

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

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6 **Abstract**

I provide a brief synthesis of ecological research in stochastic phenomena. 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” (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.

7 *Key words:* stochasticity, demographic noise, environmental noise, colored
8 noise, quasi-cycles, tipping points,

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9 Introduction: Noise the nuisance

10 Stochasticity is most often thought of as something which obscures patterns
11 we are trying to infer. This is a simple consequence of modeling: as discussed
12 above, variables of interest to the processes in question are modeled explicitly
13 (e.g. change in population density as it depends on the current density), everything
14 else is just noise. Most statistical inference in ecology is built solely to deal
15 with this problem: pulling back the veil of noise to reveal processes of interest.
16 Unfortunately, given the high levels of variation and relatively limited data
17 typical in ecological analyses, this can be a significant challenge, and even as
18 statistical and computational advances provide more powerful and accessible
19 inference tools, the task only gets harder.

20 For instance, few ecological concepts are more central than the notion of
21 density dependence: that competition in some form or other should limit a
22 species ability to grow without bound. Yet establishing statistical evidence
23 for density dependence is remarkably difficult, as illustrated by Knape & de
24 Valpine (2011). Using time series from the Global Population Dynamics Database
25 (GPDD) Knape & de Valpine show that once one accounts for the potential for
26 measurement error in addition to environmental stochasticity – an unavoidable
27 source of noise in most ecological data – it becomes difficult to find evidence for
28 even the simplest models of density dependence in the majority of available time
29 series. Faced with such uncertainty, it is tempting to throw up our hands and
30 wait until some prophesied deluge of streaming micro-sensors stapled to every
31 organism provide enough signal to beat back the noise. Fortunately, this has not
32 been the path taken.

33 Over the past twenty years, ecological theory, modelling, and methods have
34 increasingly elucidated the role of noise not only to *obscure* patterns but to
35 *create* them. This period marked a transition away from the intense focus on
36 simple models which exhibited deterministic chaos that had enchanted much
37 of theoretical ecology in the previous two decades (Bjørnstad & Grenfell 2001)
38 in favor of more complex and stochastic models. Of particular interest has

39 been those conceptual advances that have bridged the divide from theoretical to
40 empirical interest – not merely the introduction of “real data” in a theoretical
41 paper, but rather the concepts that take on a life of their own in the larger
42 research community. Consequently, this paper seeks to be a bridge between two
43 audiences: theoretical researchers already expert in noisy phenomena but in
44 interested in reaching wider empirical application, and also primarily empirical
45 researchers seeking an entrance into noisy phenomena.

46 In this spirit, each of the examples illustrated here is coupled with concise
47 and efficient R code in the appendix to both reproduce and further explore the
48 simulations. While examples of noisy phenomena in natural systems are also
49 crucial, matching the pattern does not necessarily mean we have also matched
50 the process behind the data. The examples cited from the literature here offer
51 some of the best empirical evidence of these phenomena, but I encourage readers
52 to also experiment with the example code provided. Simulations permit poking
53 and prodding of empirical investigation quickly and with little mathematical
54 formalism in the way. In the code provided, most stochastic models are expressed
55 in the BUGS language, which may be more familiar to empirical readers than
56 corresponding mathematical formulas. This also permits both efficient simulation
57 and potential estimation of parameters given sample data using the R package,
58 NIMBLE (de Valpine *et al.* 2017); allowing the deductive models illustrated here
59 to readily function as inductive models with parameters inferred from time-series
60 data. A copy of this appendix is maintained at [https://github.com/cboettig/
61 noise-phenomena](https://github.com/cboettig/noise-phenomena), and bug reports, suggestions or help requests are welcome
62 through the issue tracker. A second appendix provides more mathematical
63 details for interested readers. With these in place, we are ready to begin our
64 tour through three major areas of noisy phenomena: Origins of noise, emergent
65 phenomena, and noise-driven inference.

66 Our first stop will be into research into the origins of noise. This will
67 not only let us set up definitions for terms and concepts we will encounter
68 throughout, but also introduce some of the fundamental mathematical and
69 computational tooling needed in our tour of noisy phenomena. From origins of

noise, we will then explore some of the phenomena that noise can create. These examples are central to the conceptual transition away from viewing noise only as a nuisance that obscures patterns and realize the rich set of patterns and phenomena that can emerge. Our tour will be by no means exhaustive, but as with chaos before it, theoretical allure does not always reflect ecological relevance. Having looked at some of the phenomena that can be created by noise, our third stop will try to run this in reverse: using noise to infer underlying phenomena. Examples here are rarer but potentially the most rewarding, bridging the gap from theoretical construct to empirical investigation. The most compelling examples have come from ways in which noisy phenomena are used to infer stability and forecast changes in resilience of populations or ecosystems. Though not without weaknesses or missteps, the resulting dialog between theoretical and empirical aspects have made this particularly a rich area of research. We end our tour by considering what features best enable the translation and ecological relevance of noisy phenomena.

Origins of noise

What is noise? Where does it come from? It is important to bear in mind that 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. Simply put, *noise is all that we leave out of our model*. 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 (Coulson *et al.* 2004). 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 (Ovaskainen & Meerson 2010; Black & McKane 2012).

With the exception of quantum mechanics (and there only at scales that

99 have no relevance to ecology), stochasticity is not an inherent property of nature
 100 but rather an emergent property of many events occurring at a different scale.
 101 Coins and dice obey the physical laws of motion; only variation in how they are
 102 tossed (i.e. something complex we do not usually model) creates randomness.
 103 The term “noise” itself reflects this emergent rather than fundamental origin:
 104 the combination of hundreds of voices and sounds each individually distinct
 105 blends together into a background of noise. Statistical mechanics tells us that
 106 temperature is a measure of the average speed of individual molecules in a
 107 gas – any given molecule will experience a range of possible speeds but by
 108 itself has no notion of temperature. Likewise, stochasticity enters our ecological
 109 models because our quantities of interest, such as the density of a population,
 110 is but an average over a lower-level, discrete process of individual births and
 111 deaths. Stochasticity that emerges directly from discrete individual events that
 112 underlie the process described by our model are considered *intrinsic stochasticity*,
 113 commonly referred to as *demographic stochasticity* in ecological literature, as
 114 it usually arises in the context scaling from individual demographic events
 115 to population level descriptions. An important aspect of this demographic
 116 stochasticity is that it scales with the square root of the “system size,” so that
 117 for very large populations the resulting fluctuations are relatively small. On
 118 the other hand, *extrinsic stochasticity*, usually referred to as *environmental*
 119 *stochasticity* in the ecological literature, arises in processes that are not described
 120 by our model, but merely impact the value of some parameter of our model; for
 121 instance, fluctuations in temperature may drive variation in a death rate, or
 122 fluctuations in rainfall drive variation in carrying capacity.

123 *Demographic stochasticity*

124 Demographic stochasticity refers to fluctuations in population sizes or densi-
 125 ties that arise from the fundamentally discrete nature of individual birth and
 126 death events. Demographic stochasticity is a particularly instructive case for
 127 illustrating a mechanism for how noise arises as an aggregate description from a
 128 lower-level mechanistic process. We summarize the myriad lower-level processes

129 that mechanistically lead to the event of a ‘birth’ in the population as a proba-
130 bility: in a population of N identical individuals at time t , a birth occurs with
131 probability $b_t(N_t)$ (*i.e.* a rate that can depend on both the population size N)
132 and increases the population size, N to $N + 1$, and deaths occur with probability
133 $d_t(N_t)$, decreasing the population size, N to $N - 1$. Assuming each of these
134 events are independent, this is a state-dependent Poisson process. The change
135 in the probability of being in state N is given by the sum over the ways to enter
136 the state, minus the ways to leave the state: a simple expression of probability
137 balance known as the “master equation.”

138 It is possible to simulate such a process exactly using Gillespie’s exact
139 stochastic simulation algorithm (SSA; Gillespie 1977), which simulates each
140 individual birth or death as a separate event. Figure 1 uses this algorithm to
141 compare simulations of the Levins’ patch model; see Appendix A for example
142 code. In the Levins’ model, n individuals compete for a finite number of suitable
143 habitats N . Individuals die a constant rate e , and produce offspring at a constant
144 rate c who then have a probability of colonizing an open patch that is simply
145 proportional to the fraction of available patches, $1 - n/N$.

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

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

148 The van Kampen system size expansion provides a convenient way to explicitly
149 approximate the “macroscopic” (*i.e.* population level, see Black & McKane (2012))
150 dynamics from an individual-based description of events in a Markov process
151 (based on Kurtz 1970, 1971; Kampen 2007). In addition to illustrating how
152 common stochastic models (in particular, Gaussian noise) arise from lower-level
153 descriptions, this result will also provide us a useful framework for interpreting
154 the behavior of stochastic models more generally. In Appendix B I illustrate the
155 derivation of the following equations for the mean and expected population sizes

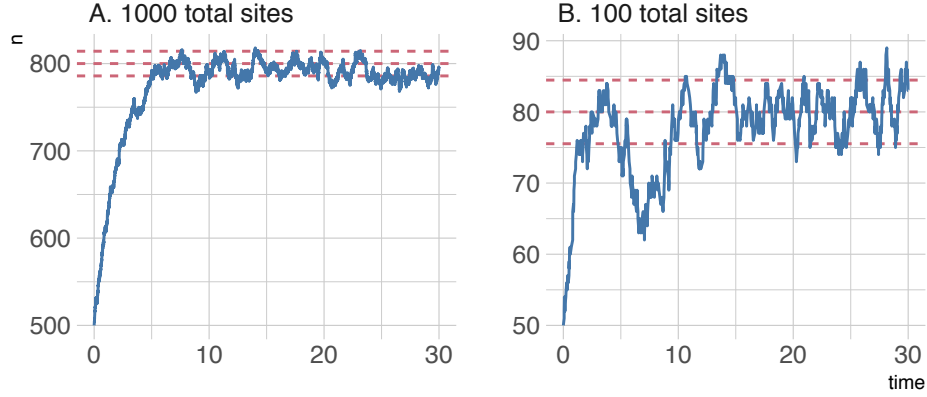


Figure 1: Population dynamics from a Gillespie simulation of the Levins model with large ($N=1000$, panel A) and small ($N=100$, panel B) number of sites (blue) show relatively weaker effects of demographic noise in the bigger system. Models are otherwise identical, with $e = 0.2$ and $c = 1$ (code in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

156 for a generic density dependent birth-death process:

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

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

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

161 The change in variance can be seen as a balance between the stochastic
 162 contribution, $b(x) + d(x)$ and the deterministic contribution, $\partial_x (b(x) - d(x))$.
 163 The deterministic contribution is the slope of the macroscopic equation, that

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 (Gonzalez & Holt 2002), 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

is, the eigenvalue indicating the stability of the equilibrium point. For stable points, this value must be negative and precisely balance the strictly positive stochastic contribution of $b(x) + d(x)$ (the greater the rate of stochastic events involved, the greater the fluctuations). This balance at steady-state is known as the fluctuation-dissipation theorem (Kampen 2007), and will prove a useful expression in understanding stochastic dynamics. Because Eq (3) also describes the time-evolution of these fluctuations, we can similarly solve for the correlation between two points separated by time τ .

For our Levins' model, $b(n) = n(1 - \frac{n}{N})$ and $d(n) = cn$, we find the average number of occupied patches $\langle n \rangle = N \frac{c}{c}$ with variance at steady-state of $\sigma_n^2 = N \frac{c}{c}$. Observe that the variance scales proportionally to the system size, N , which explains the standard deviation increases only as \sqrt{N} while the steady state itself increases in direct proportion to N , resulting in the smaller relative size of fluctuations in the larger system in Figure 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

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

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

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

195 Note that the contribution of environmental stochasticity is independent of
196 system size and directly proportional to the variance in the environment. This
197 derivation provides a useful illustration of the difference between demographic
198 noise and environmental noise: the latter simply describes the variation intro-
199 duced by some other dynamic variable that we are not modelling explicitly, and
200 whose dynamics are independent of the state of our system, x . This environmen-
201 tal variation no doubt also arise from some more detailed lower level process,
202 but we need not be explicit about those dynamics – the expansion tells us that
203 it is sufficient to know the overall variance and the degree of auto-correlation.
204 Recent work has also highlighted the importance of including both demographic
205 and environmental noise (Bonsall & Hastings 2004; Melbourne & Hastings 2008).
206 The system size expansion still requires the assumption that the noise is small
207 relative to the system size. In the case of large fluctuations, this approximation
208 must be replaced with a different approach, such as the WKB approximation, as
209 discussed in Ovaskainen & Meerson (2010).

210 The importance of τ_c , or the degree of auto-correlation, which emerges from
211 our derivation above, has also been and continues to be a subject of significant
212 interest in the study of stochastic population dynamics (e.g. Roughgarden
213 1975; Lawton 1988; Ripa & Heino 1999; Fieberg & Ellner 2000; Marshall &
214 Burgess 2015). Early work rarely often assumed environmental noise would be
215 uncorrelated as a mathematical convenience. As the derivation of Eq (4) makes
216 clear, for a continuous-time process, the relevant metric is the timescale of auto-
217 correlation in the environmental noise process relative to the auto-correlation
218 timescale of the population dynamics. The Gaussian noise that emerges out

219 of the system-size approximation is always auto-correlated to some degree – if
 220 we measure our environment at consecutive times infinitesimally far apart, we
 221 expect nearly identical values. At intervals much longer than the correlation
 222 time, consecutive measurements are effectively independent (i.e. white noise).
 223 The degree of auto-correlation in noise is all about *relative* timescales.

224 *Other forms of stochasticity*

225 Stochasticity frequently enters our models in other ways as well. For instance,
 226 most population-level models treat all individuals within the population, or
 227 at least within a particular age or stage class, as identical. *Individual hetero-*
 228 *geneity* in relevant traits (growth rates, dispersal ability) can be represented
 229 probabilistically as a distribution rather than a fixed value, making it function
 230 as another form of random variation in a model (Coulson 2001; Schreiber 2010).
 231 *Spatial heterogeneity* can likewise be reflected in stochastic parameters of a
 232 spatially implicit model, or as spatially varying environmental stochasticity in
 233 a spatially explicit model. As with other forms of noise (Bonsall & Hastings
 234 2004; Melbourne & Hastings 2008), interaction between individual or spatial
 235 variation and other sources of noise can drive patterns including the potential
 236 for persistence, coexistence, and dispersal of species (Schreiber 2010, 2017; Hart
 237 *et al.* 2016). *Observational error* acts much like another form of stochasticity,
 238 arising from sampling effects or limitations of instruments, etc. Yet unlike the
 239 sources described above, this uncertainty does not impact the actual state of our
 240 system, and thus does not give rise to any additional phenomena or information
 241 about that process, though it can obscure it (de Valpine & Hastings 2002; Knappe
 242 & de Valpine 2011).

243 Other forms of uncertainty common in models are not stochastic phenomena.
 244 This includes any form of *reducible uncertainty*: In constructing and estimating
 245 mathematical models of ecological processes, we encounter uncertainty over our
 246 parameter estimates and possible choice of models (Ellison 2004). In some ways,
 247 this uncertainty can act like the stochasticity described above: for instance, both
 248 introduce variation into any forecast of future outcomes. Yet unlike stochasticity,

249 this uncertainty is reducible: with additional observations, we can narrow the
250 uncertainty over parameters or candidate models, while stochasticity remains
251 an inherent source of variation. We will this not consider model and parameter
252 uncertainty, as they are not sources of noise. *Deterministic chaos* (Desharnais
253 *et al.* 2001) is another mechanism of introducing significant variation into a
254 simple model. Chaos can a look a lot like noise: indeed, it can be observationally
255 indistinguishable from a stochastic process (Ellner & Turchin 2005; Werndl
256 2009). Despite substantial interest in previous decades and the relative ease
257 of encountering chaos in simple ecological models (particularly in differences
258 equations), and convincing reconstructions of chaotic dynamics in laboratory
259 manipulations (Costantino *et al.* 1997) the prevalence of chaotic dynamics as a
260 driving factor in most ecological systems remains unclear. After all, the great
261 variation of natural populations is hardly surprising: the undeniable influences
262 of variation created by all those things left out of our models, all that individual
263 detail from intrinsic, lower level processes and external environmental processes
264 that becomes aggregated in our simple models all but begs for a stochastic
265 description.

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

271 **Noise the creator: Noise can induce novel phenomena**

272 Stochasticity can give rise to a wide array of interesting phenomena that are
273 often at odds with our intuition. As these examples will illustrate, such behavior
274 arises through an interaction between stochastic and non-linear elements of
275 a system, underscoring the importance of explicitly including stochasticity in
276 ecological models (Higgins 1997; Coulson *et al.* 2004). Importantly, the noise
277 itself does not have to be large to give rise to these phenomena. In this section,

278 I highlight several examples that have shown up frequently in the literature and
279 prove sufficiently tractable to provide a simple intuition for the mechanisms
280 involved.

281 *Persistence and coexistence*

282 A natural focus of much research into stochastic ecological systems has been
283 on understanding the implications for persistence of individual and coexistence of
284 interacting species. Demographic noise in particular has fundamental implications
285 for the long-term equilibrium: any finite population, however big, is guaranteed
286 to eventually go extinct under demographic noise. However, in most models it is
287 possible to define a notion of quasi-stationary distribution concentrated around
288 the deterministic attractor, and to prove the probability of extinction decreases
289 exponentially with system size (e.g. see Ovaskainen & Meerson (2010); Schreiber
290 (2017) also reviews more recent literature which has established these results
291 more generally). Generalizations about persistence and stable coexistence of
292 interacting species in stochastic models are difficult due to complex interactions
293 between demographic and environmental noise, population structure, spatial
294 heterogeneity, magnitude of noise, degree of auto-correlation and so forth (e.g.
295 Higgins 1997; Coulson 2001; Melbourne & Hastings 2008; Hart *et al.* 2016);
296 indeed care must be taken even in defining the appropriate notion of persistence
297 (e.g. Schreiber 2006). Instead of these long-term limits, here we will focus
298 on a few examples of stochastic phenomena that can emerge on shorter time
299 scales and provide some intuition for how the interaction between stochastic and
300 nonlinear dynamics can create these surprising results.

301 *Quasi-cycles*

302 Understanding the origin of sustained oscillations has long been a central
303 question in ecology (Hastings 1996; Bjørnstad & Grenfell 2001). The simple Lotka
304 Volterra model produces only neutrally stable centers, while the more realistic
305 model that introduces carrying capacity for prey as they compete for resources
306 results in a model that produces only damped oscillations, eventually settling into

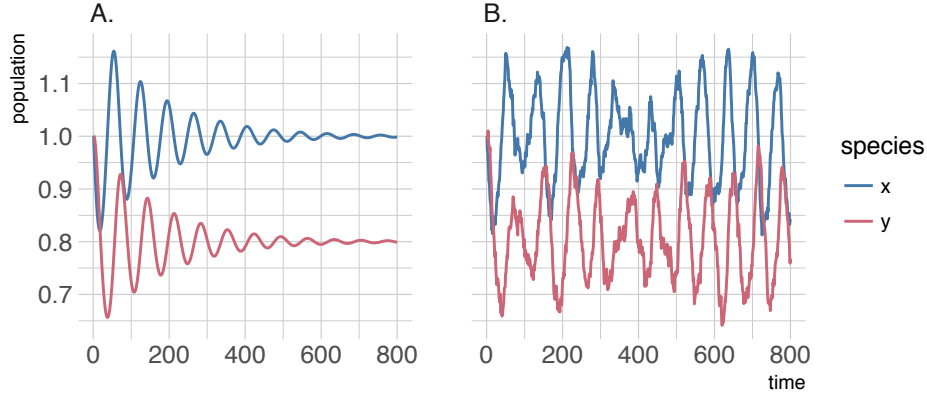


Figure 2: Panel A: under negligible environmental noise, the introduction of a carrying capacity damps Lotka-Volterra oscillations which eventually settle to a stable state. Panel B: small noise induces quasi-cycles in the same model: sustained long-term oscillations predominately around the natural 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.

307 a stable state (Figure 1A). However, the introduction of relatively small noise
 308 into the system can be sufficient to excite the system into sustained oscillations
 309 (Figure 1B). In the example shown here, a simple predator-prey system is driven
 310 by environmental white noise ξ_t , with prey following the equation:

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

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

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

313 with c the conversion ratio and d the predator mortality rate. Here we have
 314 assumed for the prey, $\xi_x \sim \mathcal{N}(t, \sigma_x^2)$, and similarly for the predator driven by
 315 ξ_y . Figure 1A shows examples for noise $\sigma_x = \sigma_y = 10^{-5}$, while Figure 1B shows
 316 $\sigma_x = \sigma_y = 0.01$.

317 Oscillations arise through the process of stochastic resonance. The damped
 318 oscillations seen in Figure 1a are analogous to a child sitting still on a swing: fric-

319 tion slowly damps the magnitude of each successive oscillation, while the period
 320 of pendulum remains unchanged. Driving the pendulum through perturbations
 321 timed to match that natural period can quickly create sustained oscillations with
 322 large magnitudes, but such perfect timing is not required. In the model above,
 323 white noise effectively drives the pendulum at all frequencies, though at very low
 324 magnitude, since the noise is small relative to the scale of the dynamics. However,
 325 frequencies that most closely match the natural period of the damped oscillator
 326 are amplified, resonating with the natural oscillations. This process is sufficient
 327 to permit even small noise to drive sustained oscillations in the model indefinitely.
 328 The power spectrum (the squared norm of the Fourier transform, a measure
 329 of what frequencies are present; see, e.g. Black & McKane (2012)) provides a
 330 convenient way to visualize the effects of these oscillations. The power spectrum
 331 for a deterministic limit cycle would create a perfect sinusoidal oscillation and a
 332 resulting power spectrum of a delta spike at that single frequency. The power
 333 spectrum for the quasi-cycle instead shows a distribution of frequencies, centered
 334 at the the resonant frequency of the damped oscillator.

335 Early work by Blarer & Doebeli (1999) identified quasi-cycles as a possible
 336 explanation for oscillations and periodic outbreaks in pest ecosystems. Bjørnstad
 337 *et al.* (2004) analyzes the potential for such stochastic effects to drive cyclic
 338 behavior in population abundances of Atlantic bluefin tuna and Atlantic Cod,
 339 while Black & McKane (2010) illustrates the use of power-spectrum approaches
 340 to examine the behavior of quasi-cycles in common disease outbreak models,
 341 focusing on a case where noise arises explicitly from demographic stochasticity,
 342 rather than generic environmental noise as in the model above and elsewhere.
 343 Pineda-Krch *et al.* (2007) compare patterns from these stochastically generated
 344 cycles to stable limit cycles they resemble. Stochastic resonance highlights
 345 one way in which even small noise can play an important role in driving large
 346 scale patterns where we had previously only sought deterministic explanations.
 347 This example also illustrates the interplay between nonlinear dynamics and
 348 stochasticity that is the hallmark of stochastically driven phenomena. A stable
 349 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).

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 May (1977) 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.

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

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

380 where in our model $f(y)$ is vegetation growth minus consumption, $f(y) =$
 381 $g(y) - c(y)$. The motivation comes from physics, where f is a force and U
 382 the corresponding potential energy. This suggests a convenient analogy to
 383 gravity, often implied by drawing a ball inside the curve and referring to this
 384 as a “ball-in-cup” diagram. The potential function is particularly instructive
 385 for understanding stochastic switching under small noise, as in our simulation
 386 in Figure 3, where it is straight-forward to show (e.g. Feller 1968; Kampen
 387 2007) that the probability of a transition is proportional the exponential of
 388 the depth of the well from the lowest point to the separation barrier, (a result
 389 that is familiar as Arrhenius law of activation energy to grade-school students
 390 of chemistry). This effect is visible even in the short simulation shown in
 391 3A, which spends longer times in the lower state which has the deeper well.
 392 (Readers are encouraged to experiment with this by adjusting the parameters of
 393 the simulation in the included code). Unfortunately, the literature is not always
 394 careful in describing how this potential well diagram arises, which has caused it
 395 to become a source for as least as much confusion as it is of insight. While the
 396 curves in Figure 3B can be clearly associated with underlying mechanisms of
 397 rates: logistic growth and consumption with handling time, the same is not true
 398 of the potential: it is much harder to have a good intuition about the ‘negative
 399 integral of the difference growth and consumption,’ and how it would change
 400 in response to, say, a larger carrying capacity K or higher consumption rate a .
 401 While the x-axis of the potential diagram remains the same: the system state,
 402 the conceptual problem is clearly evident in the usual ambiguity describing the
 403 y-axis in such ball-in-cup models.

404 Despite the nearly ubiquitous association of a ball-in-cup model with ecolog-

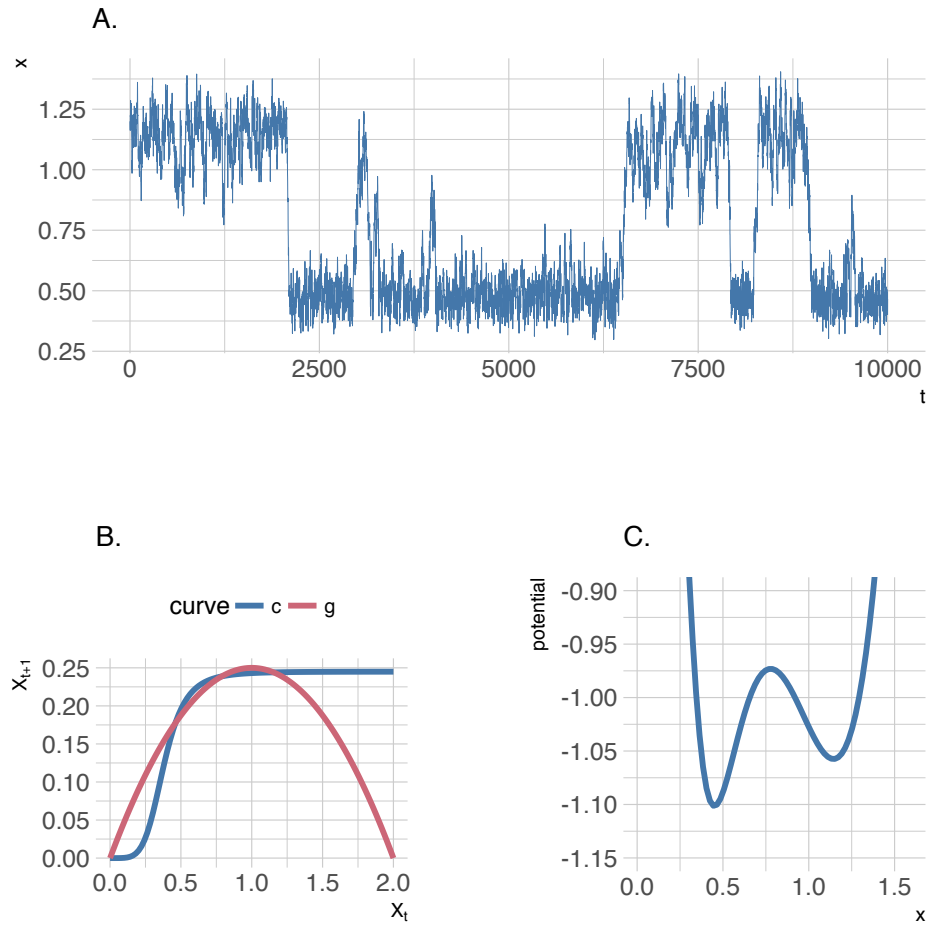


Figure 3: Stochastic switching in May's model of alternative stable state dynamics. $r = .5$, $K = 2$, $Q = 5$, $H = .38$, $\sigma = .04$, $a = 0.245$, $N = 10000$

ical 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. 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 (Boettiger & Hastings 2012a; Drake 2013). 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 (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). 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).

436 Noise the informer: Noise can provide novel information

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

446 Noise can provide novel information in other ways as well. Stochastic fluctua-
 447 tions act like a continual miniature perturbation experiment, constantly pushing
 448 a system away from an equilibrium to reveal its behavior elsewhere in state
 449 space. Observing the size and auto-correlation of these fluctuations thus provides
 450 insight on the stability of an equilibrium point, (as can be seen, for instance
 451 in the fluctuation-dissipation result we found for generic birth death models).
 452 This observation has been exploited with particular success as a potential *early*
 453 *warning sign* that a system is loosing stability; possibly due to an approach-
 454 ing catastrophic transition or saddle-node bifurcation. This pattern, known as
 455 critical slowing down (in reference to the auto-correlation time in the physics
 456 literature) was first proposed as an early warning sign for ecological systems
 457 by Wissel (1984), but has received considerable empirical as well as theoretical
 458 attention only more recently (Scheffer *et al.* 2009, 2015). Increases in two of these
 459 early warning indicators, variance and auto-correlation, are illustrated along
 460 with the timeseries of a simulation of the dynamics of yeast population growth
 461 in Figure 4. This simulation is based on a mechanistic model developed by Dai
 462 *et al.* (2012) that closely matches the population dynamics they observed in
 463 serial dilutions of budding yeast *Saccharomyces cerevisiae* on a sucrose medium.
 464 Because the relevant proteins are located in the extra-cellular matrix rather than
 465 inside the cells, budding yeast break down sucrose collaboratively, creating an

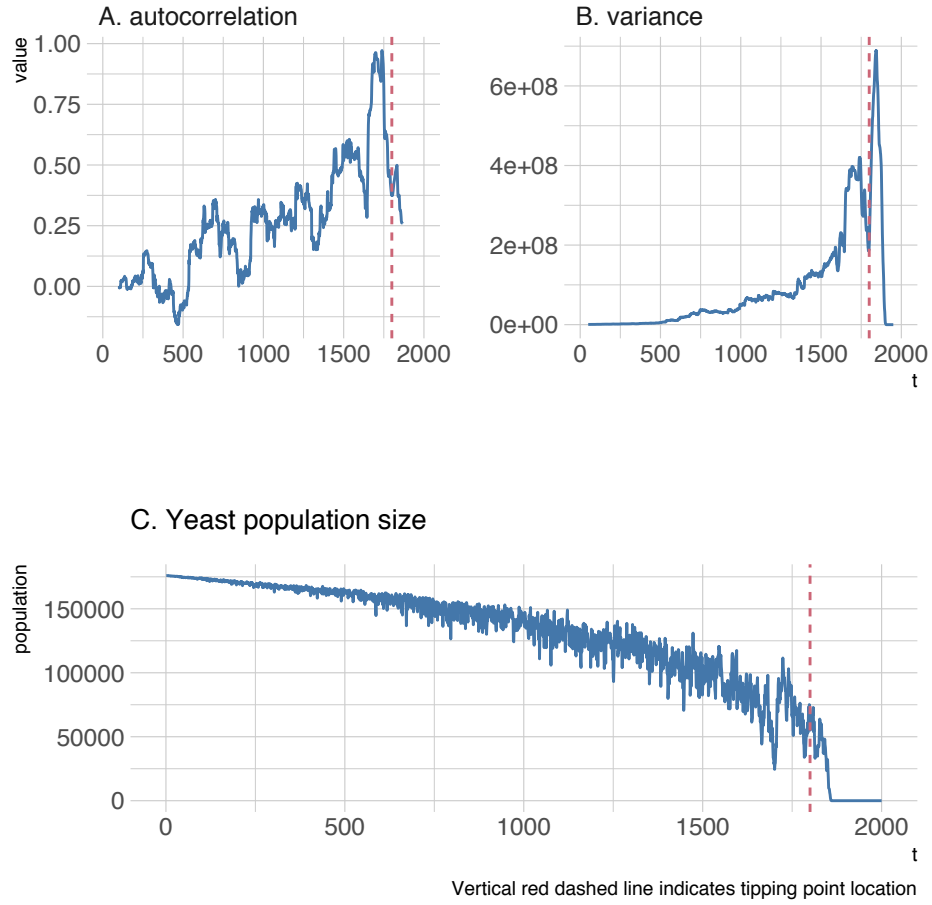


Figure 4: Early warning signs of a critical transition in a simulation of increasing serial dilution of budding yeast. Panel A: Rolling variance autocorrelation Time series is shown in panel C. Model details and simulation parameters in Appendix A.

466 Allee effect below which the population is too small to sustain itself. Increasing
467 the serial dilution rate slowly over time drives the stable population towards a
468 fold bifurcation, which is accompanied by the patterns of increasing variance
469 and increasing auto-correlation seen empirically in lab populations (Dai *et al.*
470 2012) as well as the numerical simulation shown in Figure 4.

471 As we saw in the equations from the system-size approximation, the variance
472 and auto-correlation in question are technically properties of an ensemble, and
473 should be computed over replicate simulations. While the laboratory experiments
474 of Dai *et al.* (2012) do precisely this, conducting identical, independent replicate
475 manipulations in separate beakers, this is not an option in natural populations.
476 If the environmental change is sufficiently slow relative to the measurements, one
477 can assume that the system is close to its stationary state over a given window
478 in time, computing these averages over a rolling time window as we illustrate
479 here, rather than across an ensemble of replicates.

480 The challenge of identifying warning signs that a system is approaching a
481 tipping point has proven a rich area for applications of stochastic processes.
482 We have already seen how in addition to the patterns of increasing variance
483 and auto-correlation, our survey of stochastic phenomena has highlighted the
484 increased potential to observe stochastic switching, or flickering, as the system
485 approaches the tipping point. Challenges remain in distinguishing these patterns
486 from other causes (Boettiger *et al.* 2013). For instance, as we have seen, variance
487 in a system can increase due to external drivers without changing the auto-
488 correlation, and both variance and auto-correlation can increase if a system
489 loses stability without approaching a saddle-node bifurcation, but will not show
490 flickering. The greater our suite of stochastic indicators, the better our ability to
491 pin down the processes involved. Such examples suggest that stochastic processes
492 could play a similar role in identifying other critical transitions. For instance,
493 stochastic resonance may be visible in advance of a Hopf bifurcation, in which a
494 stable node becomes a limit cycle.

495 Most importantly, the framing of stochastic processes as indicators of changes
496 in an ecosystem that might otherwise go unnoticed has proven a rich catalyst

497 for bringing these concepts beyond the realm of abstract theory. A rich array of
 498 experimental and observational tests of early warning signals (*i.e.* Carpenter *et*
 499 *al.* 2011; Dai *et al.* 2012; and many others, *e.g.* see Scheffer *et al.* 2015 review)
 500 has served not merely to illustrate these phenomena can be seen in laboratory and
 501 field ecosystems, but also to spark suggestions of additional possible indicators
 502 and surface a wide array of practical (Boettiger & Hastings 2013; Scheffer *et*
 503 *al.* 2015), statistical (e.g. Boettiger & Hastings 2012b, 2012a), and theoretical
 504 (Hastings & Wysham 2010; e.g. Dai *et al.* 2015) challenges to such application.
 505 This creates a two-way dialog between empirical and theoretical work that does
 506 much to advance the field as a whole.

507 **Conclusions**

508 The past two decades have seen widespread recognition of the central role
 509 that stochasticity plays through the use of mechanistic models can have in
 510 creating and understanding ecological phenomena (Coulson *et al.* 2004; Black &
 511 McKane 2012). We have seen increasing use of master-equation approaches to
 512 individual-based models to reflect demographic stochasticity that is amenable to
 513 analytical treatment (Black & McKane 2012), and much work in understanding
 514 the importance of environmental noise, particularly the more realistic but less
 515 mathematically convenient notion of colored or auto-correlated noise on pop-
 516 ulation dynamics, persistence, and coexistence (Ovaskainen & Meerson 2010;
 517 Schreiber 2017). These deductive models can generate phenomena that resemble
 518 familiar patterns such as population cycles for which we have previously sought
 519 deterministic explanations, as well as stochastic phenomena with no such analog
 520 such as stochastic switching. Yet too many of these advances have remained
 521 limited to the domain of theory; limited to deductive models which may seek to
 522 mimic observed patterns but are rarely used to confront empirical data directly.
 523 There is good reason for this: statistical inference of even relatively simple models
 524 with multiple sources of noise will always be difficult given limited ecological
 525 data (Knappe & de Valpine 2011). However, many stochastic phenomena may

526 suggest new ways to infer rather than merely obscure underlying processes.

527 The eruption of interest in early warning signals for critical transitions
528 (Scheffer *et al.* 2009) provides an excellent illustration of this potential. A range
529 of stochastic phenomena have been suggested and a tested for their potential to
530 reveal subtle signs of ecosystem change prior to a dramatic shift, and prompted
531 a rich dialog between further theory and new experiment. Changes in stochastic
532 properties such as variance or auto-correlation provide evidence of resilience
533 loss that would be invisible to a deterministic model, and non-linear stochastic
534 phenomena such as stochastic switching are observed as evidence of ‘flickering’
535 prior to a critical transition. In this way, our understanding of stochastic
536 dynamics is translated into novel sources of information about a system which
537 has sparked a wealth of empirical investigation and further theoretical work to
538 test the potential of this approach. The study and application of stochastic
539 phenomena to detect ecosystem change is unlikely to be limited to this simple
540 scenario of a critical transition or fold bifurcation.

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

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