

1 From noise to knowledge: how randomness generates novel phenomena and
2 reveals information

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15 [phenomena](https://github.com/cboettig/noise-phenomena)), and if accepted, will be archived with provided DOI in an appropriate scientific data repository.

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Noise, as the term itself suggests, is most often seen a nuisance to ecological insight, a inconvenient reality that must be acknowledged, a haystack that must be stripped away to reveal the processes of interest underneath. Yet despite this well-earned reputation, noise is often interesting in its own right: noise can induce novel phenomena that could not be understood from some underlying deterministic model alone. Nor is all noise the same, and close examination of differences in frequency, color or magnitude can reveal insights that would otherwise be inaccessible. Yet with each aspect of stochasticity leading to some new or unexpected behavior, the time is right to move beyond the familiar refrain of “everything is important” [1]. Stochastic phenomena can suggest new ways of inferring process from pattern, and thus spark more dialog between theory and empirical perspectives that best advances the field as a whole. I highlight a few compelling examples, while observing that the study of stochastic phenomena are only beginning to make this translation into empirical inference. There are rich opportunities at this interface in the years ahead.

19 Introduction: Noise the nuisance

20 To the empirical ecologist, stochasticity, or more simply, “noise,” is just that – something which obscures
21 patterns we are trying to infer [2]; and an ever richer batteries of statistical methods are developed largely
22 in an attempt to strip away this undesirable randomness to reveal the patterns beneath [3]. Over the past
23 several decades, theoretical ecology has transitioned from thinking of stochasticity in such terms; where noise
24 is a nuisance that obscures the “deterministic skeleton” of the underlying mechanisms, to the recognition that
25 stochasticity can itself be a mechanism for driving many interesting phenomena [4]. Yet this transition from
26 “noise the nuisance” to “noise the creator” of ecological phenomena has had, with a few notable exceptions,
27 relatively little impact in empirical thinking about stochasticity. One of the most provocative of those
28 exceptions has turned the classical notion of noise the nuisance on its head: recognizing that noise driven
29 phenomena can become a tool to reveal underlying processes: to become “noise the informer.” Here I argue
30 that this third shift in perspective offers an opportunity to better bridge the divide between respective
31 primarily theoretical and primarily empirical communities by seeing noise not as mathematical curiosity or
32 statistical bugbear, but as a source for new opportunities for inference.

33 Few topics have received greater attention than the question of the persistence of a given species [3,5–9]
34 or the coexistence of multiple species [10–17]

35 and the role of stochasticity in more complex models, particularly in structured populations (matrix
36 models), [18–21]

37 in spatial structure [9,22–24]

38 Individual heterogeneity [25]; [26]

39 Excellent reviews and textbook introductions

40 [6] [1] [3] [27]

41 See in particular reviews by [28] and [29]

42 [30]

43 The extensive literature on demographic and environmental noise has been frequently reviewed elsewhere
44 [31]

45 [32]

46 I approach this synthesis in three parts. First, I will sketch the ground-work for the origins of noise in any
47 model as statistical summary of large number of additional processes from some lower level that are modeled
48 only in aggregate. This will provide the fundamentals we need to illustrate several key examples of noise
49 driven phenomena in ecological dynamics: noise the creator. Finally, we will be able to invert some of these

examples; instead of going from process to pattern, we will go from pattern to process: noise the informer.

I will anchor each of these sections using concrete examples from simple models. It is easy to critique such simple models: ecology is complex, and much effort has been spent on illustrating the importance that complexity: age and stage structure, spatial structure, individual heterogeneity, evolution, non-stationary environments, species network interactions, and much more [1,22]. While acknowledging more realistic examples and more general results where available, using specific and familiar simple models that – just complex enough to illustrate the phenomenon but no more – will provide us with a platform that is more accessible to both intuition and exploration and extension either through mathematical manipulation or computer simulation. In this spirit, I provide concise, detailed and commented code for simulating each of the models presented in Appendix A. Simulations permit poking and prodding of empirically-minded investigation unencumbered by either experimental design or mathematical formalism. Most stochastic models are expressed in the BUGS language, which may be more familiar to empirical readers than corresponding mathematical formulas. This also permits both efficient simulation and potential estimation of parameters given sample data using the R package, NIMBLE [33]; allowing the deductive models illustrated here to readily function as inductive models with parameters inferred from time-series data. A copy of this appendix is maintained at <https://github.com/cboettig/noise-phenomena>, and bug reports, suggestions or help requests are welcome through the issue tracker. A second appendix provides more mathematical details for interested readers. With these in place, we are ready to begin our tour through three major areas of noisy phenomena: Origins of noise, emergent phenomena, and noise-driven inference.

Origins of noise

What is noise? Where does it come from? Simply put, noise is all that we leave out of our model. Whenever stochasticity is introduced into a model, it is only as a simplification or summary of the effects of a large number of other processes, often occurring at different scales. A central theme of stochastic modeling research over the past several decades has been an emphasis on making this relationship between stochasticity and underlying processes more precise: that is, on the origins of noise [4]. This literature has largely divided the origins of stochasticity between *intrinsic* factors: where stochasticity is introduced to reflect the reality that our variables of interest are intrinsically statistical averages of lower-level processes, and *extrinsic* factors: where stochasticity reflects the impact of other variables we are not explicitly modeling at all [34]. **Demographic stochasticity** is the primary (though not the only) example of an intrinsic factor, which reflects the fact that the continuous variable we often think of a “population size” or “population

density” is an average over a lower level process of births and deaths among a finite number of individuals [35]. **Environmental stochasticity** is the primary example of an extinsic factor, reflecting the fact that parameters we may treat as constants in a model in fact depend on variables such as temperature or soil moisture that are not explicitly modeled by our equations, but simplified into statistical summaries of those processes [36].

The Gillespie simulation provides a simple and exact algorithm for simulating demographic stochasticity at an individual level.

Free from both the approximations and mathematical complexity of more common formulations using stochastic differential equations (SDEs), (or their partial differential equation counterparts the Fokker-Planck equation), the Gillespie algorithm offers a simple and powerful approach to simulating stochastic phenomena that remains underutilized.

The mathematical proofs [37] & [38], popularized by ???’s intuitive “system size” expansion, provide a far more explicit framework to interpret demographic stochasticity than the better known diffusion approximation [39,40].

It is often suggested that stochasticity is “inherent” or “fundamental,” e.g. “demographic stochasticity arises because the birth of an individual is probabilistic” [35]. It is easy to forget that this is merely an assertion about a model, not an assertion about reality. Only in quantum mechanics do we find inherently probabilistic properties: births and deaths of organisms all have far more mechanistic explanations which we simply summarize in statistical terms: on average – that is, summing over a wide range of possible mechanisms we have chosen not to explicitly model – an individual death occurs at rate λ .

This is in fact an extrinsic factor (variables not modeled explicitly), which makes birth appear probabilistic; (just as we describe the toss of a coin as probabilistic when in fact it is a mechanistic outcome of Newton’s laws).

Demographic stochasticity arises only subsequently, when we change scales from a description at the individual level to one at the population level.

[34]; [35]; [36]

This does not attempt to summarize all of the literature on the origins and types of noise, which have been reviewed elsewhere [4,28,29,31,32,41]

justify simple models, citations adapting this to complex models:

Early quantitative ecological models first formulated at the population level as differential or difference equations: deterministic models that seek to capture the essential features of a system while neglecting

any random component as mere noise [4]. Advances in both theoretical understanding and the advent of widely available and efficient numerical methods have helped drive research towards increasingly more explicit descriptions of how stochasticity enters into quantitative models [28,31].

Demographic stochasticity

Demographic stochasticity refers to fluctuations in population sizes or densities that arise from the fundamentally discrete nature of individual birth and death events. Demographic stochasticity is a particularly instructive case for illustrating a mechanism for how noise arises as an aggregate description from a lower-level mechanistic process. We summarize the myriad lower-level processes that mechanistically lead to the event of a ‘birth’ in the population as a probability: In a population of N identical individuals at time t , a birth occurs with probability $b_t(N_t)$ (*i.e.* a rate that can depend on the population size, N), which increases the population size to $N + 1$. Similarly, death events occur with probability $d_t(N_t)$, decreasing the population size by one individual, to $N - 1$. Assuming each of these events are independent, this is a state-dependent Poisson process. The change in the probability of being in state N is given by the sum over the ways to enter the state, minus the ways to leave the state: a simple expression of probability balance known as the “master equation” [42].

It is possible to simulate such a process exactly using Gillespie’s exact stochastic simulation algorithm [43], which simulates each individual birth or death as a separate event. Figure 1 uses this algorithm to compare simulations of [44] patch model; (see Appendix A for example code). In the Levins’ model, n individuals compete for a finite number of suitable habitats N . Individuals die a constant rate e , and produce offspring at a constant rate c who then have a probability of colonizing an open patch that is simply proportional to the fraction of available patches, $1 - n/N$.

$$\frac{dn}{dt} = \underbrace{cn \left(1 - \frac{n}{N}\right)}_{\text{birth}} - \underbrace{en}_{\text{death}}, \quad (1)$$

Figure 1 shows the results of two exact SSA simulations of this model with identical parameters except for the total number of available sites, N .

The van Kampen system size expansion provides a convenient way to explicitly approximate the “macroscopic” (*i.e.* population level, see [31]) dynamics from an individual-based description of events in a Markov process [37,38,42]. In addition to illustrating how common stochastic models (in particular, Gaussian noise)

137 arise from lower-level descriptions, this result will also provide us a useful framework for interpreting the
 138 behavior of stochastic models more generally. In Appendix B I illustrate the derivation of the following
 139 equations for the mean and expected population sizes for a generic density dependent birth-death process:

$$\frac{dx}{dt} = b(x) - d(x) + O(N^{-1}) \quad (2)$$

$$\frac{d\sigma^2}{dt} = 2(\partial_x b(x) - \partial_x d(x))\sigma^2 + b(x) + d(x) \quad (3)$$

140 where $x = \langle n \rangle$, the average or expected population size of an ensemble of replicates, assuming the
 141 transitions (+/- 1 in this case) are much smaller than the system size (N in the Levins model). The dynamics
 142 for the average population match the population-level equation.¹

143 The change in variance can be seen as a balance between the stochastic contribution, $b(x) + d(x)$ and the
 144 deterministic contribution, $\partial_x (b(x) - d(x))$. The deterministic contribution is the slope of the macroscopic
 145 equation, that is, the eigenvalue indicating the stability of the equilibrium point. For stable points, this value
 146 must be negative and precisely balance the strictly positive stochastic contribution of $b(x) + d(x)$ (the greater
 147 the rate of stochastic events involved, the greater the fluctuations). This balance at steady-state is known
 148 as the fluctuation-dissipation theorem [42], and will prove a useful expression in understanding stochastic
 149 dynamics. Because Eq (3) also describes the time-evolution of these fluctuations, we can similarly solve for
 150 the correlation between two points separated by time τ .

151 For our Levins' model, $b(n) = n(1 - \frac{n}{N})$ and $d(n) = en$, we find the average number of occupied patches
 152 $\langle n \rangle = N \frac{e}{c}$ with variance at steady-state of $\sigma_n^2 = N \frac{e}{c}$. Observe that the variance scales proportionally to
 153 the system size, N , which explains the standard deviation increases only as \sqrt{N} while the steady state
 154 itself increases in direct proportion to N , resulting in the smaller relative size of fluctuations in the larger
 155 system in Figure 1. We can also see that different ways of partitioning the same macroscopic equation into
 156 components of birth and death will create the same mean dynamics but with different levels of noise. For
 157 instance, in a logistic model with $b = rn$ and $d = rn^2/N$, we instead find the variance at steady state is
 158 $\sigma^2 = K$; significantly larger than in the Levins model.

¹up to fluctuations of order $\frac{1}{N}$. We can actually both observe and successfully approximate this higher-order correction from additional terms in the system size expansion to recover the phenomenon of stochastic inflation [45], where the average population size can be larger or smaller than predicted by the deterministic model – see Appendix A for examples in simulations compared to predictions of the system size expansion

Whereas demographic noise reflects processes at a lower scale (the individual, rather than the population), environmental stochasticity reflects processes whose dynamics we are not explicitly modelling. Once again, this can best be illustrated through an explicit formulation of the master equation. For a generic population model that depends not only on population state x but also on environmental factors y , it is possible to derive the steady-state variance (Appendix B) as:

$$\sigma_x^2 = \frac{(\partial_y f(x, y))^2}{(\partial_x f(x, y))^2 + \partial_x f(x, y) \tau_c} \sigma_e^2 + \sigma_d^2 \quad (4)$$

where σ_e^2 is the variance in the environmental noise and τ_c the auto-correlation of that noise, σ_d^2 the equilibrium variance contributed by demographic noise from before, $(\frac{b+d}{-2\partial_x(b-d)})$ and where we have defined $f(x, y) = b(x, y) - d(x, y)$ for notational convenience. For example, if extinction rate e in our Levins' model is allowed to vary stochastically as Gaussian white noise with variance σ_e^2 and mean e , we find the expected variance introduced in the population to be:

$$\sigma_n^2 = \frac{e^2}{(c+e)^2} \sigma_e^2 + \frac{e}{c} N$$

Note that the contribution of environmental stochasticity is independent of system size and directly proportional to the variance in the environment. This derivation provides a useful illustration of the difference between demographic noise and environmental noise: the latter simply describes the variation introduced by some other dynamic variable that we are not modelling explicitly, and whose dynamics are independent of the state of our system, x . This environmental variation no doubt also arises from some more detailed lower level process, but we need not be explicit about those dynamics – the expansion tells us that it is sufficient to know the overall variance and the degree of auto-correlation. Recent work has also highlighted the importance of including both demographic and environmental noise [46,47]. The system size expansion still requires the assumption that the noise is small relative to the system size. In the case of large fluctuations, this approximation must be replaced with a different approach, such as the WKB approximation, as discussed in [28].

The importance of τ_c , or the degree of auto-correlation, which emerges from our derivation above, has also been and continues to be a subject of significant interest in the study of stochastic population dynamics [48–52]. Early work often assumed environmental noise would be uncorrelated as a mathematical convenience. As the derivation of Eq (4) makes clear, for a continuous-time process, the relevant metric is the timescale of

auto-correlation in the environmental noise process relative to the auto-correlation timescale of the population dynamics. The Gaussian noise that emerges out of the system-size approximation is always auto-correlated to some degree – if we measure our environment at consecutive times infinitesimally far apart, we expect nearly identical values. At intervals much longer than the correlation time, consecutive measurements are effectively independent (i.e. white noise). The degree of auto-correlation in noise is all about *relative* timescales.

Other forms of stochasticity

Stochasticity frequently enters our models in other ways as well. For instance, most population-level models treat all individuals within the population, or at least within a particular age or stage class, as identical. *Individual heterogeneity* in relevant traits (growth rates, dispersal ability) can be represented probabilistically as a distribution rather than a fixed value, making it function as another form of random variation in a model [3,9,25]. *Spatial heterogeneity* can likewise be reflected in stochastic parameters of a spatially implicit model, or as spatially varying environmental stochasticity in a spatially explicit model. As with other forms of noise [46,47], interaction between individual or spatial variation and other sources of noise can drive patterns including the potential for persistence, coexistence, and dispersal of species [9,17,26]. *Observational error* acts much like another form of stochasticity, arising from sampling effects or limitations of instruments, etc. Yet unlike the sources described above, this uncertainty does not impact the actual state of our system, and thus does not give rise to any additional phenomena or information about that process, though it can obscure it [2,53].

Other forms of uncertainty common in models are not stochastic phenomena. This includes any form of *reducible uncertainty*: In constructing and estimating mathematical models of ecological processes, we encounter uncertainty over our parameter estimates and possible choice of models [54]. In some ways, this uncertainty can act like the stochasticity described above: for instance, both introduce variation into any forecast of future outcomes. Yet unlike stochasticity, this uncertainty is reducible: with additional observations, we can narrow the uncertainty over parameters or candidate models. Thus we will not consider model and parameter uncertainty, as they do not reflect intrinsic phenomena of the dynamics but only our own ignorance about those dynamics.

Deterministic chaos [55] is another mechanism of introducing significant variation into a simple model. Chaos can look a lot like noise: indeed, it can be observationally indistinguishable from a stochastic process [56,57]. Despite substantial interest in previous decades and the relative ease of encountering chaos in simple ecological models (particularly in difference equations), and convincing reconstructions of chaotic dynamics in laboratory manipulations [58] the prevalence of chaotic dynamics as a driving factor in most ecological

systems remains unclear. After all, the great variation of natural populations is hardly surprising: the undeniable influences of variation created by all those things left out of our models, all that individual detail from intrinsic, lower level processes and external environmental processes that becomes aggregated in our simple models all but begs for a stochastic description.

Much active research continues to explore the consequences of introducing these more explicitly motivated and interacting sources of noise. With some grounding in the origins of different types of noise in place, we are ready to move to our second stop to see how this noise can drive the creation of novel phenomena on a macroscopic level.

Noise the creator: Noise can induce novel phenomena

Stochasticity can give rise to a wide array of interesting phenomena that are often at odds with our intuition. As these examples will illustrate, such behavior arises through an interaction between stochastic and non-linear elements of a system, underscoring the importance of explicitly including stochasticity in ecological models [4,59]. Importantly, the noise itself does not have to be large to give rise to these phenomena. In this section, I highlight several examples that have shown up frequently in the literature and prove sufficiently tractable to provide a simple intuition for the mechanisms involved.

Persistence and coexistence

Few topics have recieved greater attention then the question of the persistence of a given species [???,3,5,7–9]

and coexistence of multiple species

[10–17]

Structured populations [18–21]

See in particular reviews by [28] and [29]

Individual heterogeneity [25]; [26]

[30]

A natural focus of much research into stochastic ecological systems has been on understanding the implications for persistence of individual and coexistence of interacting species. Demographic noise in particular has fundamental implications for the long-term equilibrium: any finite population, however big, is guaranteed to eventually go extinct under demographic noise [5,27]. However, in most models it is possible to define a notion of quasi-stationary distribution concentrated around the deterministic attractor, and to

prove the probability of extinction decreases exponentially with system size (e.g. see [28]; [17] also reviews more recent literature which has established these results more generally). Generalizations about persistence and stable coexistence of interacting species in stochastic models are difficult due to complex interactions between demographic and environmental noise, population structure, spatial heterogeneity, magnitude of noise, degree of auto-correlation and so forth [3,26,46,59]; indeed care must be taken even in defining the appropriate notion of persistence [60]. Instead of these long-term limits, here we will focus on a few examples of stochastic phenomena that can emerge on shorter time scales and provide some intuition for how the interaction between stochastic and nonlinear dynamics can create these surprising results.

Quasi-cycles

Understanding the origin of sustained oscillations has long been a central question in ecology [1,61]. The simple Lotka Volterra model produces only neutrally stable centers, while the more realistic model that introduces carrying capacity for prey as they compete for resources results in a model that produces only damped oscillations, eventually settling into a stable state (Figure 2A). However, the introduction of relatively small noise into the system can be sufficient to excite the system into sustained oscillations (Figure 2B) [62–64].

In the example shown here, a simple predator-prey system is driven by environmental white noise ξ_t , with prey following the equation:

$$x_{t+1} = x_t + x_t r \left(1 - \frac{x_t}{K}\right) - b x_t y_t + \xi_{x,t}$$

where x_t is the prey density at time t , r the growth rate, K the carrying capacity, b an encounter rate with the predator y , who obeys the equation:

$$y_{t+1} = y_t + c x_t y_t - d y_t + \xi_{y,t}$$

with c the conversion ratio and d the predator mortality rate. Here we have assumed for the prey, $\xi_x \sim \mathcal{N}(\iota, \sigma_x^2)$, and similarly for the predator driven by ξ_y . Figure 2A shows examples for noise $\sigma_x = \sigma_y = 10^{-5}$, while Figure 2B shows $\sigma_x = \sigma_y = 0.01$.

Oscillations arise through the process of stochastic resonance. The damped oscillations seen in Figure 2A are analogous to a child sitting still on a swing: friction slowly damps the magnitude of each successive oscillation, while the period of pendulum remains unchanged. Driving the pendulum through perturbations timed to match that natural period can quickly create sustained oscillations with large magnitudes, but

such perfect timing is not required. In the model above, white noise effectively drives the pendulum at all frequencies, though at very low magnitude, since the noise is small relative to the scale of the dynamics. However, frequencies that most closely match the natural period of the damped oscillator are amplified, resonating with the natural oscillations. This process is sufficient to permit even small noise to drive sustained oscillations in the model indefinitely. The power spectrum (the squared norm of the Fourier transform, a measure of what frequencies are present; see, e.g. [31]) provides a convenient way to visualize the effects of these oscillations. The power spectrum for a deterministic limit cycle would create a perfect sinusoidal oscillation and a resulting power spectrum of a delta spike at that single frequency. The power spectrum for the quasi-cycle instead shows a distribution of frequencies, centered at the the resonant frequency of the damped oscillator.

Early work by [62] identified quasi-cycles as a possible explanation for oscillations and periodic outbreaks in pest ecosystems. [65] analyzes the potential for such stochastic effects to drive cyclic behavior in population abundances of Atlantic bluefin tuna and Atlantic Cod, while [64] illustrates the use of power-spectrum approaches to examine the behavior of quasi-cycles in common disease outbreak models, focusing on a case where noise arises explicitly from demographic stochasticity, rather than generic environmental noise as in the model above and elsewhere [66,67].

[68] compare patterns from these stochastically generated cycles to stable limit cycles they resemble. Stochastic resonance highlights one way in which even small noise can play an important role in driving large scale patterns where we had previously only sought deterministic explanations. This example also illustrates the interplay between nonlinear dynamics and stochasticity that is the hallmark of stochastically driven phenomena. A stable node with linear dynamics, such as an Ornstein-Uhlenbeck process, has no resonant frequency, and could not produce sustained oscillations (unless the environmental driver itself had a periodic pattern) [40,64].

Stochastic switching

We turn from stochastic resonance to oscillations of a very different sort, which do not resemble any deterministic process, as seen in Figure 3A. This pattern is characterized by long stretches during which fluctuations in the state variable remain concentrated around a high average value followed by sudden, rapid transitions into fluctuations concentrated around a lower value. This behavior arises through the interaction of stochasticity and alternative stable state dynamics. The simulation shown in Figure 3A for the is based on an resource consumption model first proposed by [69] as one of the early examples of the potential for alternative stable state dynamics. The resource grows according to a logistic growth model and is consumed

according to a Holling Type-III functional response curve, to which I have simply introduced the addition of environmental noise:

$$X_{t+1} = X_t + \underbrace{X_t r \left(1 - \frac{X_t}{K}\right)}_{\text{growth, } g(X_t)} - \underbrace{\frac{aX_t^Q}{X_t^Q + H^Q}}_{\text{consumption, } c(X_t)} + \xi_t,$$

where ξ_t is normally distributed environmental variation with mean zero and standard deviation σ . Figure 3B shows separate curves corresponding the parts of the model describing vegetation growth and vegetation consumption, using the same parameters as shown in the simulation panel, 3A. Equilibria exist whenever growth balances consumption. For the parameters shown, the S-shaped curve of the Type-III consumption pattern crosses the quadratic curve of logistic growth at four separate locations. When growth is larger than consumption before the crossing, and thus smaller after, the point is stable, otherwise it is unstable. Consequently, we can see two stable points, in the neighborhood of $X_t \approx 1.2$ and $X_t \approx 0.5$, closely matching the average fluctuations seen in the simulation in 3A. Stochastic fluctuations drive spontaneous shifts between these alternative stable states.

The concept of a potential well, Figure 3C, is often invoked when describing the behavior of alternative stable states. The curve for the potential well, $U(x)$ is defined as the negative integral of the population growth rate,

$$U(x) = - \int_0^x f(y) dy$$

where in our model $f(y)$ is vegetation growth minus consumption, $f(y) = g(y) - c(y)$. The motivation comes from physics, where f is a force and U the corresponding potential energy. This suggests a convenient analogy to gravity, often implied by drawing a ball inside the curve and referring to this as a “ball-in-cup” diagram. The potential function is particularly instructive for understanding stochastic switching under small noise, as in our simulation in Figure 3, where it is straight-forward to show [42,70] that the probability of a transition is proportional to the exponential of the depth of the well from the lowest point to the separation barrier, (a result that is familiar as Arrhenius law of activation energy to grade-school students of chemistry). This effect is visible even in the short simulation shown in 3A, which spends longer times in the lower state which has the deeper well. (Readers are encouraged to experiment with this by adjusting the parameters of the simulation in the included code). Unfortunately, the literature is not always careful in describing how this potential well diagram arises, which has caused it to become a source for as least as much confusion as it

is of insight. While the curves in Figure 3B can be clearly associated with underlying mechanisms of rates: logistic growth and consumption with handling time, the same is not true of the potential: it is much harder to have a good intuition about the ‘negative integral of the difference growth and consumption,’ and how it would change in response to, say, a larger carrying capacity K or higher consumption rate a . While the x-axis of the potential diagram remains the same: the system state, the conceptual problem is clearly evident in the usual ambiguity describing the y-axis in such ball-in-cup models.

Despite the nearly ubiquitous association of a ball-in-cup model with ecological discussions of resilience and stability, this potential well diagram (Figure 3C) is also a source of confusion on the topic. As we have seen, the most salient feature of this diagram is the depth of each well: transition probabilities (under small noise) depend only on the depth of the well and not the steepness of the well, the distance between the wells or between well and tipping point barrier. However, it is important to remember that because the potential function is defined by the above integral, it in fact already combines two more elementary and mechanistically precise quantities from the growth equation: the slope of the growth rate (stability) and the distance to the tipping point (size of the basin of attraction). Both a steeper negative slope or a longer distance to integrate over between stable and unstable points will create a deeper well.

Empirical evidence for stochastic switching in ecological timeseries is limited by the long time scale usually required [71–73]. Because a single stochastic transition between alternative stable states appears as such a dramatic deviation from the previous pattern (as illustrated in Figure 3A), it is often tempting to assume the change could only be the result of some sudden external force or change in the environment, so it is worth remembering that given long enough, these transitions can happen entirely by chance stochasticity [74,75]. However, these transitions are most likely to be observed in systems with relatively shallow potential wells. This is mostly likely to occur if some external change is slowly making the potential well shallower and thus transitions more likely – a phenomenon that has become to be known as “flickering” and suggested as a potential early warning sign of an approaching transition [76]. Examples of flickering between alternative stable states have been suggested in data ranging from geological timescales at the end of glaciation in the Pleistocene [77] to ecological scales over a few decades in lake ecosystems [78]. Stochastic transitions between bi-stable states are thought to play an important role in genetic switches, where among other phenomena this mechanism can explain the emergence of two alternative phenotypes in clonal microbial populations, which can act to buffer the population in a changing environment [79].

Noise the informer: Noise can provide novel information

One of the most interesting aspects of noise is as a source of additional information. This can be realized in a variety of ways. For instance, in deriving expressions for the variance created by demographic noise above, we observed that different partitions of a logistic growth model can lead to the same macroscopic dynamics (same values for $b - d$), while having different variance (due to different values for $b+d$). This suggests that the variation observed in such a population could potentially help resolve how dynamics are partitioned between individual birth and death rates (though in practice one would have to first account for any contribution of environmental noise).

Noise can provide novel information in other ways as well. Stochastic fluctuations act like a continual miniature perturbation experiment, constantly pushing a system away from an equilibrium to reveal its behavior elsewhere in state space. Observing the size and auto-correlation of these fluctuations thus provides insight on the stability of an equilibrium point, (as can be seen, for instance in the fluctuation-dissipation result we found for generic birth death models). This observation has been exploited with particular success as a potential *early warning sign* that a system is loosing stability; possibly due to an approaching catastrophic transition or saddle-node bifurcation. This pattern, known as critical slowing down (in reference to the auto-correlation time in the physics literature) was first proposed as an early warning sign for ecological systems by [80], but has received considerable empirical as well as theoretical attention only more recently [81,82]. Increases in two of these early warning indicators, variance and auto-correlation, are illustrated along with the timeseries of a simulation of the dynamics of yeast population growth in Figure 4. This simulation is based on a mechanistic model developed by [83] that closely matches the population dynamics they observed in serial dilutions of budding yeast *Saccharomyces cerevisiae* on a sucrose medium. Because the relevant proteins are located in the extra-cellular matrix rather than inside the cells, budding yeast break down sucrose collaboratively, creating an Allee effect below which the population is too small to sustain itself. Increasing the serial dilution rate slowly over time drives the stable population towards a fold bifurcation, which is accompanied by the patterns of increasing variance and increasing auto-correlation seen empirically in lab populations [83] as well as the numerical simulation shown in Figure 4.

As we saw in the equations from the system-size approximation, the variance and auto-correlation in question are technically properties of an ensemble, and should be computed over replicate simulations. While the laboratory experiments of [83] do precisely this, conducting identical, independent replicate manipulations in separate beakers, this is not an option in natural populations. If the environmental change is sufficiently slow relative to the measurements, one can assume that the system is close to its stationary state over a

given window in time, computing these averages over a rolling time window as we illustrate here, rather than across an ensemble of replicates.

The challenge of identifying warning signs that a system is approaching a tipping point has proven a rich area for applications of stochastic processes. We have already seen how in addition to the patterns of increasing variance and auto-correlation, our survey of stochastic phenomena has highlighted the increased potential to observe stochastic switching, or flickering, as the system approaches the tipping point. Challenges remain in distinguishing these patterns from other causes [84]. For instance, as we have seen, variance in a system can increase due to external drivers without changing the auto-correlation, and both variance and auto-correlation can increase if a system loses stability without approaching a saddle-node bifurcation, but will not show flickering. The greater our suite of stochastic indicators, the better our ability to pin down the processes involved. Such examples suggest that stochastic processes could play a similar role in identifying other critical transitions. For instance, stochastic resonance may be visible in advance of a Hopf bifurcation, where a stable state gives way to stable oscillations (limit cycle) of growing magnitude [85,86].

Most importantly, the framing of stochastic processes as indicators of changes in an ecosystem that might otherwise go unnoticed has proven a rich catalyst for bringing these concepts beyond the realm of abstract theory. A rich array of experimental and observational tests of early warning signals [72,73,82,83,87] has served no merely to illustrate these phenomena can be seen in laboratory and field ecosystems, but also to spark suggestions of additional possible indicators and surface a wide array of practical [82,88], statistical [74,89], and theoretical [90,91] challenges to such application. This creates a two-way dialog between empirical and theoretical work that does much to advance the field as a whole.

Conclusions

The past two decades have seen widespread recognition of the central role that stochasticity plays through the use of mechanistic models can have in creating and understanding ecological phenomena [4,31]. We have seen increasing use of master-equation approaches to individual-based models to reflect demographic stochasticity that is amenable to analytical treatment [31], and much work in understanding the importance of environmental noise, particularly the more realistic but less mathematically convenient notion of colored or auto-correlated noise on population dynamics, persistence, and coexistence [17,28]. These deductive models can generate phenomena that resemble familiar patterns such as population cycles for which we have previously sought deterministic explanations, as well as stochastic phenomena with no such analog such as stochastic switching. Yet too many of these advances have remained limited to the domain of theory; limited

to deductive models which may seek to mimic observed patterns but are rarely used to confront empirical data directly. There is good reason for this: statistical inference of even relatively simple models with multiple sources of noise will always be difficult given limited ecological data [2]. However, many stochastic phenomena may suggest new ways to infer rather than merely obscure underlying processes.

The eruption of interest in early warning signals for critical transitions [81] provides an excellent illustration of this potential. A range of stochastic phenomena have been suggested and tested for their potential to reveal subtle signs of ecosystem change prior to a dramatic shift, and prompted a rich dialog between further theory and new experiment. Changes in stochastic properties such as variance or auto-correlation provide evidence of resilience loss that would be invisible to a deterministic model, and non-linear stochastic phenomena such as stochastic switching are observed as evidence of ‘flickering’ prior to a critical transition. In this way, our understanding of stochastic dynamics is translated into novel sources of information about a system which has sparked a wealth of empirical investigation and further theoretical work to test the potential of this approach. The study and application of stochastic phenomena to detect ecosystem change is unlikely to be limited to this simple scenario of a critical transition or fold bifurcation.

Precisely because most stochastic phenomena arise through their interaction with non-linearity, the patterns that result can become a lens into better understanding those nonlinear processes and detecting how they may change. Meanwhile, the widespread adoption of computational tools and the ability to express theoretical results in numerical algorithms can make any new approaches more readily accessible to application in empirical research. In the past two decades, we have set to rest those deterministic skeletons that see noise only as nuisance and embraced the central role noise plays as the creator of ecological phenomena. Going forward, I hope and predict that we will see greater discussion and use of stochastic phenomena to infer underlying processes in empirical patterns in similar interactions between theoretical and empirical research.

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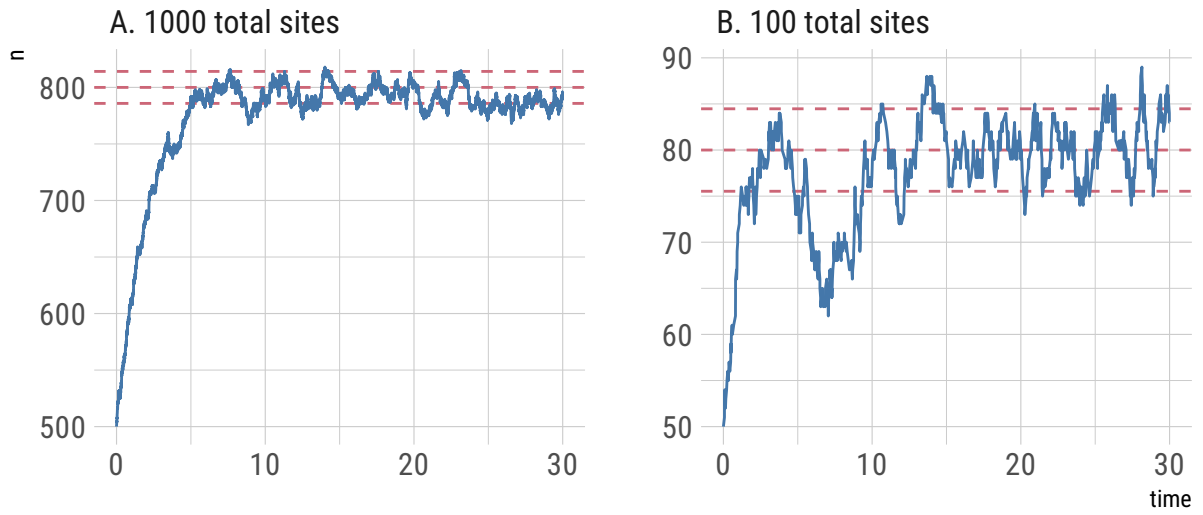


Figure 1: Population dynamics from a Gillespie simulation of the Levins model with large ($N=1000$, panel A) and small ($N=100$, panel B) number of sites (blue) show relatively weaker effects of demographic noise in the bigger system. Models are otherwise identical, with $e = 0.2$ and $c = 1$ (code in appendix A). Theoretical predictions for mean and plus/minus one standard deviation shown in horizontal red dashed lines.

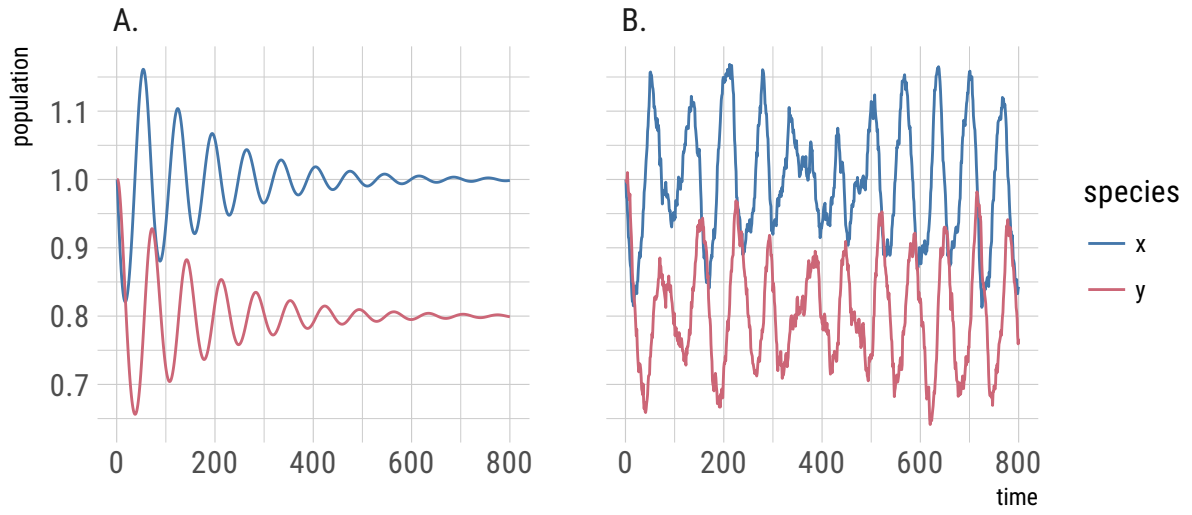


Figure 2: Panel A: under negligible environmental noise, the introduction of a carrying capacity damps Lotka-Volterra oscillations which eventually settle to a stable state. Panel B: small noise induces quasi-cycles in the same model: sustained long-term oscillations predominately around the natural frequency of the original damped oscillations. Parameters for models shown are $r = .1$, $K = 5$, $b = .1$, $c = .1$, $d = .1$, $N = 800$; code in Appendix A.

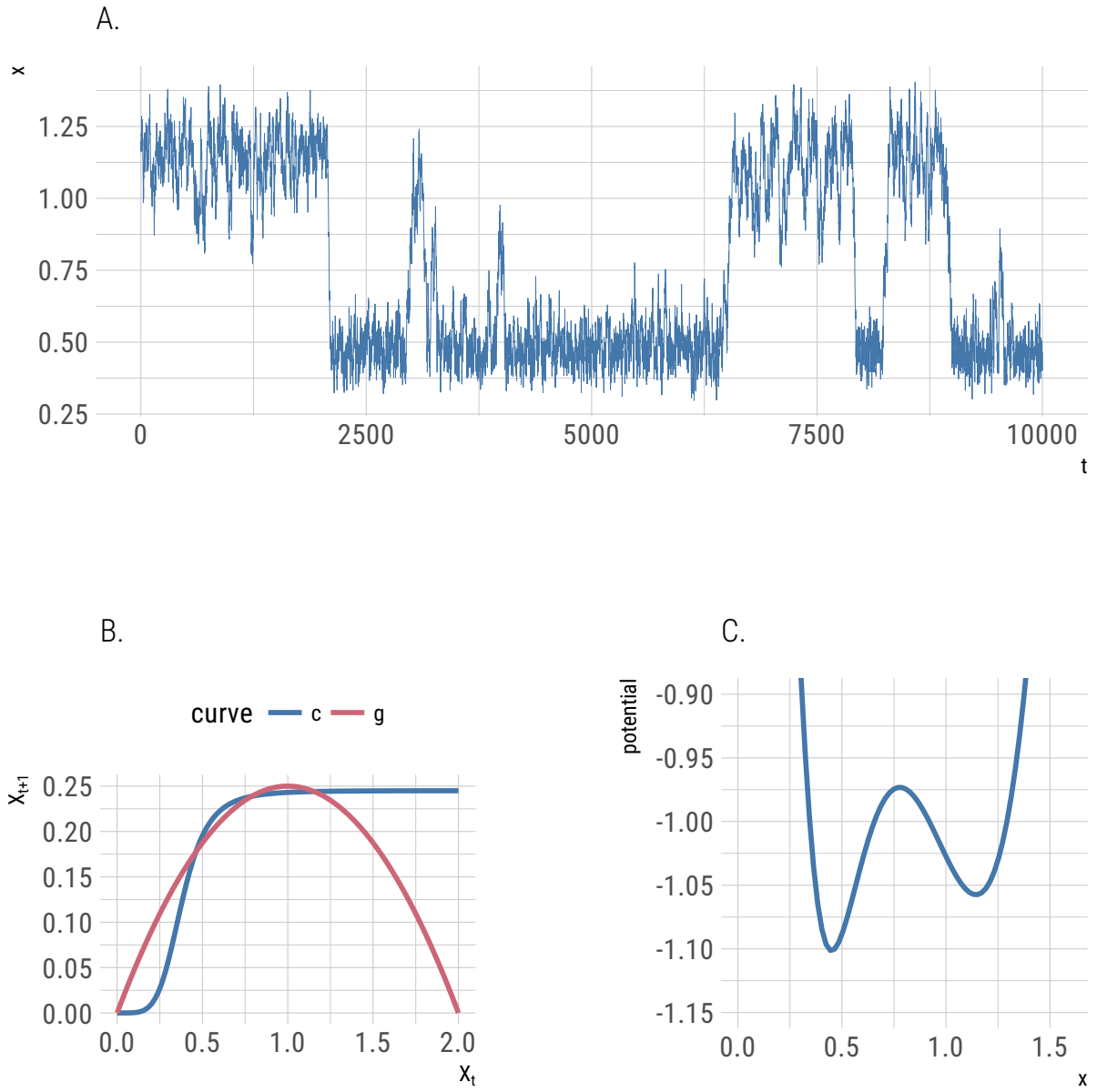


Figure 3: Stochastic switching in May's model of alternative stable state dynamics. $r = .5$, $K = 2$, $Q = 5$, $H = .38$, $\sigma = .04$, $a = 0.245$, $N = 10000$.

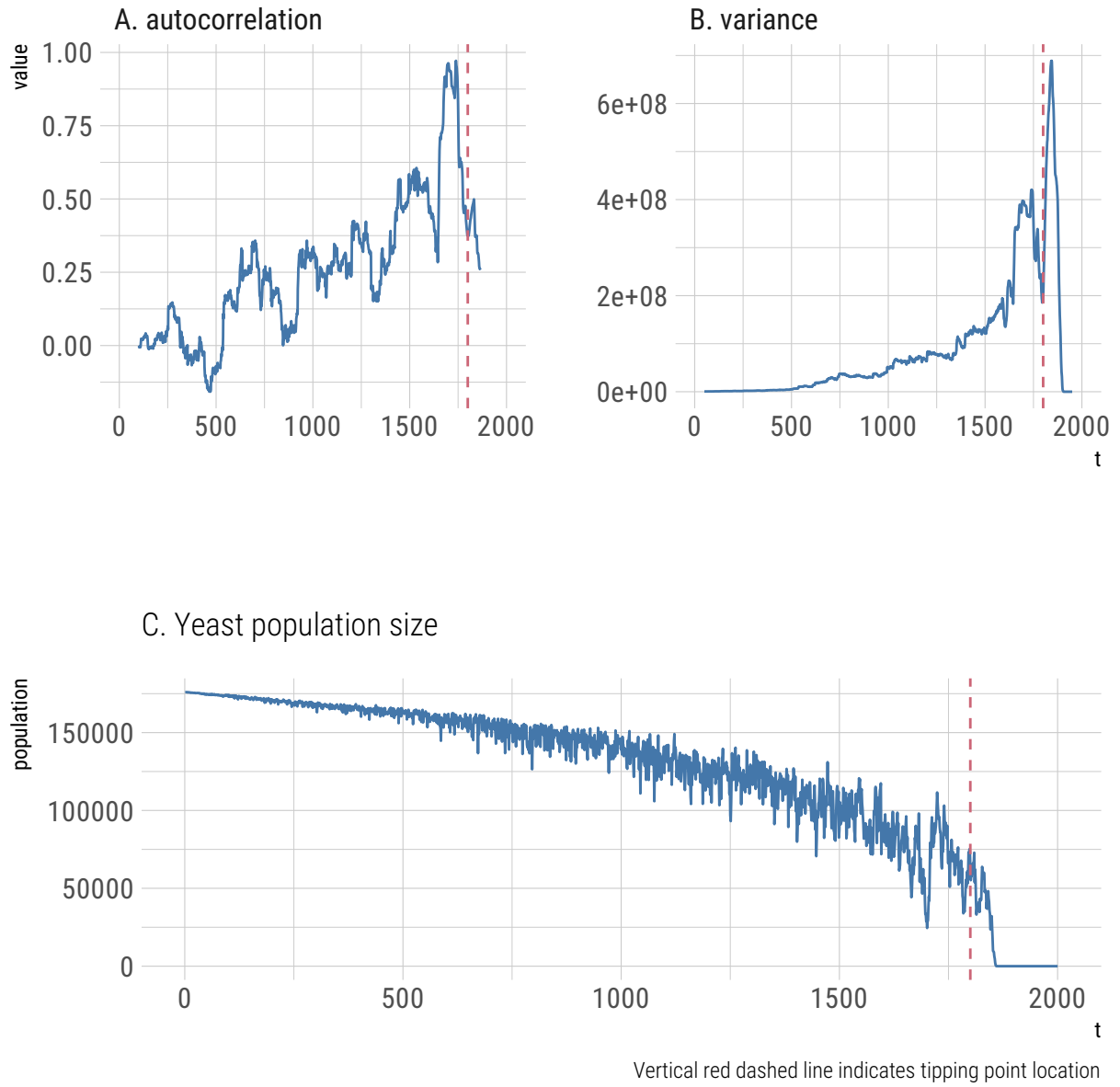


Figure 4: Early warning signs of a critical transition in a simulation of increasing serial dilution of budding yeast. Panel A: Rolling variance autocorrelation Time series is shown in panel C. Model details and simulation parameters in Appendix A.