LETTERS

Extinction risk depends strongly on factors contributing to stochasticity

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Extinction risk in natural populations depends on stochastic factors that affect individuals, and is estimated by incorporating such factors into stochastic models[1–9]. Stochasticity can be divided into four categories, which include the probabilistic nature of birth and death at the level of individuals (demographic stochasticity[2]), variation in population-level birth and death rates among times or locations (environmental stochasticity[1,3]), the sex of individuals[6,8] and variation in vital rates among individuals within a population (demographic heterogeneity[7,9]). Mechanistic stochastic models that include all of these factors have not previously been developed to examine their combined effects on extinction risk. Here we derive a family of stochastic Ricker models using different combinations of all these stochastic factors, and show that extinction risk depends strongly on the combination of factors that contribute to stochasticity. Furthermore, we show that only with the full stochastic model can the relative importance of environmental and demographic variability, and therefore extinction risk, be correctly determined. Using the full model, we find that demographic sources of stochasticity are the prominent cause of variability in a laboratory population of *Tribolium castaneum* (red flour beetle), whereas using only the standard simpler models would lead to the erroneous conclusion that environmental variability dominates. Our results demonstrate that current estimates of extinction risk for natural populations could be greatly underestimated because variability has been mistakenly attributed to the environment rather than the demographic factors described here that entail much higher extinction risk for the same variability level.

An essential question in ecology and conservation biology is the determination of the likelihood of extinction within a biological system[10]. This clearly depends on understanding the relative importance of different processes that affect the stochastic dynamics of biological populations, and how these interact with both density-dependent and density-independent processes[5,6]. Ecologists have long sought simple approaches to predicting the likelihood of extinction[11,12]. In conservation biology, the simple idea of a population level that determines which kind of forces might lead to extinction has been appealing[4,13–15]. However, a more detailed and more mechanistic approach is clearly needed to answer these questions more carefully in a way that uses available data.

There is a long history of models that incorporate stochasticity to examine its effect on population growth and extinction[1–6,13,16–21]. The first stochastic models showed that populations could become extinct even if deterministic models concluded they would persist indefinitely[16]. Early results also showed that the variance of population fluctuations and the probability of extinction depend on which biological processes are subject to stochasticity, and that the long-term growth rate of a stochastic population differs from an equivalent population with deterministic dynamics[16,17]. These general results

have proved to be robust, and later studies have concentrated on how different sources of stochasticity in the life history of organisms affect population growth and extinction.

There are many sources of stochasticity that contribute to variance in population growth and thus contribute to the risk of stochastic extinction. Two broad classes are most commonly recognized[6]. Demographic stochasticity occurs because the birth or death of an individual is a random event, such that individuals identical in their probability distributions for reproduction or longevity nevertheless differ by chance in how many offspring they produce or when they will die[2,20]. Environmental stochasticity occurs because fluctuations in exogenous environmental factors such as temperature and rainfall drive population-level fluctuations in birth and death rates[3,20]. In small populations, demographic stochasticity increases extinction risk due to unfortunate coincidences in the fate of individuals, which are cancelled out in larger populations. In contrast, environmental stochasticity increases extinction risk over a larger range of population sizes because the whole population is affected simultaneously.

Two further sources of stochasticity have long been recognized[17] but only recently analysed, namely stochastic sex determination[6,8,22,23] and demographic heterogeneity[7,9], with the former strictly an extreme form of the latter. These can both be viewed as components of demographic stochasticity[6,7], although we separate them here because they are fundamentally different to randomness in births and deaths. In sexually reproducing species, the sex of an offspring is often randomly determined, giving rise to a stochastically fluctuating sex ratio in the population. Most current models of extinction risk only include females; however, a stochastic sex ratio can increase the variance in population growth and extinction risk over and above the effects of demographic stochasticity on females alone. This is because males contribute to density-dependent regulation or because the lack of males reduces female mating success[8,23,24].

Demographic heterogeneity refers to variation in birth or death rates among individuals within a population, such as might occur among individuals of different size[7,9]. This contrasts with demographic stochasticity, which in its original definition and subsequent application concerns chance events assuming a fixed value of the birth or death rate of an individual[2,20]. Demographic stochasticity, sex ratio stochasticity and demographic heterogeneity all contribute to the total demographic variance. Demographic heterogeneity can either increase or decrease the demographic variance, depending on the details of the stochastic process, and so can either increase or decrease the extinction risk[7].

A problem that remains to be addressed is how to combine the various sources of stochasticity into an analytically tractable model. Many current approaches begin by assuming a deterministic skeleton to which noise terms are added, where the statistical distribution of the noise is chosen to reflect a broad class of stochasticity[6,25]. Among

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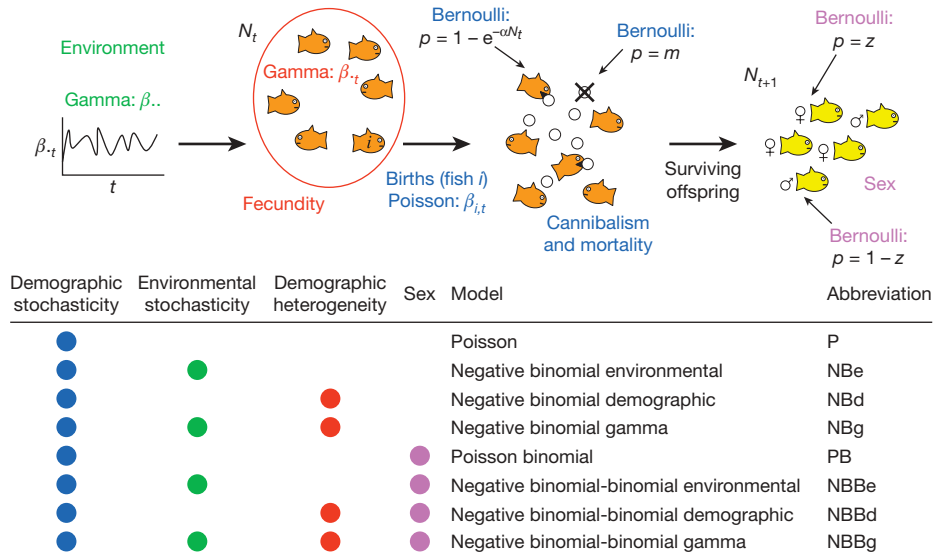
Figure 1 | A family of stochastic Ricker models based on Ricker's[26] assumptions about the life cycle of a fish species that cannibalises its eggs. The stochastic models incorporate stochasticity in various parts of the life cycle, including gamma variation in environmentally determined birth rates, gamma variation in birth rates between individuals, Poisson variation in birth rates within individuals, Bernoulli variation in mortality within individuals, and Bernoulli variation in the sex of an individual at birth.

other models, the Ricker model[26] has often been used as a deterministic skeleton[25,27]. Here we incorporate stochasticity directly into the birth and death processes, allowing the mean and variance of population growth to arise mechanistically from the underlying process assumptions. Our models are for discrete individuals. We derive our stochastic models from Ricker's assumptions but extend these by specifying the stochastic mechanisms at different stages in the life history of an individual and scaling up to the population level (Supplementary Methods). Ricker's assumptions[26] lead to the Poisson–Ricker model, which contains demographic stochasticity arising from the number of eggs laid by individuals and the survival of individual eggs from predation by adults. To this basic model we add environmental stochasticity and demographic heterogeneity in the number of offspring and stochasticity in the sex of offspring. We focus on births because variability in births has greater or equal effects than mortality, but our models extend generally to mortality variation (Supplementary Discussion). We use different combinations of the various stochastic sources to derive a family of nested stochastic Ricker models (Fig. 1).

The stochastic models are true Ricker models because they all have conditional mean N_{t+1} equal to the deterministic Ricker model[26], that is, $E[N_{t+1}] = RN_t\exp(-\alpha N_t)$, where N_t is the population size in generation t, R is the density-independent mean per capita growth rate (finite rate of growth), and α is a measure of density-dependent effects (Supplementary Methods). However, the various stochastic models have different distributions of numbers next year as a function of numbers this year (Supplementary Table 1) and so differ substantially in their variance characteristics for the number of individuals in a subsequent generation (Fig. 2 and Supplementary Fig. 1). As expected, the variance in the number of individuals in the next generation increases as more sources of stochasticity are included in the models. The Poisson–Ricker model, a model of pure demographic stochasticity, has the smallest variance (Fig. 2).

When the total variance is held at the same value (Supplementary Methods), there is an important difference between models of environmental stochasticity and demographic heterogeneity in the variance for the number of individuals the following generation (Fig. 2). For environmental stochasticity, the variance in numbers peaks at the stationary point of the deterministic Ricker function, whereas for demographic heterogeneity, the variance is concentrated at low abundance to the left of the stationary point. This is because environmental stochasticity results in a density-independent variance parameter, whereas demographic heterogeneity generates one that is density dependent (Supplementary Methods). Consequently, demographic heterogeneity entails a greater risk of extinction than environmental stochasticity for the same total variance (Fig. 3). As we highlight below, the similarities in the two variance functions allow these processes to be easily confused, yet their differences have large effects on extinction risk.

The stochastic sex ratio increases the variance at low to intermediate initial abundance, and substantially so at abundances less than the stationary point of the Ricker model (Fig. 2). The effect of the sex ratio is greatest in the demographic models (Fig. 2; compare Poisson (P) with Poisson binomial (PB) models, and negative binomial
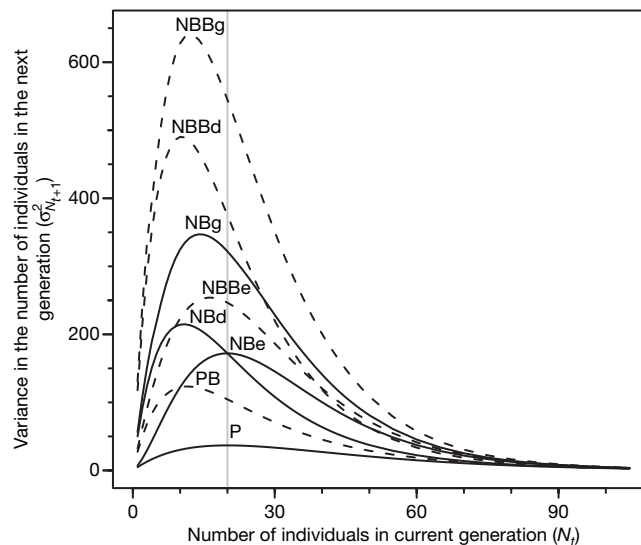

Figure 2 | Variance in the number of individuals in the next generation (N_{t+1}) as a function of the number of individuals in the current generation (N_t) for the stochastic Ricker models. The model parameters were: $R = 5$, $\alpha = 0.05$, $k_D = 0.5$, $k_E = 10$. The stochastic parameters (k_D, k_E) were set so that the total variance due to demographic heterogeneity was equal to the total variance due to environmental stochasticity. The vertical bar indicates the position of the stationary point in the Ricker production function. Abbreviations identify the models listed in Fig. 1.
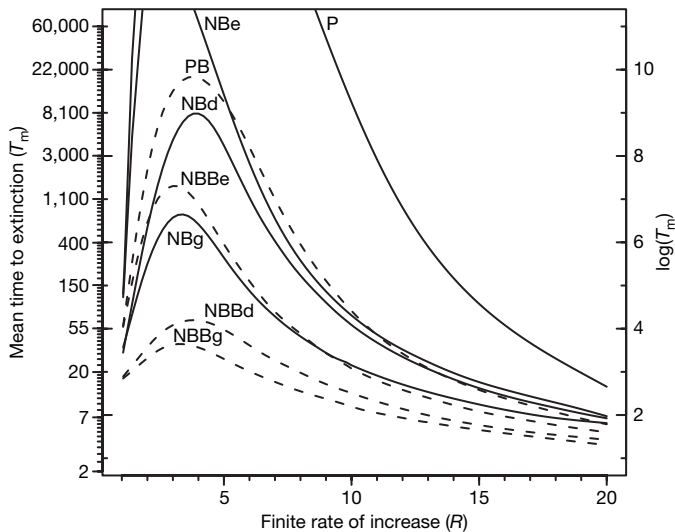
Figure 3 | Intrinsic mean time to extinction[30] (T_m) for the stochastic Ricker models as a function of the finite rate of increase (R). The model parameters were: $k_D = 0.5$; k_E was adjusted so that the total variance in N^{t+1} due to demographic heterogeneity was equal to the total variance due to environmental stochasticity; α was adjusted to hold the equilibrium density at 30 individuals. Internal ticks show the natural logarithm scale. Abbreviations identify the models listed in Fig. 1.

demographic (NBd) with negative binomial-binomial demographic (NBBd) models). The combined variance of demographic stochasticity, environmental stochasticity, demographic heterogeneity and stochastic sex ratio is higher than in models of their individual effects and is additive (Fig. 2).

Extinction risk for the stochastic Ricker models differs substantially depending on the combination of factors in the life cycle that contribute to stochasticity (Fig. 3). The lowest extinction risk is for the Poisson–Ricker model, which includes only demographic stochasticity, whereas the highest extinction risk is for the model that includes all sources of stochasticity. Notably, for the same total variance, extinction risk is enhanced more by demographic heterogeneity or a stochastic sex ratio than by environmental stochasticity, often by orders of magnitude. Extinction risk is also dependent on the finite rate of growth, R (Fig. 3). Increasing R from 1 initially promotes higher persistence times but it also enhances the contribution of nonlinear dynamics to the variance in population fluctuations, causing persistence times to eventually fall. For populations with growth rates R larger than the value producing the first bifurcation in the Ricker model (7.4), fluctuations due to nonlinear dynamics increase and persistence times rapidly drop below those of populations with R equal to 1 (the minimum R required for persistence in the absence of fluctuations).

The characteristic probability mass functions (Supplementary Table 1) of the different stochastic Ricker models provide an opportunity to distinguish between models by fitting them to data. Using

likelihood approaches and information criteria[28], we fitted the models to data from a laboratory experiment on *Tribolium castaneum* growing in discrete time cultures in temperature-controlled incubators. As in Ricker's models of a fish species (Fig. 1), cannibalism of eggs by adults is the main density-regulating process in laboratory populations of *T. castaneum* in discrete time cultures[29]. The best-fitting model was the negative binomial-binomial gamma model, which is the only model to include all four sources of stochasticity (Table 1; the fitted model is shown in Supplementary Fig. 2). No other model fitted as well (Table 1) and the experimental design provided a robust distinction between the models (Supplementary Discussion). In addition, the second-best model (also by a substantial amount) was the negative binomial gamma model, which left out only the stochastic sex ratio that is then partly absorbed by the demographic heterogeneity parameter (Table 1).

The likelihood analysis revealed several important features of the stochastic system. The Poisson model was the worst model by a large margin (Table 1, $\Delta AIC = 336$), suggesting that the most basic assumptions of demographic stochasticity in births, density-dependent survival and density-independent survival are completely unable to describe the variance in abundance even when environmental variability is tightly controlled within the laboratory. In addition, the estimated vital rates of the population were not very different among the models but the estimates of the stochastic parameters were very sensitive to which stochastic factors were included in the fitted model (Table 1). This highlights the importance of a full model specification for correctly identifying the important stochastic factors and therefore correctly estimating extinction risk. Notably, the full model revealed that demographic heterogeneity was much more important than environmental stochasticity, whereas simpler models without demographic heterogeneity erroneously suggest that environmental variability dominates because any demographic heterogeneity is absorbed by the environmental variance parameter (Table 1).

These results show that many species currently viewed as at risk of extinction from environmental stochasticity could instead be at much higher risk from undetected demographic variance. This demographic variance is driven by sex ratio variation and demographic heterogeneity that has been mistakenly attributed to environmental stochasticity. The increased extinction risk is a consequence of the fact that, for the same overall level of variance in abundance for one generational step, sex ratio stochasticity and demographic heterogeneity give rise to greater variance than environmental stochasticity when population sizes are small and vulnerable. Thus, identifying the relative contribution of different stochastic processes is vital to understanding fluctuations and estimating extinction risk because variability differs at different population levels for different processes. As natural populations are likely to have greater demographic heterogeneity than our laboratory stock of *T. castaneum*, the effect we have uncovered here will be larger in natural populations. Suitable data could include time series of population abundance using the methods we have developed here, or individual level data, with special effort needed to encompass a range of population

Table 1 | Fit of stochastic Ricker models to *T. castaneum* data

Model	R	α	k_D	k_E	L	ΔAIC
Poisson	2.526	0.003636	-	-	−406.5	336
Negative binomial demographic	2.638	0.003744	0.1463	-	−246.3	18
Negative binomial environmental	2.706	0.003800	-	1.9913	−265.3	56
Negative binomial gamma	2.598	0.003727	0.2610	29.2262	−238.9	5
Poisson binomial	2.697	0.003753	-	-	−282.0	87
Negative binomial-binomial demographic	2.621	0.003731	0.3876	-	−245.8	17
Negative binomial-binomial environmental	2.770	0.003831	-	13.1014	−242.6	10
Negative binomial-binomial gamma	2.613	0.003731	1.1475*	26.6221*	−236.4	0

The models were fitted to the data by maximizing the log likelihood (L), calculated from the probability mass function of each stochastic Ricker model (Supplementary Table 1). The estimated parameters were: R, the density-independent mean per capita growth rate; α, the density-dependent parameter; k_D and k_E, the variance parameters for demographic heterogeneity and environmental stochasticity, respectively, where small values indicate large variance. The difference in the Akaike information criterion (ΔAIC) was used to compare models[28].
* Bias-corrected estimates for k_D and k_E were 1.07 and 17.62, respectively (see Supplementary Discussion).

densities to capture the density-dependent nature of the variance in abundance. With field data, care will also be needed to factor in measurement error as this will further hide the importance of demographic heterogeneity relative to environmental stochasticity (Supplementary Discussion). We suggest that extinction risk for many populations of conservation concern needs to be urgently re-evaluated with full consideration of all factors contributing to stochasticity.

METHODS SUMMARY

We placed adult *T. castaneum* into $4\,cm \times 4\,cm \times 6\,cm$ acrylic containers with 20 g of standard medium (95% flour, 5% brewer's yeast) to lay eggs for 24 h, after which time the adults were removed. We set up 60 separate containers with adult numbers ranging from 2 to 1,000. Containers were kept in a constant-temperature incubator at $31\,°C$ for the full beetle life cycle and their positions within the incubator were randomized weekly. The 24-h egg-laying period was followed by a further 34 days during which individuals passed through the egg, larval and pupal stages. The number of adults emerging at the end of the 35-day life cycle was recorded for each container. The stochastic Ricker models were fitted to the emergence data by maximum likelihood[28].

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Author Contributions B.A.M. derived and analysed the models, and analysed the data. B.A.M. and A.H. conceived the study, planned and directed the experiments, and wrote the paper.

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