Demographic Noise

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Abstract

Populations are finite. Birth and death are separate events. Demographic noise is important. A simple expression describes this.

Key words: fluctuation-dissipation, demographic stochasticity, ecological models

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1. Introduction

We present a dynamical treatment of demographic noise in population models. We derive a simple and general expression to estimate the fluctuations in a population from a given deterministic model. We demonstrate that demographic noise can be derived directly from deterministic models by specifying birth and death terms explicitly. Our method is based upon an expansion of individual dynamics that explicitly accounts for system size and distinguishes between macroscopic (average) quantities and observed quantities.

1.1. *The Poisson process description*

The Poisson process is a common description of demographic noise. It arises as the limit of a binomial distribution (coin flipping) when the events are rare and the population large. This model is commonly applied as follows. Consider a model of the form:

$$N_{t+1} = f(N_t) \tag{1}$$

This approach chooses with probability P the number in the next generation N_{t+1} at random from a Poisson distribution with mean $f(N)$:

$$P(N_t)_{t+1} = \text{Poisson}(N, f(N_t)), \tag{2}$$

while the variance of the Poisson distribution will also be $f(N)$. If the population has some equilibrium size $N^* \neq 0$ such that $f(N^*) = N^*$, then at equilibrium the population will have size N^* and fluctuate around that value with standard deviation $\sqrt{N^*}$. In the continuous time limit this approaches a Gaussian with the same mean and variance. Observe that $P(0) > 0$ for any N, hence a population can always go extinct. Further, if we naturally assume the population is isolated, then $f(0) = 0$, and extinction is the only long-term stable state. This description provides a first pass at describing demographic noise, and captures some of its important phenomena:

- Finite populations fluctuate around there equilibrium.
- Any isolated population that cannot grow without bound will eventually go extinct.
- The magnitude of the steady-state fluctuations relative to the equilibrium decreases with increasing population size (as $\sqrt{N^*}/N^*$), decreasing the extinction risk of larger populations proportionally.

While we have started to capture one aspect of demographic noise (populations are finite), we have ignored the second (population dynamics come from birth and death processes). Too often we stop at this description of demographic noise. By using only $f(N)$, we have not specified births and deaths separately. This is quite common in population models, where the choice of $f(N)$ does not obviously suggest which are the birth and which are the death terms. Our second introductory example illustrates the importance of doing so.

1.2. *The importance of birth and death*

Consider a population that is of size n with probability p_n, with birth and death rates given by b_n and d_n respectively, diagrammed in Fig 1 This representation is known as a single step Markov process. The rate of transitions to the $n+1$ state b_n, the rate of transitions to $n-1$ is d_n. Both of these are transitions away from the state p_n, hence the

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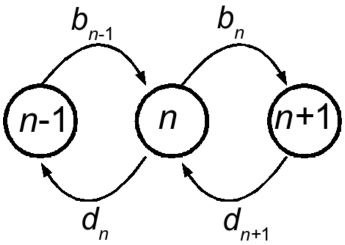

Fig. 1. The birth-death process as a Markov process.

decrease the probability of p_n. The probability p_n increases by transitions into the state n, from either side: births enter from the state below at rate b_{n-1} and deaths from the state above, d_{n+1}. Hence the rate of change in p_n is given by

$$\dot{p}_n = b_{n-1}p_{n-1} + p_{n+1}d_{n+1} - [b_n + d_n]p_n \tag{3}$$

This probability balance is known for historical reasons as a master equation. This equation will form the center of our treatment. Master equations of this form can be written more concisely by introducing the step operator, $\mathbb{E}^k$ such that $\mathbb{E}^k f_n = f_{n+k}$, giving us

$$\dot{p}_n = (\mathbb{E}^{-1} - 1)b_n p_n + (\mathbb{E} - 1)d_n p_n \tag{4}$$

which for historical reasons is known as a master equation. From this we can directly calculate the mean and variance for this process by multiplying by n or n^2 and summing over all n. These calculations are greatly simplified by observing the following property of the step operator: for any pair of test functions f_n, g_n,

$$\sum_{n=0}^{N-1} g_n \mathbb{E} f_n = \sum_{n=1}^{N} f_n \mathbb{E}^{-1} g_n$$

For example, the mean is:

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\langle n \rangle &= \sum n(\mathbb{E}^{-1} - 1)b_n p_n + \sum n(\mathbb{E} - 1)d_n p_n \\ &= \sum b_n p_n(\mathbb{E} - 1)n + \sum d_n p_n(\mathbb{E}^{-1} - 1)n \\ &= -\langle d_n \rangle + \langle b_n \rangle \end{aligned} \tag{5}$$

and similarly

$$\frac{\mathrm{d}}{\mathrm{d}t}\langle n^2 \rangle = 2\langle n(b_n - d_n)\rangle + \langle b_n + d_n \rangle \tag{6}$$

The key observation here is that the variance includes the sum of birth and death, not just the difference. Intuitively we would expect a population with large numbers of births and deaths that average to a small difference to fluctuate much more than one in which this difference is very small. Despite this simple observation, countless models purporting to include demographic noise ignore this distinction. While all moments can be derived as above, it is often impossible to solve these equations for nonlinear models. Instead, we introduce an approximation of Eq (4) that is physically motivated and intuitive. The method has its roots in physics [van Kampen, 1981]. The reader familiar with the diffusion equation, Appendix A, may be interested in the similarities and differences of the approach.

2. The linear noise approximation

2.1. *Introduction, a change of variables*

In this section, we expand the master equation (4) in terms of a measure of the system size, Ω. The heart of this approximation is a change of variables, the rest is simply book-keeping. We begin by explaining this change of variables, which replaces n by some average value ϕ and some fluctuations ξ. Understand this, and the rest is mechanics.

Observe that (4) is written in terms of discrete individuals, represented by the integer n. Many population models permit real-valued variables for the population, usually interpreted as the density of individuals, for which fractional values have meaning. If we go out to the field and mark off a very large area and count all the individuals within it, we can expect to get the population density, ϕ. Over some appropriate region, we expect the population density to be independent of our survey area. Knowing the density, we can predict how many individuals we'd expect to find in any given area Ω, simply $\phi\Omega$. We also know that the larger the area, the more accurate our prediction. We call ϕ a macroscopic variable – it describes what we expect to see over an entire population (the macroscopic level) on average, rather than at the individual level. It is an intensive (bulk) variable, because it does not depend on the area surveyed, while number n will depend on the area Ω considered. We expect n to deviate around an average value of $\phi\Omega$ by some amount that depends on the system size. For several reasons (such as the error term we found in the simple Poisson process), we will guess that the size of the fluctuations ξ scale with system size as $\Omega^{1/2}$. Mathematically,

$$n = \Omega\phi(t) + \Omega^{1/2}\xi \tag{7}$$

We will change Eq (4) into the variables ϕ and ξ. We begin with the step operator, which can be approximated by a Taylor expansion.

$$\mathbb{E}^k = 1 + \Omega^{-1/2}k\frac{\partial}{\partial \xi} + \Omega^{-1}\frac{k^2}{2}\frac{\partial^2}{\partial \xi^2} + \ldots \tag{8}$$

Taking $P(n,t) = \Pi(\xi,t)$, we can rewrite the time derivative as

$$\frac{\partial}{\partial t}P(n,t) = \frac{\partial \Pi}{\partial t} - \Omega^{1/2}\frac{\mathrm{d}\phi}{\mathrm{d}t}\frac{\partial \Pi}{\partial \xi} \tag{9}$$

To complete the transformation, we put (9) on the left side, replace all the $\mathbb{E}$'s in (4) with (8), and all the n's appearing in the functions b_n and d_n with (7):

$$\begin{aligned} &\frac{\partial \Pi(\xi,t)}{\partial t} - \Omega^{1/2}\frac{\mathrm{d}\phi}{\mathrm{d}t}\frac{\partial \Pi}{\partial \xi} = \\ &\quad \left(-\Omega^{-1/2}\frac{\partial}{\partial \xi} + \frac{\Omega^{-1}}{2}\frac{\partial^2}{\partial \xi^2} + \ldots\right) b(\phi\Omega + \xi\Omega^{1/2})\Pi(\xi,t) \\ &+ \left(\Omega^{-1/2}\frac{\partial}{\partial \xi} + \frac{\Omega^{-1}}{2}\frac{\partial^2}{\partial \xi^2} + \ldots\right) d(\phi\Omega + \xi\Omega^{1/2})\Pi(\xi,t) \end{aligned} \tag{10}$$

Collecting terms of order $\Omega^{1/2}$ on both sides, we have:

$$\frac{\mathrm{d}\phi(t)}{\mathrm{d}t} = b(\phi) - d(\phi) = \alpha_1(\phi) \tag{11}$$

Where we have the part of the birth and death functions that depend on the macroscopic variable ϕ alone. This is known as the macroscopic equation, and corresponds to the density equations commonly written down. We call this difference $\alpha_1(\phi)$ as a shorthand [1]

Collecting terms of order Ω^0 we recover the diffusion equation:

$$\frac{\partial \Pi}{\partial t} = -\alpha'_{1,0}(\phi)\frac{\partial}{\partial \xi}\xi\Pi + \tfrac{1}{2}\alpha_{2,0}(\phi)\frac{\partial^2}{\partial \xi^2}\Pi \tag{12}$$

Where we define $\alpha_2(\phi) = b(\phi) + d(\phi)$ as an analogous short hand. From this it is a straight forward exercise to calculate the moments of the distribution (multiply by ξ, ξ^2 and integrate),

$$\partial_t\langle\xi\rangle = \alpha'_{1,0}(\phi)\langle\xi\rangle \tag{13}$$

$$\partial_t\langle\xi^2\rangle = 2\alpha'_{1,0}(\phi)\langle\xi\rangle + \alpha_{2,0}(\phi) \tag{14}$$

The variance $\sigma^2_\xi = \langle\xi^2\rangle - \langle\xi\rangle^2$ obeys the same relation as the second moment. These equations must be solved using $\phi(t)$ from the macroscopic solution, solved with the appropriate initial condition n_0. Then we can transform back to the original variables:

$$\langle n\rangle = \phi(t|n_0)\Omega + \Omega^{1/2}\langle\xi\rangle \tag{15}$$

$$\sigma^2 = \Omega\sigma^2_\xi \tag{16}$$

It is possible to prove that any solution to (12) must be Gaussian. Consequently, knowing these two moments completely determines the distribution of n. This is often assumed for demographic noise. We have justified this common Gaussian noise assumption by showing it is simply a consequence of expanding the master equation to linear order, $\mathcal{O}(\Omega^0)$. From (15) we can also conclude that the macroscopic (average) variable obeys the deterministic law.

2.2. *Fluctuation dissipation theorem*

Eq (14) is particularly instructive. Note that $\alpha_2(\phi)$ is always positive, and hence will try to increase the fluctuations $\langle\xi^2\rangle$. As this term increases, it increases the influence of its coefficient $\alpha'_1(\phi)$. If this term is negative (as it must be near a stable equilibrium) then it serves to dissipate these fluctuations. Note the dissipation comes from the macroscopic behavior alone, and does not depend on knowing b and d separately. Since this dissipation is strongest for large fluctuations and small for very small fluctuations, ξ^2 will exponentially approach an equilibrium:

$$\langle\xi^2\rangle = \frac{-\alpha_2(\phi)}{2\alpha_1(\phi)} \tag{17}$$

However, $\alpha'_1(\phi)$ need not be negative everywhere. This is easy to see by plotting the macroscopic growth rate $\dot{(\phi)} = \alpha_1(\phi)$ against ϕ, as in Fig 3, where α'_1 is simply the slope. Equilibria ϕ_s occur wherever this curve crosses zero. If it does so with a negative slope, $\alpha'_1(\phi^s) < 0$ then this point is stable. Hence there will be a region around any stable point where this fluctuation-dissipation relationship given by (17) provides a good description of the fluctuations. Consequently, for any birth-death process $b > d$ we can write down the equilibrium fluctuations as:

$$\sigma^2 = \frac{b+d}{2[d' - b']} \tag{18}$$

This expression has the wonderful properties of being both simple and general. For instance, we can calculate the fluctuations of the logistic equation around its equilibrium $n^* = K$. Taking $b = rn$ and $d = rn^2/K$:

$$\sigma^2 = \frac{rn^* + rn^{*2}/K}{2(2rn^*/K - r)} = K$$

Which agrees with calculations elsewhere [Nisbet & Gurney, 1982]. Note that the result could have been different had we used a different interpretation of the birth and death terms of the same equation. However, there will almost always be a region where α'_1 is positive, since $\phi = 0$ will be an equilibrium point for any closed non-zero population. In this region, equation (14) still holds as long as those fluctuations do not reach of order the system size, though they will generally far exceed the equilibrium value of the fluctuations, as seen in Fig 2. For these large transient fluctuations the equilibrium (18) will be a very poor estimate, though they can still be calculated from (14). While (18) gives results that agree with other estimates of fluctuations found in the literature, we am unaware of another description of these very large transient fluctuations.

3. Examples with birth-death processes

3.1. *Levins patch model*

In this section we compare the theory to exact individual-based simulations of the Levins model. The Levins metapopulation model is given by

$$\dot{n} = cn\left(1 - \frac{n}{N}\right) - en \tag{19}$$

where n is the number of occupied patches, N the total number of patches, c is the colonization rate, and e the extinction rate. The colonization term provides our birth rate function and the extinction rate the death rate function. The total number of patches N is an obvious choice

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[1] This notation suggests it is the first jump moment, defined as first moment of the transition rate between states in a Markov process. It so happens this term will give the macroscopic law for any Markov process, not only a birth-death process. The second moment of the transition rates, a_2, will be for us simply the sum of the birth and death rates. We use this notation as it generalizes to processes that have a different master equation from (4).

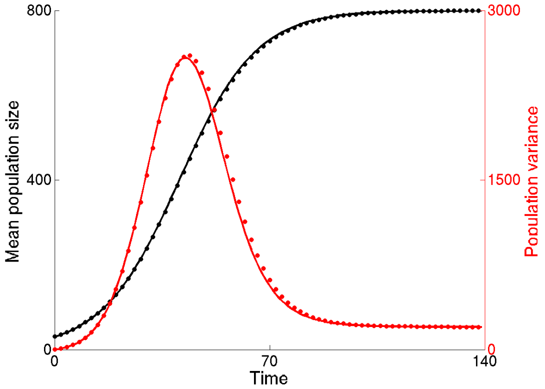


Fig. 2. The mean (black) and variance (red) of the simulation (dots) closely match those predicted by the theory (solid lines). Fluctuations grow quite large since the simulation starts outside the regime specified by (24), but never reach $\mathcal{O}(\Omega)$ ($\sqrt{3000} \ll 1000$), hence the approximation does not break down. When system reaches $n = 400$, fluctuations begin to dissipate to their equilibrium levels. For this simulation, $c = 0.1$, $e = 0.02$, $N = 1000$, $n_o = 30$. Data are averaged over ensembles of 10^5 realizations.

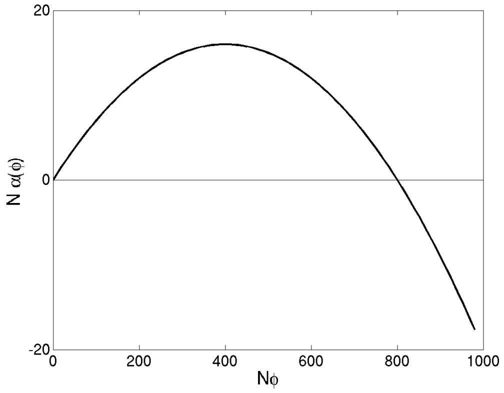


Fig. 3. The function $\alpha_1(\phi)$ for the Levins model simulation. The function $\alpha_1(\phi)$ determines the macroscopic dynamics. Where it crosses the horizontal axis with a negative slope determines the stable point ($n = 800$). When the slope is negative, (population sizes greater than 400), fluctuations exponentially approach the equilibrium given by the fluctuation-dissipation equation, (17). When the slope is positive fluctuations will grow, as seen in Fig 2. Model parameters are identical to Fig (2).

for the system size Ω. From this we can immediately apply the above theory. The jump moments written in the macroscopic variable are:

$$\alpha_1(\phi) = c\phi(1-\phi) - e\phi \tag{20}$$

$$\alpha_2(\phi) = c\phi(1-\phi) + e\phi \tag{21}$$

From which the macroscopic equation (11), the fluctuations (14) can be solved. According to (12) the distribution is simply the Gaussian with the mean given by (15) and variance (16). The equilibrium of the macroscopic equation is:

$$\langle n \rangle_s = N\left(1 - \frac{e}{c}\right) \tag{22}$$

while the steady-state fluctuations are given by (17), (16):

$$\sigma_n^2 = N\frac{e}{c} \tag{23}$$

It is worth noting that this model has the same macroscopic form as the logistic model we examined earlier, but with a different interpretation of the birth and death terms, and consequently different fluctuations. These fluctuations will exponentially approach this in the region where $\alpha_1'(\phi) < 0$,

$$\phi_{\text{crit}} > \frac{c-e}{2c} \tag{24}$$

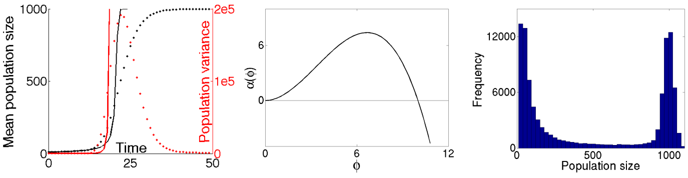
When the population size is less than $N\phi_{\text{crit}}$, fluctuations will grow exponentially, as seen in Fig 2. Our approximation will remain valid as long as the population can reach the critical size before the fluctuations become of order N, the system size. As long as the system reaches the critical value fast enough, the fluctuations will not have time to grow too large. This can be visualized by plotting the macroscopic dynamics $\alpha_1(\phi)$ against ϕ, as in Fig 3. Fluctuations grow when the slope is positive, relax to their equilibrium when the slope is negative. Where the curve crosses the horizontal axis are the stationary states, which are stable if the curve is decreasing at that point. The fluctuations are clearly more likely to achieve this for smaller system sizes, as the rate of growth is given by the macroscopic quantity ϕ. However, in these population models small populations in small system sizes are more likely to face stochastic extinction instead, which is not described by this approach. When the curve is symmetric around its maximum, it is difficult for fluctuations to ever reach the system size. However, if this curve grows very slowly initially, then the deterministic approach to equilibrium is initially very slow, and fluctuations have time to grow. This violates our approximation and results in bimodal distributions of populations, as seen in the next example.

3.2. *Growing fluctuations*

A simple way to create fluctuations which will have enough time to grow to the order of the system size requires going beyond quadratic order. Very ecological models for a single species with single stable will have this form, making the linear noise approximation valid in almost all scenarios. We briefly present this example to illustrate what can go wrong. Weak alee effects can produce this behavior, though the simplest are again symmetric (composed of positive and negative quadratics). Consider the deterministic dynamics given by

$$\dot{\phi} = a\phi^2 - b\phi^3 \tag{25}$$

where $b < a$. The equilibrium population size is Nb/a, and the fluctuation dissipation basin around it is $n > \frac{2a}{3b}N$. Starting sufficiently outside the basin, the macroscopic equation is no longer a good approximation of the mean trait, since fluctuations reach of order system size, $\sqrt{2 \cdot 10^5} \sim 100$, as seen in Fig 4(a). The fluctuation equation diverges under these conditions before the popula-



(a) (b) (c)

Fig. 4. (a) The macroscopic equation and the variation over time. (b) the macroscopic dynamics as a function of the intensive variable ϕ. (c) The distribution of population sizes in the ensemble at $t = 23$. Model parameters: $N = 100$, $n_0 = 10$, $a = 0.5$, $b = 0.05$, ensemble of 10^5 realizations.

tion reaches the fluctuation dissipation basin. This behavior is characteristic of deterministic dynamics starting in a region of a small positive slope seen in 4(b). Under this regime, fluctuations are so large that some realizations remain trapped in the early, slow dynamics while others fall into the equilibrium basin, resulting in a bimodal distributions at intermediate times, as seen in 4(c). Starting inside the basin of dissipation this system closely matches the predictions of our expansion (simulation not shown). While this pathological behavior may be rare in ecological models, it arises in evolutionary descriptions where the fluctuations are driven by mutations and the dissipation by selection.

3.3. *Multivariate equations: a competition model*

We consider the Crowley model [Crowley *et al.*, 2005] of competition for space:

$$\dot{x} = b_1 x(1 - x - y) - d_1 x + cxy \tag{26}$$

$$\dot{y} = b_2 y(1 - x - y) - d_2 y - cxy \tag{27}$$

Where x and y are the macroscopic variables independent of system size. Taking $n_x = \Omega x + \Omega^{1/2}\xi$ and $n_y = \Omega y + \Omega^{1/2}\eta$, we proceed much as before to derive the fluctuation equations:

$$\begin{aligned}\partial_t \sigma_\xi^2 = {} & 2(b_1(1 - 2x - y) \\ & + cy - d_1)\sigma_\xi^2 + 2(-b_1 x + cx)\langle xy\rangle \\ & + b_1 x(1 - x - y) + cxy + d_2 x)\end{aligned} \tag{28}$$

$$\begin{aligned}\sigma_\eta^2 = {} & 2(b_2(1 - 2y - x) - cx - d_2)\sigma_\eta^2 \\ & + 2(-b_2 y - cy)\langle \xi\eta\rangle \\ & + b_2 y(1 - x - y) + cxy + d_2 y)\end{aligned} \tag{29}$$

$$\begin{aligned}\langle \xi\eta\rangle = {} & b_1(1 - 2x - y) + cy - d_1)\langle \xi\eta\rangle \\ & + (-b_1 x + cx)\sigma_\eta^2 \\ & + (-b_2 y - cy)\sigma_\xi^2 \\ & + (b_2(1 - 2y - x) - cx - d_2)\langle \xi\eta\rangle - cxy;\end{aligned} \tag{30}$$

These three coupled equations can be solved by numerical integration, which we compare to individual-based simulation of the Crowley competition model, Fig 5.

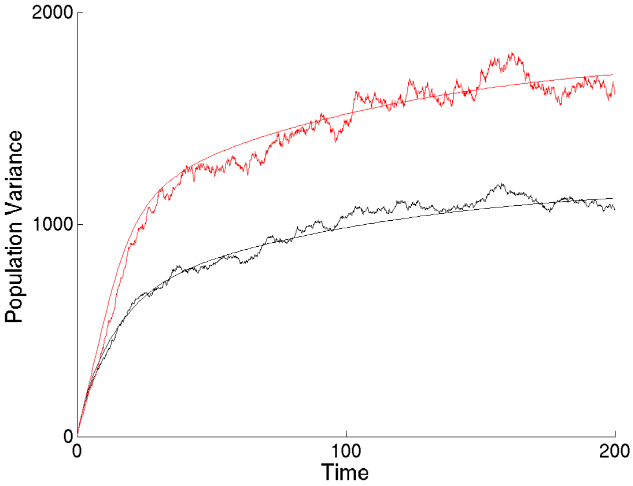


Fig. 5. Fluctuations for species x in black and y in red. Smooth curves are theoretical predictions. Model parameters: $b_1 = 0.2$, $b_2 = 0.6$, $d_1 = d_2 = c = 0.1$, $N = 1000$, plots based on an ensemble of 10^2 realizations.

4. Discussion

Demographic noise is inherent part of all populations. Demographic noise is a consequence of populations being finite; it creates fluctuations in population abundance and is responsible for extinction and fixation events. An accurate description of demographic noise requires both birth and death rates. We have presented a simple way (18) to estimate the scale of these demographic fluctuations by explicitly making use of the observation that the size of the fluctuations is smaller for bigger systems. Further, we identify a fully dynamical theory of these fluctuations from individual based models. We demonstrate that the theory can also be applied to multivariate dynamics, such as multi-species interactions or structured population models.

Faced with any time-series data on population abundances, we see demographic noise. Often, this noise is ignored, while models try to explain the general trends using deterministic models. One is particularly likely to look for deterministic explanations when faced with large deviations, invoking rich dynamical behavior such as phase transitions between alternate stable states [Ives *et al.*, 2008] or chaos. If the population is near equilibrium, (18) accurately describes fluctuations over time as well as those between populations. Given candidate deterministic models, one should predict the associated demographic noise for the models. This determines how far from the deterministic trajectory we might expect a particular model to be. The deterministic (macroscopic) dynamics of a model with higher fluctuations should not be expected to match the data as closely as one that predicts small fluctuations – in fact it would be possible to weight the goodness of fit by the expected demographic variation. Second, it may be possible to directly compare the predicted fluctuations against those observed if the population is thought to be within the fluctuation-dissipation domain described here. One should always bear in mind that any of these analyses require the model identify births and deaths separately.

From the distribution (9) it should be possible to estimate the distribution of extinction times.

The theory presented here can be applied in situations other than birth-death process of individuals in a population. For instance, genetic drift is a familiar phenomenon driven by demographic noise. The steady-state mutation-selection balance is an instance of the fluctuation dissipation result (17). This evolutionary scenario can also be subject to the fluctuation enhancement we observed here whenever the population is far enough away from equilibrium that the selection gradient has a positive derivative. Behavioral models could allow for fluctuations of resources or other consumers in finite patches. Fluctuation dissipation is also an important part of genetic circuits and chemical signalling [Bialek & Setayeshgar, 29] which are often driven by relatively small numbers of interacting chemicals due to the much smaller system size of a cell compared to a beaker experiment. Non-equilibrium stochastic processes with system sizes that are very finite are ubiquitous in biological systems, making dynamical theory for nonlinear dynamics that accounts for system size is crucial.

Appendix A. The diffusion approximation

A somewhat different approach to deriving a diffusion equation predominates in the literature. This approach does not make system size explicit, but instead hinges on taking a simultaneous limit of both short time and small step size. We prefer the derivation given in the text, since it appeals to system size rather than an arbitrary small parameter going to zero. It also provides a more natural treatment for nonlinear systems, for which the diffusion equation requires extra care. With these notes in mind, the classical derivation goes as follows. Consider small steps $x = \epsilon n$, and hence $p_n = \epsilon P_x$, where $\epsilon \ll 1$. To keep the process from slowing down we consequently have to scale up the rates by ϵ as well:

$$b_n - d_n = \frac{A_x}{\epsilon} \tag{A.1}$$

Where A is independent of ϵ. Similarly we have to scale the sum, which being proportional to the variance must be scaled by

$$b_n + d_n = \frac{B_x}{\epsilon^2} \tag{A.2}$$

We Taylor expand the step operator $\mathbb{E}$ in the new variable:

$$\mathbb{E}^k = 1 + \epsilon k \frac{\partial}{\partial x} + \frac{\epsilon^2 k^2}{2} \frac{\partial^2}{\partial x^2} + \dots \tag{A.3}$$

Then (4) becomes:

$$\begin{aligned} \frac{\partial P(x,t)}{\partial t} &= \left(\epsilon \frac{\partial}{\partial x} + \epsilon^2 \tfrac{1}{2} \frac{\partial^2}{\partial x^2} + \dots \right) \left(\frac{B_x}{2\epsilon^2} - \frac{A_x}{2\epsilon} \right) P \\ &\quad + \left(-\epsilon \frac{\partial}{\partial x} + \epsilon^2 \tfrac{1}{2} \frac{\partial^2}{\partial x^2} - \dots \right) \left(\frac{B_x}{2\epsilon^2} + \frac{A_x}{2\epsilon} \right) P \end{aligned} \tag{A.4}$$

Collecting terms of common order ϵ,

$$= -\frac{\partial A_x P}{\partial x} + \tfrac{1}{2} \frac{\partial^2 B_x P}{\partial x^2} + \mathcal{O}(\epsilon^2) \tag{A.5}$$

For small ϵ we can ignore the terms of $\mathcal{O}(\epsilon^2)$, and we have recovered the diffusion approximation. Unfortunately, nature does not give us a parameter ϵ that goes to zero. We expect that larger populations will have relatively smaller fluctuations (recall the introductory example) and hence this limit should have something to do with increasing the system size. We make these notions more precise by expanding equation (4) explicitly in terms of the system size. This will lead us to a much richer and more satisfying description of demographic noise than the mathematical limit above.

Appendix B. The Ω expansion

To see the Taylor expansion of the step operator (where k can be a positive or negative integer), first consider it in the variable n:

Take as the definition

$$\mathbb{E}^k f(n) = f(n+k)$$

Then

$$\begin{aligned} \mathbb{E}^k n &= n + k \\ \mathbb{E}^k n^2 &= \mathbb{E}^k n n = (n+k)(n+k) = n^2 + 2kn + k^2 \end{aligned}$$

This suggests we can approximate the step operator by a Taylor series

$$\mathbb{E}^k = 1 + k \frac{\partial}{\partial n} + \frac{k^2}{2} \frac{\partial^2}{\partial n^2} + \dots \tag{B.1}$$

To change variables, recall the chain rule,

$$\frac{\partial}{\partial \xi} f(n(\xi)) = \frac{\partial n}{\partial \xi} \frac{\partial}{\partial n} f(n(\xi))$$

hence

$$\frac{\partial}{\partial n} = \left(\frac{\partial n}{\partial \xi} \right)^{-1} \frac{\partial}{\partial \xi}$$

Making this substitution to (B.1) we recover (8) in the text.

To derive (9) in the text, note that the derivative of the probability distribution in the master equation, $\frac{\partial}{\partial t} P(n,t)$ is taken with n held constant,

$$\frac{\mathrm{d}n}{\mathrm{d}t} = \Omega \frac{\mathrm{d}\phi(t)}{\mathrm{d}t} + \Omega^{1/2} \frac{\mathrm{d}\xi}{\mathrm{d}t} = 0,$$

therefore

$$\frac{\mathrm{d}\xi}{\mathrm{d}t} = -\Omega^{1/2} \frac{\mathrm{d}\phi(t)}{\mathrm{d}t}. \tag{B.2}$$

Also by the chain rule, we have

$$\frac{\partial}{\partial t} P(n,t) = \frac{\partial \Pi}{\partial t} + \frac{\partial \Pi}{\partial \xi} \frac{\mathrm{d}\xi}{\mathrm{d}t} \tag{B.3}$$

Substituting in (B.2), we recover (9).

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