

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

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16 [//github.com/cboettig/noise-phenomena](https://github.com/cboettig/noise-phenomena)), and if accepted, will be archived with
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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.

21 **Introduction: Noise the nuisance**

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

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

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

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

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

78 Our first stop will be into research into the origins of noise. This will
79 not only let us set up definitions for terms and concepts we will encounter
80 throughout, but also introduce some of the fundamental mathematical and
81 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

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

135 *Demographic stochasticity*

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

141 that mechanistically lead to the event of a ‘birth’ in the population as a proba-
142 bility: in a population of N identical individuals at time t , a birth occurs with
143 probability $b_t(N_t)$ (*i.e.* a rate that can depend on both the population size N)
144 and increases the population size, N to $N + 1$, and deaths occur with probability
145 $d_t(N_t)$, decreasing the population size, N to $N - 1$. Assuming each of these
146 events are independent, this is a state-dependent Poisson process. The change
147 in the probability of being in state N is given by the sum over the ways to enter
148 the state, minus the ways to leave the state: a simple expression of probability
149 balance known as the “master equation.”

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

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

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

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

for a generic density dependent birth-death process:

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

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

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

The change in variance can be seen as a balance between the stochastic contribution, $b(x) + d(x)$ and the deterministic contribution, $\partial_x(b(x) - d(x))$. The deterministic contribution is the slope of the macroscopic equation, that 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 $d(n) = en$, we find the average number of occupied patches $\langle n \rangle = N \frac{e}{c}$ 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 only as \sqrt{N} while the steady state itself increases in direct proportion to N , resulting in the smaller relative size

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

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

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

Note that the contribution of environmental stochasticity is independent of system size and directly proportional to the variance in the environment. This derivation provides a useful illustration of the difference between demographic noise and environmental noise: the latter simply describes the variation introduced by some other dynamic variable that we are not modelling explicitly, and whose dynamics are independent of the state of our system, x . This environmental variation no doubt also arise from some more detailed lower level process,

but we need not be explicit about those dynamics – the expansion tells us that it is sufficient to know the overall variance and the degree of auto-correlation. Recent work has also highlighted the importance of including both demographic and environmental noise (Bonsall & Hastings 2004; Melbourne & Hastings 2008). The system size expansion still requires the assumption that the noise is small relative to the system size. In the case of large fluctuations, this approximation must be replaced with a different approach, such as the WKB approximation, as discussed in Ovaskainen & Meerson (2010).

The importance of τ_c , or the degree of auto-correlation, which emerges from our derivation above, has also been and continues to be a subject of significant interest in the study of stochastic population dynamics (e.g. Roughgarden 1975; Lawton 1988; Ripa & Heino 1999; Fieberg & Ellner 2000; Marshall & Burgess 2015). Early work rarely often assumed environmental noise would be uncorrelated as a mathematical convenience. As the derivation of Eq (4) makes clear, for a continuous-time process, the relevant metric is the timescale of auto-correlation in the environmental noise process relative to the auto-correlation timescale of the population dynamics. The Gaussian noise that emerges out of the system-size approximation is always auto-correlated to some degree – if we measure our environment at consecutive times infinitesimally far apart, we expect nearly identical values. At intervals much longer than the correlation time, consecutive measurements are effectively independent (i.e. white noise). The degree of auto-correlation in noise is all about *relative* timescales.

Other forms of stochasticity

Stochasticity frequently enters our models in other ways as well. For instance, most population-level models treat all individuals within the population, or at least within a particular age or stage class, as identical. *Individual heterogeneity* in relevant traits (growth rates, dispersal ability) can be represented probabilistically as a distribution rather than a fixed value, making it function as another form of random variation in a model (Coulson 2001; Schreiber 2010). *Spatial heterogeneity* can likewise be reflected in stochastic parameters of a

244 spatially implicit model, or as spatially varying environmental stochasticity in
 245 a spatially explicit model. As with other forms of noise (Bonsall & Hastings
 246 2004; Melbourne & Hastings 2008), interaction between individual or spatial
 247 variation and other sources of noise can drive patterns including the potential
 248 for persistence, coexistence, and dispersal of species (Schreiber 2010, 2017; Hart
 249 *et al.* 2016). *Observational error* acts much like another form of stochasticity,
 250 arising from sampling effects or limitations of instruments, etc. Yet unlike the
 251 sources described above, this uncertainty does not impact the actual state of our
 252 system, and thus does not give rise to any additional phenomena or information
 253 about that process, though it can obscure it (de Valpine & Hastings 2002; Knappe
 254 & de Valpine 2011).

255 Other forms of uncertainty common in models are not stochastic phenomena.
 256 This includes any form of *reducible uncertainty*: In constructing and estimating
 257 mathematical models of ecological processes, we encounter uncertainty over our
 258 parameter estimates and possible choice of models (Ellison 2004). In some ways,
 259 this uncertainty can act like the stochasticity described above: for instance, both
 260 introduce variation into any forecast of future outcomes. Yet unlike stochasticity,
 261 this uncertainty is reducible: with additional observations, we can narrow the
 262 uncertainty over parameters or candidate models, while stochasticity remains
 263 an inherent source of variation. We will this not consider model and parameter
 264 uncertainty, as they are not sources of noise. *Deterministic chaos* (Desharnais
 265 *et al.* 2001) is another mechanism of introducing significant variation into a
 266 simple model. Chaos can a look a lot like noise: indeed, it can be observationally
 267 indistinguishable from a stochastic process (Ellner & Turchin 2005; Werndl
 268 2009). Despite substantial interest in previous decades and the relative ease
 269 of encountering chaos in simple ecological models (particularly in differences
 270 equations), and convincing reconstructions of chaotic dynamics in laboratory
 271 manipulations (Costantino *et al.* 1997) the prevalence of chaotic dynamics as a
 272 driving factor in most ecological systems remains unclear. After all, the great
 273 variation of natural populations is hardly surprising: the undeniable influences
 274 of variation created by all those things left out of our models, all that individual

275 detail from intrinsic, lower level processes and external environmental processes
276 that becomes aggregated in our simple models all but begs for a stochastic
277 description.

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

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

284 Stochasticity can give rise to a wide array of interesting phenomena that are
285 often at odds with our intuition. As these examples will illustrate, such behavior
286 arises through an interaction between stochastic and non-linear elements of
287 a system, underscoring the importance of explicitly including stochasticity in
288 ecological models (Higgins 1997; Coulson *et al.* 2004). Importantly, the noise
289 itself does not have to be large to give rise to these phenomena. In this section,
290 I highlight several examples that have shown up frequently in the literature and
291 prove sufficiently tractable to provide a simple intuition for the mechanisms
292 involved.

293 *Persistence and coexistence*

294 A natural focus of much research into stochastic ecological systems has been
295 on understanding the implications for persistence of individual and coexistence of
296 interacting species. Demographic noise in particular has fundamental implications
297 for the long-term equilibrium: any finite population, however big, is guaranteed
298 to eventually go extinct under demographic noise. However, in most models it is
299 possible to define a notion of quasi-stationary distribution concentrated around
300 the deterministic attractor, and to prove the probability of extinction decreases
301 exponentially with system size (e.g. see Ovaskainen & Meerson (2010); Schreiber
302 (2017) also reviews more recent literature which has established these results

more generally). Generalizations about persistence and stable coexistence of interacting species in stochastic models are difficult due to complex interactions between demographic and environmental noise, population structure, spatial heterogeneity, magnitude of noise, degree of auto-correlation and so forth (e.g. Higgins 1997; Coulson 2001; Melbourne & Hastings 2008; Hart *et al.* 2016); indeed care must be taken even in defining the appropriate notion of persistence (e.g. Schreiber 2006). Instead of these long-term limits, here we will focus on a few examples of stochastic phenomena that can emerge on shorter time scales and provide some intuition for how the interaction between stochastic and nonlinear dynamics can create these surprising results.

Quasi-cycles

Understanding the origin of sustained oscillations has long been a central question in ecology (Hastings 1996; Bjørnstad & Grenfell 2001). The simple Lotka Volterra model produces only neutrally stable centers, while the more realistic model that introduces carrying capacity for prey as they compete for resources results in a model that produces only damped oscillations, eventually settling into a stable state (Figure 1A). However, the introduction of relatively small noise into the system can be sufficient to excite the system into sustained oscillations (Figure 1B). In the example shown here, a simple predator-prey system is driven by environmental white noise ξ_t , with prey following the equation:

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

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

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

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

329 Oscillations arise through the process of stochastic resonance. The damped
 330 oscillations seen in Figure 1a are analogous to a child sitting still on a swing: fric-
 331 tion slowly damps the magnitude of each successive oscillation, while the period
 332 of pendulum remains unchanged. Driving the pendulum through perturbations
 333 timed to match that natural period can quickly create sustained oscillations with
 334 large magnitudes, but such perfect timing is not required. In the model above,
 335 white noise effectively drives the pendulum at all frequencies, though at very low
 336 magnitude, since the noise is small relative to the scale of the dynamics. However,
 337 frequencies that most closely match the natural period of the damped oscillator
 338 are amplified, resonating with the natural oscillations. This process is sufficient
 339 to permit even small noise to drive sustained oscillations in the model indefinitely.
 340 The power spectrum (the squared norm of the Fourier transform, a measure
 341 of what frequencies are present; see, e.g. Black & McKane (2012)) provides a
 342 convenient way to visualize the effects of these oscillations. The power spectrum
 343 for a deterministic limit cycle would create a perfect sinusoidal oscillation and a
 344 resulting power spectrum of a delta spike at that single frequency. The power
 345 spectrum for the quasi-cycle instead shows a distribution of frequencies, centered
 346 at the the resonant frequency of the damped oscillator.

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

360 stochasticity that is the hallmark of stochastically driven phenomena. A stable
 361 node with linear dynamics, such as an Ornstein-Uhlenbeck process, has no
 362 resonant frequency, and could not produce sustained oscillations (unless the
 363 environmental driver itself had a periodic pattern).

364 *Stochastic switching*

365 We turn from stochastic resonance to oscillations of a very different sort,
 366 which do not resemble any deterministic process, as seen in Figure 3A. This
 367 pattern is characterized by long stretches during which fluctuations in the state
 368 variable remain concentrated around a high average value followed by sudden,
 369 rapid transitions into fluctuations concentrated around a lower value. This
 370 behavior arises through the interaction of stochasticity and alternative stable
 371 state dynamics. The simulation shown in Figure 3A for the is based on an
 372 resource consumption model first proposed by May (1977) as one of the early
 373 examples of the potential for alternative stable state dynamics. The resource
 374 grows according to a logistic growth model and is consumed according to a
 375 Holling Type-III functional response curve, to which I have simply introduced
 376 the addition of environmental noise:

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

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

387 in 3A. Stochastic fluctuations drive spontaneous shifts between these alternative
 388 stable states.

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

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

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

415 y-axis in such ball-in-cup models.

416 Despite the nearly ubiquitous association of a ball-in-cup model with ecolog-
417 ical discussions of resilience and stability, this potential well diagram (Figure
418 3C) is also a source of confusion on the topic. As we have seen, the most salient
419 feature of this diagram is the depth of each well: transition probabilities (under
420 small noise) depend only on the depth of the well and not the steepness of the
421 well, the distance between the wells or between well and tipping point barrier.
422 However, it is important to remember that because the potential function is
423 defined by the above integral, it in fact already combines two more elementary
424 and mechanistically precise quantities from the growth equation: the slope of the
425 growth rate (stability) and the distance to the tipping point (size of the basin of
426 attraction). Both a steeper negative slope or a longer distance to integrate over
427 between stable and unstable points will create a deeper well.

428 Empirical evidence for stochastic switching in ecological timeseries is limited
429 by the long time scale usually required. Because a single stochastic transition
430 between alternative stable states appears as such a dramatic deviation from the
431 previous pattern (as illustrated in Figure 3A), it is often tempting to assume
432 the change could only be the result of some sudden external force or change
433 in the environment, so it is worth remembering that given long enough, these
434 transitions can happen entirely by chance stochasticity (Boettiger & Hastings
435 2012a; Drake 2013). However, these transitions are most likely to observed
436 in systems with relatively shallow potential wells. This is mostly likely to
437 occur if some external change is slowly making the potential well shallower and
438 thus transitions more likely – a phenomenon that has become to be known as
439 “flickering” and suggested as a potential early warning sign of an approaching
440 transition (Brock & Carpenter 2010). Examples of flickering between alternative
441 stable states have been suggested in data ranging from geological timescales
442 at the end of glaciation in the Pleistocene (Taylor *et al.* 1993) to ecological
443 scales over a few decades in lake ecosystems (Wang *et al.* 2012). Stochastic
444 transitions between bi-stable states are thought to play an important role in
445 genetic switches, where among other phenomena this mechanism can explain the

446 emergence of two alternative phenotypes in clonal microbial populations, which
447 can act to buffer the population in a changing environment (Balaban 2004).

448 **Noise the informer: Noise can provide novel information**

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

458 Noise can provide novel information in other ways as well. Stochastic fluctua-
459 tions act like a continual miniature perturbation experiment, constantly pushing
460 a system away from an equilibrium to reveal its behavior elsewhere in state
461 space. Observing the size and auto-correlation of these fluctuations thus provides
462 insight on the stability of an equilibrium point, (as can be seen, for instance
463 in the fluctuation-dissipation result we found for generic birth death models).
464 This observation has been exploited with particular success as a potential *early*
465 *warning sign* that a system is loosing stability; possibly due to an approach-
466 ing catastrophic transition or saddle-node bifurcation. This pattern, known as
467 critical slowing down (in reference to the auto-correlation time in the physics
468 literature) was first proposed as an early warning sign for ecological systems
469 by Wissel (1984), but has received considerable empirical as well as theoretical
470 attention only more recently (Scheffer *et al.* 2009, 2015). Increases in two of these
471 early warning indicators, variance and auto-correlation, are illustrated along
472 with the timeseries of a simulation of the dynamics of yeast population growth
473 in Figure 4. This simulation is based on a mechanistic model developed by Dai
474 *et al.* (2012) that closely matches the population dynamics they observed in

475 serial dilutions of budding yeast *Saccharomyces cerevisiae* on a sucrose medium.
 476 Because the relevant proteins are located in the extra-cellular matrix rather than
 477 inside the cells, budding yeast break down sucrose collaboratively, creating an
 478 Allee effect below which the population is too small to sustain itself. Increasing
 479 the serial dilution rate slowly over time drives the stable population towards a
 480 fold bifurcation, which is accompanied by the patterns of increasing variance
 481 and increasing auto-correlation seen empirically in lab populations (Dai *et al.*
 482 2012) as well as the numerical simulation shown in Figure 4.

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

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

stable node becomes a limit cycle.

Most importantly, the framing of stochastic processes as indicators of changes in an ecosystem that might otherwise go unnoticed has proven a rich catalyst for bringing these concepts beyond the realm of abstract theory. A rich array of experimental and observational tests of early warning signals (*i.e.* Carpenter *et al.* 2011; Dai *et al.* 2012; and many others, *e.g.* see Scheffer *et al.* 2015 review) has served not merely to illustrate these phenomena can be seen in laboratory and field ecosystems, but also to spark suggestions of additional possible indicators and surface a wide array of practical (Boettiger & Hastings 2013; Scheffer *et al.* 2015), statistical (e.g. Boettiger & Hastings 2012b, 2012a), and theoretical (Hastings & Wysham 2010; e.g. Dai *et al.* 2015) challenges to such application. This creates a two-way dialog between empirical and theoretical work that does much to advance the field as a whole.

Conclusions

The past two decades have seen widespread recognition of the central role that stochasticity plays through the use of mechanistic models can have in creating and understanding ecological phenomena (Coulson *et al.* 2004; Black & McKane 2012). We have seen increasing use of master-equation approaches to individual-based models to reflect demographic stochasticity that is amenable to analytical treatment (Black & McKane 2012), and much work in understanding the importance of environmental noise, particularly the more realistic but less mathematically convenient notion of colored or auto-correlated noise on population dynamics, persistence, and coexistence (Ovaskainen & Meerson 2010; Schreiber 2017). These deductive models can generate phenomena that resemble familiar patterns such as population cycles for which we have previously sought deterministic explanations, as well as stochastic phenomena with no such analog such as stochastic switching. Yet too many of these advances have remained limited to the domain of theory; limited to deductive models which may seek to mimic observed patterns but are rarely used to confront empirical data directly.

535 There is good reason for this: statistical inference of even relatively simple models
536 with multiple sources of noise will always be difficult given limited ecological
537 data (Knappe & de Valpine 2011). However, many stochastic phenomena may
538 suggest new ways to infer rather than merely obscure underlying processes.

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

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

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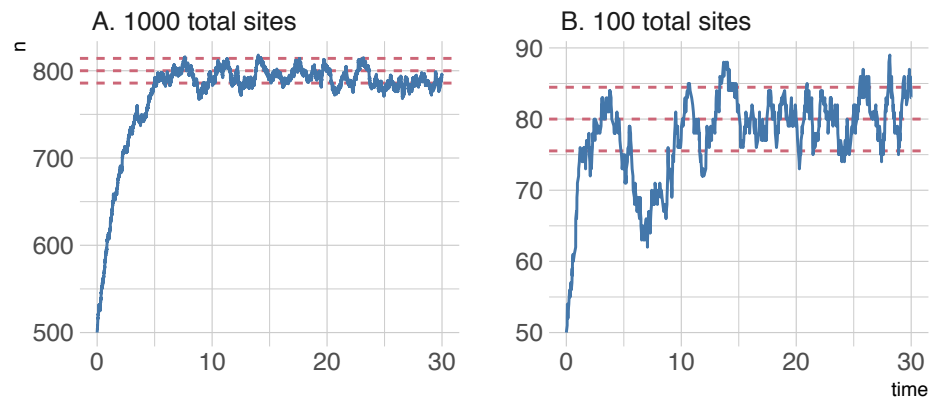


Figure 1: Population dynamics from a Gillespie simulation of the Levins model with large ($N=1000$, panel A) and small ($N=100$, panel B) number of sites (blue) show relatively weaker effects of demographic noise in the bigger system. Models are otherwise identical, with $e = 0.2$ and $c = 1$ (code in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

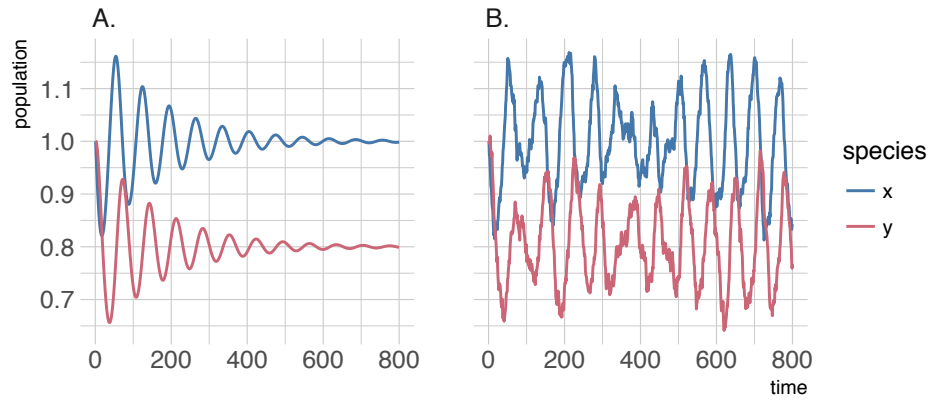


Figure 2: Panel A: under negligible environmental noise, the introduction of a carrying capacity damps Lotka-Volterra oscillations which eventually settle to a stable state. Panel B: small noise induces quasi-cycles in the same model: sustained long-term oscillations predominately around the natural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

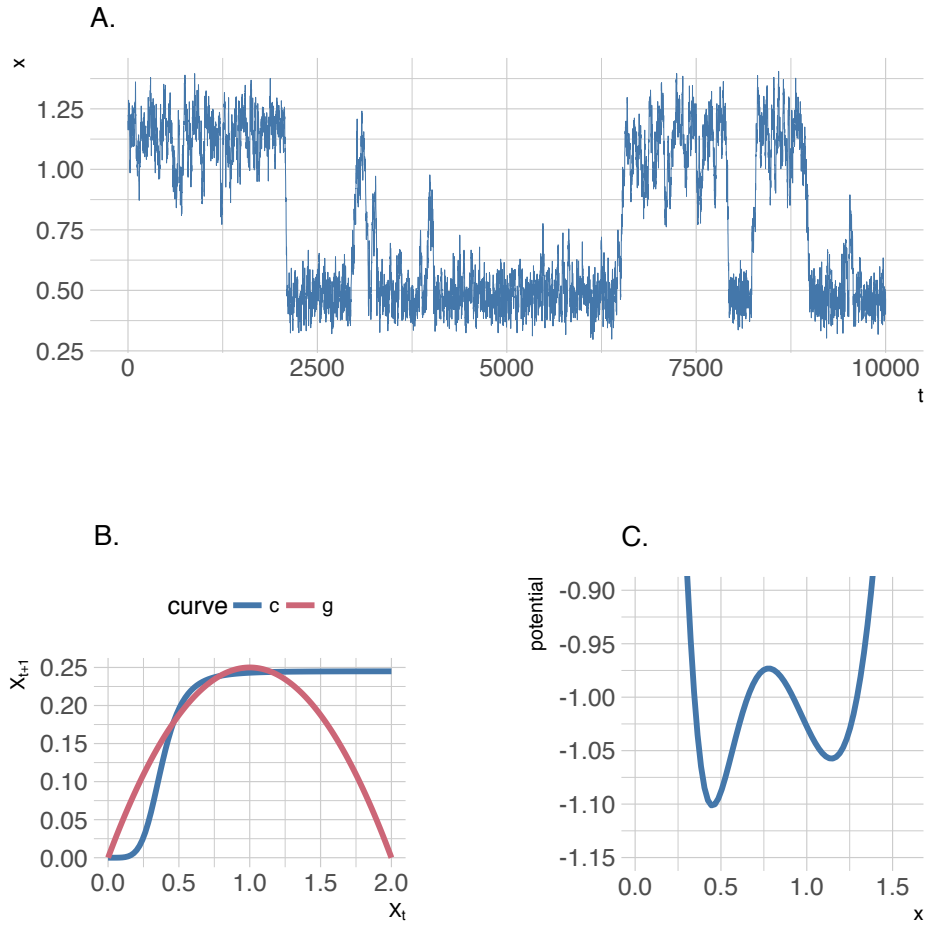


Figure 3: Stochastic switching in May's model of alternative stable state dynamics. $r = .5$, $K = 2$, $Q = 5$, $H = .38$, $\sigma = .04$, $a = 0.245$, $N = 10000$

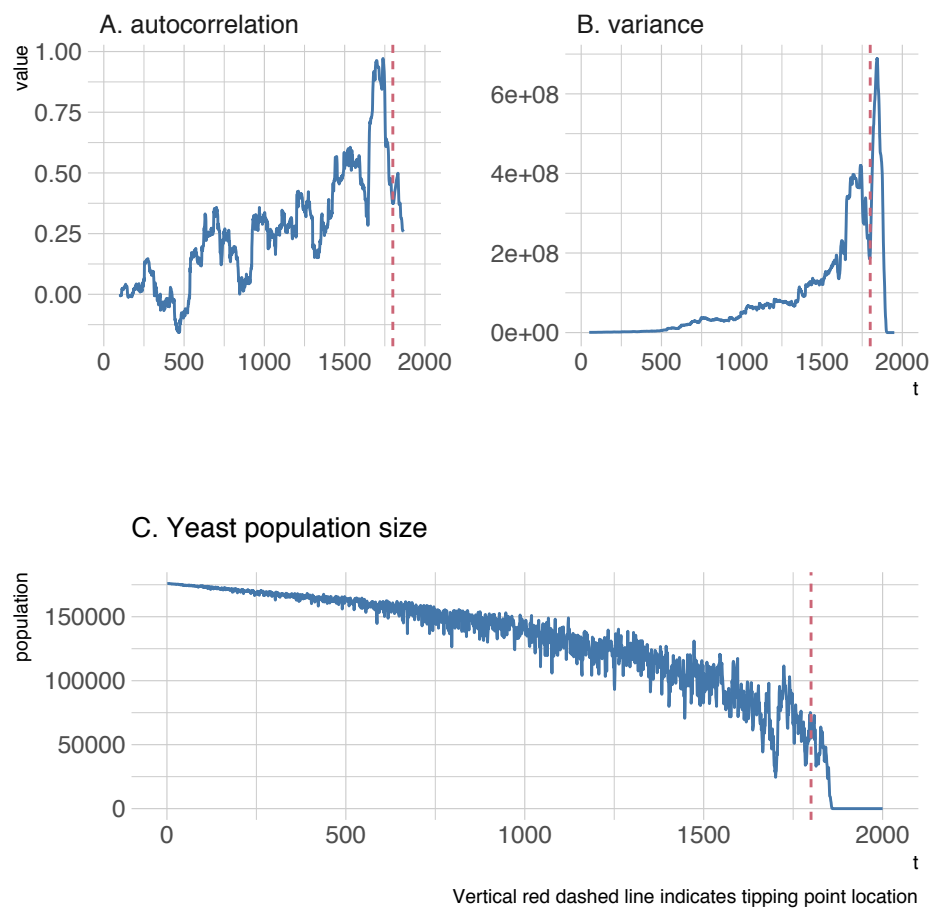


Figure 4: Early warning signs of a critical transition in a simulation of increasing serial dilution of budding yeast. Panel A: Rolling variance autocorrelation Time series is shown in panel C. Model details and simulation parameters in Appendix A.