

A general relationship between population size and extinction risk

Authors

Thomas S Ball, Ben Balmford, Andrew Balmford, Daniele Rinaldo, Piero Visconti, and Rhys E. Green.

Abstract

Understanding the relationship between a population's probability of extinction and its carrying capacity is key in assessing conservation status, and critical to efforts to understand and mitigate the ongoing biodiversity crisis. Despite this, there has been limited research into the form of this relationship. We conducted around five billion population viability assessments which reveal that the relationship is a modified Gompertz curve. This finding is consistent across around 1700 individual model populations which between them span different breeding systems and widely varying rates of population growth, levels of environmental stochasticity, adult survival rate, age at first breeding, and starting population size. Applying analytical methods to equations describing population dynamics showed that minimal assumptions were required to prove this is a general relationship which holds for any extant population subject to density-dependent growth. Finally, we discuss the implications of these findings and consider the practical use of our results by conservationists.

Introduction

How does the risk of extinction of a population alter with changes in its environment? We propose a framework with which to consider such changes, focusing on the impact of reductions in carrying capacity on extinction risk. This is fundamental to many critically important questions in conservation. Which species are at greatest risk and therefore need most urgent attention? Which sites, if protected, offer the best prospects of retaining populations of concern? And how are changes in area of habitat or climate envelopes likely to affect extinction risk? Despite substantial progress, we still lack a generalised understanding of the shape of the relationship between a population's probability of extinction and the carrying capacity of the environment in which it lives. Here, we attempt to address this shortfall. By conducting a suite of population simulations we discover a generally applicable model relating extinction risk to carrying capacity, then show that the model has a theoretical basis. We hope that our discovery might be used to inform future conservation efforts, and lay the foundation for further understanding and mitigation of anthropogenic harms to natural life on Earth.

The applied importance of assessing extinction risk was first brought into focus by the pioneering work of Mace and Lande (1991), who developed quantitative and repeatable procedures, which have since been used to assess the conservation status of >160,000 species (www.iucnredlist.org). In parallel with this, much progress has been made modelling the expected time to extinction of populations (Lande 1993), and the minimum size needed to reduce the risk of extinction below an acceptable threshold within a specified period – usually 100 years. Here, 'population' is used here to describe a set of individuals interacting with the same environment; a species global meta-population may be comprised of several sub-populations. The small population paradigm highlights the substantial increase in probability of extinction (P_E)

with smaller carrying capacity (K) (Caughley 1994), yet surprisingly little attention has been given to the precise form of this relationship. Several high-profile studies (Thomas et al. 2004; Phalan et al. 2011; Strassburg et al. 2012, 2018; Armsworth et al. 2020) have assumed, by analogy with the species-area relationship, that the probability of survival P_S (i.e. $1 - P_E$) increases with K according to a power law. Pioneering work by Brook et al. (2006) and Hilbers et al. (2016) used simulation models and parameter values estimated using population time-series data to model the effects of changes in K on P_E . Building upon this, Wolff et al. (2023) use the data from Hilbers et al. (2016) to consider the functional form of the relationship between P_S and K . They find that a Gompertz curve offers accurate predictions for most mammals, although they provide no assessment of whether the Gompertz is the true underlying relationship, nor how the shape changes with different parameter and demography assumptions.

We argue that it is essential to better understand the shape of the P_E vs. K relationship, and its generality, because it will strongly influence the effects on biodiversity of recent and ongoing habitat destruction and degradation. Here we tackle this problem using simulation models which characterise a broad diversity of population processes across widely varying demographic parameters. Remarkably, we discover that one particular curve – defined by a modified Gompertz curve – provides an exceptionally and consistently good fit to our simulation results across a wide range of combinations of model input parameters and four different model structures. We go on to provide a theoretical explanation for why the curve takes this form, and, with the assumption of density-dependent growth, show the form of the curve will be similar for all extant populations. We believe these discoveries, and the underpinning framework, substantially enhance our understanding of, and capacity to mitigate, the dynamics of the unfolding extinction crisis.

The shape of the curve

We conducted simulations for four population models with increasingly complex structures, each allowed to run for 100 years.. All of our models assumed density-dependent growth between years, reflected by a logistic relationship between population growth rate and current population size relative to carrying capacity. Model A assumed separate populations of males and females with independent growth rates, though each sex was subject to the same realisation of environmental stochasticity each year. In Model B the growth rate of males and females was dependent on the total number of both sexes combined, rather than separately for each sex. Model C extended Model B to biparental care, such that non-paired individuals did not reproduce. This model also required assumptions regarding adult annual survival rate and age of first breeding. For Models A, B, and C, environmental stochasticity in each year was independent of all proceeding years. Model D built upon C but differed in that it allowed for temporal autocorrelation in environmental stochasticity between years, making consecutive good or bad growth rates years more likely. Models A and B had two input parameters, r_{\max} and σ , which are the maximum population growth rate and extent of environmental stochasticity respectively. Model C had two additional inputs: S_a , which is the annual survival probability for an adult in the population, and B , the age at first breeding. Model D had a further input parameter Z , which controlled the degree of temporal autocorrelation. Detailed descriptions of the four models and their parameters are given in Supplementary Appendix A.

We ran simulations for all four models across a broad range of input parameters, for values of carrying capacity K ranging from 1 to 3 million (for an explanation of the chosen range of inputs see Supplementary Appendix B). We contend that given that species lifetimes are typically in the

range of 10^5 - 10^7 years (Barnosky et al. 2011), species will only be extant today if, at reasonably large K they have life history parameters which ensure their persistence for at least 100 years. We therefore only consider sets of input parameters as “viable” if $P_E \approx 0$ in 100 years when $K = 3$ million.

We initialised 10,000 populations for each viable parameter combination and value of K , calculating the probability of survival (P_S) as the proportion of those 10,000 populations that remain extant by 100 years of simulation. We then model the change in P_S as a function of K (denoted $P_S(K)$) using a Gompertz curve, modified through the addition of a “shape” parameter (γ). P_E as a function of K (denoted $P_E(K)$) within 100 years is then given by $1 - P_S(K)$; this relationship is thus a transformed and modified Gompertz curve, but hereafter we refer simply to it as a “modified Gompertz” curve, which is an asymmetric sigmoid. Formally:

$$\begin{aligned} P_S(K) &= \exp(-\exp(a + b K^\gamma)), \\ P_E(K) &= 1 - P_S(K) \end{aligned} \quad (1)$$

where a , b , and γ are constants. Fitting this model to simulations for each plausible parameter set and population model (A-D), using a process described in Supplementary Appendix C, generated r^2 -values every one of which exceeded 0.995. Figure 1 shows an example for each of our four types of population and illustrates the extremely close fit of the modified Gompertz despite marked differences in model assumptions. This comparison also makes the noteworthy point that moving from models A-D – that is to say adding realism - increases the probability of extinction (i.e. the $P_E(K)$ curve shifts to the right).

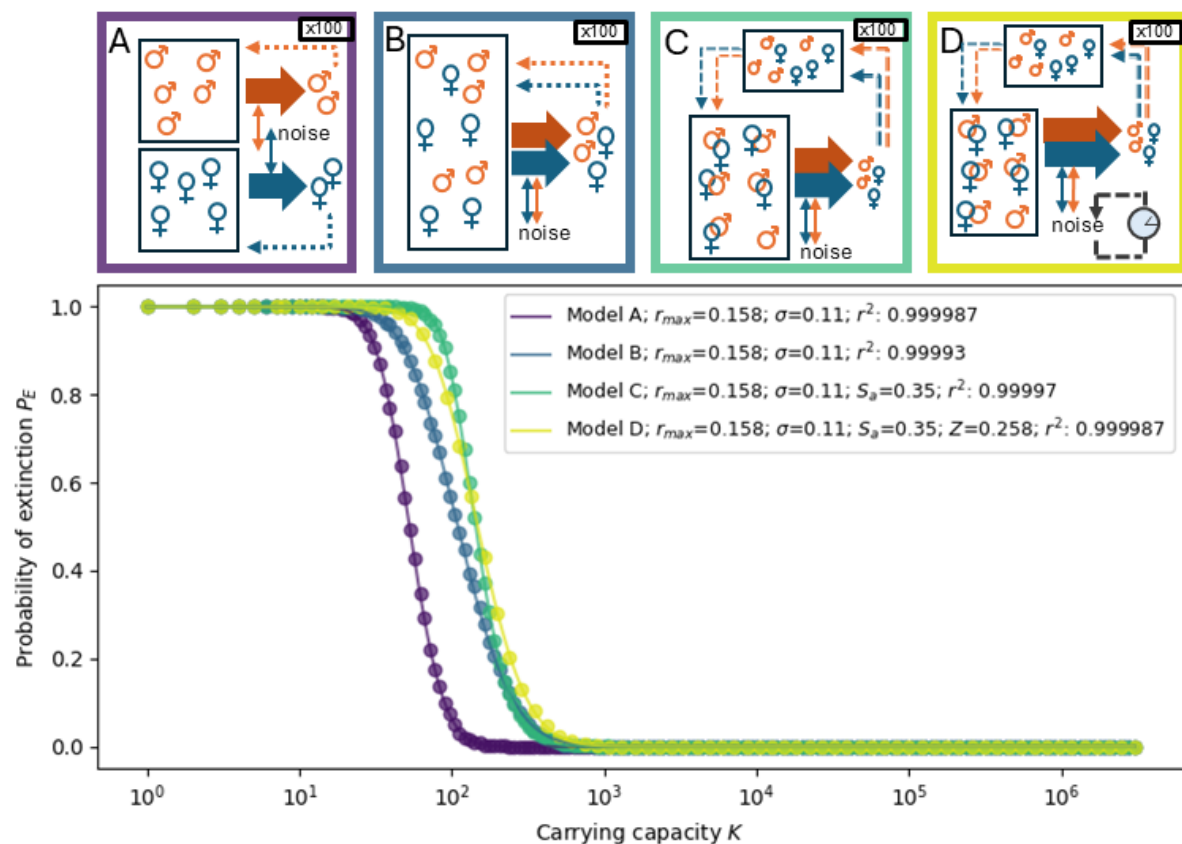


Figure 1. Modelled probabilities of extinction (circles) for a range of carrying capacities and fitted modified Gompertz curves (lines) for Models A, B, C, and D, along with a diagrammatic

representation of each model. In each diagram, the individuals contained within the box represent the ‘current’ population, with those outside and the various arrows representing the mechanism by which individuals are recruited at next time step. Model A with male and female growth rates (large arrows) dependent only on the number of individuals of each sex respectively. Model B with growth rate for each sex being dependent on the number of individuals in each sex together. Model C with a ‘delay’ to growth caused by the time taken for juveniles to reach breeding maturity, and Model D: the same as Model C, but with temporally autocorrelated environmental stochastic noise. Associated r^2 values as shown in the figure legend are extremely high. We used middle-of-the-road values for the input parameters: $r_{\max}=0.158$, $\sigma=0.11$ for all four models, $S_a=0.35$ for Models C and D, and $Z=0.258$ for D.

The modified Gompertz is generally applicable

A modified Gompertz curve thus generally describes the relationship between probability of extinction and carrying capacity across a broad range of input parameters and model types. It is also interesting to consider the case when the initial population size deviates from carrying capacity (Figure 2), a very plausible circumstance, for example when an area of a species’ habitat is suddenly lost (initial population exceeding carrying capacity) or an extirpated population is re-introduced into its former range (likely with fewer individuals in the initial population than the carrying capacity). We find that under these circumstances the relationships continue to follow modified Gompertz curves – albeit with slightly different shapes. Using Model A, but with initial population size (N_0) set at a fraction of K (Figure 2a), larger carrying capacities are required to prevent increases in the extinction risk when the initial population is a smaller proportion of K . Setting initial populations as some fixed number, wholly independent of K , provides slightly counterintuitive results (Figure 2b). Holding K fixed, P_E increases with initial population size. Density-dependence means that the first changes from the initial population are to push the population towards K . When the initial population exceeds K , density dependence pushes the population down. Moreover, the environmental stochasticity scales with population size, so that larger populations face more extreme environmental stochasticity driven changes in absolute terms. Density-dependent growth, and a higher likelihood of relatively large environmental stochastic shocks, both act to increase the extinction risk faced by a population exceeding the carrying capacity of its environment.

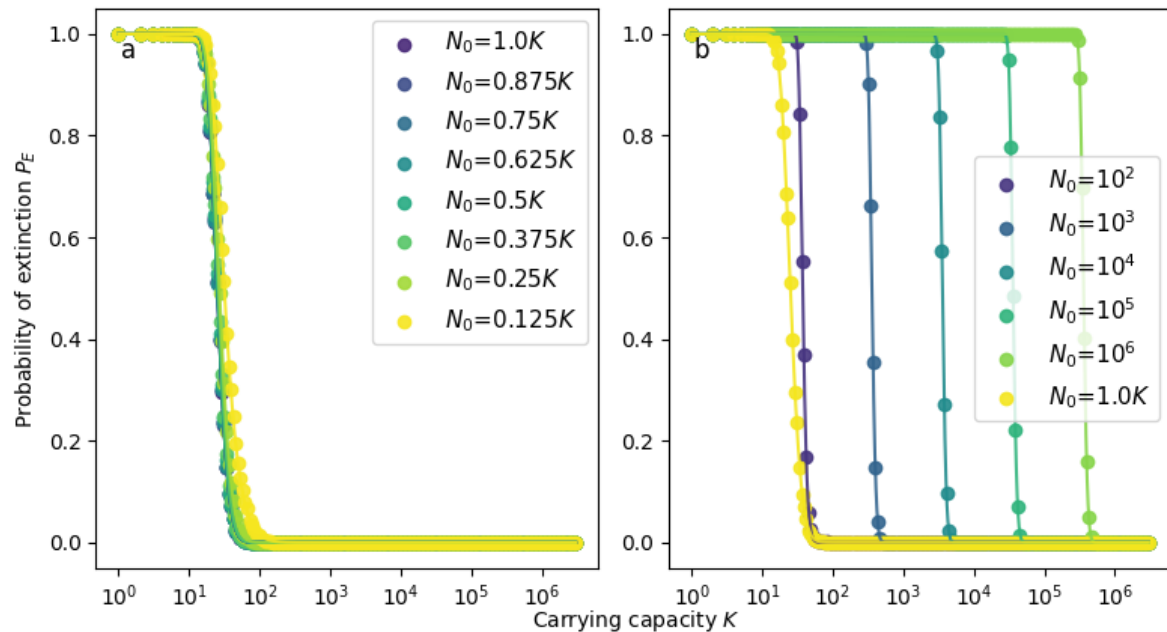


Figure 2. Empirical probabilities of extinction (circles) for a range of carrying capacities and fitted modified Gompertz curves (lines) when initial population size (N_0) in Model A ($r_{max}=0.56$, $\sigma=0.15$) differs from the carrying capacity K either as some proportion of K (a) or is an absolute number independent of K (b). Associated r^2 values for the modified Gompertz curves remain extremely high ($r^2>0.9999$ for all curves).

We also explored the performance of the modified Gompertz curve in approximating a wholly different population model parameterised using population-specific demographic rates estimated from field studies. Shaffer and Samson (1985) provide a sex- and age-structured, density-dependent, population model for brown bears (*Ursus arctos*) using data from a 12-year study in Yellowstone National Park. They report estimates of probability of extinction within 100 years for seven hypothetical carrying capacities. Fitting the modified Gompertz curve (Equation 1) to their data again shows an extremely close approximation (see Supplementary Figure D1; $r^2 = 0.9991$).

The theoretical basis for the modified Gompertz

In order to understand the apparent generality of the modified Gompertz curve, we complement these simulations with a theoretical analysis of Model A (all technical details and formal derivations are set out in Supplementary Appendix E). We selected Model A is because its relative simplicity allows for analytical tractability; the additional features of Models B through D do not affect the key insight we gain from our analysis: the mean-reverting nature of extant populations around the steady state as function of the carrying capacity. This result allows us to generalise our theoretical foundation to the rest of the models, unless one adds features that break this fundamental feature, such as persistent non-Gaussian fluctuations, or changing drastically the type of density dependence. We focus on the continuous-time, logistic stochastic differential equation (SDE) and study its properties. We then obtain its expected time to extinction as a function of K and define the parameter space that allows extant species to exist. Coherently with the numerical analysis, we focus on a population starting at carrying capacity and show how its probability of survival P_S can be well approximated by a Gompertz curve in K . We achieve this

result by approximating the transition density of the logistic SDE with the one of an Ornstein-Uhlenbeck process centred on carrying capacity and then integrating it over all achievable (i.e. non-extinct) states. The intuition behind this result is that for all viable parameter sets, following an environmental fluctuation the population will tend to revert towards carrying capacity. As ecosystem carrying capacity increases, the role played by the initial fluctuation becomes increasingly less relevant and the probability of long-run persistence increases. Indeed, this theoretical analysis reveals the modified Gompertz relationship to be general to all populations, provided two assumptions are met. First, that population growth rate is governed by density dependence, such that the population cannot grow infinitely. This density dependence could take any form and is not restricted to logistic growth. Second, that the population demographics give rise to a steady state population that is above 0 (i.e. its demographic parameters are contained in the viable parameter set we suggest describes extant species). Given these highly defensible assumptions, the relationship between extinction risk and carrying capacity will be well approximated by a Gompertz curve.

Prioritising conservation interventions

As one of many conservation implications of understanding the population extinction risk-carrying capacity relationship, consider setting priorities among competing alternatives. Other things being equal, if the primary goal is to limit extinctions, which recent work has indicated to be the preference of both experts and a general audience (Meier 2024), priority for interventions could be given to those for which a marginal increase in carrying capacity is likely to have the largest reduction in extinction risk, i.e. those for which the first derivative of the modified Gompertz curve is greatest, the point of inflection of the curve. For all models, this occurs when the probability of extinction is greater than 50%, with median P_E values at the point of inflection being 0.65, 0.75, 0.74, 0.75 for Models A, B, C, and D respectively (Supplementary Figure F1). These results, which are remarkably consistent across different parameter combinations, suggest that conservation efforts might yield the highest benefits for populations for which $P_E \approx 0.75$. An important caveat here is that potential interventions will of course vary in other ways too – particularly in net costs, which may often be higher in situations where anthropogenic pressures are such that populations are closer to extinction.

Compatibility with Red List criteria

Finally, we believe that the modified Gompertz relationship described here can be directly integrated with IUCN's Red List process for assessing extinction risk. Red List Criterion E categorises species that have a 10% probability of extinction within 100 years as Vulnerable, the least threatened at-risk category (IUCN 2001). We thus examine the relationship between our simulation parameters and K_{10} , which we define as the carrying capacity for which the population has a 10% probability of extinction within 100 years. For Models A (Figure 3a) and B (Figure 3b) K_{10} decreases with increasing r_{\max} , but is relatively invariant across population parameter combinations for r_{\max} values >0.4 . The K_{10} value of the plateau is approximately 200 greater for Model B than A. In those models, K_{10} also increases with environmental stochasticity (σ). See Supplementary Appendix G for the rationale behind the choice of 10%, along with results for Models C and D.

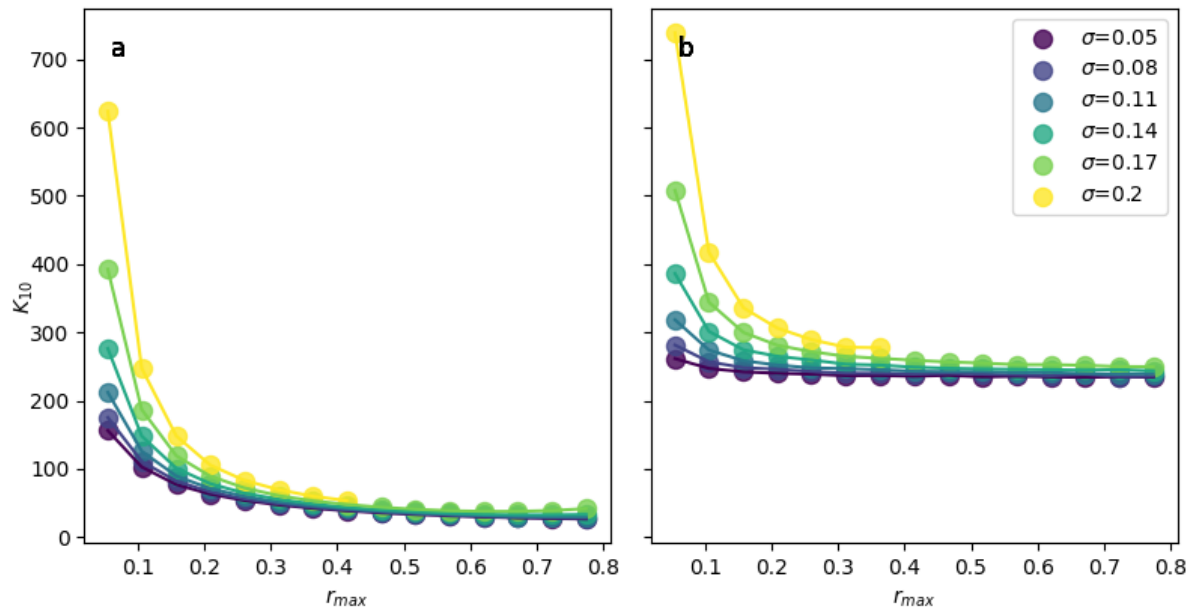


Figure 3. The relationship between K_{10} – the K value at which $P_E = 0.1$ – and maximum growth rate r_{\max} for various values of environmental stochasticity σ for (a) Model A and (b) Model B.

Discussion

Using simple population dynamic models, we have discovered that the relationship between population carrying capacity and probability of extinction is well approximated by a modified Gompertz function, and that this is robust across many different permutations of the parameter inputs and modelling assumptions. We have shown theoretically why the curve is approximated by a modified Gompertz, and crucially that this is general across extant species so long as they face some form of density dependence.

Further work is needed to understand how the findings of this study translate into estimates of species-level extinction risk. For the great majority of our model populations the probability of extinction decreases to near-zero very quickly as K increases, with negligible risk of extinction being observed at (and commonly below) values of $K < 10,000$. Real-world global species often have total populations numbering in the millions (Callaghan 2021). However, our models are of individual populations. The density-dependent behaviour of the logistic growth rate may not apply in the same way at global scales. Nevertheless, global metapopulations of species might well be characterised as a set of coupled sub-populations, interacting through the transfer of individuals and resources. Some species may be well-represented by a single population of the type we have simulated here, whilst dispersal, migration, habitat and resource fragmentation, amongst other things, will necessitate a more complex approach for others. Successful modelling of global metapopulations will require understanding of the dynamics of subpopulations as well as their interactions; we believe that we have gone some way to addressing the former in this study.

This paper follows the small population paradigm in focusing on the role of stochasticity in driving populations extinct. Future research could extend our modelling framework to assess the impacts of human-driven deterministic changes – such as the increases in extinction risk caused by anthropogenic reductions in population growth rates or adult survival, or ongoing declines in

habitat available and corresponding carrying capacity. Understanding the likely extinction impacts of such changes – acting either independently or synergistically – is crucial if we are to begin to halt and reverse biodiversity loss. To this end, we believe this study represents a significant step forward in understanding the dynamics of the extinction crisis and in prioritising, guiding and evaluating efforts to mitigate it.

Methods

We devised a series of population simulations with which to explore the relationship between population carrying capacity and probability of extinction. Each of our models is based upon a logistic growth model, in which the growth rate at a given time is based upon the number of current individuals in the population N over the carrying capacity K , and the maximum growth rate r_{\max} , such that realised growth rate is maximised when $N = 1$ and is zero when $N = K$. For a mathematical formalisation of this and the following models, see Supplementary Appendix A. We set the time step for our simulations to be one year, since empirical species data, for example survival rates and breeding rates, are typically expressed on annual timescales.

In Model A, the growth rates of the two sexes are calculated independently of each other. To represent demographic stochasticity, at each time step the new number of individuals of each sex was drawn from a Poisson distribution. Environmental stochasticity was implemented as a random variable normally distributed about zero, with standard deviation σ . We reasoned that environmental factors affecting one sex would probably affect the other equally, so we applied the same environmental stochasticity at each time step. Model B is similar to Model A but introduces demographic dependence such that the growth rate of each sex is dependent on the number of individuals in both sexes: if there is a reduced number of males at a given timestep, the growth rate of females would also be affected.

Model C builds on Model B but introduces more complex features of demographic stochasticity: biparental care, and a representation of an age at first breeding (a time to maturity). The growth rate of each sex is now governed by the number of adult males and females in the population at some time before the current time step, determined by the age at first breeding. This necessitated a reformulation of the model, and the inclusion of additional parameters S_a , the annual survival rate of adults in the population, and B , the age at first breeding. Combinations of S_a and r_{\max} give plausible values of B , as described in Supplementary Appendix B.

Model D is an extension of Model C incorporating a representation of temporally autocorrelated environmental stochasticity. We replaced the normally distributed random variable from the previous models with a random walk with a central tendency, such that the realisation of environmental noise at a given time was more likely to be closer to that of the previous time step. This necessitated the inclusion of a final model parameter Z , which is a ‘reversion’ factor: the tendency of the noise to ‘walk’ back to zero. For $Z = 0$, the environmental noise is effectively a random walk with no tendency to revert to zero, and for $Z = 1$, the environmental noise is effectively drawn from a normal distribution about zero at each timestep (as is the case in Models A, B, and C).

For each model, we ran simulations across a range of parameters, varying r_{\max} between 0.055 and 0.774, σ between 0.05 and 0.55, S_a between 0.35 and 0.95, and Z between 0.01 and 1.0. For the methodology behind the selection of these parameter spaces see Supplementary Appendix B. For each set of inputs, we ran simulations for a range of K values, which were geometrically

distributed between 1 and 3 million. For each individual value of K we ran 10,000 repeats, recording the probability of extinction P_E as the proportion of those repeats that reached extinction at or before 100 years. The modified Gompertz model was fitted to the results for each set of input parameters following a process described in Supplementary Appendix C.

In the basic runs for Models A through D, the simulation was initialised with the number of individuals equal to the carrying capacity K . To explore the effect of beginning with populations not at the carrying capacity, we initialised Model A with $r_{max}=0.56$ and $\sigma=0.15$, varying the starting population N_0 in two ways. First, such that N_0 was proportional to K in 8 increments between 0.125 and 1.0, second such that N_0 was a constant, regardless of the value of K , in incremental values between 1 and 1 million in factors of 10. As before, the number of individuals in each sex was set at half the total carrying capacity. We then varied K , running 10,000 repeats for each value as before, and examined the relationship between P_E and K .

Identifying the carrying capacity at which a population has a 10% probability of extinction (K_{10}), shown in Figure 3, was a matter of re-arranging the modified Gompertz curve equation as follows:

$$K_Q = \left(\frac{\ln(-\ln(1-Q)) - a}{b} \right)^{\frac{1}{\gamma}} \quad (2)$$

Where K_Q is the carrying capacity at the probability of interest Q , and a , b , and γ are the previously defined curve parameters. Calculation of K_{10} is then a simple matter of setting Q to 0.1 and inputting the curve parameters obtained via the fitting process described in Supplementary Methods C.

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