Demographic stochasticity

Brett A. Melbourne

Department of Ecology and Evolutionary Biology, University of Colorado, Boulder,

USA.

Demographic stochasticity describes the random fluctuations in population size that occur

because the birth and death of each individual is a discrete and probabilistic event. That

is, even if all individuals in the population are identical and thus have the same

probabilities associated with birth and death, the precise timing and other details of birth

and death will vary randomly between individuals causing the size of the population to

fluctuate randomly. Demographic stochasticity is particularly important for small

populations because it increases the probability of extinction.

I. Probabilistic births and deaths

Demographic stochasticity arises because the birth and death of an individual is

probabilistic. As an illustration of the concept of probabilistic births and deaths, imagine

a small founding population of an asexually reproducing organism. This population is

made up of identical individuals, each of which has the same probability of dying and the

same probability of giving rise to a new individual within some unit of time. In a

deterministic setting these conditions would give rise to exponential growth but

probabilistic births and deaths give rise to a wider range of dynamical behavior. Probabilistic births and deaths means that if one were to repeat an experiment starting with the same number of individuals, a plot of the number of individuals through time would be different for each replicate of the experiment. Indeed, the dynamical outcomes of the stochastic process would include populations that go extinct and populations that experience a long lag period of low population size before exponential growth occurs (Fig. 1).

[Place figure 1 near here]

A key feature of biological systems that contributes to demographic stochasticity is that individuals are discrete units. The probability of birth or death applies to the individuals. An important consequence is that biological outcomes are discrete: an individual is either born or it is not, or an individual dies or it does not. There can be no partial events, such as the birth or death of a fraction of an individual. When these discrete events are probabilistic they lead to random fluctuations in population size, such as those illustrated in Fig. 1. These discrete, probabilistic events are particularly important when the population is small because then the number of events is small and these events can combine with high probability in such a way as to drive the population size away from the expected value. The expected value of population size is the number of individuals averaged over an infinitely large number of realizations of the stochastic process. In larger populations, the large number of discrete events tend to average each other out and

the dynamics of population size tends toward the expected value and is often well approximated by an equivalent deterministic model.

II. Demographic variance

Demographic stochasticity causes variance in population size around the expected value. This variance comes about because each individual within the population contributes a deviation from the expected value of the per capita growth rate of the population. The variance in these individual deviations from the per capita growth rate is called the demographic variance. Sometimes the expected value can be calculated using a deterministic model, so one can think of demographic stochasticity as adding variance to the deterministic component of the dynamics. For all models, the variance of the change in population size due to demographic variance scales with population size such that $\text{Var}(\Delta N) = \text{Var}(d)N$, or alternatively on a per capita basis

$$\text{Var}\left(\frac{\Delta N}{N}\right) = \frac{\text{Var}(d)}{N} \quad (1),$$

where $\Delta N/N$ is the per capita change in population size N, and $\text{Var}(d)$ - the demographic variance - is the variance in the individual deviations, d, from the expected growth rate. Synonymously, d may be thought of as the deviations in the fitness contributions of the individuals from the expected fitness. Eq. 1 shows an important property of demographic variance: the contribution of demographic variance to fluctuations in population size diminishes as population size increases because the demographic variance is divided by population size (see also Fig. 2 (b)). This contrasts with the effects of environmental stochasticity for which the contribution to population fluctuations does not diminish with increasing population size. This diminishing contribution of the demographic variance

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means that its effect can be largely ignored compared to the environmental variance when the population size is sufficiently large. Precisely how large depends on the ratio of demographic to environmental variance for a particular population but empirical studies suggest that this is often around a population size of 100, although it ranges over several orders of magnitude.

III. Sources of demographic variance

There are several sources of demographic variance that combine together to cause variance in population size (Fig. 2). These can be divided into contributions from the within-individual scale and the between-individual scale. The classic notion of demographic stochasticity is the contributions from the within-individual scale - the probabilistic births and deaths that occur even if all of the individuals within a population are identical. However, variation between individuals also contributes to the demographic variance, perhaps more so than within-individual variance, although empirical studies of the relative contributions in natural populations are lacking. Variation between individuals can have both stochastic and deterministic components, so it is sometimes called demographic heterogeneity. Examples of demographic heterogeneity include variation in fecundity or survival between individuals due to genotype, body size, life stage, or age. In the case of sessile organisms, such as plants, the immediate environment of the individual can also contribute to between-individual variation.

[Place figure 2 near here]

Sexually reproducing species provide an important example of demographic heterogeneity because there are two types of individuals, males and females, whereas only females can give birth to new individuals. The sex of offspring is probabilistic in most species giving rise to stochastic variation in the sex ratio of the population (Fig. 3). As for probabilistic births and deaths, variation in the sex ratio is enhanced when the population is small. One strategy often used to avoid this complication is to model only females and to assume that the abundance of males is sufficient for normal reproduction. If the assumption holds, this can be a good strategy, while recognizing that the demographic variance of the total population is necessarily greater than that of the female population alone. For example, when male and female offspring are equally likely, the demographic variance of the total population is often twice as high.

However, variance in the sex ratio can increase the demographic variance beyond this simple numerical contribution of males to the population size. There are at least two reasons for this. First, if males contribute to density-dependent regulation, fluctuations in the sex ratio will have a more dramatic effect on female fecundity or survival. For example, if availability of food is a key determinant of female reproductive success, the sex ratio is important because males will reduce fecundity by competing with females for food. Second, a stochastic sex ratio can mean that there are times when male abundance is low enough to reduce the mating success of females. The effect of the sex ratio on mating success is sensitive to the mating system. For example, a high female to male sex ratio will result in more unmated females in a monogamous population compared to a polygamous population.

[Place figure 3 near here]

IV. Modeling and analyzing demographic stochasticity

There are several ways to model the stochastic behavior of a population and to incorporate demographic stochasticity. Monte Carlo simulation is the most straightforward approach and can be used with any stochastic model regardless of the complexity of the model. Monte Carlo simulation uses computational algorithms to generate random numbers that simulate the probabilistic events in the stochastic model. In continuous-time the Gillespie algorithm can be used to model demographic stochasticity. In the Gillespie algorithm a random time interval is generated between the individual birth or death events. This random time interval is assumed to have an exponential distribution to model demographic stochasticity. An example is shown in Fig. 1. In discrete-time models of demographic stochasticity random numbers of births and deaths are generated from probability distributions. Common choices to model demographic stochasticity are the Poisson distribution for births and the binomial distribution for deaths. An example is shown in Fig. 3. These approaches for continuous and discrete time explicitly account for the discrete nature of individuals yet do not track each individual. Individual based models track the state of each individual in the population and may be necessary to model between-individual variation (demographic heterogeneity) or other detailed phenomena such as dispersal behavior. Individual based models require much greater computation time.

A disadvantage of simulation is that it is difficult to draw generalizations beyond the particular parameter combinations studied because the results are in a numerical format. For a few simple models of demographic stochasticity, exact analytical results can be calculated for some quantities of interest, such as the probability distribution of abundance at a particular time or the mean time to extinction. However, this is not practical or possible for most models. A more general approach uses approximations of the master equation. The master equation is important in the theory of stochastic processes. It describes the evolution in time of the probability distribution of abundance and can be written down for both continuous time and discrete time models. Many classic results for stochastic ecological models have been obtained using the Fokker-Planck approximation of the master equation, also called the diffusion approximation. The Fokker-Planck approximation is most accurate for fluctuations around the carrying capacity and for small growth rates but is often inaccurate otherwise.

V. Field measurement of demographic stochasticity

There are two general approaches to field measurement of demographic stochasticity: observation of individual reproduction and survival, and inference from the dynamics of population size. Key concerns are distinguishing demographic stochasticity from effects of observation uncertainty, density dependence and environmental stochasticity. Individual observations are the most efficient and precise but are often not possible. A random sample of individuals are observed and the birth of surviving offspring and death of the individual are recorded. Typically these observations are made within a single year or other period appropriate to the organism's reproductive biology. The demographic

variance is then estimated as the sample variance of individual fitness. The demographic variance can be density dependent; meaning the variance in individual fitness is a function of population density. Observations from multiple years together with records of population density are required to measure the effect of density on the demographic variance, as well as to measure environmental stochasticity. Environmental stochasticity is fluctuation in the mean growth rate between years and so is easily distinguished from the demographic variance (e.g. by analysis of variance), although care is needed to separate environmental stochasticity from fluctuations due to density dependence.

A second approach estimates the demographic variance from a time series of population size. In this approach, different probability distributions are used to represent demographic and environmental stochasticity. These probability distributions are fitted to the data. For example, the Poisson distribution might be used to represent purely demographic stochasticity, whereas the negative binomial distribution might be used to represent the combined variation from demographic and environmental stochasticity. In the latter case, the variance parameter of the negative binomial distribution measures the independent contribution of environmental stochasticity, whereas the remaining (Poisson) variation is assumed to be due to demographic stochasticity. To correctly separate environmental and demographic variance, sources of demographic heterogeneity also need to be represented by probability distributions in the statistical model. An obvious drawback of this approach is that a long time series is needed, typically twenty or more time points. However, a long time series is also required to measure density dependence in the demographic variance when only individual fitness is observed. Because of these

constraints, it is common to measure demographic variance at only one time point using observations from individuals, even though the demographic variance is unlikely to be constant or density independent.

VI. Extinction

The most important consequence of demographic stochasticity is an increased probability of extinction in small populations. This is not only important for the extinction risk of populations of conservation concern but is fundamental to a wide range of ecological processes. For example, colonization and biological invasion first require small populations to persist, which they do with probability equal to one minus the probability of extinction. Similarly, for a disease epidemic to occur, the disease must first avoid extinction when few hosts are infected. Extinction is fundamental also to community processes such as the coexistence of competitors, or predator and prey. To coexist with each other in the long term, species must be able to recover from low population density, at which time the probability of extinction is increased by demographic stochasticity. Finally, extinction of small populations is also important for spatial dynamics, such as in metapopulations because demographic stochasticity contributes to the extinction of smaller local populations.

For most stochastic models that are ecologically realistic, extinction is ultimately certain (the probability of extinction equals 1) because population size is bounded above by the carrying capacity. This ensures that population size fluctuates between zero and an upper bound, and will eventually hit zero at some time because of demographic and

environmental stochasticity. On the other hand, even when extinction is certain, the expected time to extinction due to demographic stochasticity alone is often extremely long. For these reasons the ultimate probability of extinction is often a meaningless measure for assessing extinction risk or comparing models of demographic stochasticity.

There is debate about the best measure to assess extinction in models. One approach, often used to assess the viability of threatened populations, is to calculate the probability of extinction over a defined time interval, say 100 generations. However, a standard time interval has not been agreed upon and studies cannot be easily compared if they use different time intervals. An alternative measure of extinction is the arithmetic mean time to extinction, MTE. This allows models and studies to be compared on the same scale. A related measure is the intrinsic mean time to extinction, T_m, equal to MTE when the population dynamics have passed any transient dynamics and reached an established phase. This established phase is called the quasi-stationary distribution in stochastic process theory. The probability of extinction over any time interval can be calculated from T_m together with an additional parameter, c, that describes transient effects or dependence on initial conditions (Box 1).

[Place Box 1 near here]

For a wide range of models, the mean time to extinction under demographic stochasticity scales exponentially with carrying capacity, K,

$$MTE = ae^{bK},$$

where *a* and *b* are positive constants and their values are determined by the particular model being considered. Thus, as carrying capacity (and hence population size) increases, the mean time to extinction increases exponentially (Fig. 4). The rate of exponential increase depends on the factors contributing to the demographic variance. In particular, between-individual variance keeps the extinction risk high despite an increase in carrying capacity (Fig. 4). The exponential relationship for demographic stochasticity contrasts with environmental stochasticity in which there is a power law relationship between *MTE* and *K*. Thus, under environmental stochasticity the mean time to extinction increases more slowly with carrying capacity, and hence extinction risk remains high.

[Place figure 4 near here]

VI. Calculating extinction measures

There are several ways to calculate extinction measures for a given model, including simulation, deriving exact results, or approximating the master equation. Monte Carlo simulation is the most straightforward approach. For example, to calculate extinction risk over a defined time horizon, simulate the stochastic model for that time period and record whether the population goes extinct in the simulation. Repeat the simulation many times, each time generating new random numbers. The proportion of simulations that become extinct is an estimate of the extinction risk over that time horizon. For example, for the exponential growth model in Fig. 1, 62 out of 1000 simulated populations went extinct within a total period of 60 time units. The calculated probability of extinction due to demographic stochasticity for that time horizon is therefore 0.062 (about 6 percent).

Simulation can be used similarly to estimate the mean time to extinction, *MTE*. However, this brute force approach to estimate the *MTE* is often not practical for demographic stochasticity since the time to extinction in an individual simulation can be extremely long. Instead, a method called the $\ln(1-P_0)$ plot can be used to estimate the intrinsic mean time to extinction, T_m, without needing to wait for all runs to go extinct (Box 1).

VII. Origins of the concept

One of the earliest questions about demographic stochasticity was posed toward the end of the 19th century by the English scientist and statistician Francis Galton. The Victorians were worried that the aristocracy was dying out. Lineages of important families were becoming extinct. It was popular to muse that the comforts enjoyed by the upper classes were leading to the biological decline of the aristocracy. Galton himself entertained this idea but challenged it with an alternative hypothesis (perhaps proposed to him by the French-Swiss botanist Alphonse de Candolle) that the extinction of aristocratic lineages could instead be due to probabilistic births and deaths. Galton and the mathematician Rev. Henry Watson offered a mathematical solution for surname extinction in the Journal of the Anthropological Institute of Great Britain in 1874 but it wasn't until 1930 that it was correctly and independently solved by the Danish mathematician Johan Steffensen. A year later in 1931, the American mathematical biologist Alfred Lotka applied Steffensen's solution to US census data - perhaps the first time a model of demographic stochasticity was confronted with data. Lotka determined that the probability of extinction of a male line of descent was 0.88. Demographic stochasticity became a hot topic for about the next 30 years as part of the emerging field of stochastic processes.

Fundamental contributions to the idea of demographic stochasticity were made during this period by such luminaries as the English statistician Ronald Fisher, the Croatian-American mathematician William Feller, and the Russian mathematician Andrey Kolmogorov. The English statisticians Maurice Bartlett and David Kendall in particular made many important contributions. Considerations about demographic stochasticity developed during this period include density dependence, disease epidemics, age structured populations, interspecific competition, predator-prey dynamics, spatially structured populations, maximum likelihood estimation, and analytical derivations for the mean time to extinction. The term "demographic stochasticity" appears to have been coined by the Australian theoretical ecologist Robert May in 1973.

Glossary

demographic heterogeneity random or deterministic variation in intrinsic vital rates between individuals that contributes to the demographic variance.

demographic stochasticity the random fluctuations in population size that occur because the birth and death of each individual is a discrete and probabilistic event.

demographic variance variance in the deviations of individuals from the expected fitness of the population. The demographic variance can have components contributed by both within and between-individual variation.

expected value the average over an infinitely large number of realizations of a stochastic process.

Monte Carlo simulation to simulate the probabilistic events in a stochastic model, random numbers are generated using a computational algorithm.

MTE the arithmetic mean time to extinction, or expected time to extinction.

T_m intrinsic mean time to extinction. Equal to *MTE* when the population dynamics have passed any transient dynamics due to initial conditions and reached an established phase called the quasi-stationary distribution.

Gillespie algorithm a Monte Carlo algorithm used to simulate probabilistic births and deaths in continuous time. A random time interval between the individual birth or death events is generated from an exponential distribution.

Further Reading

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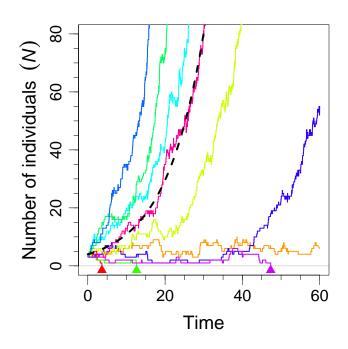

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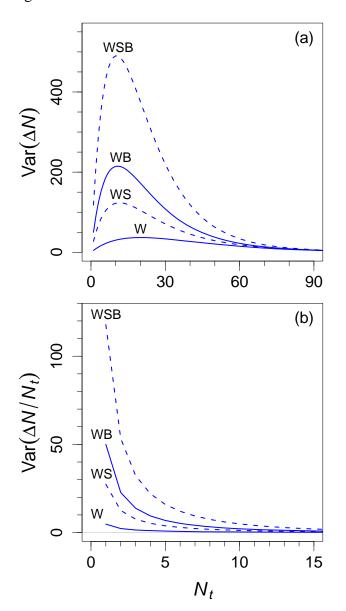

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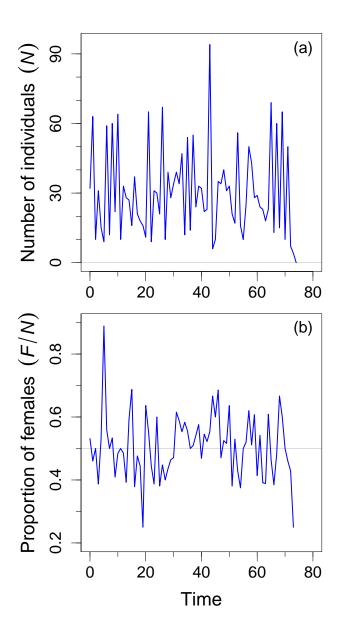
Figures

Figure 1. Demographic stochasticity caused by probabilistic births and deaths of discrete individuals. Variation from demographic stochasticity is illustrated here by ten representative realizations of population growth from 1000 Monte Carlo simulations of the same stochastic model. Dynamical outcomes included populations that experienced exponential growth (some fast, some slow), populations that experienced a long period of low population size before exponential growth occurred, populations that did not grow at all during the period, and 62 populations that went extinct. This contrasts with the equivalent deterministic model of exponential growth (dashed black line). Of simulations that did not go extinct, shown are the simulations with the highest and lowest number of individuals at the end of the simulation, as well as the 2.5th, 25th, 50th, 75th, and 97.5th percentiles. Of simulations that went extinct, shown are the shortest, median, and longest extinction times. Triangles show the time of extinction. Model details: individuals were identical and reproduced asexually; births and deaths were density independent with rates

0.2 and 0.1 respectively; initial population size was 4 individuals. The Gillespie

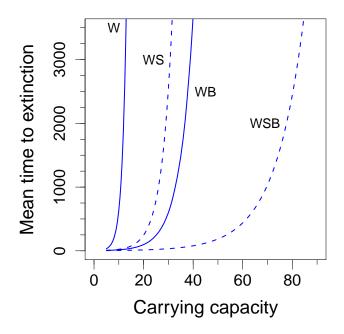algorithm was used to simulate the continuous time stochastic process.

Figure 2. How sources of demographic variance combine together to cause variance in

population size illustrated with a stochastic Ricker model. In this example, sources of

demographic variance can be divided into contributions from probabilistic births and

deaths at the within-individual scale (W), probabilistic sex determination (S), and

differences in female fecundity at the between-individual scale (B). (a) Stochastic

fluctuations in population size measured by Var(ΔN). The Ricker model is a discrete time model, so the change in population size is $\Delta N = N_{t+1} - N_t$. Compared to probabilistic births and deaths alone (W), the stochastic fluctuations are increased by probabilistic sex determination (WS). Stochastic fluctuations are further increased when fecundity differs between females (WSB). (b) As in (a) but with stochastic fluctuations measured on a per capita basis to show the declining importance of demographic stochasticity with population size. Model details: births for individual females were Poisson; variation in intrinsic birth rate between females was gamma with mean 20 and variance 55; density independent mortality was Bernoulli with probability 0.5; density dependent mortality was Bernoulli with probability $1 - e^{-\alpha N}$, where N is the size of the population and $\alpha = $ 0.05; probability of female offspring was 0.5.

Figure 3. One Monte Carlo simulation of a stochastic Ricker model with several sources of demographic variance, including stochastic sex determination. The population went extinct after 74 generations. (a) Fluctuations in total population size. (b) Fluctuations in the proportion of females. The model is the WSB model in Fig. 2 with the same details.

Figure 4. The mean time to extinction increases exponentially with carrying capacity due to demographic stochasticity. Populations go extinct more rapidly when the carrying capacity is low. The example is a stochastic Ricker model as in Fig. 2. Compared to probabilistic births and deaths alone (W), extinction risk is increased by probabilistic sex determination (WS) and when fecundity differs between females (WB, WSB). Model details were the same as in Fig. 2 except: variation in intrinsic birth rate between females was gamma with mean 10 and variance 10; density independent mortality was Bernoulli with probability 0.6.

Box 1. Estimating the mean time to extinction.

An approach called the $\ln(1-P_0)$ plot can be used to estimate the intrinsic mean time to extinction, T_m, for a stochastic population model by simulation (Grimm and Wissel 2004, *Oikos* 105: 501-511). In most stochastic population models the probability distribution function of extinction times is well approximated by an exponential structure or is exactly exponential. The $\ln(1-P_0)$ plot takes advantage of this exponential structure. The approach has four steps:
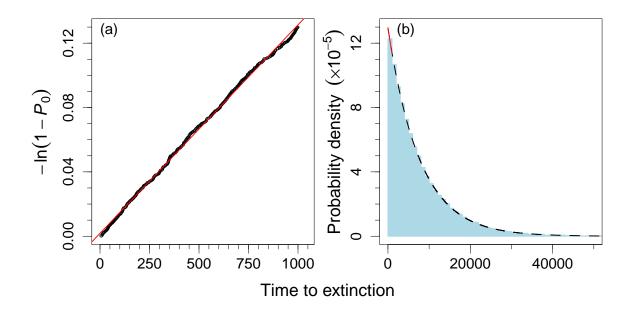
1) Simulate the model a moderate number of times (e.g. 1000-5000) over a defined time interval (e.g. 1000 years).

2) Calculate $P_0(t)$, the probability of becoming extinct by time t, from the empirical cumulative distribution function for the simulated extinction times.

3) Plot $-\ln(1-P_0)$ against t. This should show a linear relationship as in panel (a). If the relationship is not linear, the $\ln(1-P_0)$ plot should not be used to estimate T_m.

4) Fit a linear regression to estimate the parameters of this linear relationship (panel a). The inverse of the slope gives the intrinsic mean time to extinction, T_m, while the intercept, c, gives the probability of reaching the established phase.

This approach relies on extrapolating the distribution function to long extinction times that are beyond the simulation time. That is, simulations that went extinct within say the first 1000 years are used to estimate the parameters of the exponential distribution for all possible extinction times (panel b). The approach can also be used when all simulations are allowed to go extinct. Sources of error in the estimation of T_m include Monte Carlo error and extrapolation error. Monte Carlo error can be reduced by increasing the number of replicate simulations.

The example given here is for a stochastic Ricker model with two sources of demographic variance: within-individual variance (probabilistic births and deaths) and between-individual variance generated because the sex of individuals is stochastically determined. (a) The $\ln(1-P_0)$ plot showing the expected linear relationship and the fitted linear regression. The estimated slope was 1.3×10^{-4}. The inverse of the slope is the estimated intrinsic mean time to extinction $T_m = 7719$ generations. The estimated intercept was $c = 0.9982$, which is very close to 1.0 and indicates that transient effects were minimal. The model was simulated 5000 times for 1000 generations starting from near the carrying capacity of the population (35 individuals). (b) Comparison of the extrapolated distribution of extinction times from the $\ln(1-P_0)$ plot with the known distribution, showing that the $\ln(1-P_0)$ plot accurately extrapolates to the full distribution. The known distribution is represented by a histogram of extinction times from about 67 000 simulations of the model, each time allowing the simulation to run to extinction. The lines show the fitted distribution of extinction times from the $\ln(1-P_0)$ plot. Red indicates the area where the distribution was fitted by the $\ln(1-P_0)$ plot while the dashed line shows

the extrapolated distribution. The estimated mean time to extinction from the full simulation was 7705 with standard error 30, so the mean time to extinction of 7719 estimated by the ln(1-P_0) plot was within the error bounds and within 0.2% of this more precise estimate. Model details: births for individual females were Poisson with mean 10; density independent mortality was Bernoulli with probability 0.6; density dependent mortality was Bernoulli with probability $1 - e^{-\alpha N}$, where N is the size of the population and $\alpha = 0.02$; probability of female offspring was 0.5.