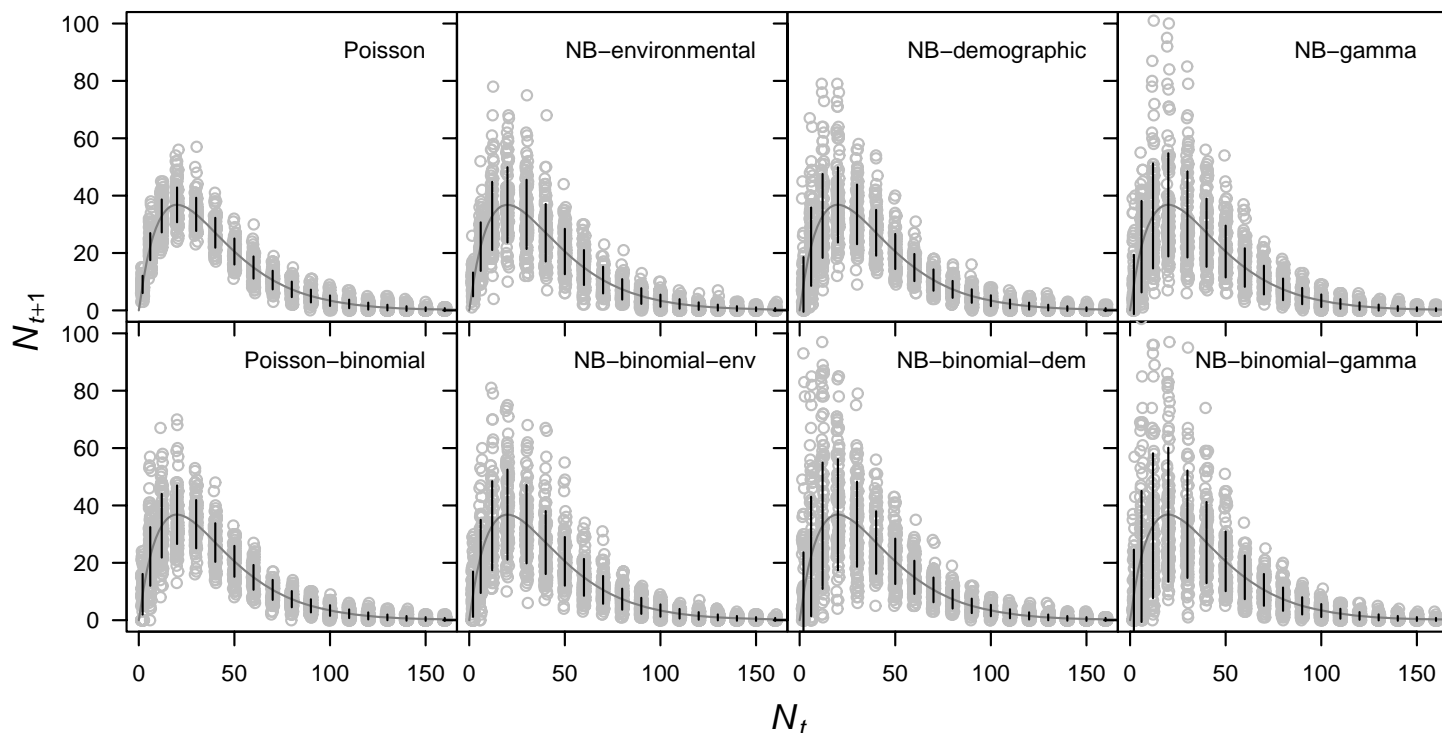


# Extinction risk depends strongly on factors contributing to stochasticity

Brett A. Melbourne<sup>1</sup> & Alan Hastings<sup>2</sup>

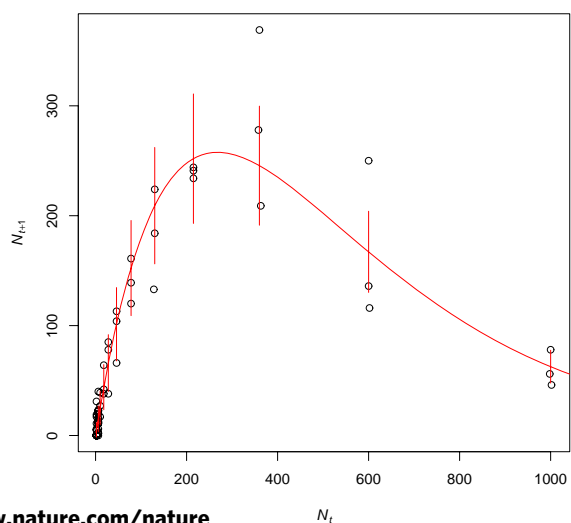
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**Supplementary Figure 1 | Stochastic realisations of the production functions for a family of stochastic Ricker models.** For each level of initial abundance  $N_t$ , 100 realisations of the abundance in the next generation  $N_{t+1}$  were simulated. Points are jittered along the x-axis for clarity. The curve shows the theoretical mean of the distribution. Error bars show the theoretical standard deviation. Model

parameters:  $R = 5$ ,  $\alpha = 0.05$ ,  $k_D = 0.5$ ,  $k_E = 10$ . The stochastic parameters ( $k_D$ ,  $k_E$ ) were set so that the total variance due to demographic heterogeneity was equal to the total variance due to environmental stochasticity; this also corresponds to equal variance at the stationary point in the production function. Abbreviations identify the models listed in Fig. 1 of the main text.



**Supplementary Figure 2 | Data from the *Tribolium* experiment showing the best fitting stochastic Ricker model.** The best fitting model was the negative binomial-binomial-gamma Ricker model, which is a model for the combined effects of all stochastic sources: demographic stochasticity, stochastic sex determination, environmental stochasticity, and demographic heterogeneity. The curve shows the theoretical mean of the distribution. Error bars show the theoretical standard deviation. Details of the model fit are given in Table 1 of the main text.

## Supplementary Methods

**Derivation of stochastic Ricker models.** The original derivation of the deterministic Ricker model was for fish populations undergoing cannibalism of eggs by adults<sup>26</sup>. Ricker assumed first that eggs were laid in a short discrete event at the beginning of the year. For the rest of the year, adults were free to cannibalise eggs and juveniles. Here, we extend Ricker's model to derive a family of stochastic models that include stochasticity in various aspects of the lifecycle (see Fig. 1 in the main text).

The foundation of the stochastic models is the Poisson Ricker model, which we derive first. It includes three sources of demographic stochasticity in the lifecycle: births, density-dependent mortality, and density-independent mortality. To this basic model we then add either environmental heterogeneity (variation in the birth rate in time or space), demographic heterogeneity (variation in the birth rate between individuals within the population), or both to derive respectively the negative binomial-environmental (NBe), the negative binomial-demographic (NBd), and the negative binomial-gamma (NBg) Ricker models.

We then derive models where sex is determined stochastically. We first add stochastic sex determination to the Poisson Ricker model, which leads to the Poisson-binomial (PB) Ricker model. Finally, we add environmental heterogeneity, demographic heterogeneity, or both to the Poisson-binomial Ricker model to derive respectively the negative binomial-binomial-environmental (NBBe), the negative binomial-binomial-demographic (NBBd), and the negative binomial-binomial-gamma (NBBg) Ricker models. These models form a nested family of stochastic Ricker models, where the NBBg model is the full model.

**Poisson Ricker model.** The Poisson Ricker model is a basic model of demographic stochasticity. There are  $N_t$  adults in the population at time  $t$ , the beginning of the lifecycle. Let individual adults give birth randomly according to a Poisson process at a constant rate  $\beta$  in a short, defined period at the beginning of the lifecycle. Then,  $B_{i,t}$ , the number of eggs or young produced by adult  $i$  at the beginning of the lifecycle, is a Poisson random variable (e.g. ref. 31):

$$B_{i,t} \sim \text{Poisson}(\beta), \quad (\text{S1})$$

where  $\beta$  is the mean number of births per adult.

To become an adult, each individual offspring must now survive being cannibalised or dying from

density-independent causes. Ricker assumed that an individual adult encounters and eats eggs or young randomly with constant probability and no handling time<sup>26</sup>. With these assumptions about the stochastic search process, the probability  $c_i$  that an individual offspring is not eaten by adult  $i$  by the end of the period of exposure to predation is

$$c_i = e^{-\alpha}, \quad (\text{S2})$$

where  $\alpha$  is the adult search rate (see e.g. p 53 ref. 32). The probability  $c$  that an individual offspring is not eaten by any adults is thus

$$c = \prod_i^{N_t} c_i = e^{-\alpha N_t}. \quad (\text{S3})$$

The probability that an individual survives all forms of mortality during the lifecycle is then

$$s = (1 - m)c, \quad (\text{S4})$$

where  $m$  is the probability of density-independent mortality.

Summing up survival of all offspring from adult  $i$  gives a binomial distribution for  $S_{i,t+1}$ , the number surviving to the adult stage, given that  $B_{i,t}$  were produced by that adult. That is

$$S_{i,t+1} \sim \text{Binomial}(B_{i,t}, s). \quad (\text{S5})$$

Since  $B_{i,t}$  is Poisson (Eq. S1),  $S_{i,t+1}$  has a compound binomial-Poisson distribution. By the law of total probability this compound distribution reduces to a Poisson distribution (see e.g. ref. 31):

$$S_{i,t+1} \sim \text{Poisson}(R e^{-\alpha N_t}), \quad (\text{S6})$$

where  $R = \beta(1-m)$  and is immediately identifiable as the finite rate of population increase of the deterministic Ricker model.

Finally, we add up the surviving offspring produced by all of the adults. Since the sum of independent Poisson random variables is also Poisson (see e.g. ref. 33), the total offspring surviving to become adults is:

$$N_{t+1} = \sum_i^{N_t} S_{i,t+1} \sim \text{Poisson}(N_t R e^{-\alpha N_t}). \quad (\text{S7})$$

Thus, with Ricker's assumptions we find that  $N_{t+1}$  has a Poisson distribution with mean equal to the deterministic Ricker model. The probability mass function (pmf) for the Poisson Ricker model is given in Supplementary Table 1. Dennis *et al.* also derived a Poisson Ricker model for demographic stochasticity from similar assumptions<sup>25</sup>.

**Supplementary Table 1. Probability mass functions (pmfs) of stochastic Ricker models with discrete individuals.**

Model	pmf
Poisson	$\frac{e^{-\mu} \mu^{n_{t+1}}}{n_{t+1}!}, \mu = n_t R e^{-\alpha n_t}$
Negative binomial - environmental	$\binom{n_{t+1} + k_E - 1}{k_E - 1} \left( \frac{\mu}{k_E + \mu} \right)^{n_{t+1}} \left( \frac{k_E}{k_E + \mu} \right)^{k_E}, \mu = n_t R e^{-\alpha n_t}$
Negative binomial - demographic	$\binom{n_{t+1} + n_t k_D - 1}{n_t k_D - 1} \left( \frac{\mu}{n_t k_D + \mu} \right)^{n_{t+1}} \left( \frac{n_t k_D}{n_t k_D + \mu} \right)^{n_t k_D}, \mu = n_t R e^{-\alpha n_t}$
Negative binomial - gamma	$\int_{R_E=0}^{\infty} G(R_E) \binom{n_{t+1} + n_t k_D - 1}{n_t k_D - 1} \left( \frac{\mu}{n_t k_D + \mu} \right)^{n_{t+1}} \left( \frac{n_t k_D}{n_t k_D + \mu} \right)^{n_t k_D}, G(R_E) = R_E^{k_E-1} \exp\left(-\frac{R_E k_E}{R}\right) \left(\frac{k_E}{R}\right)^{k_E} \frac{1}{\Gamma(k_E)}, \mu = n_t R_E e^{-\alpha n_t}$
Poisson-binomial	$\sum_{F=0}^{n_t} \binom{n_t}{F} z^F (1-z)^{n_t-F} \frac{e^{-\lambda} \lambda^{n_{t+1}}}{n_{t+1}!}, \lambda = F \frac{R}{z} e^{-\alpha n_t}$
Negative-binomial-binomial-environ.	$\sum_{F=0}^{n_t} \binom{n_t}{F} z^F (1-z)^{n_t-F} \binom{n_{t+1} + k_E - 1}{k_E - 1} \left( \frac{\lambda}{k_E + \lambda} \right)^{n_{t+1}} \left( \frac{k_E}{k_E + \lambda} \right)^{k_E}, \lambda = F \frac{R}{z} e^{-\alpha n_t}$
Negative-binomial-binomial-demog.	$\sum_{F=0}^{n_t} \binom{n_t}{F} z^F (1-z)^{n_t-F} \binom{n_{t+1} + F k_D - 1}{F k_D - 1} \left( \frac{\lambda}{F k_D + \lambda} \right)^{n_{t+1}} \left( \frac{F k_D}{F k_D + \lambda} \right)^{F k_D}, \lambda = F \frac{R}{z} e^{-\alpha n_t}$
Negative-binomial-binomial-gamma	$\int_{R_E=0}^{\infty} G(R_E) \sum_{F=0}^{n_t} \binom{n_t}{F} z^F (1-z)^{n_t-F} \binom{n_{t+1} + F k_D - 1}{F k_D - 1} \left( \frac{\lambda}{F k_D + \lambda} \right)^{n_{t+1}} \left( \frac{F k_D}{F k_D + \lambda} \right)^{F k_D}, G(R_E) = R_E^{k_E-1} \exp\left(-\frac{R_E k_E}{R}\right) \left(\frac{k_E}{R}\right)^{k_E} \frac{1}{\Gamma(k_E)}, \lambda = F \frac{R_E}{z} e^{-\alpha n_t}$

The pmf is the conditional probability  $\Pr\{N_{t+1} = n_{t+1} | N_t = n_t\}$ ,  $\binom{a}{b}$  is the binomial coefficient, and  $\Gamma(x)$  is the gamma function. Parameters:  $R$  finite rate of growth,  $\alpha$  density dependent parameter (adult search rate),  $R_E$  finite rate of growth for a particular condition of the environment,  $F$  the number of females,  $z$  the probability that an individual is female,  $k_E$  the shape parameter of the gamma distribution for environmental stochasticity,  $k_D$  the shape parameter of the gamma distribution for demographic heterogeneity. Parameters are defined in the Supplementary Methods.

### Negative-binomial-environmental Ricker model.

This is a model for the combined effects of demographic and environmental stochasticity. We allow the environment to vary stochastically in time, space, or both. The model development follows that for the Poisson Ricker model. The birth rate  $\beta_{t,x}$  now varies stochastically in time and space ( $x$ ), representing environmental stochasticity. The number of births summed over all adults at a particular time and place is a sum of Poissons, so is also Poisson:

$$B_{t,x} = \sum_i^{N_t} B_{i,t,x} \sim \text{Poisson}(N_t \beta_{t,x}). \quad (\text{S8})$$

We represent variation in  $\beta_{t,x}$  in time or space as a gamma random variable with mean  $\beta$  and shape parameter  $k_E$ :

$$\beta_{t,x} \sim \text{Gamma}(\beta, k_E). \quad (\text{S9})$$

Since the distribution is conditional on  $N_{t,x}$ , the distribution of  $N_{t,x} \beta_{t,x}$  is also gamma but with mean  $N_{t,x} \beta$  and shape parameter  $k_E$ ,

$$N_{t,x} \beta_{t,x} \sim \text{Gamma}(N_{t,x} \beta, k_E). \quad (\text{S10})$$

The distribution of total offspring  $B_{t,x}$  is then a gamma mixture of Poissons (Eq. S8), which is one

form of the negative binomial distribution (see e.g. ref. 33):

$$B_{t,x} \sim \text{NegBinom}(N_{t,x} \beta, k_E), \quad (\text{S11})$$

where  $\beta$  is the mean birth rate in time or space.

As for the Poisson Ricker model (Eqs S2-S5), survival of offspring is binomial:

$$S_{t+1,x} \sim \text{Binomial}(B_{t,x}, s). \quad (\text{S12})$$

Since  $B_{t,x}$  is negative binomial (Eq. S11), the number of surviving offspring from time  $t$  at location  $x$  has a compound binomial-negative binomial distribution. This compound distribution reduces to a negative binomial distribution:

$$N_{t+1,x} \sim \text{NegBinom}(N_{t,x} R e^{-\alpha N_{t,x}}, k_E), \quad (\text{S13})$$

where again  $R = \beta(1-m)$ . The pmf is given in Supplementary Table 1. The variance parameter,  $k_E$ , of this model is not density dependent. That is, the variance in final abundance  $N_{t+1}$  varies only with the final abundance and does not depend on the initial abundance  $N_t$ . Ludwig<sup>5</sup> also derived a negative binomial Ricker model for demographic and environmental stochasticity but since he did not

incorporate density dependent mortality, the model has a different parameterisation

**Negative-binomial-demographic Ricker model.** This is a model for the combined effects of demographic stochasticity and demographic heterogeneity. The model development also follows that for the Poisson Ricker model. Let adult  $i$  give birth randomly at a constant rate  $\beta_i$  specific to that adult. Then,  $B_{i,t}$ , the number of offspring produced by adult  $i$  at the beginning of the lifecycle, is a Poisson random variable:

$$B_{i,t} \sim \text{Poisson}(\beta_i), \quad (\text{S14})$$

where  $\beta_i$  is the mean number of births for adult  $i$ . The mean birth rate for a particular adult reflects the tendency of that individual to produce more or less offspring than other adults. For example, a large adult might consistently produce more offspring than a small one. To capture variation in birth rate between individuals we assume that  $\beta_i$  follows a gamma distribution, with mean  $\beta$  and variance determined by the shape parameter  $k_D$ , and therefore the distribution of  $B_{i,t}$  is negative binomial (gamma mixture of Poissons):

$$B_{i,t} \sim \text{NegBinom}(\beta, k_D). \quad (\text{S15})$$

Survival is binomial (Eqs S2-S5),

$$S_{i,t+1} \sim \text{Binomial}(B_{i,t}, s). \quad (\text{S16})$$

and so the distribution of  $S_{i,t+1}$  is a compound binomial-negative binomial distribution, which reduces to a negative binomial (as previously):

$$S_{i,t+1} \sim \text{NegBinom}(R e^{-\alpha N_t}, k_D), \quad (\text{S17})$$

where again  $R = \beta(1-m)$ .

Since the sum of independent negative binomials with the same  $k$  parameter is also a negative binomial (see e.g. ref. 33), the survivors summed over all adults is:

$$N_{t+1} = \sum_i^{N_t} S_{i,t+1} \sim \text{NegBinom}(N_t R e^{-\alpha N_t}, k_D N_t). \quad (\text{S18})$$

Thus, with demographic heterogeneity in addition to demographic stochasticity in births and deaths,  $N_{t+1}$  has a negative binomial distribution with mean equal to the deterministic Ricker model. The pmf is given in Supplementary Table 1. The nature of the variance in the final abundance for this model is particularly interesting, since the variance parameter of the negative binomial,  $k' = k_D N_t$ , is density-dependent; it is a function of the initial abundance  $N_t$ . At low initial abundance,  $k'$  is small, yielding larger variance to mean

ratios for  $N_{t+1}$ , whereas as at high initial abundance  $k'$  is large and the variance approaches the Poisson limit (Fig. 2 in the main text). This contrasts with the model for environmental stochasticity (Eq. S13) in which the variance does not depend on the initial abundance.

**Negative-binomial-gamma Ricker model.** This is a model for the combined effects of demographic stochasticity, demographic heterogeneity, and environmental stochasticity. We combine the assumptions of the previous three models, specifically that the number of offspring produced by an adult is a Poisson random variable, variation in birth rate between individuals within a population (demographic heterogeneity),  $\beta_i$ , follows a gamma distribution with mean  $\beta_{t,x}$ , variation in the population mean at different times and locations,  $\beta_{t,x}$ , follows a gamma distribution with mean  $\beta$ , and survival is binomial. With these assumptions, the distribution of  $N_{t+1,x}$  is a compound negative binomial-gamma distribution (gamma mixture of negative binomials) with mean equal to the deterministic Ricker model and two variance parameters,  $k_D$  and  $k_E$ . The pmf is given in Supplementary Table 1.

**Poisson-binomial Ricker model.** This is a model for the combined effects of demographic stochasticity and stochastic sex determination. The derivation is similar to the Poisson Ricker model. The number of offspring  $B_{i,t}$  from female  $i$  at the beginning of the lifecycle, is a Poisson random variable:

$$B_{i,t} \sim \text{Poisson}(\beta), \quad (\text{S19})$$

where  $\beta$  is now the mean number of births per female, rather than per adult. Survival of offspring is as before (Eqs S2-S5):

$$S_{i,t+1} \sim \text{Binomial}(B_{i,t}, s), \quad (\text{S20})$$

where, importantly, predation involves both sexes (Eq. S3). Adding up the surviving offspring produced by all of the females yields a Poisson distribution:

$$N_{t+1} = \sum_i^{F_t} S_{i,t+1} \sim \text{Poisson}(F_t \beta (1-m) e^{-\alpha N_t}), \quad (\text{S21})$$

where  $F_t$  is the number of females at the beginning of the lifecycle. Since  $F_t$  is a binomial random variable,

$$F_t \sim \text{Binomial}(N_t, z), \quad (\text{S22})$$

where  $z$  is the probability that an individual is female, the distribution of  $N_{t+1}$  is a Poisson-binomial distribution (or Bernoulli mixture of Poissons) with mean equal to the deterministic Ricker model and  $R = z\beta(1-m)$ . The pmf is given in Supplementary Table 1.

**Negative binomial-binomial-environmental Ricker model.** This is a model for the combined effects of demographic stochasticity, stochastic sex determination, and environmental stochasticity. The derivation is substantially the same as the Poisson-binomial and negative binomial-environmental Ricker models. Adding up the surviving offspring produced by all of the females yields a negative binomial distribution:

$$N_{t+1} = \sum_i^{F_t} S_{i,t+1} \sim \text{NegBinom}(F_t \beta(1-m)e^{-\alpha N_t}, k_E). \quad (\text{S23})$$

Since  $F_t$  is a binomial random variable, the distribution of  $N_{t+1}$  is a negative-binomial-binomial distribution (or Bernoulli mixture of negative binomials) with mean equal to the deterministic Ricker model and  $R = z\beta(1-m)$ . The pmf is given in Supplementary Table 1.

**Negative binomial-binomial-demographic Ricker model.** This is a model for the combined effects of demographic stochasticity, stochastic sex determination, and demographic heterogeneity. The derivation is substantially the same as the previous model. The number of surviving offspring from all females has a negative binomial distribution:

$$N_{t+1} = \sum_i^{F_t} S_{i,t+1} \sim \text{NegBinom}(F_t \beta(1-m)e^{-\alpha N_t}, k_D F_t). \quad (\text{S24})$$

The distribution of  $N_{t+1}$  is thus a negative-binomial-binomial distribution with mean equal to the deterministic Ricker model and  $R = z\beta(1-m)$ . The pmf is given in Supplementary Table 1. The variance in the final abundance,  $N_{t+1}$ , depends on the initial abundance, which contrasts with the previous model for environmental stochasticity (Eq. S23) in which the variance does not depend on the initial abundance.

**Negative binomial-binomial-gamma Ricker model.** This is a model for the combined effects of all stochastic sources: demographic stochasticity, stochastic sex determination, environmental stochasticity, and demographic heterogeneity. This is the full model. We combine the assumptions of the previous three models, which includes the assumptions for the negative binomial-binomial Ricker model plus the assumption that the number of females is a binomial random variable. With these assumptions, the distribution of  $N_{t+1,x}$  is a compound negative binomial-binomial-gamma distribution (gamma mixture of negative binomial-binomials) with mean equal to the deterministic Ricker model and  $R = z\beta(1-m)$ . In addition to the two variance parameters,  $k_D$  and  $k_E$ , the

probability that an individual is female,  $z$ , also influences the variance in  $N_{t+1,x}$ . The pmf is given in Supplementary Table 1.

**Total variance due to environmental stochasticity or demographic heterogeneity.** To compare models including environmental stochasticity with models including demographic heterogeneity, we set the variance parameters of these models (respectively  $k_E$  and  $k_D$ ) so that the total variance in  $N_{t+1}$  was equal. The total variance is given by integrating the variance function over  $N_t$ , thus

$$\int_0^\infty \sigma_{N_{t+1}|N_t}^2 . dN_t, \quad (\text{S25})$$

which, when the total variance for environmental stochasticity and demographic heterogeneity are equated, yields:

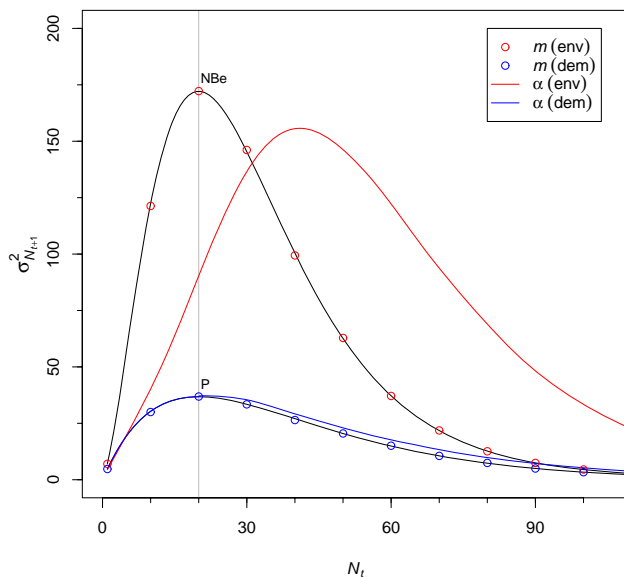
$$k_E = \frac{k_D}{\alpha}. \quad (\text{S26})$$

## Supplementary Discussion

**Extensions to the models.** Several extensions and variations on our family of models are possible. While the models described above and in the main text include demographic stochasticity in all stages of the lifecycle (births, density independent and density dependent mortality), we included environmental stochasticity and demographic heterogeneity only in births. Mortality is also subject to environmental stochasticity and demographic heterogeneity. However, we show here that adding environmental stochasticity and demographic heterogeneity in mortality to our mechanistic models does not alter our conclusions, either because the effect of mortality variance is negligible compared to variance in births, or its effects are fully accounted for by the models described in the main text.

Inclusion of stochasticity in density independent mortality is straightforward. For example, an appropriate form for stochastic variation in the probability of density independent survival ( $1-m$ ) is the beta distribution. Then, when demographic stochasticity and environmental stochasticity are the only sources of mortality variation, the resulting model is the Poisson-beta-environmental Ricker model. Since the finite rate of increase,  $R = \beta(1-m)$ , is the multiple of births and density independent survival, the effects of environmental stochasticity in mortality on population growth and extinction are indistinguishable from the effects of environmental stochasticity in births

(Supplementary Figure 3). The key effect of environmental stochasticity in either births or mortality is on the variance of  $R$ ; the form of the distribution is not important. Furthermore, because mortality is bounded between zero and one, variance in mortality is bounded, reaching a maximum of  $m(1-m)$ . In contrast, variance in births is unlimited. Thus, we expect the greatest potential for stochasticity in  $R$  to be contributed by births. Nevertheless, when mortality makes an important contribution to stochasticity in  $R$ , it is captured phenomenologically (as demonstrated in Supplementary Figure 3) by the NBe or NBBg Ricker models used in the main text, which model variation in  $R$  as a gamma distribution.



**Supplementary Figure 3 | Variance in the number of individuals in the next generation  $N_{t+1}$  as a function of the number of individuals in the current generation  $N_t$  for models with stochasticity in mortality.** Model parameters:  $R = 5$ ,  $\bar{\alpha} = 0.05$ ,  $\bar{m} = 0.9$ . Density independent mortality ( $m$ ) was included as a beta random variable, for either environmental stochasticity ( $\sigma^2_m = 0.02$ ),  $m$  (env), or demographic heterogeneity ( $\sigma^2_m = 0.08$ ),  $m$  (dem). To model density dependent mortality variation,  $\alpha$  was included as a gamma random variable ( $k_\alpha = 25$ ;  $\sigma^2_\alpha = 0.001$ ) for either environmental stochasticity,  $\alpha$  (env), or demographic heterogeneity,  $\alpha$  (dem). All models include demographic stochasticity, as in the Poisson Ricker model. Variances in  $N_{t+1}$  were estimated by simulation. Exact variances for the Poisson Ricker model (P) and Negative-binomial-environmental Ricker model (NBe;  $k_E = 10$ ,  $\sigma^2_R = 2.5$ ) are shown for reference (black curves). The vertical bar indicates the position of the stationary point in the Ricker production function.

The effect of demographic heterogeneity in density independent mortality is severely restricted, so that it never increases the variance in abundance<sup>7</sup>. When individual mortality is described by a Bernoulli

distribution and the probability of dying varies independently among individuals, demographic heterogeneity has no effect on the variance of survival; the variance in survival is always equal to the variance due to ordinary demographic stochasticity for the same mean probability of mortality. The lack of an effect of demographic heterogeneity is demonstrated in Supplementary Figure 3 where the variance in  $m$  is set close to the maximum possible, yet the variance in abundance in the next generation is indistinguishable from the Poisson Ricker model.

The effect of environmental stochasticity or demographic heterogeneity in mortality in the density dependent cannibalism parameter,  $\alpha$ , is more complex. There are similar restrictions on the magnitude of the effect of stochasticity, as the variance in the density dependent probability of survival,  $c$ , is bounded by  $c(1-c)$ . Variance in  $\alpha$  also changes the form of the mean model, either by modifying the Ricker parameters or altering the mean model away from the Ricker form. Using a gamma distribution for  $\alpha$ , we show by simulation that stochasticity in  $\alpha$  results in a variance profile for  $N_{t+1}$  that peaks well to the right of the stationary point in the Ricker production function, which is in dramatic contrast to models with stochasticity in  $m$  or  $R$  (Supplementary Figure 3). This feature is absent from our data, and so we are confident that this is not important in our laboratory system.

**Robustness of the model fit.** To examine the robustness of the model selection process for our data and experimental design, we generated artificial data assuming that alternative models to the best fitting NBBg model were in fact the true model, and then refitted the models and carried out model selection using AIC as done with the real data. Each simulation experiment was initiated with  $N_t$  equal to that used in the laboratory experiment, using the same level of replication, and with model parameters as estimated from the data for the alternative models (Table 1 in the main text). We examined the NBBg and NBBd models as alternative true models. The simulations show that our experimental design was excellent for distinguishing between models, and that our inference that the NBBg model was the best fitting model is robust.

When the true model in the simulation was pure environmental stochasticity (NBBg), it was correctly identified as the best model ( $\Delta\text{AIC} > 2$ ) in 99.1% of 1000 simulation runs when compared to the model for pure demographic heterogeneity (NBBd). The probability of wrongly accepting the NBBd model was extremely low (1 in 1000 simulation runs). The mixed



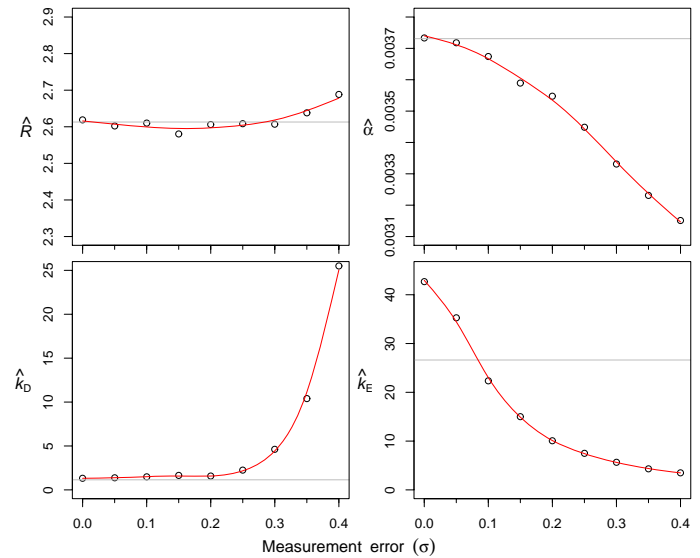
model (NBBg) was rarely (2.1%) identified as the best model when NBBe was the true model. Conversely, when the true model was pure demographic heterogeneity (NBBd), it was correctly identified as the best model in 99.8% of simulation runs when compared to the model for pure environmental heterogeneity (NBBe). The probability of wrongly accepting the NBBe model was extremely low (0 in 1000 simulation runs). The mixed model (NBBg) was rarely (0.8%) identified as the best model when NBBd was the true model.

**Bias and measurement error.** Measurement error in our laboratory data was negligible (we estimate less than one percent based on repeat counts) but can be considerable in field data<sup>34</sup> and has a large influence on estimating extinction risk<sup>35</sup>. To examine the potential effect of measurement error on parameter estimates we generated artificial data, assuming that the NBBg model was the true model, to which we added increasing amounts of measurement error noise and then re-estimated the model parameters. Each simulation experiment was initiated with  $N_t$  equal to that used in the laboratory experiment, using the same level of replication, and with "true" model parameters as estimated from the data for the NBBg model (Table 1 in the main text). We added lognormal error to both  $N_t$  and  $N_{t+1}$  (rounded to the nearest integer), simulating the common field situation where the magnitude of the error variance increases with abundance. For particular field systems, a mechanistic model of the measurement process would be desirable to properly account for the various contributions to the measurement error (e.g. ref 36).

The simulation results show that parameter estimates were biased by measurement error (Supplementary Figure 4). In particular, the variance parameters, which are critical to estimating extinction risk, were severely biased by measurement error. As measurement error increased, the apparent contribution from environmental stochasticity increased relative to that from demographic heterogeneity (small values of  $k_D$  or  $k_E$  indicate higher variance), so that at high levels of measurement error their apparent relative importance was reversed from the true model. This has important implications for estimating extinction risk because underestimating the role of demographic heterogeneity will underestimate the extinction risk.

The simulation results also show that the maximum likelihood estimates of the biological rate parameters ( $R$ ,  $\alpha$ ) were unbiased, but that the variance parameters were biased, especially  $k_E$  (Supplementary Figure 4; measurement error equal to zero). We

calculated bias corrected estimates of the variance parameters by subtracting the relative deviation (natural logarithm scale) observed in the simulation study from the maximum likelihood estimate (Table 1).



**Supplementary Figure 4 | The effect of lognormal measurement error on parameter estimates from the Negative-binomial-binomial-gamma Ricker model.**  $\sigma$  is the standard deviation of the measurement error on the natural logarithm scale. Each point is the mean of 850 replicate simulations.

## Supplementary Notes

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## Additional references.

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