in population dynamics (ToE_{pop}). We identify the dependence of ToE_{pop} on the magnitude of both trends and variability in climate and also explore the effect of intrinsic demographic controls on ToE_{pop}. We demonstrate that different life histories (fast species vs. slow species), demographic processes (survival, reproduction) and the relationships between climate and demographic rates, yield population dynamics that filter climate trends and variability differently. We illustrate empirically how to detect the point in time when anthropogenic signals in populations emerge from stochastic noise for a species threatened by climate change: the emperor penguin. Finally, we propose six testable hypotheses and a road map for future research.

1 Introduction

Climate change is expected to have significant effects on biological populations [Mason *et al.*, 2019]. Many studies have assessed the influence of particular climate variables on demographic rates (e.g., survival) and population sizes [e.g., see review Gaillard *et al.*, 2013; Jenouvrier, 2013; Reed *et al.*, 2021]. However, while the primacy of climate influence is commonly accepted, specific detection and attribution of population trends to anthropogenic changes in climate is complicated by substantial stochastic noise related to observation error (i.e., errors due to measurement imprecision) and process error in biological processes (i.e., unexplained variation in true abundance driven by unobserved biotic such as species interactions or abiotic processes such as habitat quality, resource variability...) and climate variability [Che-Castaldo *et al.*, 2017; Parmesan *et al.*, 2013] (Table 1). Climate variability is an important characteristic of the climate system and a driver of population dynamics [Boyce *et al.*, 2006; Vázquez *et al.*, 2015] that may occlude the population response to the underlying climate change signal.

Natural climate variability is noise from unforced variability generated internally within the climate system Mann *et al.* [2021]) (Table 1). Natural variability in the climate system occurs over a broad range of temporal and spatial scales, with spectral properties in the seasonal, interannual to decadal bands. It arises from different sources, including variations that are (1) driven by a periodic external forcing, like the diurnal or the seasonal cycle of insolation, (2) due to the non-linear interplay of feedbacks within the climate system, such as coupled mode of variability (e.g. El Niño-Southern Oscillation, North Atlantic Oscillation, Pacific Decadal Oscillation), and (3) associated with random fluctuations in the external or internal climate system [Ghil, 2002]. In addition, climate change is characterized by an anthropogenic climate change signal (Table 1). This secular trend is the deterministic response of the climate system to an external forcing driven by anthropogenic emissions of greenhouse gases and changes in land use. Hence, the detection of

4

27 anthropogenic forced change is a signal to noise problem.

28 To detect and attribute the threats to a species posed by climate, climate-driven sig-
29 nals in population should be distinguished from stochastic noise. The concept of time
30 of emergence (ToE) exactly does that: it identifies when the signal of anthropogenic cli-
31 mate change can be formally distinguished from noise associated with natural variability
32 (Table 1). In climate science, the ToE has been studied extensively [Hawkins *et al.*, 2020;
33 Hawkins & Sutton, 2012]. It is used to detect climatic changes and to describe whether
34 climate changes are potentially beyond the known natural environmental variability of
35 ecosystems [Giorgi & Bi, 2009; Mahlstein *et al.*, 2013].

36 Although, this concept of ToE has yet to be formally applied to ecological time se-
37 ries, some studies have quantified when novel climate conditions relevant for ecological
38 processes will emerge from natural variability. For example, Beaumont *et al.* [2011] have
39 characterized the standard deviation (SD) of surface air temperature for a baseline pe-
40 riod (1961-1990) and then evaluated the number of months that the temperature exceeds
41 2 SDs by 2070 for various ecoregions of exceptional biodiversity. They found that more
42 than 83% of terrestrial and freshwater ecoregions will be exposed to temperature exceed-
43 ing 2 SDs by 2070.

44 The ToE explicitly characterizes the point in time when anthropogenic climate change
45 can be formally distinguished from noise associated with natural variability. Hence, it
46 informs on how fast changes exceed natural variability and can help prioritize decisions
47 about when, where and for which conservation and management actions may be neces-
48 sary. Some studies have characterized explicitly the ToE of ecosystem drivers in marine
49 ecosystems [Henson *et al.*, 2017; Schlunegger *et al.*, 2020]. For example, Henson *et al.* [2017]
50 found that climate change signals of pH and SST emerge rapidly while climate change
51 trends in interior oxygen content and primary productivity emerge later. In terrestrial
52 ecosystems, Rojas *et al.* [2019] focused on the timing when the precipitation changes will
53 emerge outside the range of natural variability during the 21th century relevant for agri-

5

cultural activities. They found early timing of emergence in precipitation trends for the production regions of four major crops (wheat, soybean, rice, and maize) even under a low-emission scenario. Sorte *et al.* [2019] characterized the seasonal and spatial variations in the emergence of novel climates characterized by precipitation, minimum and maximum temperature, along the migration routes of 77 passerine bird species. They found that earlier ToE occur for migrants that winter within the tropics. However, none of these studies have applied directly the concept of ToE to time series of population dynamics.

Here, we apply the concept of ToE to characterize climate-driven signals in population dynamics. We present a new perspective on detecting climate-related impacts in populations by characterizing the ToE in population growth rate (herefater, ToE_{pop}), the point in time when climate-driven signals in population dynamics can be quantitatively distinguished from noise associated with year-specific stochastic variations in population growth rates (Fig. 1). While in climate science the noise is associated with climate natural variability, applying this approach to population dynamics does not exclude other sources of noise (e.g., observation and process errors; demographic and environmental variability, the later being driven by fluctuations in physical habitat, resource availability, and biological interactions).

For species threatened by climate change, ToE_{pop} can represent the time at which the population will detectably decline to a level below its historical variability. This point in time potentially corresponds to the time at which the species will be exposed to high extinction risk, to the time at which individuals will migrate massively to track ecological niches, or to the time at which individuals may have to adapt to new conditions through evolutionary adaptations. The earlier the ToE_{pop} occurs, the faster novel conditions emerge out of the natural range of variability, the faster the population will reach a non-historical level, with less time for the organisms to adapt or migrate. The ToE_{pop} is one illustrative metric that acknowledges the dual role of natural variability and an anthropogenic climate change signal, also useful for populations increasing under cli-

6

mate change [Román-Palacios & Wiens, 2020; Stephens *et al.*, 2016]. Importantly, ToE allows meaningful comparative studies of when the signal of anthropogenic climate change emerges from natural variability across ecosystem drivers [Henson *et al.*, 2017], species [Sorte *et al.*, 2019], ecosystems [Beaumont *et al.*, 2011] and for future socio-economic processes relevant for climate mitigation [Schlunegger *et al.*, 2020].

From a conceptual viewpoint, ToE_{pop} occurs earlier when the slope of the population climate-driven trend is large and/or when the population variability is small (Fig. 1). Both the population climate-driven trend and variability depend on the species' life history and the functional relationships between climate and the demographic rates (Barraquand & Yoccoz [2013]). Specifically, species of both plant and animal kingdoms can be ranked along a main axis of life history variation, the so called "slow-fast continuum" [Gaillard *et al.*, 2016; Oli, 2004; Sæther, 1987; Salguero-Gómez *et al.*, 2016; Stearns, 1983]. Species with fast life history are characterized by early maturity, high reproductive output and short lifespan; while species with slow life history have opposite characteristics. Previous work has shown that depending on their position along this continuum, species exhibit contrasting demographic responses to climate change with various spectrum of variability and amplitude of the response [Compagnoni *et al.*, 2021; Doak & Morris, 2010; Jenouvrier *et al.*, 2005; Morris *et al.*, 2008; Paniw *et al.*, 2017]. In addition, the population responses to climate change depend on the function that links climate variables to demographic rates (survival, growth, reproduction) that drive population growth rate and structure (i.e. functional relationships, Fig. S 1).

After briefly reviewing the time of emergence in climate (section 2), we present this concept in the context of population dynamics (section 3). Then, we characterize and compare the time of emergence of climate-driven signals in population dynamics in a theoretical context to address five questions (section 4):

- How does ToE_{pop} in populations relate to ToE in climate?

- How does ToE_{pop} vary across life histories (e.g. slow- fast species)?

- How does ToE_{pop} vary across demographic processes (e.g. survival, reproduction)?

- How does ToE_{pop} vary among different functional relationship between climate and demographic rates?

- Do some species, demographic processes or functional relationship magnify the signal of anthropogenic climate change?

We find that different life histories (e.g., long vs. short-lived species) and demographic processes by which climate affects the population (i.e., through survival, reproduction) provide different "scale-dependent" filters so that some life histories magnify signal-to-noise ratios while other demographic dynamics prolong ToE_{pop}. Furthermore, to illustrate our theoretical results, we quantify the ToE_{pop} of an iconic species endangered by climate change: the emperor penguin (*Aptenodytes forsteri*) [Jenouvrier *et al.*, 2021] (section 5). Finally, we propose a set of six testable hypotheses based on the patterns of ToE in climate (hereafter $ToE_{climate}$) and the demographic processes across life histories and propose a road map for future studies on the ToE_{pop} (section 6).

2   Time of emergence in climate

The concept of $ToE_{climate}$ has been discussed for several decades in the climate sciences with studies attempting to detect the carbon dioxide warming signal published more than 80 years ago ([Callendar, 1938; Revelle & Suess, 1957], see review in Hawkins *et al.* [2020]). The time of emergence has been characterized in temperature [Mahlstein *et al.*, 2011], precipitation [Giorgi & Bi, 2009], climate extremes [King *et al.*, 2015], in sea level [Lyu *et al.*, 2014], in Arctic climate [Landrum & Holland, 2020] and biogeochemical variables [e.g., Henson *et al.*, 2017; Long *et al.*, 2016; Schlunegger *et al.*, 2020].

Different methods have been used to quantify $ToE_{climate}$, most of them using climate model simulations (but see Hawkins *et al.* [2020] for an application using observation of temperature). The common methods for estimating $ToE_{climate}$ are the signal threshold

method (section 3), and the signal-to-noise ratio method with a particular cutoff [Hawkins & Sutton, 2012]; a variant of this approach is the identification of the signal-to-noise ratio using a predefined threshold across multiple consecutive years (refereed as the exceedance threshold) [Mora *et al.*, 2013]. Various statistical methods have been developed, from statistical test to assess for significant differences between time periods [Zappa *et al.*, 2015], estimation of the standard error of the regression to estimate the lead-time required for a linear trend to emerge from natural variability [Mahlstein *et al.*, 2012], development of hierarchical statistical state-space model [Barnhart *et al.*, 2016] or artificial neural networks [Barnes *et al.*, 2018].

Recently, the availability of large ensembles of climate (or Earth system) models have open new doors to quantify climate natural variability and hence evaluations of the ToE$_\text{climate}$. An ensemble is a collection of coupled climate simulations (Table 1) that are integrated in parallel, typically with small differences in initial conditions applied to each ensemble member. Climate model generate internal variability as a product of interactions between components internal to the climate system [Hasselmann, 1976]. Since the climate system is chaotic, perturbations in initial conditions grow with time, randomizing the phase of natural variability and leading to spread across the ensemble. This spread can be interpreted as a measure of the amplitude of natural climate variability. As all the ensemble members are subject to the same external forcing (i.e., emissions scenario), the deterministic response of the climate system can be assessed as the mean across the ensemble members, which effectively filters out the noise associated with natural variability [Kay *et al.*, 2015]. Modeling centers usually contribute a small number of ensemble members to international climate change projection assessments, typically ranging from 3 to 10 ensemble members for a given model. Large ensembles with ensemble sizes ranging from 30 to 100 members permit climatologists to compute emergence thresholds to formally consider the uncertainty in the forced response due to natural climate variability [Barnhart *et al.*, 2016].

9

₁₆₀ Here, we use signal threshold method (section 3) based on a large ensemble by con-

₁₆₁ structing prediction interval of the climate and population projections, and estimate the

₁₆₂ time taken by the system to emerge from the background of natural variability [Barnhart

₁₆₃ *et al.*, 2016]. For example, the left part of Figure 2 shows an idealized climate trajectory

₁₆₄ corresponding to a single ensemble member (red line) and the associated envelope of nat-

₁₆₅ ural variability based on a 95% prediction interval (gray). ToE$_{\text{climate}}$ is the time when the

₁₆₆ projected future conditions under the influence of climate change, "forced conditions"

₁₆₇ (red lines), exceeds a pre-defined threshold for emergence that is based on the histori-

₁₆₈ cal unperturbed conditions (gray area, with the horizontal line illustrating the baseline

₁₆₉ threshold at which climate change is defined to emerge).

₁₇₀ The emergence thresholds are typically based on the percentile of the distribution of

₁₇₁ the historical and forced projections. They define the prediction intervals at which the

₁₇₂ signal of climate change emerges from the natural climate variability. We present the re-

₁₇₃ sults for one threshold of wide confidence envelope with a 95% prediction interval based

₁₇₄ on emergence thresholds defined by the 2.5 or 97.5 percentile values of the distribution,

₁₇₅ where impacts are triggered by the extreme historical conditions only. The analysis with a

₁₇₆ narrow confidence envelope with emergence thresholds defined by the 20 or 80 percentile

₁₇₇ values of the confidence interval (i.e. 60% prediction interval) is shown in appendix (Fig.

₁₇₈ S 3). In that case, the system is likely highly sensitive to climate as severe impacts are

₁₇₉ thought to occur for lower percentile of the climate conditions distribution experienced

₁₈₀ during the historical run. Our results are qualitatively the same between 95% and 60%

₁₈₁ prediction intervals (Figs. 3 versus S 3).

₁₈₂ In our simulations, we construct a large ensemble of climate time series for both the

₁₈₃ historical and forced environment for various natural climate variability (σ^2) and warm-

₁₈₄ ing trends (α). Specifically, the historical climate time series are obtained by sampling

₁₈₅ into a normal distribution – centered on a zero mean and with a specific standard devia-

₁₈₆ tion σ – with independent draws each year (i.e. Independent and Identically Distributed

random variables (IID)). The forced climate time series are calculated by adding to this natural variability a linear trend of slope α. In that context, this ToE calculation in an IID environment is directly related to the signal-to-noise ratio: $ToE = \frac{2P}{SNratio}$ with P the climate value corresponding the threshold of the prediction interval.

In our theoretical study, we explore a range of parameters consistent with the observed standard deviation of the inter-annual temperature variability (Fig. 1 of Hawkins & Sutton [2012]) and the projected climate warming by 2100 (IPCC), with $\sigma_C \in [0.2\ 1.5]$ and $\alpha_C \in [0.01\ 0.15]$ (Fig. 2). In our empirical example, we used 40-members from the Community Earth System Model Large Ensemble (CESM-LE, Kay *et al.* [2015]) to characterize the confidence envelope of sea ice, hence the ToE$_{climate}$ and ToE$_{pop}$.

3 Conceptual model of the time of emergence in population

The time of emergence depends both on (1) the time varying signal, $T(t)$ estimated as the long term monotonic trend (red trend on Fig. 1) and (2) the noise based on the range of natural variability over some historical period (variations of the black time series on Fig. 1, section 2). Hence, it is important to understand how the climate-driven trend in population growth rate and its year-specific stochastic variations are related to climate trend and variability (section 3.2, Fig. 1). Although, previous theoretical studies have shown that the variance in annual population growth rates depends on the variance in climate in a stationary environment [Engen *et al.*, 2005], we still lack a theoretical understanding on how the population trend and variability respond to climate in a non-stationary environment. Hence, after introducing the methods to estimate the time of emergence in population (section 3.1), we discuss conceptually the links between the trend and variability of population and climate (section 3.2, Fig. 1). In addition, to partially shedding light on those concepts, we build on previous theoretical studies [Engen *et al.*, 2005; Morris *et al.*, 2008] to show analytically how the variance in annual population growth rates can

11

be related (linearly for small environmental changes) to the climate variance in a stochastic and stationary environment by explicitly accounting for the functional relationship between climate and demographic rates (section 3.3, eq. 8).

3.1 Methods to estimate ToE_{pop}

As in climate (section 2), population ecologists can use various methods to estimate the time of emergence in population ToE_{pop}. Figure 2 illustrates the signal threshold method used here (section 2), where the time of emergence is the first year when the projected future state of a variable crosses a pre-defined emergence threshold based on the historical variations. For example, the projected future state of a population can be depicted by the gray envelope of future projections (red lines on Figs. 1, 2) under a specific forcing scenarios based on a range of emissions of greenhouse gases (GHGs), while the emergence threshold can be determined from the gray envelope of historical population projections (black lines on Figs. 1, 2)).

In ecological impact studies, the emergence threshold (e.g., horizontal lines on Figs. 1, 2) can be interpreted as thresholds beyond which management-relevant impacts will occur and depend on the management sensitivity to changes in climate conditions. Indeed, emergence thresholds are not necessarily set at the extreme 2.5% high or 2.5% low of the range of historical population variations ($\sim 2\sigma$) usually used in risk impact studies but can be set at any thresholds at which the decline or increase in population is perceived as unsustainable. For example, high management sensitivity threshold may be desirable for increasing species, whereby management actions are triggered by low emergence thresholds e.g. 60% prediction interval of population growth distribution during the baseline period (Fig. S 3).

3.2 Factors influencing the ToE_{pop}

Figure 2 shows that the time of emergence in populations varies among species. From a conceptual viewpoint, this depends on the sensitivity of the population growth rate to climate: $\frac{\partial \lambda}{\partial C}$ (Fig. 1). This sensitivity can be decomposed into two main components.

12

First, it depends on the sensitivity of the demographic rates themselves θ_i (e.g. survival, reproduction) to climate $\frac{\partial \theta_i}{\partial C}$ (panel 1 in the demographic rates box on Fig. 1). Therefore, the functional relationships between climate and the demographic rates likely play a key role in the sensitivity of the population growth rate to climate. Second, $\frac{\partial \lambda}{\partial C}$ depends on the sensitivity of the population growth rate to demographic rates $\frac{\partial \lambda}{\partial \theta_i}$ (panel 2 in the demographic rates box on Fig. 1). The latter is influenced by the species' life history [Saether & Bakke, 2000]. For instance, the "demographic buffering" hypothesis posits that in long-lived species, adult survival is expected to be buffered against environmental changes (environmental canalization sensu Gaillard & Yoccoz [2003]) and reproduction is expected to be more variable with stronger functional relationships with climate. The opposite patterns are expected in short-lived species (see Hilde *et al.* [2020] for a review). Therefore, demographic rates of species with contrasting life histories are expected to be differently influenced by climate, influencing in turn the sensitivity of the population growth rate to climate, the variance in annual population growth rates and the climate-driven change in population. As a result, time of emergence in populations is expected to vary among species, but the pattern of such variations are difficult to predict conceptually. Indeed, in next section, we show that the magnitude of the demographic response to climate (i.e. $\frac{\partial \theta_i}{\partial C}$) increase both the variance and the climate-driven trend of the population, with effect size that vary with the mean state of climate (see Supplementary Appendix 1 and Fig. 1), hence unknown resulting impact on ToE_{pop}.

3.3 Population variability in a stationary environment

In this section,, we show how the variance in annual population growth rates depends on the variance in climate, σ^2, and the functional relationship between the mean climate $\overline{C}$ and demographic rates, assuming a stationary environment (i.e., one in which the mean $\overline{C}$ and variance σ^2 do not vary over time). For a structured population model of the form $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$ (see section 4, Fig. 1) in a stationary environment characterized by small variations, the environmental variance of the population growth rate λ_t (such that

13

$N_{t+1} = \lambda_t N_t$) can be approximated (first degree Taylor approximation) by [see Engen *et al.*, 1998, 2005]:

$$\text{var}(\lambda_t) = \sum_{i,j} \frac{\partial \lambda}{\partial \theta_i}\bigg|_{\theta_i=\bar{\theta}_i} \frac{\partial \lambda}{\partial \theta_j}\bigg|_{\theta_j=\bar{\theta}_j} \text{Cov}(\theta_i, \theta_j) \tag{1}$$

with $\bar{\theta}$, the vector of mean demographic parameters including fertility, survival of juveniles and adult and maturation rates (Table 1).

This variance is important as it influences the long-term stochastic growth rate of the population:

$$\log \lambda_s = \lim_{T \to \infty} \frac{1}{T} \log \|\mathbf{A}_{T-1} \cdots \mathbf{A}_0 n(0)\|. \tag{2}$$

Let us assume that the environment affects only one demographic rate, θ_i (the other rates θ_j remain constant over time), then Eq 1 simplifies as:

$$\text{var}(\lambda_t) = \left(\frac{\partial \lambda}{\partial \theta_i}\bigg|_{\theta_i=\bar{\theta}_i} \right)^2 \text{var}(\theta_{it}). \tag{3}$$

The demographic rate θ_i is a function of a climatic variable C_t. θ_i is also affected by other unknown variables generating environmental stochasticity ϵ, such as observation and process errors. ϵ is a stochastic environmental noise of mean 0, and variance $\text{var}(\epsilon_t)$ and is considered as an additional variability independent from C. For example, let's assume that θ_i is an inverse logit function of a linear function of C:

$$\theta_{it} = \theta_i(C_t, \epsilon_t) = g(y = \beta_0 C_t + \beta_1 + \epsilon_t), \tag{4}$$

where β_0 and β_1 are the constant regression coefficient of the functional relationship between climate and the demographic rate (Fig. 1); g is the inverse logit link function so that $\theta_i \in [0\ 1]$. Applying the second order Taylor expansion, the variance of the demographic rate θ_i is:

$$\text{var}(\theta_{it}) \approx (g'(\bar{y}))^2 \text{var}(y) = \left(\frac{\partial \theta_i}{\partial C}\bigg|_{C=\bar{C}} \right)^2 (\beta_0^2 \sigma^2 + \text{var}(\epsilon_t)^2) \tag{5}$$

14

with σ^2 the variance of the climatic variable C and

$$\frac{\partial \theta_i}{\partial C_{C=\overline{C}}} = y' \frac{\exp(-y)}{(1+\exp(-y))^2} = \beta_0 \frac{\exp(-\beta_0\overline{C} - \beta)}{(1+\exp(-\beta_0\overline{C} - \beta_1))^2} \tag{6}$$

.

Hence Eq 3 can be simplified as:

$$\text{var}(\lambda_t) = \left(\frac{\partial \lambda}{\partial \theta_i}_{\theta_i=\overline{\theta_i}}\right)^2 \left(\frac{\partial \theta_i}{\partial C}_{|C=\overline{C}}\right)^2 (\beta_0^2\sigma^2 + \text{var}(\epsilon_t)^2). \tag{7}$$

Applying the derivative chain rule and assuming $\epsilon = 0$, i.e., that the demographic rate θ_i is a deterministic function of climate, like in our simulations, we obtain:

$$\text{var}(\lambda_t) = \beta_0^2\sigma^2 \left(\frac{\partial \lambda}{\partial C}_{|C=\overline{C}}\right)^2 \tag{8}$$

Hence the year-specific stochastic variation depends on climate internal variability σ^2, the stochastic environmental variability, as well as the sensitivity of the population growth rate to the demographic rate and the sensitivity of the demographic rate to climate in a stationary environment that both define the overall the sensitivity of the population growth rate to climate.

In a non-stationary environment (Fig. 1), $\overline{C}$ is changing, and var(λ) varies, in general, non-linearly with $\overline{C}$ depending on the sensitivity of the population growth rate to climate $\left(\frac{\partial \lambda}{\partial C}\right)$ (see Supplementary Appendix 2 and Fig. 1), this latter also influences the population trend. Hence, it is difficult to posit *a priori* how ToE$_\text{pop}$ will vary with the signal and noise in climate across life histories and demographic processes for various functional relationship between climate and demographic rates. In section 4 we use a simulation framework to answer our five questions posed in the introduction, and discuss six testable hypotheses in section 6.

15

4 Time of emergence in populations

4.1 Population projections

To project the population dynamics of species with four contrasting life histories along the slow-fast gradient (Table 2), we use a simple two-stage climate-dependent population matrix model that permits to explore some of the diversity of life cycles (Caswell [2001]; Neubert & Caswell [2000], Fig. 1). The model distinguishes non-reproducing juveniles and reproducing adults (see life cycle on Fig. 1). The population is projected from year t to year $t+1$ by:

$$\mathbf{n_{t+1}} = \mathbf{A}(\theta[(\mathbf{C_t})])\mathbf{n_t} \tag{9}$$

with $\mathbf{n_t}$ the population vector made of the abundances of juveniles and adults and $\mathbf{A}$ the population transition matrix including demographic rates $\theta[(\mathbf{C_t})]$ that are defined by specific functional relationship with climate C (Figs. 1, S 1). The demographic rates are the survival of juveniles S_j and adults S_a, the development rate of juveniles into adults γ (maturation rate), and the fertility of adults F.

$$\mathbf{A} = \begin{bmatrix} S_j(1-\gamma) & F \\ S_j\gamma & S_a \end{bmatrix} \tag{10}$$

This model permits the simulation of population dynamics of species with four contrasting life histories with increasing generation time (the mean age of mothers at child birth), which is a reliable metric to rank species along the continuum of life history variation [Gaillard *et al.*, 2005]). Species differ in terms of reproductive strategy (semelparous vs. iteroparous), age at first reproduction (precocial vs. delayed) [Neubert & Caswell, 2000] and lifespan (short vs. long) and thus range along the slow-fast continuum of life history variation [Gaillard *et al.*, 2016] from fast species with short generation time, high reproductive output and short lifespan (species 1) to slow species with opposite characteristics (species 4) (Table 2). For example, species 1 represents organisms with rapid

16

life cycle development, only one reproductive event in their lifetime and high fecundity ($b \sim 168$) (Table 2), such as many annual plants and insects. Species 2 are short-lived iteroparous species producing 7-8 offspring per unit time per female such as small mammals and birds. At the other end of the spectrum, species 4 are long-lived species with delayed first reproduction, low reproductive output per breeding event and long lifespan such as primates, whales, or albatross. While these species do not capture the full diversity of life history, especially for plants that exhibit a vast amount of life-history variations, they provide a reasonable sample of characteristic traits across a representative range. Indeed, Salguero-Gómez *et al.* [2016] showed that the first axis of life-history variations of 418 plant species worldwide representing the slow-fast continuum explains 34% of the variation in plant life-history strategies, while it explains even a higher percentage of variations (60–80%) among mammals [Oli, 2004], birds [Sæther, 1987], and reptiles [Bauwens & Diaz-Uriarte, 1997].

We include the effects of climate acting on only one demographic parameter at a time θ_i and assume that the inter-annual variability in population growth rates is induced by climate only (i.e. $\epsilon = 0$ in eq.7). In each case, the functional relationship between demographic rates and climate $\theta_i(C)$ is either linear, sigmoid or a bell shaped curve functions (Fig. 1, Fig. S 1) and is defined by the equation 4 with $\epsilon = 0$ and $\beta_1 = \overline{\theta_{ih}}$ the mean demographic parameter in the historical unperturbed environment that leads to a stable population with $\overline{C} = 0$ (Table 1). Specifically, relationships can be linear functions on the real scale, with

$$\theta_i(C_t) = \beta_0 C_t + \overline{\theta_{ih}} \tag{11}$$

and results are shown only on supplementary figure S 4 for all demographic rates. Relationships can be sigmoid functions, with

$$\theta_i(C_t) == g(y = \beta_0 C_t + \overline{\theta_{ih}}) \tag{12}$$

347 and g the inverse logit link function. Relationships can be bell shaped curves functions
348 with quadratic functional relationship between demographic rate and climate:

$$\theta_i(C_t) == g(y = \beta_0 C_t^2 + \overline{\theta_{ih}}) \tag{13}$$

349 For most demographic rates, g is the inverse logit link function so that $\theta_i \in [0\ 1]$, but not
350 for fertilities of species 1 to 3 that vary on the real scale.

351   To characterize a reasonable range of demographic rates and lifetime outcomes in the
352 set of projected environmental conditions, β_0 vary in a specific range that depends on
353 the functional relationship. For linear functional relationships between climate and de-
354 mographic parameters (equation 11), the slope varies as: $\beta_0 \in [-0.03\ 0.03]$ (Fig. S 4).
355 For sigmoid functional relationships the slope varies as: $\beta_0 \in [-0.15\ 0.15]$ (Fig. 3a). For
356 bell-shaped functional relationships the slope vary as: $\beta_0 \in [-0.025\ -0.01]$ (Fig. 3b).

357   We calculate the time of emergence of population using the threshold methods fol-
358 lowing the same methodology as for climate (section 2). We assume that the historical
359 population is stable in an unperturbed stationary environment with $\overline{C} = 0$ and variance
360 σ^2; i.e. the stochastic long-run growth rate is null: $\ln(\lambda_s) = 0$ (calculated from equation 2).
361 $\ln(\lambda_s)$ depends on variance in annual population growth rates var(λ) [Lande *et al.*, 2003;
362 Tuljapurkar & Orzack, 1980] that is driven by the natural climate variability σ^2 (section
363 3). Climate fluctuations that increase the variance of demographic rates usually decrease
364 the stochastic long-run growth rate of populations [Engen *et al.*, 2005; Lande *et al.*, 2003;
365 Tuljapurkar, 1982]. Hence, to set $\ln(\lambda_s) = 0$ across environmental historical conditions, the
366 vector of demographic parameters θ is slightly tuned for each environmental variability
367 σ.

4.2   Time of emergence in population depends on climate variability and trend

369   We found that ToE_{pop} can be predicted by the climate signal-to-noise ratio and occurs
370 earlier as the signal-to-noise in climate becomes larger (Fig. 3). Indeed, the ToE_{pop} is

18

linearly and positively correlated to the $ToE_{climate}$ (Fig. 3) as both the variability and trend in population are positively related to the natural variability and trend of climate (Fig. 4).

Remarkably, the ToE_{pop} can be earlier or later than the $ToE_{climate}$, depending on the life history strategies and the demographic processes by which climate affects demographic rates (Fig. 3). For example, the ToE_{pop} is earlier than $ToE_{climate}$ for iteroparous species for which climate affects maturation or adult survival rates for long-lived species (species 3 & 4) or juvenile survival for short-lived species (species 2). Hence, some life histories may permit an earlier detection of the time at which the signal of anthropogenic climate change emerges from the noise of natural climate variability

4.3 Time of emergence in population across life histories and demographic processes

The ToE_{pop} can be predicted by life histories and demographic processes (Fig. 3, Fig. 5). Across life histories, the ToE_{pop} is the largest for species 1 (semelparous short-lived strategy), which have on average the largest population variations (Table 2, Fig. 5). Across demographic processes, the ToE_{pop} is the longest for the fertility (Table 2). For iteroparous species, the ToE_{pop} depends on the sensitivity of the population growth rate to the demographic rate affected by climate and occurs earlier as the sensitivity increases (Fig. 5). As a consequence, the ToE_{pop} occurs later as species longevity increases when climate affects fertility and juvenile survival. However, the opposite pattern occurs when climate affects adult survival and maturation rate: ToE_{pop} occurs earlier for long-lived than short lived species (Fig. 3, Table 2).

4.4 Time of emergence in population among different functional relationships between climate and demographic rates

Surprisingly, the type of functional relationship between climate an demographic rates and its slope have little effect on the ToE_{pop} (Fig. 3, Fig. 6). While the variability of the population in the historical environment is smaller for bell shape versus linear relationships (see eq 9 section 3), both the trend and variability are larger for bell shape relationship in the non-stationary forced environment (Table 3). Indeed, the variability in the forced

19

environment increases substantially compared to the variability in the historical environment for bell shape, while it does not change for linear relationships (Table 3). However, the ratio of the trend to the magnitude of variability is very similar between bell shape and linear relationship, and the patterns of time of emergence are thus very similar regardless of the shape of the functional relationship. The slope of those relationships has also little impact of the ToE_{pop} relative to life histories and demographic processes, probably because it affects both the trend and variability simultaneously (Fig. 1).

5 Time of emergence of emperor penguin population

The emperor penguin is a relevant example to test our theoretical predictions, specifically that long lived species (comparable to species 4) may permit an earlier detection of anthropogenic climate change influences in population growth rates (Fig. 3, section 4.2). Penguins are threatened by future climate change as they rely on sea ice for breeding substrate and warming is driving reductions in sea ice cover [Jenouvrier *et al.*, 2020, 2014, 2021]. Adult survival is strongly affected by sea ice during four seasons of the life cycle resulting in complex, non-linear bell shape relationships [Jenouvrier *et al.*, 2012]. Adult survival is maximized at intermediate levels of sea ice because neither the complete absence of sea ice (low food resources and/or high predation), nor heavy and persistent sea ice (longer foraging trips), provide satisfactory conditions. Thus, in contrast to our theoretical examples, relationships between climate and demographic rates are even more complex for the emperor penguin. Indeed, sea ice affects a multitude of demographic rates during various seasons, with different functional responses among sexes. Furthermore, other processes contribute to the variability in population growth rate (i.e. $\epsilon >> 0$ in eq.7, related to sampling variance and process variance due to unmeasured environmenal conditions such as local fast ice dynamics or large-scale atmospheric perturbations, see Trathan *et al.* [2020] for a review).

5.1 Emperor penguin life cycle

The life cycle of emperor penguins includes 5 stages according to breeding status and sex (Fig. 7): male and female pre-breeders (birds that have yet to breed for the first time), breeding pairs, and male and female non-breeders (birds that have bred before but do not do so in the current year). The demographic rates describing the transitions between these stages from year t to $t + 1$ includes: the probability that an individual of a given stage returns to the breeding site, the probability of mating as a function of the availability of potential mates, the probability of breeding success (raising an offspring given that the female lays an egg), the primary sex ratio (fixed at 0.5), the survival of offspring during the first year at sea, and the annual survival of pre-breeders, non-breeders and male and female breeders.

The functional relationships between demographic parameters and sea ice concentration anomalies depend on four seasons (described in detail in Jenouvrier *et al.* [2012]):

1. The non-breeding season from January to March,

2. The arrival, copulation and laying period (April–May), hereafter called the laying period,

3. The incubation period (June–July),

4. The rearing period (August–December).

Relationships are sigmoid functions, with linear ($\beta_2 = 0$) or quadratic functional relationship between demographic rate and sea ice **x** on the logit scale:

$$\theta_i(\mathbf{x}(t)) == g(y = \beta_0 + \beta_1 \mathbf{x}(t) + \beta_2 \mathbf{x}(t)^2 + \epsilon_t) \tag{14}$$

including the parameter estimates β_k and the environmental stochasticity ϵ generated by other unknown variables. ϵ is a stochastic environmental noise of mean 0, and variance

21

445 **var**(ϵ_t) and is considered as an additional variability independent from sea ice. g is the
446 inverse logit link function so that $\theta_i \in [0, \ 1]$.

5.2 Emissions scenario, climate model and climate outputs

448   The climate outputs from multiple AOGCMs (Atmosphere Ocean General Circulation
449 Model) are publicly available in a standardized format on the Coupled Model Intercom-
450 parison Project (CMIP) website. CMIP5 provides a framework for coordinated climate
451 change experiments for assessment in the IPCC Fifth Assessment Report (AR5) in 2014
452 using four Representative Concentration Pathways (RCP) describing future GHG con-
453 centration trajectories based on socio-economic assumptions. Newer emissions forcing
454 scenarios have been developed and used for climate projections in CMIP6 for the Sixth
455 Assessment Report (AR6) released in August 2021. These "Shared Socioeconomic Path-
456 ways" [O'Neill *et al.*, 2016](SSPs) differ in the time evolution of specific climate forcers,
457 such as GHG and aerosol emissions, but bracket the same range in energy flux varia-
458 tions in the atmosphere caused by anthropogenic factors of climate change (i.e., radiative
459 forcing range) as the RCP scenarios.

460   There are several sources of uncertainties in climate projections that affect the time
461 of emergence, including the structural uncertainty associated with the different climate
462 models used to make projections, and the scenario uncertainty associated with different
463 future emission pathways [Deser *et al.*, 2012; Hawkins & Sutton, 2009; Schlunegger *et al.*,
464 2020]. However, here we use one climate model and one scenario to obtain the sea ice
465 outputs from a large ensemble [Kay *et al.*, 2015] for illustrative purposes, as large ensem-
466 ble simulations using several scenarios from several climate models were not available at
467 the time of our analysis.

468   Specifically, we used RCP 8.5 high emission scenario [Meinshausen *et al.*, 2011], that
469 represents a future in which greenhouse gas emissions continue unabated. RCP 8.5 is con-
470 sidered as a useful scenario for quantifying physical climate risk, especially over near- to
471 midterm policy-relevant time horizons [Schwalm *et al.*, 2020]. Indeed, the total cumula-

22

tive CO_2 emissions since 2005 projected under RCP8.5 by 2020 are in close agreement with historical observed total cumulative CO_2 emissions [Schwalm *et al.*, 2020]. In addition, the total cumulative CO_2 emissions since 2005 projected under RCP8.5 by 2050 agree well with energy forecasts under current and stated policies by 2050, with still highly plausible levels of CO_2 emissions by 2100 [Schwalm *et al.*, 2020].

We use sea ice outputs from a large ensemble produced by the Community Earth System Model (CESM), development of which is coordinated by the National Center for Atmospheric Research (NCAR), allowing us to characterize the natural climate variability [Kay *et al.*, 2015]. In addition, the CESM model resolves very well the Antarctic sea ice conditions that influence the most emperor penguin population growth rates [Jenouvrier *et al.*, 2020].

5.3 Sea ice and penguin projections

We calculate ToE$_{pop}$ for the 54 known colonies around the coast of Antarctica ([Fretwell *et al.*, 2012; Fretwell & Trathan, 2009], Fig. S 7) following the approach outlined in section 2 based on projections of population growth rates driven by sea ice changes. Specifically, to project emperor penguin population growth rate at each colony, we link a climate-dependent demographic matrix model to sea ice projections (section 5.2). Our sea ice-dependent demographic model includes demographic rates that depend on the sea ice conditions during four seasons (non-breeding, laying, incubating and rearing, section 5.1), and accounts for differences in the impact of sea ice conditions on adult survival between sexes (see Supporting information S3 for more details). These relationships and their estimations are described in detail in Jenouvrier *et al.* [2012]. The model includes sources of stochasticity and uncertainties: (1) parameter uncertainty describes statistical uncertainty in the estimates of demographic parameters (e.g., survival, and their responses to sea ice concentration anomalies) and (2) process variance (i.e., environmental stochasticity) reflects true "unexplained" temporal variance in demographic rates that is not accounted for by sea ice, which combined reflect the term var(ϵ) in eq.7, section 3. As

we ignored these context specific uncertainties in our theoretical simulation, we present the results with two scenario: with or without var(ϵ).

For our historical environment we used sea ice projections from 1920-1950, and for the forced environment we used sea ice projections from 1950-2100 under climate scenario RCP 8.5 (section 5.2). We assume that the population is stable in the historical, unperturbed environment and our emergence threshold are based on the 95% prediction interval. This permit us to characterize when anthropogenic signals in emperor penguin populations are *very likely* to emerge from stochastic noise.

5.4 Time of emergence in sea ice and penguin

The $\text{ToE}_{\text{climate}}$ in sea ice varies among seasons and colonies (Fig. 8, Fig. S 5) and as a consequence, the ToE_{pop} varies among colonies. The ToE in sea ice and populations are earlier for colonies in East Antarctica, than in the Ross, Bellingshausen, Amundsen and Weddell Seas (Fig. S 7). The variability and trend are negatively related (Fig. S 6), so regions showing a larger signal also exhibit larger variability in climate and population as sea ice loss are projected into the future. When the environmental stochasticity generated by other factors than sea ice (var(ϵ)) is ignored, the ToE_{pop} occurs earlier than climate for most colonies, except the ones located from Enderby Land to Terre Adelie Land in East Antarctica for which the ToE in sea ice is the earliest. When parameter uncertainty and process variance are included, the ToE_{pop} occurs later than $\text{ToE}_{\text{climate}}$ for almost all colonies, except the few colonies in the Bellingshausen and Amundsen Seas for sea ice during the rearing season.

6 Discussion

Anthropogenic climate change has triggered impacts on ecosystems world-wide, yet the timing at which these biological impacts can be formal detected has been insufficiently described [Beaumont *et al.*, 2011]. Here we focused on detecting climate-driven signals in population, but this approach can be applied to climate-related impacts on changes in

24

distribution by accounting for the temporal dynamics in those spatial changes. Heretofore, changes in distribution are often assumed to depend only on the climate signal and analyses using, for example, species distribution models often ignore climate variability (but see Zimmermann *et al.* [2009]).

We found that the time of emergence of climate-driven signals in population dynamics ToE_{pop} depends on (1) the magnitude of climate change and variability and (2) life-histories and demographic processes by which climate affects the population and we propose six testable predictions. In the context of detection and attribution of climate change, we find that some life histories magnify signal-to-noise ratios in climate ($ToE_{climate}$), enabling observations of populations to yield earlier detection of anthropogenic climate change than observations of a climate variable itself— while other demographic dynamics prolong the detection of anthropogenic climate change relative to $ToE_{climate}$.

In our emperor penguin example, density dependent processes occur because of sex-biased mortality in response to sea ice, which displays spatiotemporal autocorrelation, affecting reproduction and survival. These dynamics result in complex co-variations among demographic rates, and the life cycle is structured in several stages. Our main theoretical result – some life histories enable an earlier ToE_{pop} than $ToE_{climate}$– is well supported by our example when the noise is driven by climate natural variability and all complexities arising in natural systems discussed in the following sections are included.

However, when stochastic variations from observation error and other biotic and abiotic processes other than sea ice natural variability are included, the ToE_{pop} occurs later than $ToE_{climate}$ for almost all colonies. However, sampling and process errors can be reduced by increasing monitoring effort and improving our understanding of how the biological systems respond to biotic and abiotic factors. Furthermore, aggregating abundance across space attenuates the random component of the underlying growth rates and may permit a better detection of anthropogenic signals in populations [Che-Castaldo *et al.*, 2017].

25

Regardless of whether the stochastic noise associated with other sources than natural variability in climate occludes an earlier ToE_{pop} than $ToE_{climate}$, the time of emergence identifies when the signal of anthropogenic climate change in populations can be quantitatively distinguished from year-specific stochastic variation. Quantifying ToE_{pop} is critically needed to provide relevant cost/benefit evaluations for climate mitigation and adaptation strategies, as well as accurate assessments of the risks climate change poses to conservation and management of ecosystems [Hawkins *et al.*, 2020; Hawkins & Sutton, 2012]. In this context, we propose a road map for future research.

6.1 ToE_{pop} **is predicted from** $ToE_{climate}$

We find that the ToE_{pop} depends almost linearly on the $ToE_{climate}$ (Fig. 3). Hence, we suggest the following hypotheses.

[H1] Tropical species may permit an earlier detection of anthropogenic climate change than temperate species, especially if temperature in summer affects their demographic rates. Many climate studies have shown that the ToE in temperature is earlier for low latitude regions than for mid-latitude regions and is of intermediate duration for polar regions [Hawkins *et al.*, 2020; Hawkins & Sutton, 2012; Mahlstein *et al.*, 2012, 2011]. The emergence of signal of anthropogenic climate warming occurs the soonest in the summer season at low latitudes [Mahlstein *et al.*, 2011]. The studies of Beaumont *et al.* [2011] and Sorte *et al.* [2019] support this hypothesis: tropical and subtropical ecosystems, and mangroves, face extreme conditions earliest than boreal forests and tundra biomes because the low SD compensate for the relatively small absolute changes [Beaumont *et al.*, 2011]. Passerine bird species that migrate between temperate breeding grounds in North America and southern tropical wintering grounds experience an earlier $ToE_{climate}$ than species wintering in the subtropics [Sorte *et al.*, 2019]. $ToE_{climate}$ exceeding 2300 occurred only in the northern latitudes corresponding to the southern non-breeding grounds of some birds [Sorte *et al.*, 2019]. Studies on the thermal tolerance of terrestrial ectotherms also support this hypothesis. For example, tropical insects are relatively sensitive to temperature change and are

26

currently living very close to their optimal temperature, while species at higher latitudes have broader thermal tolerance and are living in climates that are currently cooler than their physiological optima [Deutsch *et al.*, 2008].

[H2] In terrestrial systems, species affected by temperature may yield earlier detection of anthropogenic climate change than species affected by precipitation. Climate studies have shown that changes in precipitation are often harder to detect because natural variability in precipitation is larger than in temperature [Giorgi & Bi, 2009]. For example, the $ToE_{climate}$ in precipitation extremes does not occur prior to 2100 in many regions [King *et al.*, 2015]. However, an anthropogenic signal is emerging soon in wintertime heavy precipitation events over much of Eurasia and North America, so species in these regions may experience earlier ToE_{pop}. However, this hypothesis depends also on the sensitivity of the population growth rate to temperature versus precipitation. In a comparative study of time series of 165 plants populations around the globe, Compagnoni *et al.* [2021] found that demographic responses to climate are larger for precipitation than temperature, but large noise hampers the detection of the impact of precipitation on plant populations.

[H3] In marine systems, species dependent on the upper ocean biological cycling of carbon, photosynthetic activity, or salinity may yield later detection of anthropogenic climate change than species affected by sea surface temperature or pH. Several studies found that variables integrating the effect of invading anthropogenic carbon into the global ocean (e.g. pH) and sea surface temperature emerged most rapidly while variables related to the upper ocean mixing, associated changes in biological processes (e.g. export of organic matter, primary productivity) and salinity, only emerge after several decades [Henson *et al.*, 2017; Schlunegger *et al.*, 2020].

6.2   ToE in population is predicted from life histories and demographic processes

The ToE_{pop} can be also predicted by life histories and demographic processes that will interact with our previous three hypotheses based on the relationships between ToE_{pop} and $ToE_{climate}$.

[H4] ToE$_{pop}$ *occurs later in selmeparous species.* Semelparous species, such as salmon, bamboos, and monocarpic herbs, exhibit a "big-bang reproduction" whereby individuals die immediately after the first reproduction [e.g. Metcalf *et al.*, 2003]. As a consequence, their population dynamics is often more variable than population of iteroparous species. Indeed, the various reproductive events of iteroparous species may be spread out throughout their life as a bet-hedging strategy in unpredictable environments, buffering the effect of environmental variability on population growth rate [Hilde *et al.*, 2020]. However, there is little theory available to predict how the degree of iteroparity might influence the demographic response to climate. A comparative study found no correlation between the degree of iteroparity with population responses to climate in plants [Compagnoni *et al.*, 2021]. Further work should entail a direct comparison of the influence of the generation time and degree of iteroparity on ToE$_{pop}$.

[H5] The ToE$_{pop}$ *of iteropareous species depends on the sensitivity of the population growth rate to the demographic parameter affected by climate* (Fig. 5). For population dynamics that are mainly affected by the impact of climate on adult survival during the non-breeding season ('tub' hypothesis, Sæther *et al.* [2004]), the ToE$_{pop}$ will occurs earlier in long lived species than short lived species. This might be the case for many migratory species, when the climate conditions affects survival during the migration, and in the non breeding quarters [Sorte *et al.*, 2019]. The 'tap' hypothesis [Sæther *et al.*, 2004] proposes that environmental conditions during the breeding season affect population size the following year because it influences the inflow of new recruits into the population. The ToE$_{pop}$ in population occurs earlier if climate conditions during the breeding season have carry-over effect on demographic rates influencing the number of recruits, as observed in many species [e.g. Szostek & Becker, 2015]. Specifically, this will occur when climate affects juvenile survival for short lived species and maturation rate for long lived species. Obviously, the underlying processes of the 'tub- tap' effects are not mutually exclusive, and multiple demographic rates are affected by climate, that will eventually shorten or pro-

28

long the ToE_{pop}.

[H6] Iteropareous species can act as earlier indicators of the detection of anthropogenic climate change than climate itself. Earlier ToE_{pop} than $\text{ToE}_{\text{climate}}$ occurs when climate affects the demographic rates that most influence the population growth rate: adult survival and maturity for long-lived iteroparous species and juvenile survival for short-lived ones (Fig. 3, Fig. 5). This hypothesis is supported by our empirical example: the population growth rate is mostly sensitive to the adult survival [Jenouvrier *et al.*, 2010], which is affected by sea ice conditions [Jenouvrier *et al.*, 2012]. Here, we found that the ToE_{pop} occurs earlier than $\text{ToE}_{\text{climate}}$ when process variance due to other environmental factors and demographic parameter uncertainties is ignored (Fig. 8a). In natural system, the process variance may be large, obscuring an earlier detection of anthropogenic climate change in populations than in climate variables itself (Fig. 8b, Sæther *et al.* [2007, 2004]). However, if the goal is to use earlier indicator species in the detection of anthropogenic climate change, it is possible to reduce the demographic parameter uncertainties with higher sampling effort and decrease the process variance by a better understanding of the factors affecting the demographic processes.

6.3 Road map for the future

We provide the first theoretical study of the ToE_{pop} to understand the proximate mechanisms of the impact of climate change and variability and demographic processes using a simple model. We illustrate how to use a climate explicit population model to quantify ToE_{pop} for emperor penguin, and argue that climate-dependent demographic models could be developed for several species allowing future comparative analysis. But many questions remained unanswered about the effect of more complex climate-driven demographic processes occurring in natural systems such as density dependence, autocorrelation in climate, co-variation among demographic rates, population structure, and multiple climate drivers, to name a few. We propose a road map for future research, and acknowledge that we only scratched the surface on these important topics.

29

6.3.1 Comparative studies of the ToE in population using climate explicit population models

Characterizing the time of emergence requires long-term time series to define the historical unperturbed state. For many species, the unperturbed state benchmark is not available as most long-term ecological times series cover only recent decades while profound global changes were already underway. It is challenging to characterize ToE from observations in natural systems using statistical approaches, even in climate sciences. Hence, most the climate studies have used climate outputs from atmospheric–oceanic global circulation models (AOGCMs) to quantify the $\text{ToE}_{\text{climate}}$ [Hawkins *et al.*, 2020; Hawkins & Sutton, 2012]. Similarly, we propose to develop climate explicit population models to characterize the ToE in population. We have illustrated our approach using a simple structured population matrix model [Caswell, 2001], but other demographic, trait-based or eco-evolutionary modeling frameworks can be developed.

We argue that the ToE_{pop} can be quantified for many species already [Doak & Morris, 2010; Saether *et al.*, 2019; Treurnicht *et al.*, 2016] allowing comparative studies to address our specific hypotheses on the variations of ToE_{pop} across regions, ecosystems drivers, and species life histories. In recent decades, there is an increase in the number of studies measuring the effect of climate accounting for multiple seasonal and carry-over effects of climate on the complete life cycle of a species [Cordes *et al.*, 2020; Doak & Morris, 2010; Iles & Jenouvrier, 2019; Jenouvrier, 2013; Ozgul *et al.*, 2010]. Although fewer studies have developed climate-dependent population model, the information is available in the literature to integrate the statistical relationships between climate and demographic rates into population models. The last step requires an interdisciplinary approach to use climate-dependent population models with projections of historical and future climate from AOGCMs [Iles & Jenouvrier, 2019; Jenouvrier, 2013]. AOGCMs project (often nonlinear) changes in climate over time, and critically, provide quantitative estimates of natural climate variability [Kay *et al.*, 2015]. We hope that ecologists will take advantage of

30

the free availability of climate outputs in both the pre-industrial, historical and future environment supervised by the Coupled Model Intercomparison Project (section 5.2). The most recently completed phase of the project (CMIP6) includes more climate models and output variables than previous phases, and importantly, includes several large ensemble runs of the same AOGCMs and experiment to account for natural variability in climate models [Deser *et al.*, 2020].

Finally, the key to quantifying ToE_{pop} is to characterize the population variability in the historical stationary environment. This requires careful consideration of the demographic stochasticity, especially for small populations, environmental stochasticity not driven by climate, density dependence and interactions with other species, which can be incorporated in demographic models [Lande *et al.*, 2003]. Other important environmental drivers of population dynamics such as habitat quality and resource variability can be incorporated into demographic models to reduce the process variance in the historical environment, enabling an earlier detection of the impact of climate change on populations. This is particularly important as habitat loss and resources exploitation (land-use change, fisheries and deforestation) are key threatening processes driving the global loss in biodiversity that have synergistic effects with climate change [Dobson *et al.*, 2021; Lemmer *et al.*, 2021; Mantyka-pringle *et al.*, 2012]. If the combined effects of those threats and climate change are greater than the effects of each threat individually, the climate driven trend in population maybe larger than the climate driven trend without interaction with other threats, with potentially earlier detection of anthropogenic forced change in populations. On the other hand, if those threats augment noise in the system, that may reduce the signal to noise ratio and delay the detection of anthropogenic climate change relative to $ToE_{climate}$. For example, the effects of fragmentation and loss of important habitat types will reduce population size and increase the impact of demographic stochasticity on the population dynamics [Hanski & Gaggiotti, 2004; Lande, 1998], which reduces the power of detecting any signal of climate variation. In addition, environmentally induced fluctu-

ations in population size can be magnified by harvesting (harvest–interaction hypothesis) that may also prolong the ToE_{pop} [Gamelon *et al.*, 2019].

6.3.2 Density Dependence

Our population model does not include density dependence. The impact on the ToE_{pop} will depend on the strength and type of the density dependence (negative density dependence: exact compensation, over-compensation, under-compensation, positive density dependence), the specific demographic rate that is affected by density dependence, the interaction between climate and density dependence and the life history of the species. For example, populations with undercompensating growth tend to respond slowly to environmental changes [Gamelon *et al.*, 2017; Hansen *et al.*, 2019], that may prolong the ToE_{pop}. For population declining in response to climate change the results should be qualitatively similar, except if Allee effects occur (a positive relationship between demographic rates and population), thereby accelerating extinction rate at low density [Courchamp *et al.*, 2008, 1999]. The Allee effect will increase the magnitude of the decline of the population trend and ToE_{pop} will probably occurs earlier [Lande, 1998], but that will depend if an increase variance compensate for this larger signal. For population increasing in response to climate change, the patterns found without density dependence are more likely to change, that will depend on the emergence thresholds and carrying capacity of the population. For example, for invasive species, the emergence thresholds may be defined well below the carrying capacity of the population, hence the results would be qualitatively the same as without density dependence. However, if the emergence thresholds are defined above the carrying capacity, the signal of anthropogenic climate change in population cannot be formally distinguished from population variability.

6.3.3 Temporal autocorrelation in climate and demographic rates

Our simulated environment does not include autocorrelation in the climate time series, while most environmental variables exhibit a red noise that may increase the probability of extinction of populations [Mustin *et al.*, 2013; Rescan *et al.*, 2020]. Environmen-

32

tal variables in reddened environments imply consecutive periods of favourable or un-
favourable conditions (positive autocorrelation), and a lower probability of at least one
extremely poor year compared with white noise for a given time period, which may both
decrease or increase population extinction risk [Schwager *et al.*, 2006]. The response of
species to coloured environmental variations depends on the time-scale considered, the
strength of environmental fluctuations, the particular life-history traits that are affected
by environmental change and the species life cycle defining the sensitivity of popula-
tion dynamics to these fluctuations [Engen *et al.*, 2013]. For example, a study from 454
plant and animal populations found that fast life histories show highest sensitivities to
temporal autocorrelation in demographic rates across reproductive strategies, while slow
life histories are less sensitive to temporal autocorrelation, but their sensitivities increase
for species with a large degree of iteroparity [Paniw *et al.*, 2017]. An important question
is then how the sensitivities to temporal autocorrelation in demographic rates is related
to the ToE_{pop}, and can be addressed by incorporating such autocorrelation in our current
framework. Since the patterns of the sensitivities of the population growth rate to both in-
terannual variability and temporal autocorrelation in demographic rates are similar [Iles
et al., 2019; Paniw *et al.*, 2017], and the influence of autocorrelations on the population
variability driven by environmental noise is small [Engen *et al.*, 2013], we do not expect
that including temporal autocorrelation will change our six hypothesis.

6.3.4 Correlation among demographic rates

Correlations among demographic rates can occur when climate affects rates simulta-
neously, and were ignored in our simulations. Positive covariation and autocorrelation
in demographic rates tend to increase the variability in demographic rates, decreasing
the stochastic growth rate and increasing the variability in population growth rates [En-
gen *et al.*, 2013; Tuljapurkar *et al.*, 2009]. On the opposite, negative covariation and auto-
correlation tends to decrease the variability in demographic rates, such as the survival-
fecundity-trade-offs that reduces the variance in the population growth rate [Colchero

₇₆₈ *et al.*, 2019; Sæther & Engen, 2015]. Correlations of opposite signs among the various de-

₇₆₉ mographic rates may cancel out the effect of each other, and the resulting effect on the

₇₇₀ population growth rate maybe small. In addition, the life-history strategy and density

₇₇₁ dependence affect the population responses to covariation and autocorrelation in demo-

₇₇₂ graphic rates [Colchero *et al.*, 2019; Iles *et al.*, 2019] making challenging to predict how

₇₇₃ the trend and variability in population, hence the ToE_{pop}, will be affected by covariation

₇₇₄ among demographic rates. Demographic rate correlations had the largest effect on the

₇₇₅ population growth rate for life histories with short to medium generation time [Iles *et al.*,

₇₇₆ 2019], that may amplify or dampen the detection of anthropogenic climate change.

6.3.5 Population structure

₇₇₈ Our population model includes the simplest age-structure by aggregating age-classes

₇₇₉ into two stages: juvenile and adult. Although this simple life cycle is useful to explore a

₇₈₀ wide range of life histories (Table 1), it leads to a reduced variance in annual population

₇₈₁ growth rates in an unperturbed environment [Colchero *et al.*, 2019]. In our definition,

₇₈₂ the ToE_{pop} is based on the comparison of the variability between the unperturbed and

₇₈₃ perturbed environment. Hence, the resulting ToE_{pop} should not be highly sensible to

₇₈₄ the structure of the population, except if the life cycle structure buffers or amplifies the

₇₈₅ population variability response to population structure in a non-stationary environment.

₇₈₆ The life cycle of many species are much more complex than our simulated life histo-

₇₈₇ ries. For example, the life cycles of plants include cryptic life stages such as long-term

₇₈₈ seedbanks and dormant adults. The reproduction of plants is highly variable with some

₇₈₉ plants reproducing vegetatively and seed mass and per-capita seed production ranging

₇₉₀ typically across six orders of magnitude [Kattge *et al.*, 2011]. Plants exhibits also an in-

₇₉₁ credible range of longevity, from weeks to millennia [Peñuelas & Munné-Bosch, 2010].

₇₉₂ For example, an alpine carex, *Carex curvula* is a very slow-growing rhizomatous sedge

₇₉₃ can have a lifspan of 2000 years [Steinger *et al.*, 1996]. The range of temperature vari-

₇₉₄ ations that this alpine flora can sustain (i.e. breath of thermal niche) is exceeding the

34

worst climate warming scenarios [Körner & Hiltbrunner, 2021], suggesting that the time of emergence would be prolonged for those species. Those complex life-history traits are not exclusive to the plant kingdom, and further work focusing on how age, stage and trait structure affect the dynamics of populations and potentially dampen or amplify the climate-driven variability in population (e.g. cohort resonance, Bjørnstad *et al.* [2004]), will provide fundamental insights to theoretical and applied research of the detection of anthropogenic climate change. For example, Bjørnstad *et al.* [2004] showed that spectral frequencies of the catches of cod in the Skagerrak were not the dominant frequencies of key environmental drivers, rather there was a spectral shift with a frequency peak at cod generational time scales, the so-called cohort resonance. Population dynamics may also potentially retain a memory of prior forcing, especially when climate events occurring in one season or stage of the life cycle affect individual performance in a subsequent season or stage (e.g. carry-over effects of climate; effect of climate at young age classes that may delay age at first recruitment [Hollowed & Sundby, 2014; Lindström & Kokko, 2002; Ranta *et al.*, 2005]; effect of climate on dormant stages [Hairston Jr, 1996]).

6.3.6 Multiple climate drivers

Our modeling framework includes only a single environmental time series. The cumulative integrations of white-noise atmospheric forcing in ecosystem drivers can generate population responses that are characterized by strong transitions and prolonged apparent state changes in marine ecosystems that will affect the ToE_{pop} [Di Lorenzo & Ohman, 2013]. In addition, integrating multiple drivers to characterize the ToE_{pop} is important, as different climate variables affect organisms at various seasons and stages of their life cycle, sometimes in opposite ways [Jenouvrier, 2013; Jenouvrier *et al.*, 2018]. In a butterfly species, warmer temperatures have a positive effect on the survival of eggs, prediapause larvae and pupae but a negative effect on the survival of overwintering larvae [Radchuk *et al.*, 2013]. Climatic conditions experienced at different stages cause complex patterns of environmental covariance among demographic rates even across generations,

which may either buffer or amplify the signal of anthropogenic climate change, emphasizing the importance of considering the complete life history of individuals when predicting and detecting the effect of climatic change on population dynamics [Herfindal *et al.*, 2015; Iles *et al.*, 2019; Jenouvrier, 2013].

7 Conclusion

In the current global biodiversity crisis, the development of tools to detect, quantify, and compare the signal of anthropogenic climate change is essential to understand, anticipate and adapt to climate change. Here, we provide a new perspective on how climate-induced changes in populations can be detected by quantifying the Time of Emergence in populations. We hope that ecologists will embrace the relevance of this concept in their attempt to understand population responses to climate change in non-stationary environments and provide a robust assessment of future climate risk to inform management and policy decisions.

Acknowledgments

8 References

Allen MR, Babiker M, Chen Y, *et al.* (2018) Summary for policymakers. In: *Global Warming of 1.5: An IPCC Special Report on the impacts of global warming of 1.5\C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. IPCC.

Barnes E, Anderson C, Ebert-Uphoff I (2018) An ai approach to determining the time of emergence of climate change. In: *Proc. 8th International Workshop on Climate Informatics: CI 2018*, pp. 19–22.

Barnhart KR, Miller CR, Overeem I, Kay JE (2016) Mapping the future expansion of arctic open water. *Nature Climate Change*, **6**, 280–285.

Barraquand F, Yoccoz NG (2013) When can environmental variability benefit population growth? counterintuitive effects of nonlinearities in vital rates. *Theoretical population biology*, **89**, 1–11.

Bauwens D, Diaz-Uriarte R (1997) Covariation of life-history traits in lacertid lizards: a comparative study. *The American Naturalist*, **149**, 91–111.

Beaumont LJ, Pitman A, Perkins S, Zimmermann NE, Yoccoz NG, Thuiller W (2011) Impacts of climate change on the world's most exceptional ecoregions. *Proceedings of the National Academy of Sciences*, **108**, 2306–2311.

Bienvenu F, Legendre S (2015) A new approach to the generation time in matrix population models. *The American Naturalist*, **185**, 834–843.

Bjørnstad ON, Nisbet RM, FROMENTIN JM (2004) Trends and cohort resonant effects in age-structured populations. *Journal of animal ecology*, **73**, 1157–1167.

Boyce M, Haridas C, Lee C, Thenceasstochasticdemographyw (2006) Demography in an

increasingly variable world. *Trends in Ecology & Evolution*, **21**, 141–148. doi:10.1016/j.tree.2005.11.018.

Callendar GS (1938) The artificial production of carbon dioxide and its influence on temperature. *Quarterly Journal of the Royal Meteorological Society*, **64**, 223–240.

Caswell H (2001) *Matrix population models*, vol. Second. Sinauer, Sunderland, Massachusetts, - pp.

Che-Castaldo C, Jenouvrier S, Youngflesh C, *et al.* (2017) Pan-antarctic analysis aggregating spatial estimates of adélie penguin abundance reveals robust dynamics despite stochastic noise. *Nature communications*, **8**, 832.

Colchero F, Jones OR, Conde DA, *et al.* (2019) The diversity of population responses to environmental change. *Ecology Letters*. doi:10.1111/ele.13195.

Compagnoni A, Levin S, Childs DZ, *et al.* (2021) Herbaceous perennial plants with short generation time have stronger responses to climate anomalies than those with longer generation time. *Nature Communications*, **12**. doi:10.1038/s41467-021-21977-9.

Cordes LS, Blumstein DT, Armitage KB, *et al.* (2020) Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proceedings of the National Academy of Sciences*, **117**, 18119–18126.

Courchamp F, Berec L, Gascoigne J (2008) *Allee effects in ecology and conservation*. Oxford University Press.

Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the allee effect. *Trends in ecology & evolution*, **14**, 405–410.

Deser C, Knutti R, Solomon S, Phillips AS (2012) Communication of the role of natural variability in future north american climate. *Nature Climate Change*, **2**, 775–779.

Deser C, Lehner F, Rodgers KB, *et al.* (2020) Insights from earth system model initial-condition large ensembles and future prospects. *Nature Climate Change*, **10**, 277–286. doi:10.1038/s41558-020-0731-2.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, **105**, 6668–6672. doi:10.1073/pnas.0709472105.

Di Lorenzo E, Ohman MD (2013) A double-integration hypothesis to explain ocean ecosystem response to climate forcing. *Proceedings of the National Academy of Sciences*, **110**, 2496–2499.

Doak DF, Morris WF (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*, **467**, 959–962.

Dobson A, Rowe Z, Berger J, Wholey P, Caro T (2021) Biodiversity loss due to more than climate change. *Science*, **374**, 699–700.

Engen S, Bakke Ø, Islam A (1998) Demographic and environmental stochasticity-concepts and definitions. *Biometrics*, pp. 840–846.

Engen S, Lande R, Sæther BE (2013) A quantitative genetic model of r-and k-selection in a fluctuating population. *The American Naturalist*, **181**, 725–736.

Engen S, Lande R, Sæther BE, Weimerskirch H (2005) Extinction in relation to demographic and environmental stochasticity in age-structured models. *Mathematical biosciences*, **195**, 210–227.

Fretwell PT, LaRue MA, Morin P, *et al.* (2012) An Emperor Penguin Population Estimate: The First Global, Synoptic Survey of a Species from Space. *PLoS ONE*, **7**, e33751.

Fretwell PT, Trathan PN (2009) Penguins from space: faecal stains reveal the location of emperor penguin colonies. *Global Ecology and Biogeography*, **18**, 543–552. doi:10.1111/j.1466-8238.2009.00467.x.

Gaillard J, Yoccoz N (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.

Gaillard JM, Lemaître JF, Berger V, *et al.* (2016) *Encyclopedia of Evolutionary Biology.*, chap. Life Histories, Axes of Variation, p. 312–323. Oxford: Academic Press.

Gaillard JM, Mark Hewison A, Klein F, Plard F, Douhard M, Davison R, Bonenfant C (2013) How does climate change influence demographic processes of widespread species? lessons from the comparative analysis of contrasted populations of roe deer. *Ecology letters*, **16**, 48–57.

Gaillard JM, Yoccoz NG, Lebreton JD, *et al.* (2005) Generation time: a reliable metric to measure life-history variation among mammalian populations. *The American Naturalist*, **166**, 119–123.

Gamelon M, Grøtan V, Nilsson AL, *et al.* (2017) Interactions between demography and environmental effects are important determinants of population dynamics. *Science Advances*, **3**, e1602298.

Gamelon M, Sandercock BK, Sæther BE (2019) Does harvesting amplify environmentally induced population fluctuations over time in marine and terrestrial species? *Journal of Applied Ecology*, **56**, 2186–2194.

Ghil M (2002) Natural climate variability. *Encyclopedia of global environmental change*, **1**, 544–549.

Giorgi F, Bi X (2009) Time of emergence (TOE) of GHG-forced precipitation change hotspots. *Geophysical Research Letters*, **36**. doi:10.1029/2009gl037593.

Hairston Jr NG (1996) Zooplankton egg banks as biotic reservoirs in changing environments. *Limnology and Oceanography*, **41**, 1087–1092.

Hansen BB, Gamelon M, Albon SD, *et al.* (2019) More frequent extreme climate events stabilize reindeer population dynamics. *Nature communications*, **10**, 1–8.

Hanski IA, Gaggiotti OE (2004) *Ecology, genetics and evolution of metapopulations*. Academic Press.

Hasselmann K (1976) Stochastic climate models part i. theory. *tellus*, **28**, 473–485.

Hawkins E, Frame D, Harrington L, Joshi M, King A, Rojas M, Sutton R (2020) Observed emergence of the climate change signal: From the familiar to the unknown. *Geophysical*

Research Letters, **47**. doi:10.1029/2019gl086259.

Hawkins E, Sutton R (2009) The potential to narrow uncertainty in regional climate predictions. *Bulletin of the American Meteorological Society*, **90**, 1095–1108.

Hawkins E, Sutton R (2012) Time of emergence of climate signals. *Geophysical Research Letters*, **39**, n/a–n/a. doi:10.1029/2011gl050087.

Henson SA, Beaulieu C, Ilyina T, *et al.* (2017) Rapid emergence of climate change in environmental drivers of marine ecosystems. *Nature Communications*, **8**. doi:10.1038/ncomms14682.

Herfindal I, van de Pol M, Nielsen JT, Sæther BE, Møller AP (2015) Climatic conditions cause complex patterns of covariation between demographic traits in a long-lived raptor. *Journal of Animal Ecology*, **84**, 702–711.

Hilde CH, Gamelon M, Sæther BE, Gaillard JM, Yoccoz NG, Pélabon C (2020) The demographic buffering hypothesis: evidence and challenges. *Trends in ecology & evolution*, **35**, 523–538.

Hollowed AB, Sundby S (2014) Change is coming to the northern oceans. *Science*, **344**, 1084–1085.

Iles D, Jenouvrier S (2019) *Projected population consequences of climate change*, pp. 147–164. Oxford University Press.

Iles DT, Rockwell RF, Koons DN (2019) Shifting vital rate correlations alter predicted population responses to increasingly variable environments. *The American Naturalist*, **193**, E57–E64. doi:10.1086/701043.

Jenouvrier S (2013) Impacts of climate change on avian populations. *Global Change Biology*, **19**, 2036–2057.

Jenouvrier S, Barbraud C, Weimerskirch H (2005) Long-term contrasted responses to climate of two antarctic seabirds species. *Ecology*, **86**, 2889–2903.

Jenouvrier S, Caswell H, Barbraud C, Weimerskirch H (2010) Mating behavior, popula-

tion growth, and the operational sex ratio: A periodic two-sex model approach. *The American naturalist*, **175**, 739–752. doi:10.1086/652436.

Jenouvrier S, Desprez M, Fay R, Barbraud C, Weimerskirch H, Delord K, Caswell H (2018) Climate change and functional traits affect population dynamics of a long-lived seabird. *Journal of Animal Ecology*, **87**, 906–920.

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. *Biological Conservation*, **212**, 63–73.

Jenouvrier S, Holland M, Iles D, *et al.* (2020) The paris agreement objectives will likely halt future declines of emperor penguins. *Global change biology*, **26**, 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 Biology*, **18**, 2756–2770. doi:10.1111/j. 1365-2486.2012.02744.x.

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. *Nature Climate Change*, **4**, 715.

Jenouvrier S, Judy CC, Wolf S, *et al.* (2021) The call of the emperor penguin: Legal responses to species threatened by climate change. *Global Change Biology*.

Kattge J, Diaz S, Lavorel S, *et al.* (2011) Try–a global database of plant traits. *Global change biology*, **17**, 2905–2935.

Kay J, Deser C, Phillips A, *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. *Bulletin of the American Meteorological Society*, **96**, 1333–1349.

King AD, Donat MG, Fischer EM, *et al.* (2015) The timing of anthropogenic emergence in simulated climate extremes. *Environmental Research Letters*, **10**, 094015.

Kooyman G, Ainley D, Ballard G, Ponganis P (2007) Effects of giant icebergs on two emperor penguin colonies in the ross sea, antarctica. *Antarctic Science*, **19**, 31–38.

Körner C, Hiltbrunner E (2021) Why is the alpine flora comparatively robust against climatic warming? *Diversity*, **13**, 383.

Lande R (1998) Anthropogenic, ecological and genetic factors in extinction and conservation. *Population Ecology*, **40**, 259–269.

Lande R, Engen S, Saether B (2003) *Stochastic Population Dynamics in Ecology and Conservation.* Oxford University Press.

Landrum L, Holland MM (2020) Extremes become routine in an emerging new arctic. *Nature Climate Change*, **10**, 1108–1115.

Lemmer J, Andrzejak M, Compagnoni A, Knight TM, Korell L (2021) Climate change and grassland management interactively influence the population dynamics of bromus erectus (poaceae). *Basic and Applied Ecology*, **56**, 226–238.

Lindström J, Kokko H (2002) Cohort effects and population dynamics. *Ecology Letters*, **5**, 338–344.

Long MC, Deutsch C, Ito T (2016) Finding forced trends in oceanic oxygen. *Global Biogeochemical Cycles*, **30**, 381–397.

Lyu K, Zhang X, Church JA, Slangen AB, Hu J (2014) Time of emergence for regional sea-level change. *Nature Climate Change*, **4**, 1006–1010.

Mahlstein I, Daniel JS, Solomon S (2013) Pace of shifts in climate regions increases with global temperature. *Nature Climate Change*, **3**, 739–743. doi:10.1038/nclimate1876.

Mahlstein I, Hegerl G, Solomon S (2012) Emerging local warming signals in observational data. *Geophysical Research Letters*, **39**, n/a–n/a. doi:10.1029/2012gl053952.

Mahlstein I, Knutti R, Solomon S, Portmann RW (2011) Early onset of significant local warming in low latitude countries. *Environmental Research Letters*, **6**, 034009.

Mann ME, Steinman BA, Brouillette DJ, Miller SK (2021) Multidecadal climate oscillations

1025 during the past millennium driven by volcanic forcing. *Science*, **371**, 1014–1019.

1026 Mantyka-pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habi-
1027 tat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change*
1028 *Biology*, **18**, 1239–1252.

1029 Mason LR, Green RE, Howard C, *et al.* (2019) Population responses of bird populations
1030 to climate change on two continents vary with species' ecological traits but not with
1031 direction of change in climate suitability. *Climatic Change*, **157**, 337–354. doi:10.1007/
1032 s10584-019-02549-9.

1033 Meinshausen M, Smith SJ, Calvin K, *et al.* (2011) The rcp greenhouse gas concentrations
1034 and their extensions from 1765 to 2300. *Climatic change*, **109**, 213–241.

1035 Metcalf JC, Rose KE, Rees M (2003) Evolutionary demography of monocarpic perennials.
1036 *Trends in Ecology & Evolution*, **18**, 471–480.

1037 Mora C, Frazier AG, Longman RJ, *et al.* (2013) The projected timing of climate departure
1038 from recent variability. *Nature*, **502**, 183–187.

1039 Morris W, Pfister C, Tuljapurkar S, *et al.* (2008) Longevity can buffer plant and animal
1040 populations against changing climate variability. *ecology*, **89**, 19–25.

1041 Mustin K, Dytham C, Benton TG, Travis JMJ (2013) Red noise increases extinction risk
1042 during rapid climate change. *Diversity and Distributions*, **19**, 815–824. doi:10.1111/ddi.
1043 12038.

1044 Neubert M, Caswell H (2000) Density-dependent vital rates and their population dynamic
1045 consequences. *J Math Biol*, **41**, 103–121.

1046 Oli MK (2004) The fast–slow continuum and mammalian life-history patterns: an empir-
1047 ical evaluation. *Basic and Applied Ecology*, **5**, 449–463.

1048 O'Neill BC, Tebaldi C, Vuuren DPv, *et al.* (2016) The scenario model intercomparison
1049 project (scenariomip) for cmip6. *Geoscientific Model Development*, **9**, 3461–3482.

1050 Ozgul A, Childs DZ, Oli MK, *et al.* (2010) Coupled dynamics of body mass and population

44

growth in response to environmental change. *Nature*, **466**, 482.

Paniw M, Ozgul A, Salguero-Gómez R (2017) Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters*, **21**, 275–286. doi:10.1111/ele.12892.

Parmesan C, Burrows MT, Duarte CM, Poloczanska ES, Richardson AJ, Schoeman DS, Singer MC (2013) Beyond climate change attribution in conservation and ecological research. *Ecology letters*, **16**, 58–71.

Peñuelas J, Munné-Bosch S (2010) Potentially immortal? *The New Phytologist*, **187**, 564–567.

Radchuk V, Turlure C, Schtickzelle N (2013) Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, **82**, 275–285.

Ranta E, Lundberg P, Kaitala V (2005) *Ecology of populations*. Cambridge University Press.

Reed PB, Bridgham SD, Pfeifer-Meister LE, *et al.* (2021) Climate warming threatens the persistence of a community of disturbance-adapted native annual plants. *Ecology*, **102**, e03464.

Rescan M, Grulois D, Ortega-Aboud E, Chevin LM (2020) Phenotypic memory drives population growth and extinction risk in a noisy environment. *Nature ecology & evolution*, **4**, 193–201.

Revelle R, Suess HE (1957) Carbon dioxide exchange between atmosphere and ocean and the question of an increase of atmospheric co2 during the past decades. *Tellus*, **9**, 18–27.

Rojas M, Lambert F, Ramirez-Villegas J, Challinor AJ (2019) Emergence of robust precipitation changes across crop production areas in the 21st century. *Proceedings of the National Academy of Sciences*, **116**, 6673–6678. doi:10.1073/pnas.1811463116.

Román-Palacios C, Wiens JJ (2020) Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, **117**,

4211–4217.

Roth G, Caswell H (2018) Occupancy time in sets of states for demographic models. *Theoretical Population Biology*, pp. 62–77. doi:doi:10.1016/j.tpb.2017.12.007.

Saether B, Bakke O (2000) Avian life history variation and contribution of demographic trait to the population growth rate. *Ecology*, **81**, 642–653.

Sæther BE (1987) The influence of body weight on the covariation between reproductive traits in european birds. *Oikos*, pp. 79–88.

Sæther BE, Engen S (2015) The concept of fitness in fluctuating environments. *Trends in ecology & evolution*, **30**, 273–281.

Saether BE, Engen S, Gamelon M, Grøtan V (2019) Predicting the effects of climate change on bird population dynamics. In: *Effects of Climate Change on Birds*, pp. 74–90. Oxford University Press.

Sæther BE, Lillegard M, Grøtan V, Filli F, Engen S (2007) Predicting fluctuations of reintroduced ibex populations: the importance of density dependence, environmental stochasticity and uncertain population estimates. *Journal of Animal Ecology*, **76**, 326–336.

Sæther BE, Sutherland WJ, Engen S (2004) Climate influences on avian population dynamics. *Advances in Ecological Research*, **35**, 185–209.

Salguero-Gómez R, Jones OR, Jongejans E, *et al.* (2016) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences*, **113**, 230–235.

Schlunegger S, Rodgers KB, Sarmiento JL, *et al.* (2020) Time of emergence and large ensemble intercomparison for ocean biogeochemical trends. *Global Biogeochemical Cycles*, **34**. doi:10.1029/2019gb006453.

Schwager M, Johst K, Jeltsch F (2006) Does red noise increase or decrease extinction risk? single extreme events versus series of unfavorable conditions. *The American Naturalist*, **167**, 879–888.

46

Schwalm CR, Glendon S, Duffy PB (2020) Rcp8. 5 tracks cumulative co2 emissions. *Proceedings of the National Academy of Sciences*, **117**, 19656–19657.

Sorte FAL, Fink D, Johnston A (2019) Time of emergence of novel climates for north american migratory bird populations. *Ecography*, **42**, 1079–1091. doi:10.1111/ecog.04408.

Stearns SC (1983) The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, pp. 173–187.

Steinger T, Körner C, Schmid B (1996) Long-term persistence in a changing climate: Dna analysis suggests very old ages of clones of alpine carex curvula. *Oecologia*, **105**, 94–99.

Stephens PA, Mason LR, Green RE, *et al.* (2016) Consistent response of bird populations to climate change on two continents. *Science*, **352**, 84–87.

Szostek KL, Becker PH (2015) Survival and local recruitment are driven by environmental carry-over effects from the wintering area in a migratory seabird. *Oecologia*, **178**, 643–657.

Trathan PN, Wienecke B, Barbraud C, *et al.* (2020) The emperor penguin-vulnerable to projected rates of warming and sea ice loss. *Biological Conservation*, **241**, 108216.

Treurnicht M, Pagel J, Esler KJ, *et al.* (2016) Environmental drivers of demographic variation across the global geographical range of 26 plant species. *Journal of Ecology*, **104**, 331–342. doi:10.1111/1365-2745.12508.

Tuljapurkar S, Gaillard JM, Coulson T (2009) From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1499–1509. doi:10.1098/rstb.2009.0021.

Tuljapurkar S, Orzack S (1980) Population dynamics in variable environments I. Long-run growth rates and extinction. *Theoretical Population Biology*, **18**, 314–342.

Tuljapurkar SD (1982) Population dynamics in variable environments. iii. evolutionary dynamics of r-selection. *Theoretical population biology*, **21**, 141–165.

Vázquez DP, Gianoli E, Morris WF, Bozinovic F (2015) Ecological and evolutionary im-

pacts of changing climatic variability. *Biological Reviews*, **92**, 22–42. doi:10.1111/brv. 12216.

Zappa G, Hoskins BJ, Shepherd TG (2015) Improving climate change detection through optimal seasonal averaging: The case of the north atlantic jet and european precipitation. *Journal of Climate*, **28**, 6381–6397.

Zimmermann NE, Yoccoz NG, Edwards TC, *et al.* (2009) Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences*, **106**, 19723–19728.

Figure

Figure 1: Conceptual diagram of the time of emergence (ToE) in climate (ToE$_{climate}$) and in populations (ToE$_{pop}$). ToE identifies the point in time when the signal of anthropogenic climate change (red time series) emerges from the noise associated with natural variability (black time series). ToE$_{pop}$ depends on the response of population growth rate to climate that is defined by: (1) the impact of climate on demographic rates (e.g. survival) with different functional forms that influence the sensitivity of demographic rates to climate; (2) the impact of demographic rates on the population growth rate resulting from non-linear demographic processes occurring throughout the species life cycle (described in section Population projections).

Figure 2: Illustrative figure of the time of emergence in climate (ToE$_{climate}$ on left panel) and in populations (ToE$_{pop}$ on right panels) of four species along the gradient of life histories, from fast species (species 1) to slow species (species 4). The figure shows one time series simulated during the historical environment (black line) and forced environment (red line). The emergence thresholds are based on a 95% prediction interval of 1000 simulations (grey area). The natural variability in climate is $\sigma = 0.5$. The forced perturbation occurs at years 80 years resulting in a positive trend in climate. Climate affects negatively maturation rate (slope of the linear relationship on logit scale: $\beta = -0.125$). Y-axis is different for each species.

Figure 3: Relationship between ToE$_{climate}$ (x-axis) and ToE$_{pop}$ (y-axis) for four life history strategies (from fast (species 1) to slow (species 4)), whereby climate affects only one demographic parameter at a time (colored dots: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate). Black lines represent the time when ToE$_{pop}$ = ToE$_{climate}$.

Figure 4: a) The variability in annual population growth rates depends on the natural variability of climate σ, in both in the historical and perturbed environment (example for

$\beta = 0.125 \alpha = 0.05$). (b) The trend of population growth rate at the time of emergence in population depends on the trend of climate α (example for $\beta = 0.125$ and $\sigma = 0.5$). Colors refer to the climate-dependent demographic rate: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate. The dots on (a) stand for the forced environment while square are the historical environment. Panels show four different life history strategies, from fast (species 1) to slow (species 4).

Figure 5: ToE_{pop} as function of the sensitivity of the population growth rate to the demographic rate affected by climate. The ToE_{pop} is the median across various natural variability and trend of climate and various slope in the functional relationship between climate and the demographic rate (Table 2). The sensitivity of the population growth rate to the demographic rate is calculated for the averaged population matrix in the historical environment. Symbols refer to species.

Figure 6: ToE_{pop} as function of the absolute slope of the functional relationship between climate and demographic rate β_0. Example for a climate trend of $\alpha = 0.05$ and climate variability of $\sigma = 0.5$. Colors refer to demographic pathway by which climate affects demographic rates: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate. The dots stand for $\beta_0 > 0$, while square shows $\beta_0 < 0$. Panels show four life history strategies.

Figure 7: Annual life-cycle graph for the emperor penguin. It represents a two-sex model with males (black) and females (gray). Fertilities are shown by dotted lines, and the transitions between stages of individuals already present in the population are represented by solid lines (see Figure 1 from Jenouvrier *et al.* [2010] for more details on seasonal cycle of the emperor penguin).

Figure 8: Difference between the time of emergence in sea ice and ToE_{pop} of emperor penguin ($ToE_{climate} - ToE_{pop}$) for the 54 known colonies (x-axis) and four seasons (color). The calculation of ToE_{pop} accounts for $var(\epsilon)$ generated by parameter uncertainty and process variance (i.e., environmental stochasticity) (a) or not (b).
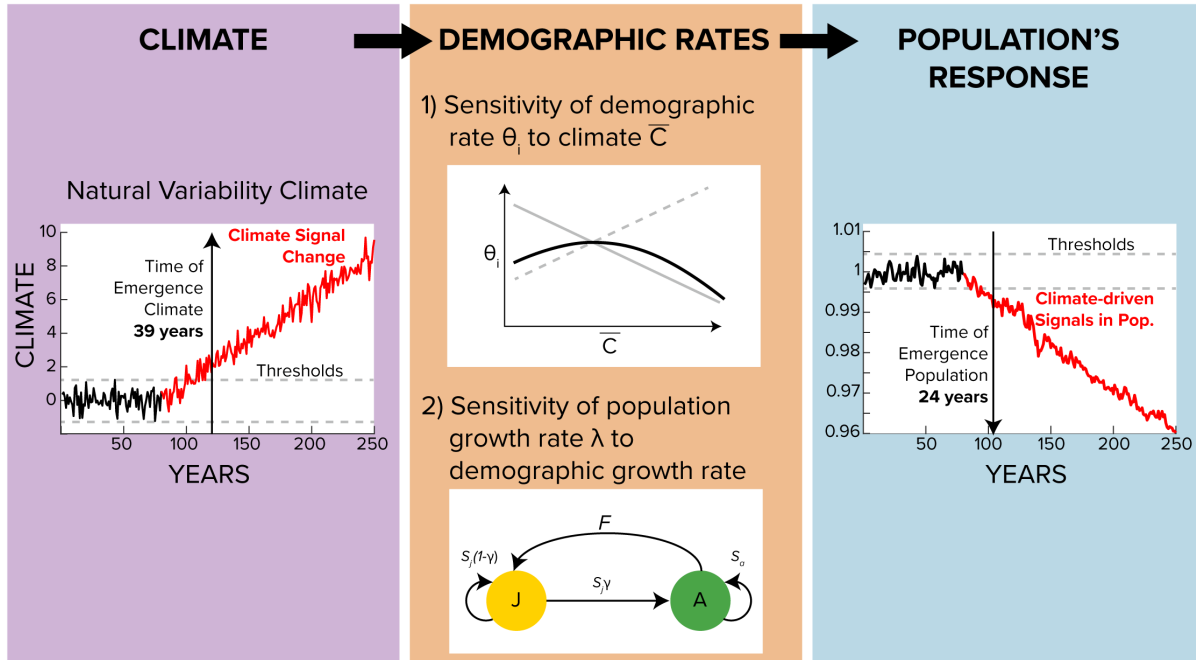
Figure 1: Conceptual diagram of the time of emergence (ToE) in climate (ToE_climate) and in populations (ToE_pop). ToE identifies the point in time when the signal of anthropogenic climate change (red time series) emerges from the noise associated with natural variability (black time series). ToE_pop depends on the response of population growth rate to climate that is defined by: (1) the impact of climate on demographic rates (e.g. survival) with different functional forms that influence the sensitivity of demographic rates to climate; (2) the impact of demographic rates on the population growth rate resulting from non-linear demographic processes occurring throughout the species life cycle (described in section Population projections).

Figure 2: Illustrative figure of the time of emergence in climate (ToE$_{\text{climate}}$ on left panel) and in populations (ToE$_{\text{pop}}$ on right panels) of four species along the gradient of life histories, from fast species (species 1) to slow species (species 4). The figure shows one time series simulated during the historical environment (black line) and forced environment (red line). The emergence thresholds are based on a 95% prediction interval of 1000 simulations (grey area). The natural variability in climate is $\sigma = 0.5$. The forced perturbation occurs at years 80 years resulting in a positive trend in climate. Climate affects negatively maturation rate (slope of the linear relationship on logit scale: $\beta = -0.125$). Y-axis is different for each species.
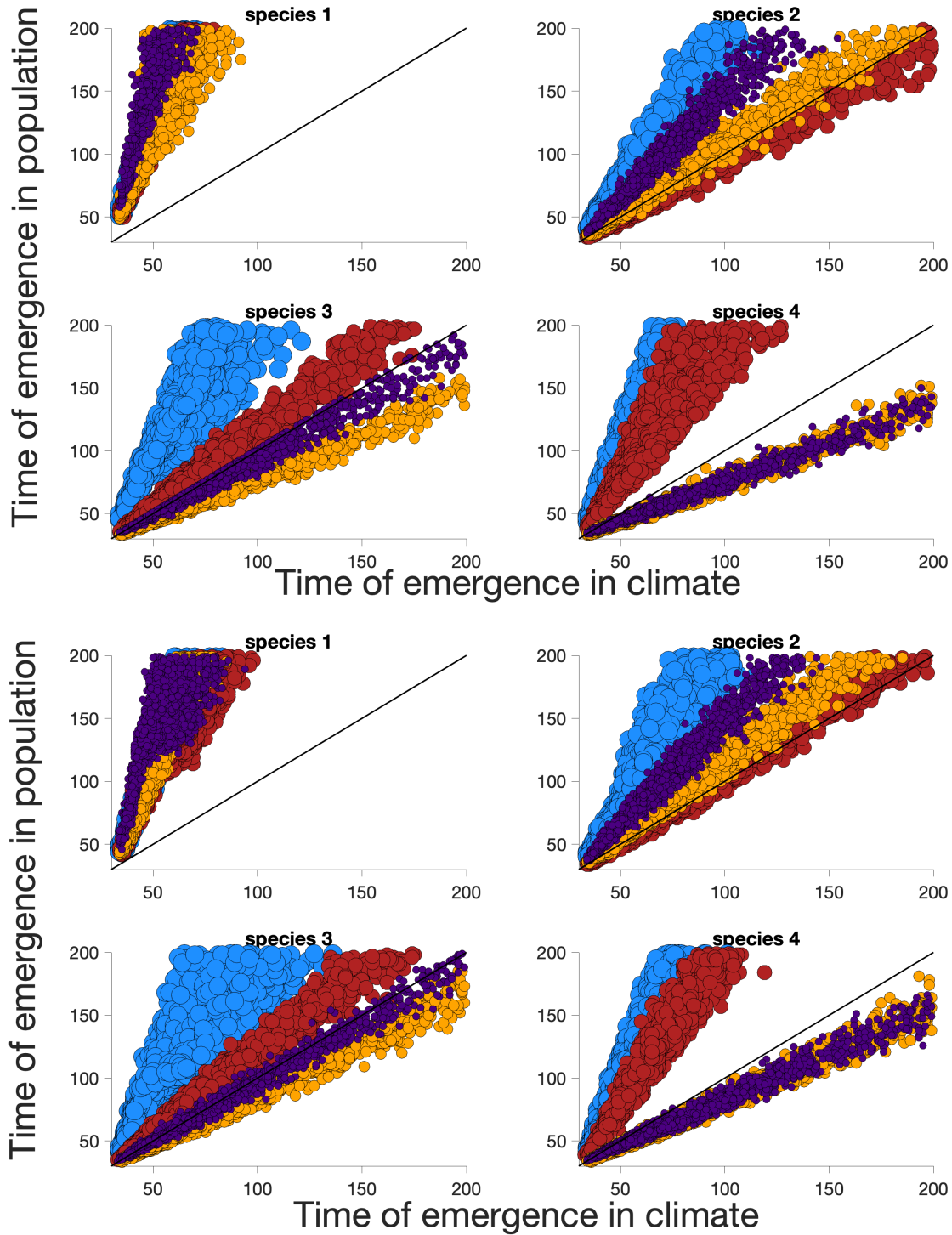
Figure 3: Relationship between ToE$_{climate}$ (x-axis) and ToE$_{pop}$ (y-axis) for four life history strategies (from fast (species 1) to slow (species 4)), whereby climate affects only one demographic parameter at a time (colored dots: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate). Black lines represent the time when ToE$_{pop}$ = ToE$_{climate}$.
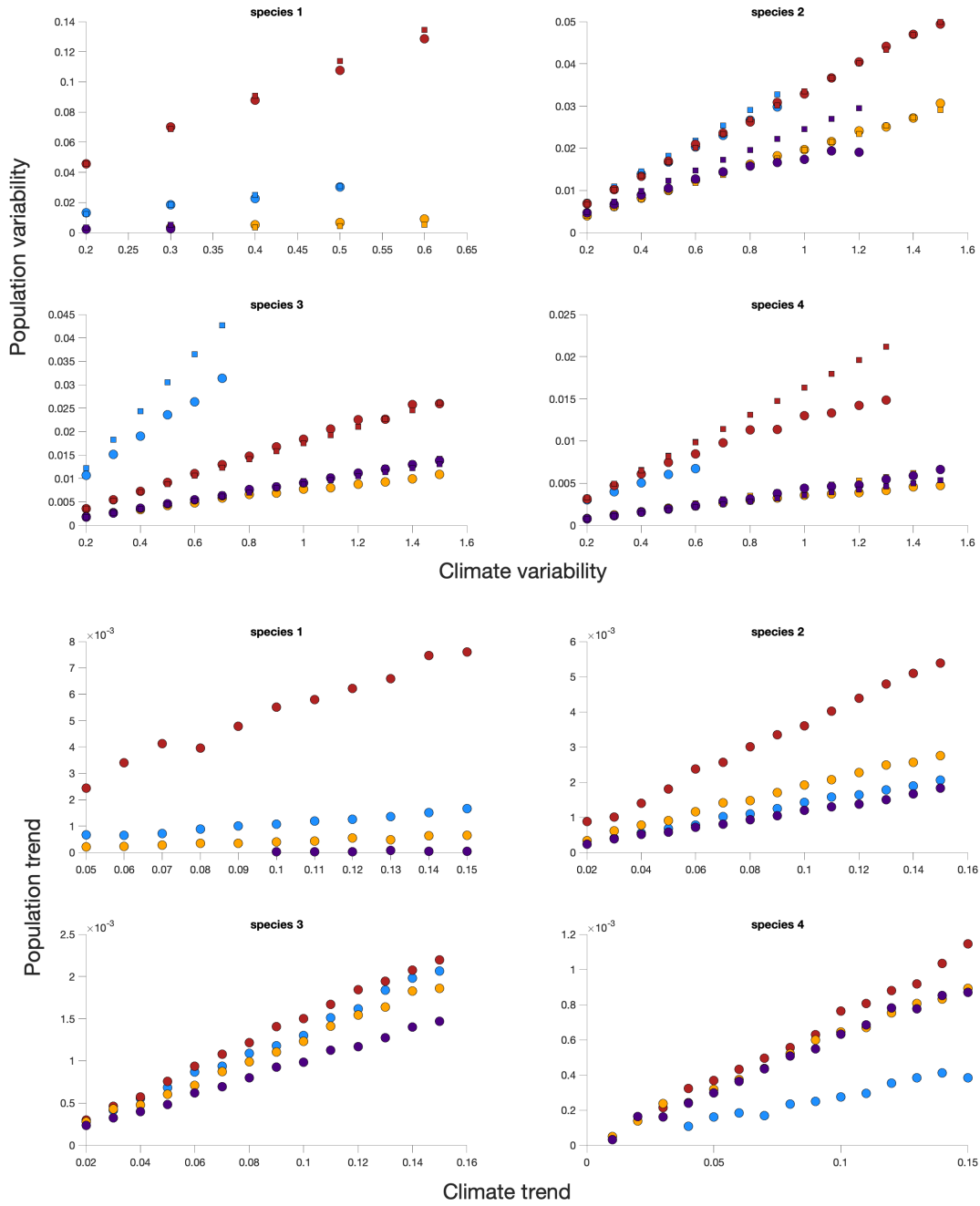
Figure 4: (a) The variability in annual population growth rates depends on the natural variability of climate σ, in both in the historical and perturbed environment (example for $\beta = 0.125$ $\alpha = 0.05$). (b) The trend of population growth rate at the time of emergence in population depends on the trend of climate α (example for $\beta = 0.125$ and $\sigma = 0.5$). Colors refer to the climate-dependent demographic rate: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate. The dots on (a) stand for the forced environment while square are the historical environment. Panels show four different life history strategies, from fast (species 1) to slow (species 4).
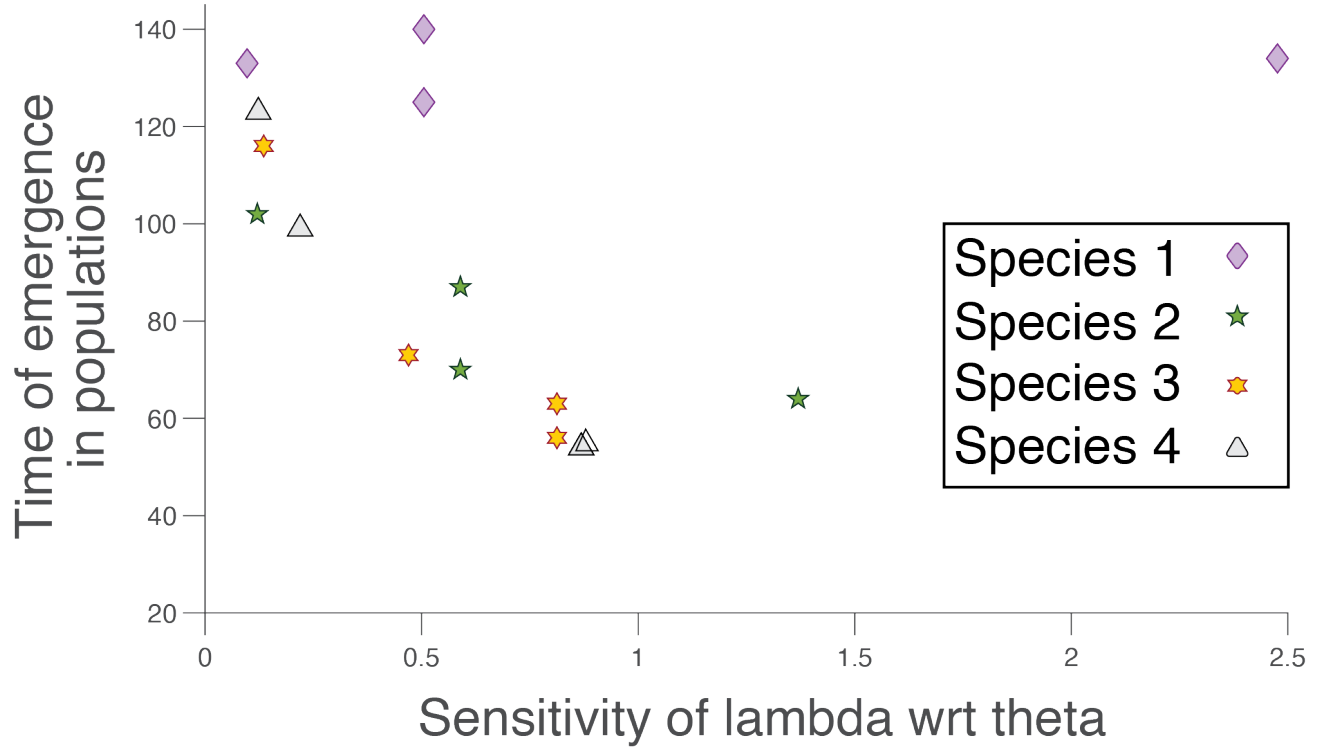
Figure 5: ToE$_{pop}$ as function of the sensitivity of the population growth rate to the demographic rate affected by climate. The ToE$_{pop}$ is the median across various natural variability and trend of climate and various slope in the functional relationship between climate and the demographic rate (Table 1). The sensitivity of the population growth rate to the demographic rate is calculated for the averaged population matrix in the historical environment. Symbols refer to species.
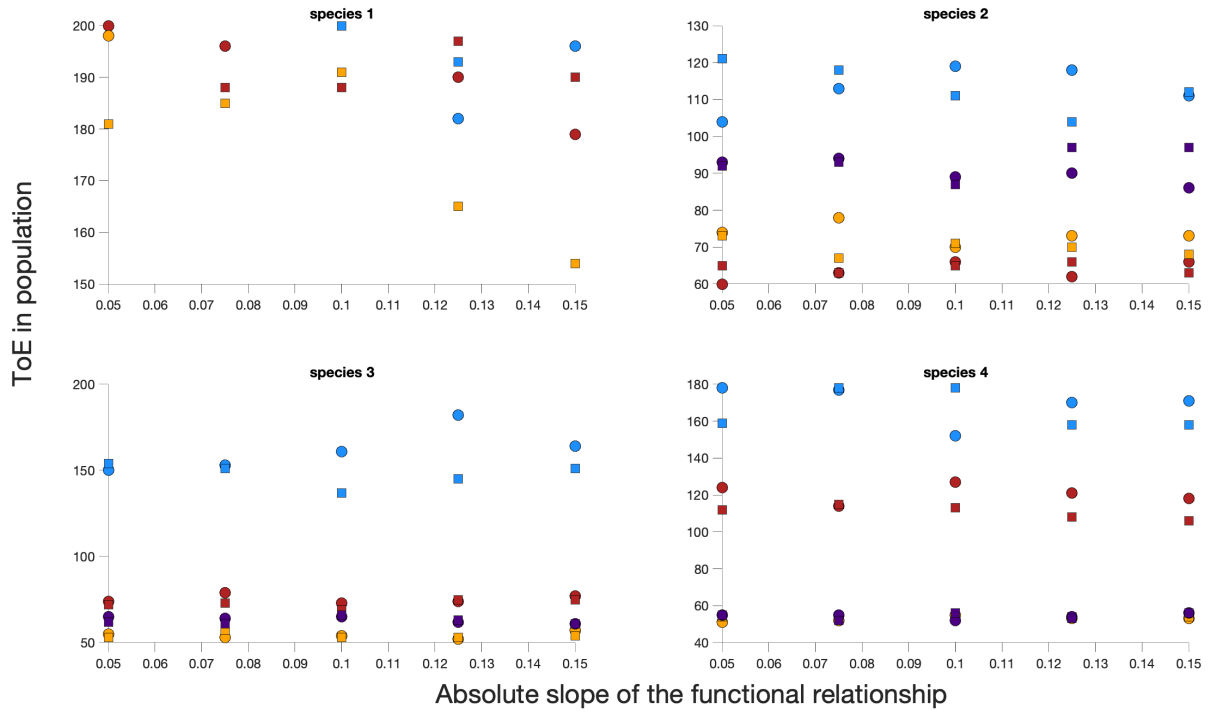
Figure 6: ToE$_\text{pop}$ as function of the absolute slope of the functional relationship between climate and demographic rate β_0. Example for a climate trend of $\alpha = 0.05$ and climate variability of $\sigma = 0.5$. Colors refer to demographic pathway by which climate affects demographic rates: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate. The dots stand for $\beta_0 > 0$, while square shows $\beta_0 < 0$. Panels show four life history strategies.
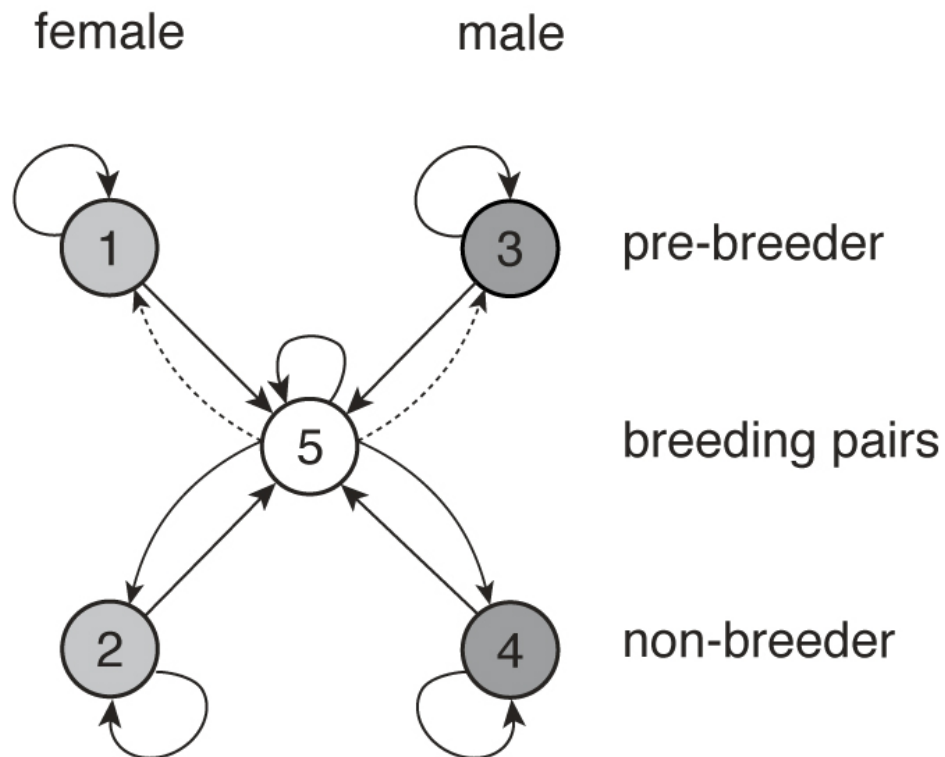
Figure 7: Annual life-cycle graph for the emperor penguin. It represents a two-sex model with males (black) and females (gray). Fertilities are shown by dotted lines, and the transitions between stages of individuals already present in the population are represented by solid lines (see Figure 1 from Jenouvrier *et al.* [2010] for more details on seasonal cycle of the emperor penguin).
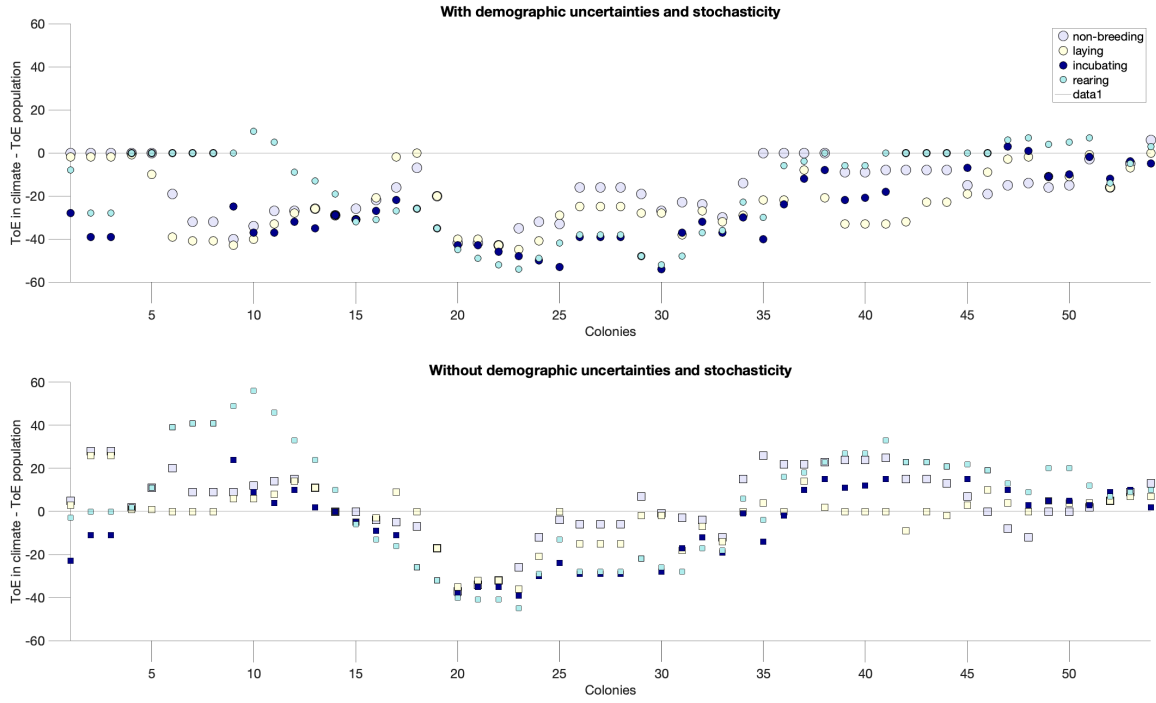
Figure 8: Difference between the time of emergence in sea ice and ToE_{pop} of emperor penguin ($ToE_{climate} - ToE_{pop}$) for the 54 known colonies (x-axis) and four seasons (color). The calculation of ToE_{pop} accounts for $var(\epsilon)$ generated by parameter uncertainty and process variance (i.e., environmental stochasticity) (a) or not (b).

1190 **Table**

Table 1: Glossary adapted from the IPCC definitions [Allen *et al.*, 2018]

Climate change
Change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forcings such as modulations of the solar cycles, volcanic eruptions and persistent anthropogenic changes in the composition of the atmosphere or in land use.

Climate model
A numerical representation of the climate system based on the physical, chemical and biological properties of its components, their interactions and feedback processes, and accounting for some of its known properties. Climate models have structural differences for example, in their spatial resolution, complexity of parameterizations, and processes that are explicitly represented.

Climate signal
Variations in the state of the climate system that have an identifiable and statistically discernible structure in time and/or space, such as a long-term warming trend.

Climate simulation
A model simulation of the climate state. This can include the simulated response of the climate system to characterize historical climate conditions, climate predictions, or climate projections.

Climate projection
A simulated response of the climate system to a forcing scenario of future emission or concentration of greenhouse gases (GHGs) and aerosols, generally derived using climate models.

Climate variability
Variations in the mean state and other statistics (such as standard deviations, the occurrence of extremes, etc.) of the climate on all spatial and temporal scales beyond that of individual weather events. Variability may be due to natural internal processes within the climate system (internal variability), or to variations in natural or anthropogenic external forcing (external variability).

Natural climate variability
Climate fluctuations from unforced variability generated internally within the climate system (e.g. weather) or associated with external forces to the climate system (e.g. volcanoes).

(Model) Ensemble
A group of parallel model climate simulations. Ensembles made with the same model but different initial conditions characterize the simulation uncertainty associated with internal climate variability, whereas multimodel ensembles including simulations by several models also include the impact of model differences.

Time of Emergence
The time at which the signal of climate change emerges from the noise of natural climate variability.

Emergence threshold
A threshold at which climate change is consider to emerge.

Table 2: Demographic rates and outcomes for the four life history strategies (species in columns). Note that the fertility (F number of offspring that are produced per adult female in year t) is reported here. The fecundity (b the number of offspring born per unit time per female) is discounted by the probability that an adult will actually survive from the time of the census to the birth pulse ($F = bS_a$). The deterministic population growth rate is one for all species. The generation time (in years) is the mean age of parents (eq 14 of Bienvenu & Legendre [2015]), from the fundamental matrix the following demographic outputs are calculated: the mean life expectancy at birth and the mean remaining life at adulthood (eq 20 of [Roth & Caswell, 2018]); the probability to return to the adult state (from eq 47 of [Roth & Caswell, 2018] using state A on Fig. 2). Ex stands for extreme.

	species 1	species 2	species 3	species 4
	Life history strategies			
Reproductive strategy	Semelparous	Iteroparous	Iteroparous	Iteroparous
Developmental strategy	Precocious	Precocious	Delayed	Ex-Delayed
Survival strategy	Short-lived	Short-lived	Long-lived	Ex-Long-lived
	Demographic rates			
Annual fertility rate	5.06	3.00	1.00	0.50
Juvenile survival prob.	0.20	0.30	0.40	0.60
Adult survival prob.	0.03	0.39	0.83	0.93
Maturation rate	0.95	0.60	0.30	0.11
	Life history outcomes			
Generation time	2.04	2.77	7.40	16.30
Life expectancy at birth	1.21	1.47	2.39	4.17
Remaining life at adulthood	1.03	1.63	6.02	14.29
Probability to return to adult state	0.03	0.39	0.83	0.93

Table 3: Time of emergence, trend and variability of population growth rate, with its sensitivity to climate across all simulations for four life history strategies (species in row) and four demographic pathways by which climate affects demography rates (columns). Median of the time of emergence of population is denoted $\mathsf{ToE_{pop}}$. At the time of emergence in the population: the median of the trend is T_{ToEpop}, the median of the variability in the forced environment is var_{ToEpop} and their ratio is $\mathsf{T}_{ToEpop}/\mathsf{var}_{ToEpop}$ at $\mathsf{ToE_{pop}}$; and the median of the sensitivity of the population growth rate to climate is $\frac{\partial\lambda}{\partial C}\Big|_{C=\overline{C}_{ToEpop}}$. Historical variability is denoted $\mathsf{var}(\lambda_t)$.

	LINEAR				BELL SHAPE			
	F	S_j	S_a	γ	F	S_j	S_a	γ
$\mathsf{ToE_{pop}}$								
species 1	133	134	125	140	133	126	125	146
species 2	102	64	70	87	106	68	73	86
species 3	116	73	56	63	107	75	60	65
species 4	123	99	54	54	120	105	58	58
$\mathsf{T}_{ToEpop}/\mathsf{var}_{ToEpop}$								
species 1	0.04	0.04	0.04	0.04	0.06	0.04	0.02	0.06
species 2	0.05	0.11	0.09	0.07	0.06	0.11	0.09	0.07
species 3	0.03	0.08	0.15	0.11	0.01	0.08	0.14	0.12
species 4	0.03	0.05	0.16	0.16	0.03	0.03	0.15	0.16
T_{ToEpop}								
species 1	0.0010	0.0032	0.0002	0.0003	0.0041	0.0067	0.0001	0.0085
species 2	0.0010	0.0021	0.0010	0.0008	0.0027	0.0021	0.0011	0.0018
species 3	0.0008	0.0008	0.0008	0.0006	0.0007	0.0010	0.0007	0.0005
species 4	0.0002	0.0004	0.0004	0.0003	0.0005	0.0004	0.0003	0.0002
var_{ToEpop}								
species 1	0.024	0.088	0.003	0.005	0.092	0.216	0.005	0.149
species 2	0.019	0.019	0.011	0.013	0.047	0.021	0.014	0.027
species 3	0.024	0.010	0.005	0.005	0.054	0.013	0.005	0.005
species 4	0.006	0.008	0.002	0.002	0.023	0.020	0.002	0.002
$\frac{\partial\lambda}{\partial C}\Big|_{C=\overline{C}_{ToEpop}}$								
species 1	0.010	0.019	0.003	0.004	0.0018	0.0060	0.0002	0.0005
species 2	0.012	0.024	0.011	0.009	0.0022	0.0048	0.0023	0.0021
species 3	0.014	0.009	0.010	0.007	0.0025	0.0019	0.0021	0.0013
species 4	0.001	0.003	0.005	0.004	0.0005	0.0009	0.0011	0.0008
$\mathsf{var}(\lambda_t)$								
species 1	0.025	0.108	0.003	0.006	0.005	0.022	0.001	0.002
species 2	0.019	0.019	0.011	0.014	0.003	0.004	0.002	0.003
species 3	0.031	0.010	0.006	0.005	0.007	0.002	0.001	0.001
species 4	0.008	0.009	0.003	0.002	0.002	0.002	0.001	0.000

Supplementary

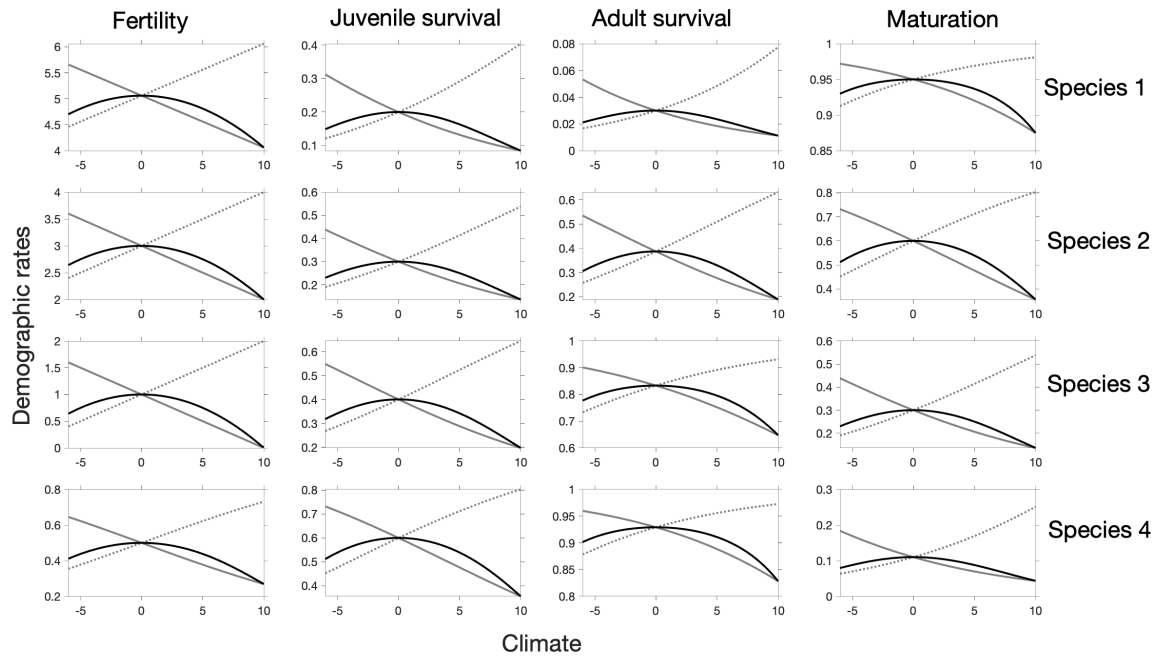# Supporting Information S1: additional figures

Figure S 1: Example of functional relationships that are linear or sigmoid with a slope $\beta_0 = 0.1$, $\beta_0 = -0.1$ for linear sigmoid functional relationship or $\beta_0 = 0.01$ for bell shape relationships for each species (row panels) and each demographic rate (column panels).
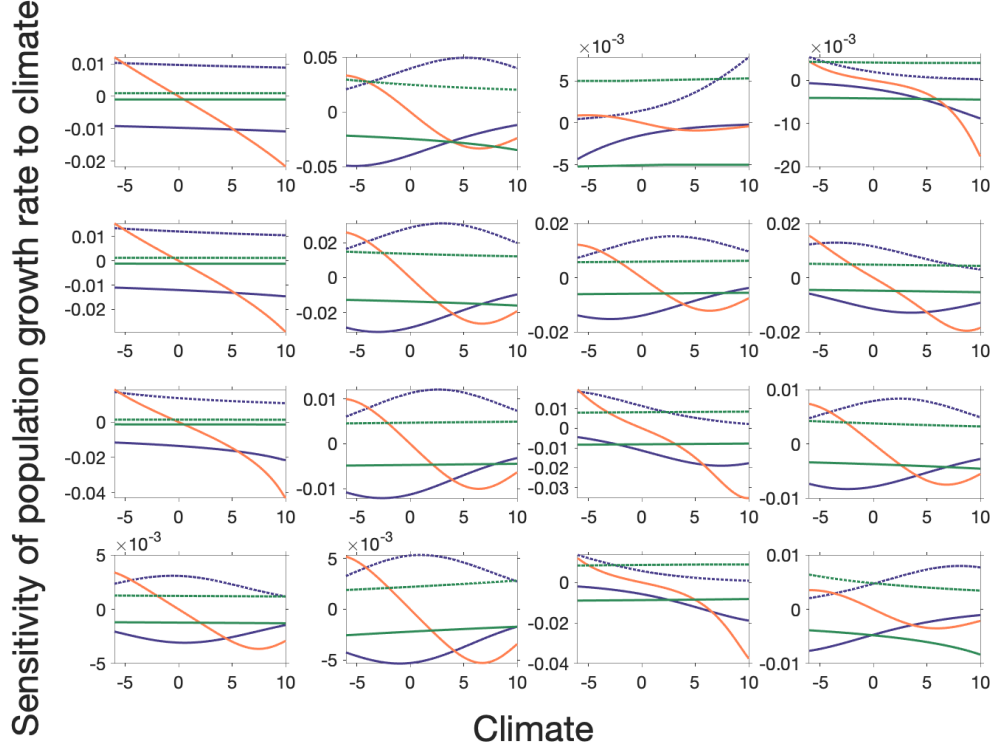
Figure S 2: Sensitivity of the population growth rate to climate for four life histories (panel in line: fast (species 1) to slow (species 4)) and demographic rates (panel in column: fertility, juvenile survival, adult survival and maturation rate) and different functional relationships between climate and demographic rates. Blue lines stands for linear on logit scale with $\beta_0 = [-0.1/0.1]$, orange line shows bell shape on logit scale with $\beta_0 = -0.01$, and green lines are linear on real scale $\beta_0 = [-0.1/0.1]$,

Figure S 3: Relationship between the time of emergence in climate (x-axis) and population (y-axis) for four life history strategies (panels), whereby climate affects only one demographic parameter at a time (colored dots: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate). The black line represent the time when the time of emergence in climate and population are equal. The functional relationships are linear or sigmoid. The emergence thresholds are defined by the 20th or 80th percentile values of the confidence interval. In that case, the system is likely highly sensitive to climate as severe impacts are thought to occur for lower percentile of the climate distribution experienced during the historical run.
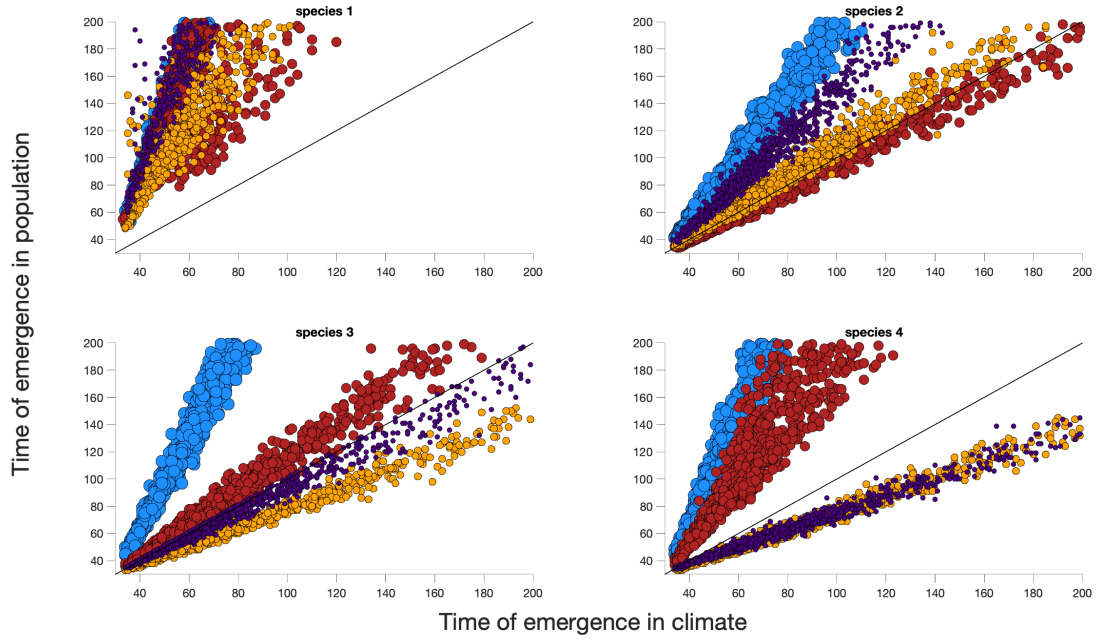
Figure S 4: Relationship between the time of emergence in climate (x-axis) and population (y-axis) for four life history strategies (panels), whereby climate affects only one demographic parameter at a time (colored dots: blue is fertility, red is juvenile survival, orange is adult survival and purple is maturation rate). The black line represent the time when the time of emergence in climate and population are equal. The functional relationships are linear on the real scale with $\beta_0 = [-0.03 \; -0.02 \; -0.01 \; 0.01 \; 0.02 \; 0.03]$.
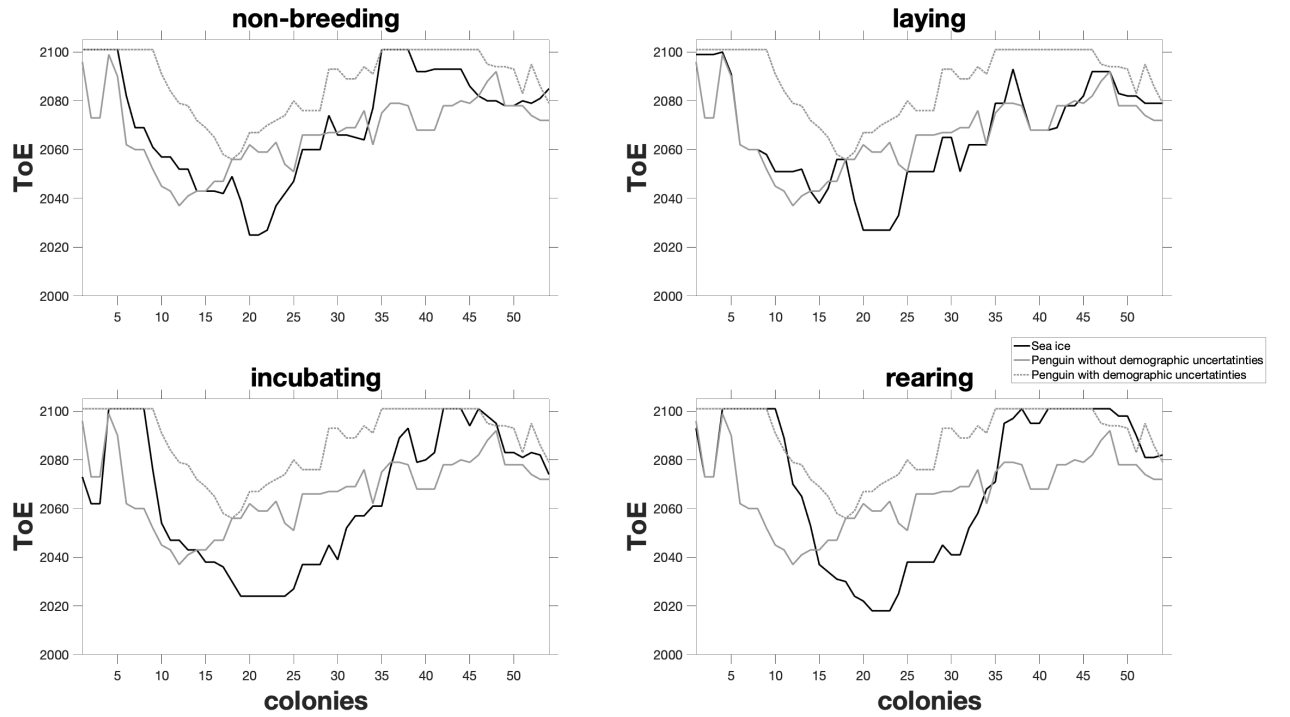
Figure S 5: Time of emergence in sea ice (black line) and in the population growth rate of emperor penguin (grey lines) for the 54 known colonies (x-axis) and season (panels). The calculation of ToE accounts for var(ϵ) generated by parameter uncertainty and process variance (i.e., environmental stochasticity) (dotted line) or not (plain line).
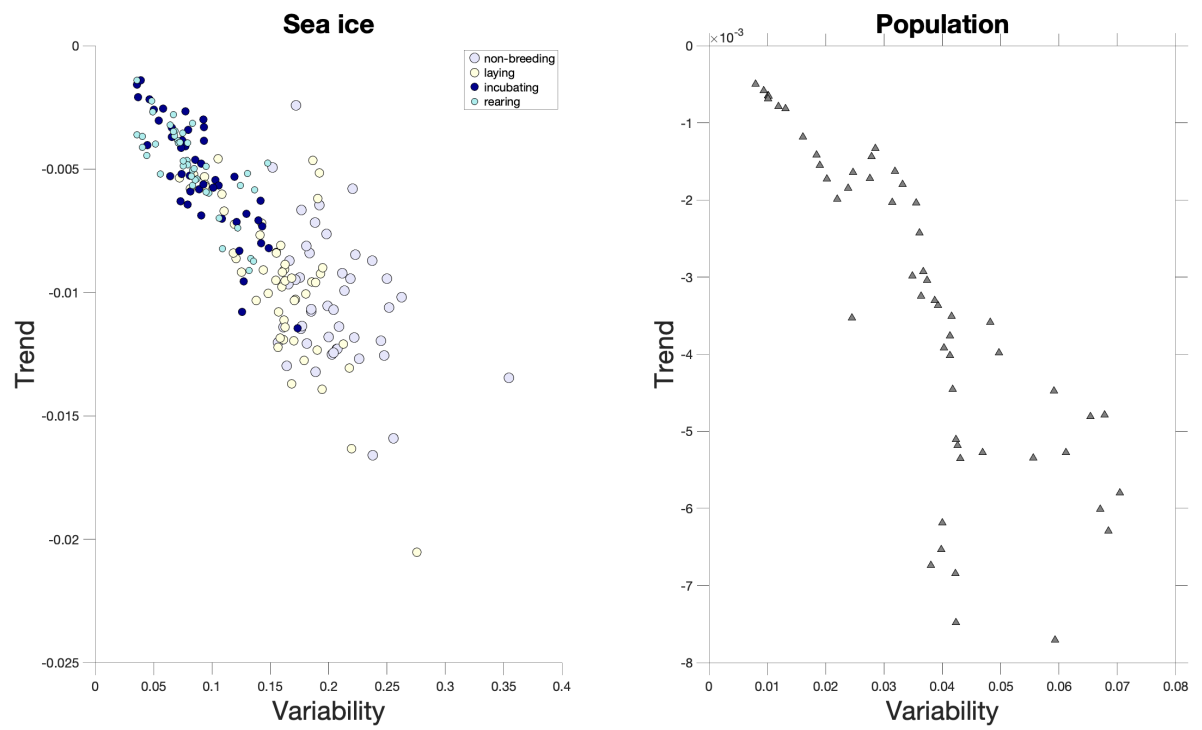
Figure S 6: Variability and trend at the time of emergence for sea ice (left panel) and for the population growth rate of emperor penguin (right panel) for the 54 known colonies (marker) and season (colors).
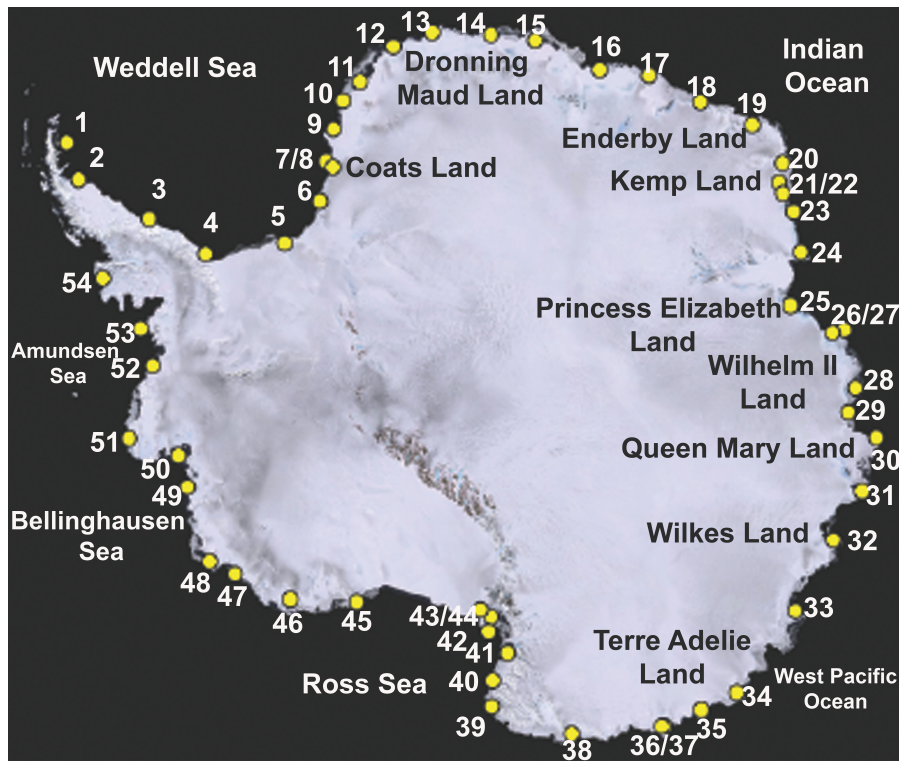
Figure S 7: Map of Emperor penguin colonies.

Supporting Information S2: population variability in a stationary environment

Equation 13 shows that the variance in annual population growth rates $\text{var}(\lambda_t)$ is linearly related to the climate variance σ^2 in a stochastic stationary environment with small variations around a climate mean $\overline{C}$.

Figure S 8 shows the variance in annual population growth rates $\text{var}(\lambda_t)$ as function of a mean climate $\overline{C}$ for different life histories when climate affects the population through different demographic rates θ_i. The functional relationships between climate and the demographic rate are linear on the real scale for fertilities (except species 4) or on the logit scale for other demographic rates. Let's assume that C represents temperature, and the population is stable for $\overline{C} = 0$.

The stationarity variability of the population growth rate varies as function of the mean climate in complex non-linear ways that depend on $\frac{\partial \lambda}{\partial C}$ and the sign of the slope of the functional relationships between climate and demographic rates β_0 that affects $\frac{\partial \lambda}{\partial C}$. The smallest $\frac{\partial \lambda}{\partial C}$, hence population growth rate variability, occurs for species 4 with an extreme long-lived history and the climate-dependent demographic rate of maturation rate regardless of the mean environmental conditions and functional relationships. Short-lived species (species 1 and 2) and the climate-dependent demographic rate of juvenile survival shows the largest $\frac{\partial \lambda}{\partial C}$, except for extreme positive mean climate. However, various patterns are observed between these extremes, which depend on the functional relationship between climate and demographic rates, the demographic rate by which climate affects population and the life histories of the species.

For example, for linear functional relationships between the fertility and climate (species 1-3), equation 13 becomes:

$$\text{var}(\lambda) = \beta_0^2 \sigma^2 \left(\frac{\partial \lambda}{\partial \theta_{i\theta_i=\overline{\theta_i}}} \right)^2 \left(\frac{\partial \theta_{i\theta_i=\overline{\theta_i}}}{\partial C_{C=\overline{C}}} \right)^2 = \beta_0^4 \sigma^2 \left(\frac{\partial \lambda}{\partial \theta_{i\theta_i=\overline{\theta_i}}} \right)^2 \tag{15}$$

If $\beta_0 > 0$, $\left(\frac{\partial \lambda}{\partial \theta_i} \right)^2$ increases as $\overline{C}$ increases, and the variance in annual population growth

9

1217   rates is larger for warmer climate than colder climate. If $\beta_0 < 0$, $\left(\frac{\partial \lambda}{\partial \theta_i}\right)^2$ decreases as $\overline{C}$

1218   increases, and the variance in annual population growth rates is larger for colder climate

1219   than warmer climate.

1220   For non-linear sigmoid functions, it is more complex, and depends on the specific

1221   shape of the $\left(\frac{\partial \lambda}{\partial \theta_i}\right)^2$ and the sign of β_0, specifically at which environment $\overline{C}$ the maximum

1222 $\left(\frac{\partial \lambda}{\partial \theta_i}\right)^2$ occurs. For example, for adult survival, the population growth rate variability

1223   is larger for warmer climate than for colder climate for long lived species when $\beta_0 < 0$

1224   (species 3 and 4). However, the opposite pattern occurs for short lived species (species

1225   1 and 2): the population growth rate variability is smaller for warmer climate than for

1226   colder climate (Fig. S 8). These patterns are opposite when $\beta_0 > 0$.

1227   For bell shape functional relationships, the variance of the population growth rate is

1228   smaller for comparable range of demographic rates (Table 2). Indeed, to obtain a realistic

1229   range of demographic rates when $\theta_{it} = g(y^* = \beta_0^* C_t^2 + \beta_1 + \epsilon_t)$ than when $\theta_{it} = g(y =$

1230 $\beta_0 C_t^2 + \beta_1 + \epsilon_t)$ (Fig. S 1), the slope of the function y^* must be smaller: $\beta_0^* < \beta_0$. Hence

1231   var(λ) is smaller despite similar magnitude for $\left(\frac{\partial \lambda}{\partial \theta_i}\right)^2$ for both function y and y^* (Fig. S
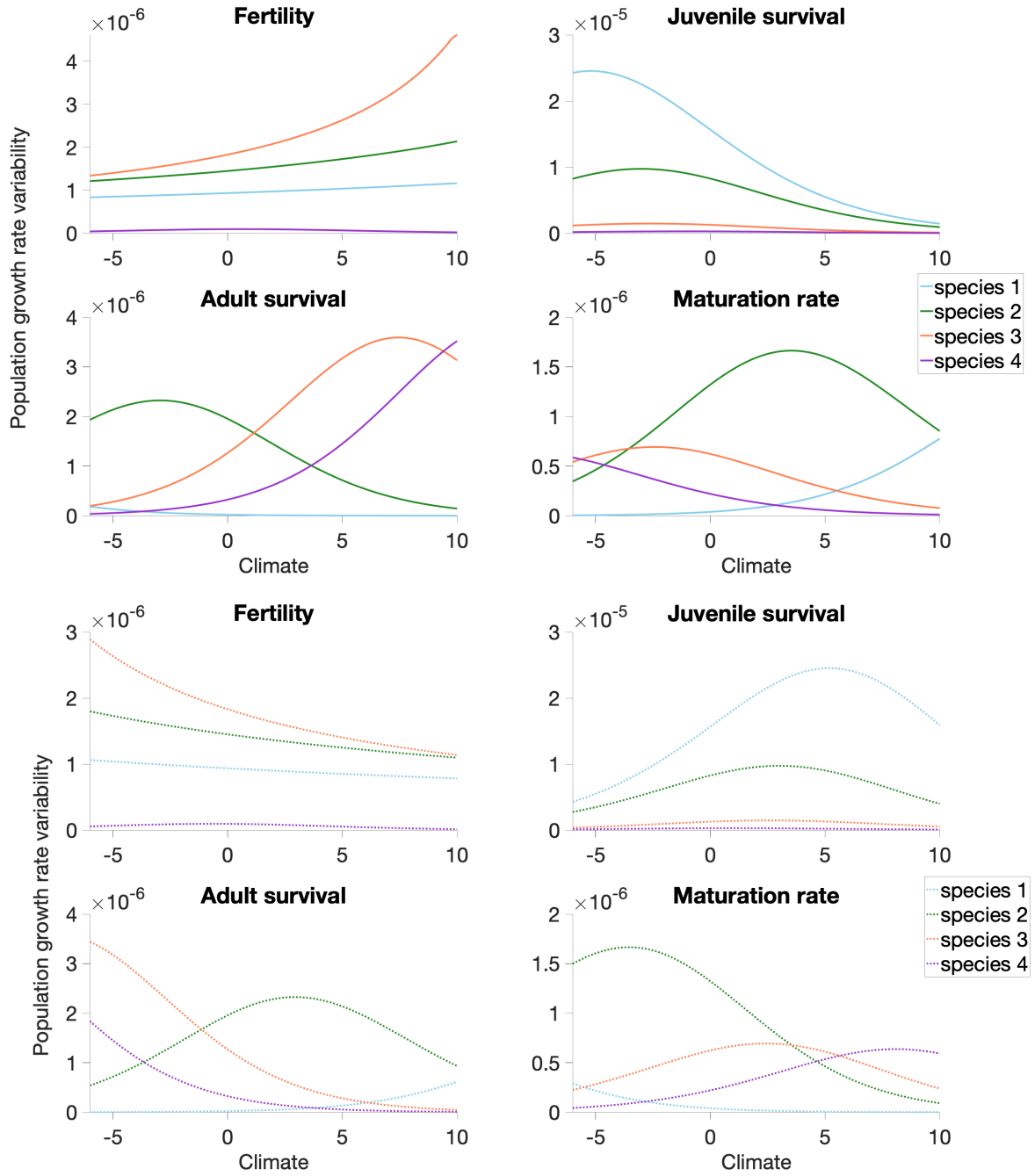
1232   2).

Figure S 8: Variability in annual population growth rates calculated from equation 8 across life histories. Panels show the variance in annual population growth rates $\text{var}(\lambda_t)$ as function of the climate mean $\overline{C}$ when climate affects population through different demographic rates: fertility, survival or maturation. Line color indicates different species along a gradient of fast-slow life histories, from fast (species 1) to slow (species 4). (a) $\beta_0 = -0.1$ and (b) $\beta_0 = 0.1$. $\sigma = 0.2$.

Supporting Information S3: the sea ice-dependent-metapopulation model for em-

peror penguins

1235

1236 Portions of the Supplementary Material are modified from Jenouvrier et al. (2010),

1237 Jenouvrier et al. (2012), Jenouvrier et al. (2017) and Jenouvrier et al. (2021) under the

1238 terms of the Publication Agreement with the University of Chicago Press, John Wiley &

1239 Sons publications and Elsevier.

1240 Our sea ice-dependent-metapopulation model projects the population vector **n**—comprising

1241 the population size n_i in each colony i—from time t to $t + 1$ using:

$$\mathbf{n}(t + 1) = \mathbf{D}\big[\mathbf{x}(t), \mathbf{n}(t)\big] \mathbf{F}\big[\mathbf{x}(t), \mathbf{n}(t)\big] \mathbf{n}(t) \tag{16}$$

1242 to indicate that the projection interval is divided into two main phases of possibly dif-

1243 ferent duration: the reproduction phase (**F**) followed by the dispersal phase (**D**) [1]. The

1244 reproduction matrix **F** is constructed using the Ricker model, which includes the intrinsic

1245 population growth rate $r_i(t)$, which vary in time, and the carrying capacity of the colony,

1246 K_i, which is set to be constant over the entire time period. The dispersal phase (**D**) com-

1247 bines various dispersal behaviors and dispersal events. The projection matrices **D** and

1248 **F** depend on both the current population density $\mathbf{n}(t)$ and the habitat characteristics (in-

1249 cluding sea ice concentrations anomalies), $\mathbf{x}(t)$, that vary among colonies and over time,

1250 t. The global population size at time t is given by $N_t = \sum_i n_i(t)$.

8.1 Reproduction phase

1252 The reproduction matrix, **F**, is constructed using the Ricker model including the in-

1253 trinsic growth rate of each colony $r_i(t)$ and the carrying capacity of each colony K_i. Neg-

1254 ative density-dependence effects occur within crowded favorable habitats ($r_i > 0$ and

1255 $n_i > K_i$) while populations tend to go extinct within poor habitat colonies ($r_i \leq 0$). Our

---

[1]Note on notation: In this paper, matrices are denoted by upper case bold symbols (e.g. **F**) and vectors by lower case bold symbols (**n**); f_{ij} is the (i, j) entry of the matrix **F**, n_i is the *ith* entry of the vector **n**.

understanding of density dependence processes is extremely limited for emperor penguins (see discussion in Appendix S1 of Jenouvrier *et al.* [2012]). Density dependence may occur at breeding ground due to competition for space. For example, the Beaufort Island colony growth is limited by the limited space available on the fast ice plate next to the island [Kooyman *et al.*, 2007]. Competition for resources may also occur, although emperor penguins are able to forage over long distances over wide areas, probably reducing intra-specific competition impact.

The intrinsic growth rate For each projection interval t, the intrinsic growth rate of each colony $r_i(t)$ is projected by a nonlinear, stochastic, sea-ice dependent, two-sex, stage-classified matrix $\mathbf{A}[\theta[\mathbf{x}(t), \mathbf{n}(t)]]$, including the demographic rates (reproduction and survival) $\theta[\mathbf{x}(t), \mathbf{n}(t)]$ (described in more detail in Jenouvrier *et al.* [2010, 2012]). The life cycle of this model is shown on Figure 7 and includes a sequence of seasonal behaviours (arrival to the colony, mating, breeding) and accounts for differences in adult survival between males and females as function of sea ice concentration anomalies $\mathbf{x}(t)$. $\mathbf{A}[\theta[\mathbf{x}(t), \mathbf{n}(t)]]$ depends on $\mathbf{n}(t)$ because the reproduction is function of the proportion of males and females within the population through mating processes [Jenouvrier *et al.*, 2010].

The carrying capacity For emperor penguins, estimating the carrying capacity of the environment is a daunting task because population time-series are limited to a few colonies around Antarctica, and no study thus far has reported the resources and breeding habitat availability. Using the population projections from the stochastic sea-ice dependent model that excludes density dependence [Jenouvrier *et al.*, 2017, 2014], Jenouvrier et al. (2017) estimated the carrying capacity of each colony as $K_i = 2N_0$, with N_0 the initial size of the population observed in 2009 [Fretwell & Trathan, 2009; Jenouvrier *et al.*, 2014].

8.2 The dispersal phase.

Finally, the model includes inter-colony movements. A dispersal event includes the three stages: (1) emigration from the resident colony, (2) search for new colony among other colonies with an average dispersal distance d (transfer), and (3) settlement in a new

13

colony. The duration of the transfer phase can vary, as the final settlement in a new colony may occur after several events (e.g., an individual may not settle in its first choice habitat if that habitat has reached its carrying capacity $n_i \geqslant K_i$.).

In our model, movements of individuals among colonies are divided into two successive dispersal events to account for a time-limited search. Indeed for emperor penguins the breeding season lasts 9 months, and thus the timing for prospecting other colonies during the non-breeding season is limited. During the first dispersal event ($\mathbf{D}^1$) individuals may select the habitat with highest quality (informed search) or settle in a random habitat. During the second dispersal event ($\mathbf{D}^2$) individuals that reached a saturated colony leave and settle randomly in a new colony (see Fig. 1 in Jenouvrier *et al.* [2017]). The later is a way to account for a dispersal cost of gathering information for the informed search (see discussion in Jenouvrier *et al.* [2017]).

The dispersal projection matrix $\mathbf{D}$ is thus

$$\mathbf{D} := \mathbf{D}^2\,\mathbf{D}^1. \tag{17}$$

and each dispersal matrix $\mathbf{D}^e$ is written

$$\mathbf{D}^e := \mathbf{S}^e[\mathbf{x}]\,\mathbf{M}^e[\mathbf{x}, \mathbf{n}_e] \tag{18}$$

to indicate that matrices for searching behavior, $\mathbf{S}^e$, and emigration, $\mathbf{M}^e$, depend on the population size at the start of the event (n_e) as well as the environmental conditions $\mathbf{x}(t)$.

The first dispersal event The emigration rate for each colony i depends on the overall quality of the habitat, which is measured by the median of the realized population growth $\overline{r_i^*}$. The emigration rate increases linearly from $m^1 = 0$ at $\overline{r} \geqslant 0$ to $m^1 = 1$ at critical value

14

$\overline{r_c^*} < 0$. The emigration matrix thus only depends on the ratio $\overline{\mathbf{r}^*(t)}/\overline{r_c^*}$,

$$\mathbf{M}^1 := \mathbf{M}^1 \left[\frac{\overline{\mathbf{r}^*(t)}}{\overline{r_c^*}} \right]. \tag{19}$$

A critical threshold $\overline{r_c^*}$ close to 0, corresponds to high dispersion scenario while a larger negative threshold reflects low dispersion.

Once individuals have left their colonies, we assume that they search for a new colony using two different behaviors: an informed searching behavior ($\mathbf{S}_I$) and a random searching behavior ($\mathbf{S}_R$).

The random search assumes that dispersers randomly seek a colony within the limits of the maximum dispersal distance. Thus the probability of selecting a colony depends on the mean dispersal distance of the emperor penguin, d, and the matrix of distance between colonies ($\text{dist}(i, j)$) included in the vector of habitat descriptors $\mathbf{x}$.

$$\mathbf{S}_R := \mathbf{S}_R[\mathbf{x}, d]. \tag{20}$$

The matrix $\text{dist}(i, j)$ corresponds to the coastal distance between colonies i and j derived from the location of know emperor penguin colonies.

Conversely, *the informed search* assumes that dispersers search for the most favorable habitat they can reach; we use $\overline{\mathbf{r}^*}$ as a descriptor of the quality of the habitat. Thus the informed search matrix is also a function of $\overline{r^*}$:

$$\mathbf{S}_I := \mathbf{S}_I[\overline{\mathbf{r}^*(t)}, \mathbf{X}, d]. \tag{21}$$

If the selected colony is not at carrying capacity, individuals settle in this new habitat. However, individuals are not able to settle in colonies that have reached their carrying capacities after the first dispersal event, and will conduct a novel search during the second dispersal event.

During the second dispersal event, the surplus individuals leave and randomly settle in another colony regardless of their dispersal strategy in their first event. Thus the emigration matrices depend on the carrying capacity $\mathbf{K}$, the population vector $\mathbf{n}$ at the end of the first dispersal event, and a random search matrix:

$$\mathbf{M}^2 := \mathbf{M}^2[\mathbf{K}, \mathbf{n}] \ \text{ and } \ \mathbf{S}^2 := \mathbf{S}_R. \tag{22}$$

Note that because of our random settlement assumption during this second dispersal event, individuals may come back to their resident colony if they first reached an overcrowded colony.