

REVIEW AND SYNTHESIS

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

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Abstract

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, colour or magnitude can reveal insights that would otherwise be inaccessible. Yet with each aspect of stochasticity leading to some new or unexpected behaviour, the time is right to move beyond the familiar refrain of “everything is important” (Bjørnstad & Grenfell 2001). 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.

Keywords

Coloured noise, demographic noise, environmental noise, quasi-cycles, stochasticity, tipping points.

Ecology Letters (2018)

INTRODUCTION: NOISE THE NUISANCE

To many, stochasticity, or more simply, noise, is just that – something which obscures patterns we are trying to infer (Knape & de Valpine 2011); and an ever richer batteries of statistical methods are developed largely in an attempt to strip away this undesirable randomness to reveal the patterns beneath (Coulson 2001). Over the past several decades, literature in stochasticity has transitioned from thinking of stochasticity in such terms; where noise is a nuisance that obscures the deterministic skeleton of the underlying mechanisms, to the recognition that stochasticity can itself be a mechanism for driving many interesting phenomena (Coulson *et al.* 2004). Yet this transition from *noise the nuisance* to *noise the creator* of ecological phenomena has had, with a few notable exceptions, relatively little impact in broader thinking about stochasticity. One of the most provocative of those exceptions has turned the classical notion of noise the nuisance on its head: recognising that noise driven phenomena can become a tool to reveal underlying processes: to become *noise the informer*. Here I argue that this third shift in perspective offers an opportunity to better bridge the divide between respective primarily theoretical and primarily empirical communities by seeing noise not as mathematical curiosity or statistical bugbear, but as a source for new opportunities for inference.

In arguing for this shift, it essential to recognise this is a call for a bigger tent, not for the rejection of previous paradigms. What I will characterize as ‘noise the nuisance’ reflects a predominately statistical approach, in which noise, almost by

definition, represents all the processes we are not interested in that create additional variation which might obscure the pattern of interest. By contrast, an extensive literature has long explored how noise itself can create patterns and explain processes from population cycling to coexistence. These broad categories should be seen as a spectrum and not be mistaken for either a sharp dichotomy nor a reference to a strictly empirical-theoretical divide. Each paradigm expands upon rather than rejects the previous notion of noise: the recognition that noise can create novel phenomena does not mean that noise cannot also obscure the signal of some process of interest. Likewise, seeking to use noise as a novel source of information about underlying processes will be informed by both previous paradigms, as our discussion will illustrate.

Accompanying this discussion, I provide concise and commented code for simulating each of the models we will discuss as Appendix S1, and more mathematical background and derivations in Appendix S2. Numerical simulations permit poking and prodding investigation unencumbered by either experimental design or mathematical formalism. A copy of these appendices is maintained at <https://github.com/cboettig/noise-phenomena>.

To emphasise the underlying trend in the changing roles in which we see and understand noisy processes, I will also restrict my focus to relatively simple models primarily from population ecology context. Simplicity not only makes examples (in equations and in code) more tractable but also allows us to focus on aspects that are germane to many contexts rather than unique to particular complexities (Bartlett 1960;

Levins 1966). Nevertheless, that complexity matters – few themes have been better emphasized in the theoretical literature (Bjørnstad & Grenfell 2001). Both the foundational literature and recent research continue to echo the theme of understanding the impact different real world complexities have in stochastic dynamics, including the importance of age and stage structure (e.g. Cohen 1979; Tuljapurkar 1989, 1997; Caswell 2009; Metcalf *et al.* 2015; Vindenes & Engen 2017), spatial structure (e.g. Durrett & Levin 1994; Dieckmann *et al.* 2000; Kerr *et al.* 2002; Schreiber 2010), Individual heterogeneity (e.g. Vindenes & Langangen 2015; Hart *et al.* 2016) or the coexistence of multiple species (Caswell 1978; Tuljapurkar & Orzack 1980; Chesson & Warner 1981; Chesson 1982, 1985; Chesson & Ellner 1989; Melbourne *et al.* 2007; Schreiber 2017); correlated (Roughgarden 1975; Ripa & Lundberg 1996; Petchey *et al.* 1997; Schreiber 2010; Lee *et al.* 2017; Spanio *et al.* 2017; Paniw *et al.* 2018) or periodic (Bjørnstad & Grenfell 2001; Coulson 2001; Keeling *et al.* 2001) structure in environmental noise, or the interaction of ecological and evolutionary processes (Sæther 1997; Lenormand *et al.* 2009; Ozgul *et al.* 2009; Schreiber 2015; Vindenes & Langangen 2015). As such, we will rely on both textbooks and recent reviews to provide a proper treatment of these issues, and focus on broader trends.

This review is structured into three sections: Origins of noise, emergent phenomena, and noise-driven inference. The first section lays the conceptual groundwork we will need, while also highlighting a shift to more and more mechanistically rooted descriptions of noise. We will see where the common formulation of ‘deterministic skeleton plus noise term’ comes from, how it is best justified, and when it breaks down. The second section introduces *noise the creator*, showing examples of ecological phenomena generated by stochasticity. These examples will be familiar to most specialists but illustrate a different way of thinking than held by most ecologists, where noise is only a nuisance to be filtered or averaged out. The third and final section, *noise the informer*, turns these examples back-to-front, asking what noise can tell us about a system: such as its underlying resilience or stability, or the approach of a catastrophic shift. Examples are fewer here, and have largely yet to benefit from the introduction of either the rigorous theorems or more complex models so plentiful in the previous sections. Yet the promise of prediction, of early warning signs before tipping points, has spurred broad interest in such noise-based inference. This review is a call to both deepen the connection to mechanism and better formalise this thinking, but also look more broadly into other ways in which noisy phenomena can help inform and predict underlying processes.

ORIGINS OF NOISE

What is noise? Where does it come from? Many stochastic models are not explicit about whether the noise terms they introduce are intended to reflect intrinsic or extrinsic factors. Early quantitative ecological models first formulated at the population level in deterministic settings. The notion of a deterministic skeleton – responsible for the phenomena of interest – that is obscured from view by the nuisance of noise

has slowly given way to recognition that stochastic and deterministic elements not only interact in interesting ways (Coulson *et al.* 2004) but also share a common origin (e.g. Black & McKane 2012). A central theme of stochastic modelling 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.

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. 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 modelling at all (e.g. Keeling 2012). *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 (Melbourne 2012). *Environmental stochasticity* is the primary example of an extrinsic 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 modelled by our equations, but simplified into statistical summaries of those processes (Ripa 2012).

It is often suggested that stochasticity is inherent or fundamental, e.g. demographic stochasticity arises because the birth of an individual is probabilistic (Melbourne 2012). It is easy to forget that this is merely an assertion about a model, not an assertion about reality (Bartlett 1960). Only in quantum mechanics do we find inherently probabilistic properties: births and deaths of organisms all have far more mechanistic explanations which we simply summarise in statistical or average terms: an individual death occurs at rate λ . This is in fact an extrinsic factor (variables not modelled 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.

In the extensive literature developing the consequences of both demographic and environmental noise in models of increasing complexity, it can be easy to miss the equally important developments in making the origins of these sources of noise more precise. Models in which stochasticity was essentially tacked on to a deterministic skeleton can be substituted for approaches that permit both the skeleton and noise to emerge from underlying processes. This more mechanistically specific approach to the origins of noise can indeed recover the classic formulations, but it can also help highlight where those models break down. Much of the literature (e.g. see Ovaskainen & Meerson 2010) has focused on the following model, established in highly influential papers of Leigh (1981), Lande (1993), Foley (1994):

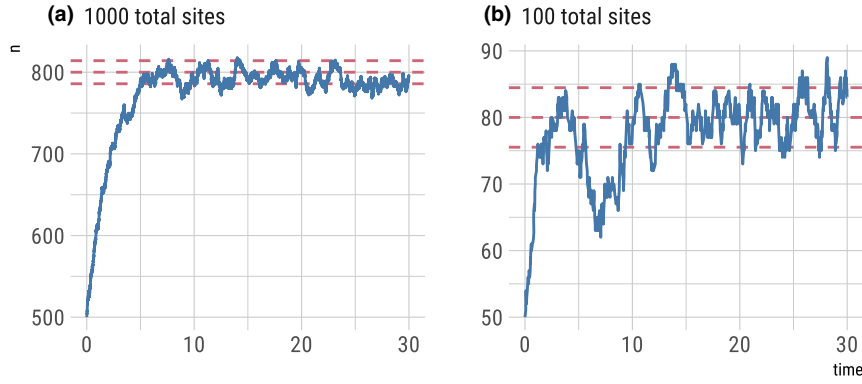


Figure 1 Population dynamics from a Gillespie simulation of the Levins model with large ($N = 1000$, panel a) and small ($N = 100$, panel b) number of sites (blue) show relatively weaker effects of demographic noise in the bigger system. Models are otherwise identical, with $e = 0.2$ and $c = 1$ (code in Appendix S1). Theoretical predictions for mean and ± 1 standard deviation shown in horizontal redashed lines.

$$dN_t = \underbrace{f(N_t)dt}_{\text{det skeleton}} + \underbrace{\sigma_d \sqrt{N_t} dB_t^{(d)}}_{\text{demographic noise}} + \underbrace{\sigma_e N_t dB_t^{(e)}}_{\text{environmental noise}} \quad (1)$$

where $dB_t^{(d)}$ and $dB_t^{(e)}$ refer to Brownian processes, (i.e. Gaussian white noise process) for demographic and environmental stochasticity respectively. When $f(n)$ is simply a Verhulst logistic function this is often referred to as the canonical model (e.g. Ovaskainen & Meerson 2010), and provides a clear illustration of the partition of separate deterministic and stochastic elements. Significant research continues to focus on extending the study of this model to consider more complex and higher-dimensional $f(n)$ (coexistence models, stage structured models) and consider the case of auto-correlated, rather than white noise of $dB_t^{(e)}$.

Here, we will examine how this canonical model can emerge from a lower-level description and how it can deviate from that description. This approach will also set the stage to see how our understanding of stochastic models can be extended to better reflect natural processes that shape not only for the so-called deterministic skeleton, but the noise terms as well. In so doing, I will highlight two tools fundamental to this analysis, one computational and one analytical: the exact simulation method of Gillespie (1977)'s stochastic simulation algorithm (SSA), and the van Kampen system size expansion (van Kampen 1976).

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 summarise 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 (van Kampen 2007). Note that in general this approach is equally applicable to stochastic transitions of any sort, not just step sizes of ± 1 and not just birth and death events, but can include transitions between stage classes or trait values, including mutations to continuously-valued traits in evolutionary dynamics (e.g. Boettiger *et al.* 2010).

The Gillespie (1977) provides an exact algorithm for simulating demographic stochasticity at an individual level, Fig. 1 and Appendix S1. The algorithm is a simple and direct implementation of the master equation, progressing in random step sizes determined by the waiting time until the next event. Free from both the approximations and mathematical complexity, the Gillespie algorithm is an interesting example of where we rely on a numerical implementation to check the accuracy of an analytic approximation, even in the case of simple models such as we will discuss. Though the algorithm is often maligned as numerically demanding, it can be run much more effectively even on large models on today's computers than when it was first developed in the 70s, and remains an under-utilised approach for writing simple and approximation-free¹ stochastic ecological models.

As our objective is to tie the origins of noise more closely to biological processes, it will be helpful to make the notion of a master equation concrete with a specific example. We will focus on the classic case of Levins (1969) patch model, to illustrate the Gillespie algorithm and the van Kampen system size expansion

$$\frac{dn}{dt} = \underbrace{cn \left(1 - \frac{n}{N}\right)}_{\text{birth}} - \underbrace{en}_{\text{death}}, \quad (2)$$

where 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

¹that is, free from the approximation made by SDE models as we see in the van Kampen example. All models are, of course, only approximations.

colonising an open patch that is simply proportional to the fraction of available patches, $1 - n/N$.

We choose this model because it has the same functional form as the ubiquitous logistic growth model, $\frac{dn}{dt} = rn(1 - n/K)$ but is explicit about how this net growth rate is divided between birth and death rate. This leads to real differences in observed stochastic properties of the model. Both the numerical approach (details in Appendix S1) and the analytical approach (Appendix S2) illustrate that it is straight-forward to use this same approach in alternate formulations.

Figure 1 shows the results of two exact SSA simulations of the classic patch model of Levins (1969), with identical parameters in both panels except for the total number of available sites, N , illustrating the magnitude of these fluctuations indeed scales in proportion to \sqrt{N} as postulated by the canonical equation, eqn 1.

The van Kampen system size expansion provides a mechanism to approximate the individual dynamics represented by the master equation (equivalently, by the Gillespie simulation) with a population-level description of the process. This is important not only because it will illustrate both origins and approximations that lie behind the population level models that predominate this literature, but will give our syntheses a chance to point out some more subtle misconceptions that have also arisen. Details of this expansion for a generic birth death process and comparison with the more familiar diffusion approximation are found in Appendix S2. Here, van Kampen's approximation follows a central-limit theorem style argument established rigorously in the theorems of Kurtz at about the same time (Kurtz 1970, 1972, 1978). The heart of the approximation is to imagine a population on some large landscape of which we sample only a fixed area to estimate the population density. That area is our system size, which as it expands includes more and more total individuals and experiences proportionally smaller fluctuations in population density. This results in the conclusion that the population density obeys a simple Gaussian distribution, whose mean size x and variance σ^2 are given by *ordinary* differential equations:

$$\frac{dx}{dt} = b(x) - d(x) + \mathcal{O}(N^{-1}) \quad (3)$$

$$\frac{d\sigma^2}{dt} = 2\partial_x[b(x) - d(x)]\sigma^2 + b(x) + d(x) + \mathcal{O}(N^{-\frac{1}{2}}) \quad (4)$$

This result is striking for a variety of reasons. First, we see the recovery of the deterministic skeleton, in which we naively replace population density x/N for population count n describes the *expected* density of the population (i.e. averaged over an ensemble of replicate realisations of the Gillespie simulations), and with remarkable accuracy, up to order $1/N$, i.e. a single individual.² The variance term is equally interesting. First, we note that noise arises from the interaction of individual birth and death events that defined our process,

illustrating the origins of this noise. Because both individual events of births and deaths add randomness, they both add to the growth of variation observed, i.e. $b(x) + d(x)$. Second, we see that dynamics for the variance σ^2 are *non-linear* whenever $b(x)$ or $d(x)$ are non-linear, so that different values of the population density will experience different noise intensities! In fact, this variance can only have an equilibrium size if the macroscopic equation has an equilibrium ($\partial_x[b(x) - d(x)] < 0$) Third, this expansion shows the variance equation is also less precise, accurate only to order $1/\sqrt{N}$. This variance equation will be important to us later as we examine the relative roles of noise and nonlinearity in noise-driven phenomena such as stochastic transitions between alternate stable states. The expected autocorrelation, $\langle x_0, x_t \rangle$ also follows from the system size expansion, e.g. at stationary state:

$$\langle x_0, x_t \rangle = \frac{b(x) + d(x)}{2\partial_x[b(x) - d(x)]} \exp\{-t|\partial_x b(x) - \partial_x d(x)|\} \quad (5)$$

which will also prove useful later on. Note this expression simply states that the equilibrium variance is a balance between noise terms, $b(x) + d(x)$ and the slope or eigenvalue of the deterministic skeleton, $2\partial_x[b(x) - d(x)]$, (a balance that forms the basis of the fluctuation-dissipation theorem) and that correlations fall off exponentially at a rate given by this slope. We will see both autocorrelation and variance play similar roles to infer this eigenvalue when we reach the role of noise as informer.

Note that this result is *different* than the canonical equation, eqn 1, or more generally the diffusion approximation (or Kramer–Moyal expansion; Kramers 1940; Moyal 1949; Gardiner 2009) which is much more typical in the ecological literature (e.g. Nisbet & Gurney 1982; Lande *et al.* 2003; Ovaskainen & Meerson 2010). Black & McKane (2012) gives an excellent introduction to the van Kampen expansion as a connection between individual-based and population-level model descriptions and applications, but fails to point out these differences, mistakenly characterising the van Kampen expansion as synonymous with the diffusion approximation. The diffusion approximation does not lead to a Gaussian distribution (equivalently, an SDE or PDE with linear noise term, see Appendix S2), but rather a *nonlinear* SDE of the form (e.g. Ovaskainen & Meerson 2010)

$$dX_t = [b(X_t) - d(X_t)]dt + \sqrt{b(X_t) + d(X_t)}dW_t \quad (6)$$

This better-known approach has several potential drawbacks. First, as noted in van Kampen (2007) or Gardiner (2009) (see Appendix S2), the Kramer–Moyal expansion approach rests on rather a more dubious double limit that often has no clear biological interpretation and can restrict its validity (though I believe theorem 3.3 of Kurtz (1978) establishes this approximation on firmer grounds). Second, the nonlinear SDE formulation can prove more difficult to work with than the convenient ODE expressions from van Kampen, eqn 4 (which can be expressed as a coupled ODE for the mean and a linear SDE for deviations). Third, while both approximations break down in the case of large deviations (see Ovaskainen & Meerson 2010), the van Kampen expansion shows that the macroscopic equation will continue to hold even when the variance does not; in contrast to the non-

²We can actually extend the van Kampen expansion to higher order and successfully approximate even this higher-order correction to the mean dynamics, recovering the phenomenon of stochastic inflation (Gonzalez & Holt 2002), where the average population size can be larger or smaller than predicted by the deterministic model depending on the curvature of the macroscopic equation.

linear SDE from the diffusion approximation. Though the limit used in the diffusion approximation can break down in cases where the van Kampen expansion is still valid (see Gardiner 2009), in most circumstances they produce similar results and both justify the postulates of the eqn 1.

Applying the system size approximation to the example of the Levins model introduced previously lets us both recover the classic model while adding some nuance in the interpretation. Taking $b(n) = n(1 - \frac{n}{N})$ and $d(n) = en$ and solving for the steady state to van Kampen's ODEs, we see the average number $\langle n \rangle$ of occupied patches is $\langle n \rangle = N \frac{e}{c}$ with variance at steady-state of $\sigma_n^2 = N \frac{e}{c}$. Observe that the variance scales proportionally to the system size, N , which explains the standard deviation increases as \sqrt{N} , as in the canonical model and as predicted by Fig. 1. We can also see that different ways of partitioning the same macroscopic equation into components of birth and death will create the same mean dynamics but with *different* levels of noise. For instance, in a logistic model with $b = rn$ and $d = rn^2/N$, we instead find the variance at steady state is $\sigma^2 = K$; significantly larger than in the Levins model.

Environmental stochasticity

The van Kampen expansion can also be useful in illustrating how extrinsic factors such as environmental noise enter into a stochastic model. Like the expansion of demographic noise, this derivation leads to environmental noise that is approximately Gaussian in distribution, but unlike the canonical model, leads to explicitly auto-correlated noise (see derivation, Appendix S2). Autocorrelated or coloured environmental noise has been a topic of significant theoretical interest (e.g. Roughgarden 1975; Lawton 1988; Ripa & Heino 1999; Fieberg & Ellner 2000; Marshall & Burgess 2015), but such formulations start from the empirical observation of autocorrelation in environmental time series rather than a process-based derivation. Any bounded continuous-time process will involve autocorrelation – measure a continuous process at ever-closer intervals in time and these measurements must converge. Appendix S2 shows that it is the *relative* time scales of the environmental process and population level process that really matter (more precisely, the relative magnitudes of the auto-correlation time of the environmental dynamics and population dynamics.) An environment with comparatively short auto-correlation scale will act effectively as white noise upon the population dynamics.

The van Kampen expansion for extrinsic factors (Appendix S2) also highlights the importance of how environmental noise couples to the population dynamics. The system size expansion illustrates how we can replace a model where stochasticity is nested inside some parameter into the simpler format of the canonical equation where this contribution can be merely added on as Gaussian noise at the end of a deterministic skeleton. (The expansion derives that the environmental noise is proportional to the square of the derivative of the deterministic skeleton with respect to the environmental variable, see Appendix S2.) Thus, for the Levins' model, we can capture the fluctuations introduced by demographic and environmental noise at equilibrium as a Gaussian distribution with variance given by the sum of demographic and environmental contributions:

$$\sigma_n^2 = \frac{\bar{e}}{c} N + \frac{[(1 - \frac{e}{c})N]^2}{(\bar{e} - c)^2} \sigma_e^2 \quad (7)$$

where $(1 - \frac{e}{c})N$ is the equilibrium population size. This justifies the assumption of the canonical equation, eqn 1 that the standard deviation (e.g. square root of the variance) scales in direct proportion to the system size N , while the demographic noise scales as the square root. Consequently, for a large system, the demographic contribution becomes proportionally smaller while the environmental contribution remains the same.

These examples of how a stochastic model arises from both intrinsic and extrinsic sources of noise through the use of the system size expansion serve both as critique and justification of the familiar notion of a stochastic model. This approximation justifies pulling out the stochasticity and adding it on the end of a deterministic skeleton (van Kampen's macroscopic equation) as Gaussian white noise term. The expansion also serves as a reminder that both noise and deterministic skeleton are the result of lower-level mechanistic processes, whose precise form will depend on the details of those processes. The Gaussian form, though convenient, is still an approximation, not suitable for small populations or rare, large deviations (see Appendix S2 and Ovaskainen & Meerson 2010). The expansion has given us three things: (1) showing us that additive Gaussian noise can be a surprisingly good approximation, (2) that noise intensity will converge to a stationary value whenever the system dynamics have a stable point, and (3) that the contribution of extrinsic (i.e. environmental) noise factors will dominate in large systems. These justifications will allow us to pursue our analysis of noise-driven phenomena using simple models in which a nonlinear deterministic skeleton is driven by Gaussian environmental noise.

NOISE THE CREATOR: NOISE CAN INDUCE NOVEL PHENOMENA

Most ecologists first encounter stochastic models in the context of statistics, where noise is a nuisance to be stripped away (Gotelli & Ellison 2004; Bolker 2007) to reveal deterministic mechanisms beneath, rather than being seen as a mechanism in and of itself. In examining the origins of noise, we were able to justify the simplistic view of noise as something merely added on to a deterministic skeleton to be less ad hoc than it appears; justified as it is by careful approximations and underlying theorems so long as our systems are sufficiently large and the fluctuations sufficiently small. If this appears to suggest that noise is somewhat negligible after all as long as we have the deterministic skeleton, then this section is all about rejecting that notion.

A major theme of the literature on stochastic models has been the illustration that, even in large systems with small noise, the qualitative behaviour of a stochastic model can be entirely unlike the behaviour of the deterministic skeleton (Higgins 1997; Bjørnstad & Grenfell 2001; Coulson *et al.* 2004). Even with our focus on population dynamics alone, examples of these differences are too numerous to do justice to all of them here – instead, we will focus on a handful of examples that show how noise interacts with nonlinearity to

create phenomena that are absent from the deterministic model. These examples will not only illustrate how ecological theory often sees noise in a very different role from ecological statistics, but will serve us well in our third section which seeks to turn that view of noise entirely on its head: not as something that obscures underlying processes but rather as a way of revealing them.

Persistence and coexistence

Perhaps there is no starker example of differences between the behaviour of a deterministic skeleton and a stochastic model than in the case of persistence of a species and the coexistence of multiple species. Demographic noise guarantees extinction in the long-run for any finite population (e.g. Kendall 1949; Bartlett 1955, 1960; Lande 1993; Saether *et al.* 1998; Coulson 2001; Lande *et al.* 2003; Schreiber 2006, 2010, 2017; Ovaskainen & Meerson 2010). Stochasticity can also do the opposite, allowing many species to coexist in scenarios where the deterministic skeleton would predict all but one of them to be doomed to extinction (Tuljapurkar & Orzack 1980; Chesson & Warner 1981; Chesson 1982, 1985; Chesson & Ellner 1989; Melbourne *et al.* 2007; Hart *et al.* 2016; Schreiber 2017). Two important trends in this literature have been establishing existing results in more general and precise language and theorems (e.g. see Schreiber 2012 for an excellent overview and synthesis of persistence and coexistence respectively), and continuing to extend such results to more complex contexts (Ovaskainen & Meerson 2010 provides one excellent review), in particular addressing auto-correlated noise (e.g. Ripa & Lundberg 1996; Petchey *et al.* 1997; Ripa & Heino 1999; Schreiber 2010; Lee *et al.* 2017; Spanio *et al.* 2017), spatial structure (e.g. Durrett & Levin 1994; Hastings & Higgins 1994; Dieckmann *et al.* 2000; Kerr *et al.* 2002; Schreiber 2010) and stage structure (e.g. Cohen 1979; Tuljapurkar 1989; Caswell 2009; Metcalf *et al.* 2015; Vindenes & Engen 2017), among other issues. We will turn our attention away from the well-trodden ground of persistence and coexistence to focus on other phenomena that can emerge in stochastic models: quasi-cycles and stochastic switching. Both examples will illustrate patterns that differ sharply from those of the deterministic skeleton, both for different underlying reasons. Interesting in their own right, these examples will also provide intuition for our third section on noise the informer.

Quasi-cycles

Understanding the origin of sustained oscillations has long been a central question in ecology (Hastings 1996; Kendall *et al.* 1999; Bjørnstad & Grenfell 2001). The simple Lotka–Volterra model produces only neutrally stable centres, 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 (Fig. 2a). However, the introduction of relatively small noise into the system can be sufficient to excite the system into sustained oscillations (Fig. 2b) (empirical discussed in Greenman & Benton 2003; Bjørnstad *et al.* 2004; Black & McKane 2010). Fig. 2c shows empirical data on records of

bluefin tuna catch that Bjørnstad *et al.* (2004) analyse as a possible example for such quasi-cycle oscillations in an important marine predator.

Nisbet & Gurney (1976) first identifies the potential for quasi-cycles to explain sustained oscillations in a simple predator–prey model with stochastic forcing, which provides a familiar formulation for us to illustrate the phenomena. Consider a predator–prey system is driven by environmental white noise ξ_t (e.g. as we have seen arise from stochastic growth rates), with prey following the equation:

$$x_{t+1} = x_t + x_t r \left(1 - \frac{x_t}{K}\right) - b x_t y_t + \xi_{x,t} \quad (8)$$

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:

$$y_{t+1} = y_t + c x_t y_t - d y_t + \xi_{y,t} \quad (9)$$

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

Oscillations arise through the process known as stochastic resonance (Nisbet & Gurney 1976; Greenman & Benton 2003). The damped oscillations seen in Fig. 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. Nisbet & Gurney (1982) for background and examples in McKane & Newman (2005), Alonso *et al.* (2007) or Black & McKane (2012)] provides a convenient way to visualise 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, centred at the resonant frequency of the damped oscillator (Nisbet & Gurney 1982).

Since Nisbet & Gurney (1976), examples of stochastic resonance have been demonstrated in common models and implicated in empirical examples of increasing complexity, (Greenman & Benton 2003), particularly in higher-dimensional disease and outbreak models (Blarer & Doebeli 1999; Greenman & Benton 2003; McKane & Newman 2005; Alonso *et al.* 2007; Black & McKane 2010). Blarer & Doebeli (1999) identified quasi-cycles as a possible explanation for oscillations and periodic outbreaks in pest ecosystems. Bjørnstad *et al.* (2004) analyses the potential for such stochastic effects

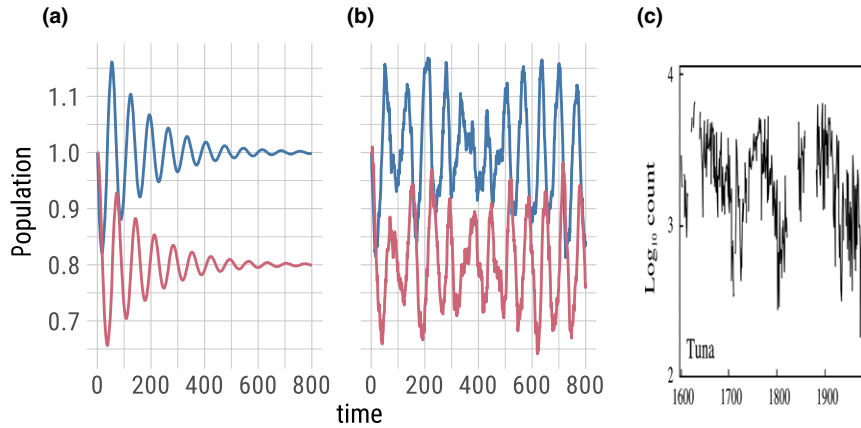


Figure 2 Panel a: under negligible environmental noise, the introduction of a carrying capacity damps Lotka–Volterra oscillations which eventually settle to a stable state. Panel b: small noise induces quasi-cycles in the same model: sustained long-term oscillations predominately around the natural frequency 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 S1. Panel c shows a potential empirical observation of stochastic resonance in historical records of bluefin Tuna, reproduced with permission from Bjørnstad *et al.* (2004).

to drive cyclic behaviour in population abundances of Atlantic bluefin tuna and Atlantic Cod. McKane & Newman (2005), Alonso *et al.* (2007), and Black & McKane (2010) illustrate the emergence of quasi-cycles in common disease outbreak models, including the use of power spectrum analysis. Pineda-Krch *et al.* (2007) compare patterns from stochastically generated cycles to stable limit cycles they resemble to ask how we can discriminate between these mechanisms. 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) (e.g. Gardiner 2009; Black & McKane 2010).

Stochastic switching

We turn from stochastic resonance to oscillations of a different sort, illustrated in Fig. 3 in empirical data on rubella outbreaks in Copenhagen, analysed by Keeling *et al.* (2001), and in simulations of a standard model shown in Fig. 3b. This pattern is characterised 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 behaviour arises through the interaction of stochasticity and alternative stable state dynamics. To sidestep some of the complexity of the disease model proposed in Keeling *et al.* (2001) we will illustrate the same stochastic switching phenomenon in the classic resource consumption model of May (1977), which has been widely used to study alternative state dynamics. As we shall see, stochastic switching is a generic property of models with alternative stable states which will have other implications later on. In May (1977) model, a resource species 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:

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

where ξ_t is normally distributed environmental variation with mean zero and standard deviation σ . Fig. 3c shows separate curves corresponding to 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 neighbourhood 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, Fig. 3d, is often invoked when describing the behaviour 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 Fig. 3, where it is straight-forward to show (e.g. Feller 1968; van Kampen 2007) that the probability of a

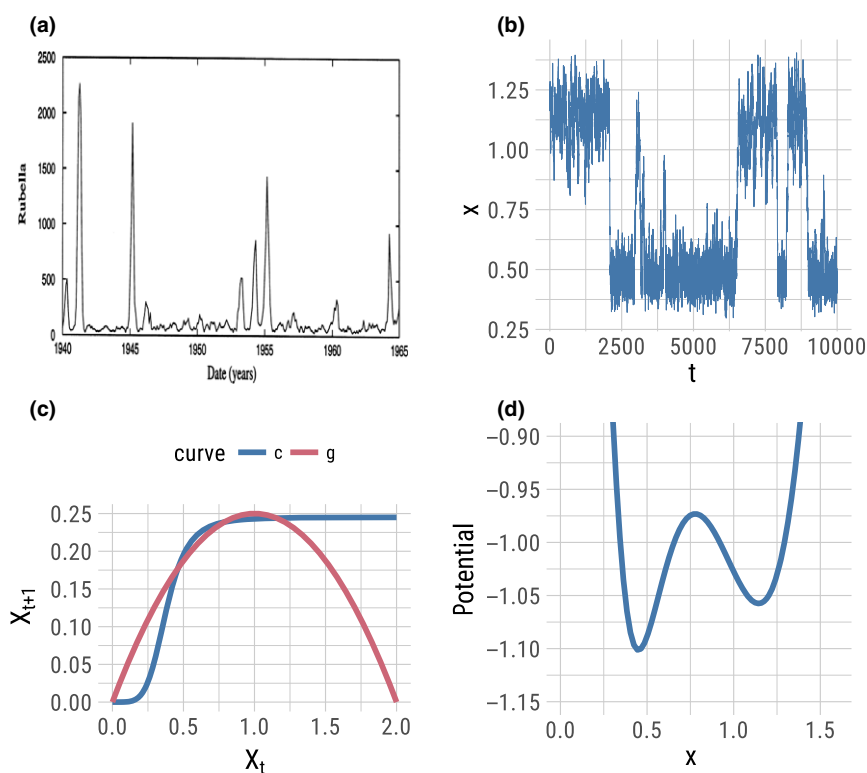


Figure 3 Panel a: Data on prevalence of rubella in Copenhagen illustrating potential stochastic switching dynamics between two regimes, reproduced with permission from Keeling *et al.* (2001). Panels b–d: Stochastic switching in May’s model of alternative stable state dynamics. Panel b: time series showing stochastic switching events between regimes. Panel c: separate nonlinear birth and death processes intersect at multiple points creating alternate stable states. Panel d: The corresponding potential well derived from the birth-death model: $U(x) = -\int b(x) - d(x)dx$. Parameter values shown $r = .5$, $K = 2$, $Q = 5$, $H = .38$, $\sigma = .04$, $a = 0.245$, $N = 10\,000$, see code in Appendix S1.

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 Fig. 3b, 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 at least as much confusion as it is of insight. While the curves in Fig. 3c 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 (Fig. 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. Because these transitions between alternative stable states appear as such a dramatic deviation from the previous pattern (as illustrated in Fig. 3a), it is tempting to assume they result from some sudden external force or change in the environment. As the numerical examples illustrate, these transitions can be explained entirely by chance (Boettiger & Hastings 2012a; Drake 2013).

Empirical evidence for stochastic switching in ecological time series is limited by the long time scale usually required (Taylor *et al.* 1993; but see Keeling *et al.* 2001; Wang *et al.* 2012; Clements & Ozgul 2016; Clements *et al.* 2017). As our discussion highlights, we are most likely to observe the phenomenon when at least one of the potential wells is relatively shallow, which results in a pattern of long periods in a single state (the deeper well) punctuated by brief excursions into and back out of the shallow well. This drives the more spike-like pattern seen in the rubella outbreaks from Keeling *et al.* (2001). 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 (Balaban 2004). This mechanism has also been explored in the emergence of multiple strategies under evolutionary dynamics in disease models (Read & Keeling 2007). This further underscores that the collection of more long-term data will be essential to our understanding of noisy phenomena and their underlying mechanisms.

NOISE THE INFORMER: NOISE CAN PROVIDE NOVEL INFORMATION

Transitions from systems with particularly shallow wells have recently taken on new empirical significance. Because such transitions become more likely as the potential well becomes less deep (i.e. the attractor has become less stable), the onset of such transitions can be interpreted as an indication of this loss of stability. This phenomenon has been dubbed flickering and suggested as a warning sign that a more permanent transition to the alternate stable state is approaching (Brock & Carpenter 2010). Examples of flickering between alternative stable states have been suggested in data ranging from geological timescales at the end of glaciation in the Pleistocene (Taylor *et al.* 1993) to ecological scales over a few decades in lake ecosystems (Wang *et al.* 2012). Flickering is then our first example of noise the informer – in which the emergence of a stochastic phenomenon is re-interpreted in a way that sheds light on an underlying process.

In examining noise the creator, we began with a tension between the interpretation of noise as it is usually presented in the context of statistical inference: a nuisance to be stripped away, and how it is viewed by the theorist, as a potentially fundamental driver of patterns, including oscillations, regime shifts, extinction & coexistence. In this third section, we attempt to reunite these two largely divergent views of the role of noise by highlighting how phenomena from the latter (noisy phenomena) can be used to address the questions of the former (inferring underlying process from pattern).

Our most provocative example of how noisy phenomena can act to reveal underlying processes comes from the literature we have just touched upon in the case of flickering – a growing set of the so-called ‘early warning signs’ of critical transitions (e.g. Scheffer *et al.* 2009). The fundamental insight behind all of these signs comes from the exploiting the ability of equations we encountered in origins of noise to reveal subtle changes in underlying processes before those changes are visible at the macroscopic (deterministic) level. This literature focuses on the phenomenon of a tipping point, in which gradual changes to the environment show essentially no changes to the behaviour of a system (i.e. the abundance of a population or health of lake ecosystem) followed by a rapid change when the tipping point is reached that cannot be easily reversed. (Scheffer *et al.* 2009, 2015). The fundamental insight of early warning signals has been to realise that though the average or deterministic dynamics of such a system do not change significantly prior to the tipping point, the dynamics of the noise must change in a consistent and predictable manner.

This pattern, known as ‘critical slowing down’ for reasons that will become obvious, was first proposed as an early warning sign for ecological transitions by Wissel (1984), but has received considerable attention only more recently, particularly owing to work in empirical systems (Scheffer *et al.* 2015). Our analysis in the origins of noise provides sufficient framework to illustrate this idea completely. The premise behind the tipping point just described is that of a fold bifurcation (which I will not detail here, but see Holling 1973; Strogatz 2001; Scheffer *et al.* 2009). The key thing we need to know about this bifurcation is that it involves changes *derivative* of the deterministic skeleton ($\partial_x[b(x) - d(x)]_{x=\hat{x}}$ in the notation of our example), which can build up or some time without significant changes to the location of the equilibrium state \hat{x} . This derivative did not appear in our macroscopic equation, $\frac{dx}{dt} = b(x) - d(x)$, but featured regularly in our equations for the noise, such as the expected variance, eqn 4 and auto-correlation, eqn 5. This derivative represents the *stability* of the equilibrium: how quickly deviations return to the stationary value. The magnitude of both variance and auto-correlation must increase as the stability ($\partial_x[b(x) - d(x)]_{x=\hat{x}}$) decreases prior to a critical transition.

The early warning signals approach views noise as a sequence of countless miniature perturbation experiments. Fig. 4 illustrates early warning indicators in an experimental manipulation and corresponding simulated model of Dai *et al.* (2012) and Dai *et al.* (2015). Though early warning signals have been reported in a growing range of systems (Scheffer *et al.* 2015), these laboratory experiments in population dynamics they observed in serial dilutions of budding yeast *Saccharomyces cerevisiae* on a sucrose medium provide the most convincing mechanistic interpretation of the underlying fold bifurcation. 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 autocorrelation. This pattern can be seen empirically in lab populations (Dai *et al.* 2012, 2015) and explored numerically in a simulation of the yeast dynamics shown in Fig. 4. As the mechanistic model of yeast population dynamics is already quite simple, the simulation shown here (code in Appendix S2) corresponds directly to the model proposed by Dai *et al.* (2015).

As we saw in the equations from the system-size approximation, the variance and autocorrelation in question are technical properties of an ensemble, and should be computed over replicate simulations. While the laboratory experiments such as Dai *et al.* (2015) 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.

In contrast to the examples, we have considered previously, work that extends this analysis into more complex scenarios

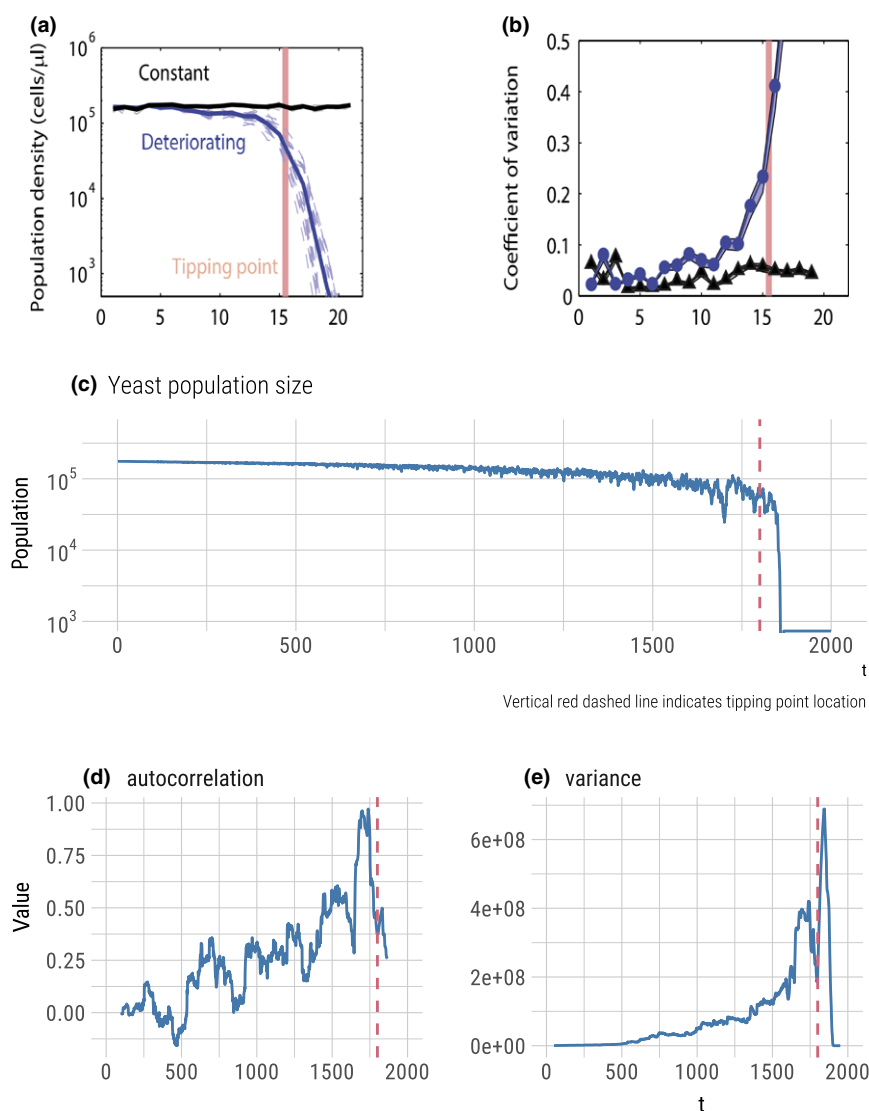


Figure 4 Early warning signs of a critical transition in a simulation of increasing serial dilution of budding yeast. Panel a: Data from replicate manipulations, reproduced with permission from Dai *et al.* (2015). Panel b: Coefficient of variation for the same experimental data. Panel c: Simulated single time series model of Dai *et al.* (2015). Panels d,e: Rolling variance and autocorrelation over simulated data show an increase in advance of the transition. Simulation details in Appendix S1. Warning signal statistics for experimental data not shown, see Dai *et al.* (2015).

of structured populations, interacting species, autocorrelated noise etc are significantly underdeveloped. Issues of spatial structure have received more attention (e.g. Guttal & Jayaprakash 2009; Dakos *et al.* 2011; Bel *et al.* 2012; Dai *et al.* 2013) but still largely idiosyncratic. Significant challenges remain in distinguishing these patterns from other causes (Boettiger *et al.* 2013). For instance, as we have seen, variance in a system can increase due to external drivers without changing the autocorrelation, and both variance and auto-correlation can increase if a system loses stability without approaching a saddle-node bifurcation, but will not show flickering. Teasing these issues apart in greater mathematical formalism and under more complex and realistic models remain largely open problems.

Interpreting stochastic processes as potential new sources of information has also proven to be an effective catalyst in bringing concepts from theory to application. An array of

experimental and observational tests of early warning signals (*i.e.* Carpenter *et al.* 2011; Dai *et al.* 2012; Scheffer *et al.* 2015; Clements & Ozgul 2016; Clements *et al.* 2017) has illustrated where these phenomena can be seen in laboratory and field ecosystems, and also sparked discussion of a wide array of practical (Boettiger & Hastings 2013; Scheffer *et al.* 2015), statistical (e.g. Boettiger & Hastings 2012a,b), and theoretical (Hastings & Wysham 2010; e.g. Dai *et al.* 2015) challenges that arise. This creates a two-way dialog between empirical and theoretical work that does much to advance the field as a whole. Similar dialog between theory and experiment in other areas of stochastic dynamics could benefit both sides.

The potential for stochastic phenomena to provide information about underlying processes goes well beyond available examples in stability and early warning signals. The examples from fold bifurcations already 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 (e.g. Fussmann *et al.* 2000; Strogatz 2001; Nelson *et al.* 2013). Noise can provide information in unrelated ways as well. 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).

CONCLUSIONS

This review has explored three paradigms in how noise is viewed throughout the ecological literature, which I have dubbed respectively: noise the *nuisance*, noise the *creator*, and noise the *informer*. Noise can be seen as a nuisance almost by definition: in examining the origins of noise, we have seen how stochasticity is introduced not because ecological processes are random in some fundamental sense, but rather, because those processes are influenced by a complex combination of forces we do not model explicitly. In this view, noise captures all that additional variation that is separate from the process of interest, and a rich array of statistical methods allow us to separate the one from the other in observations and experiments. By examining the origins of noise, we have seen that despite the complex ways in this noise can enter a model, that a Gaussian white-noise approximation (van Kampen 2007; Black & McKane 2012) is often appropriate given a limit of a large system size – a fact often invoked implicitly but rarely derived explicitly from the theorems of Kurtz (1978) and others.

Building on these foundations, we turned to noise the creator, illustrating how even small magnitude Gaussian noise could itself create and drive interesting phenomena. While a purely statistical paradigm might look to explain patterns such as oscillations or sudden transitions in terms of deterministic processes, this section highlighted how noise can create and sustain cycles (e.g. Nisbet & Gurney 1976; Bjørnstad *et al.* 2004) and switches (Keeling *et al.* 2001). While our examples focused on the most tractable systems, a wealth of literature has explored such phenomena in ever more complex contexts. These examples paint a very different picture of noise, one where ‘everything matters’ (Bjørnstad & Grenfell 2001), where it can be difficult to know what drives a pattern and where omitting any of the complexity (age or spatial structure, autocorrelation, individual heterogeneity) can qualitatively alter the behaviour of a model.

Our third paradigm seeks a more optimistic middle ground of noise the informer. Here we saw the examples from an empirically driven literature on early warning signals (Scheffer *et al.* 2009; Dai *et al.* 2012) view noise as a source of countless miniature experiments which can reveal the underlying dynamics of a system and how they may be slowly changing. In this context, noise does not act to create phenomena of interest directly. The sudden transitions we seek to anticipate are still

explained by the deterministic part of the model – bifurcations. But nor is noise a nuisance that merely cloaks this deterministic skeleton from plain view: rather, it becomes a novel source of information that would be inaccessible from a purely deterministic approach. I believe more examples of how noise can inform on underlying processes is possible, but will require greater dialog between these world views.

ACKNOWLEDGEMENTS

The author acknowledges feedback and advice from the editor, Tim Coulson and two anonymous reviewers. This work was supported in part by USDA National Institute of Food and Agriculture, Hatch project CA-B-INS-0162-H.

DATA ACCESSIBILITY STATEMENT

All data (simulated data and code) is made available on GitHub (<https://github.com/cboettig/noise-phenomena>), Data and code available from <https://doi.org/10.5281/zenodo.1219780>.

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Editor, Tim Coulson

Manuscript received 6 March 2018

First decision made 3 April 2018

Manuscript accepted 17 April 2018