Supplement to:

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NONLINEAR STOCHASTIC DYNAMICS: INTERACTING FORCES

The emergent consensus -- that both biotic interactions and abiotic random forcing are crucial -- adds a second challenge to theoretical ecology: understanding the interaction of noise and nonlinearity. We let the diversity of advances in nonlinear-stochastic ecological dynamics testify to the current level of activity and excitement in this new field.

Stochastic excitation

Higgins et al. (*1*) studied cyclic variability in the abundance of the Dungeness crab. They parameterized an age-structured model involving competitive and cannibalistic interactions between individual crabs. The resultant model predicted asymptotically stable dynamics of the stock. This contrasts starkly with the violent 10-year fluctuations observed in time series. However, when the highly variable survival of the planktonic larvae, due to starvation and expatriation of young (*1*), is incorporated as stochastic variability between years, the abundance of adults is predicted to undergo cyclic fluctuations, comparable to those seen in nature. This effect -- cyclic stochastic excitation of monostable systems -- was extensively described by Nisbet and Gurney (*2*). It has since been repeatedly rediscovered for a variety of ecological systems (*3*, *4*). These testify to how many asymptotically stable ecological systems will exhibit statistically predictable cycles in the presence of environmental or demographic stochasticity.

Reppellors and saddles

As indicated in the text, the dynamic attractors that arise from nonlinear interactions between individuals may take a variety of forms -- the well known fixed point equilibria, stable cycles, and quasiperiodic or chaotic attractors. However, there is also the possibility of multiple coexisting attractors (*5-7*) and *unstable* equilibria (‘saddles’) (Fig. 3e) (*8*) or unstable invariant sets (‘repellors’) (*9*). Attractors and saddles can be depicted geometrically in phase-space (Fig 3; supplemental figure). The geometry of these attractors is a key to understanding the interactions between noise and nonlinearity. A saddle is an equilibrium that is attracting in one dimension, but repelling in the other (supplemental figure); The Lotka-volterra competition model provide a classical example (*10*). Invariant sets -- other than point equilibria -- can also be unstable (attracting in some directions in phace-space and repelling in others). These are called ‘repellors’ (*9*). In deterministic systems, the actions of saddles and repellors are not seen. However, in the presence of even modest demographic stochasticity, saddles or repellors may have a paramount influence. Cushing et al. (*8*) tested this conjecture after having uncovered an unstable equilibrium in the theoretical dynamics of the flour beetle (Fig 3e-g). During stochastic excursions, populations are observed to linger close to the unstable equilibrium. Populations thereby alternate between the influence of the stable attractor (in this case a two-cycle) and the unstable saddle. In ecological epidemiology, small stochastic disturbances have further been found to be greatly transformed through the action of more complex unstable invariant sets (*9*).

Cohort resonance

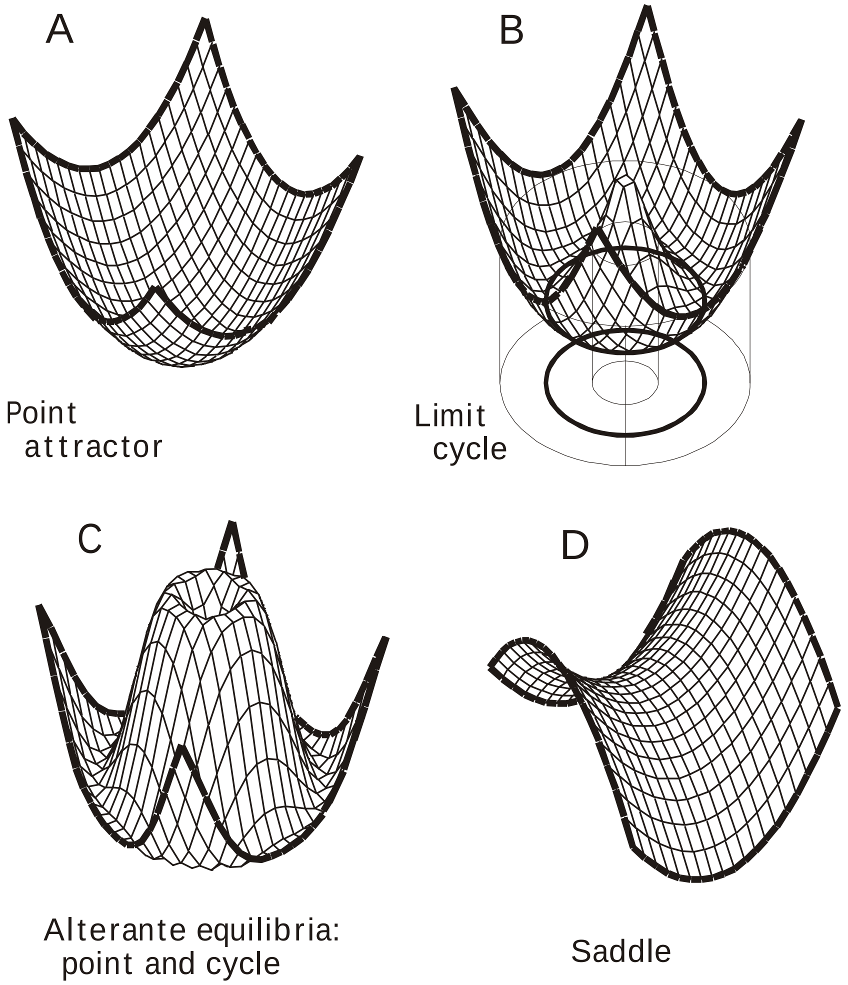
A further way in which nonlinear interactions interact with noise is illustrated by the age-structured dynamics of coastal populations of Atlantic cod (*Gadus morhua*), which exhibits both low- and high-frequency oscillations in abundance in the wild (Fig. 1). Coastal cod populations exhibit density-dependence competition, *m*, and cannibalism, *c*, within and between the two juvenile cohorts (the 0-group, X_t, and the 1-group, Y_t). The reproduction, r_t, undertaken by the stock is notoriously stochastic between years as it is affected by climatic forces directly and indirectly through the relative timing of hatching and plakton blooms (*11*, *12*). The dynamics can be modeled using a stochastic age-structured model (*13*, *14*):

$$\begin{aligned} X_t &= r_t Z_t \\ Y_t &= X_{t-1} e^{-m \ln X_{t-1}} e^{-c \ln Y_{t-1}} \qquad (1) \\ Z_t &= sY_{t-1} + sZ_{t-1} \end{aligned}$$

where, r_t is a random variable, and *s* represents the adult survival (*13*, *14*). We can rewrite the model in delay-coordinates according to (O.N. Bjørnstad and R.M. Nisbet, unpublished manuscript):

$$x_t = s(1+c) - cx_{t-1} + \sum_{k=2}^{K} \frac{s^{k-2}(1-m)}{(1-s)} x_{t-k} + r'_t + cr'_{t-1} \qquad (2)$$

where $x_t = \ln X_t$ and $r'_t = \ln r_t$. From eqn (2) it can be seen that the density-dependent interactions induces delays in regulation. The inter-cohort interaction, *c*, further echoes the random recruitment *r* in time. The deterministic dynamics of eqn (1) -- assuming



Supplemental figure: The geometry of phase-space. A. The stable point and B. the limit cycle attractor represents that is well known from, for example, predator-prey theory. C. Coexisting attractors give rise to multiple equilibria that have different domains of attraction, a system may for some period be trapped in local attractors (e.g., the stable point). D. A saddle represents an equilibrium point that is attracting in one direction and repelling in the other.

a constant reproductive rate -- give rise to a stable point attractor or a limit cycle, depending on the strength of the inter- and intracohort interaction (*13*). In the presence of stochastic reproduction, however, the dynamics exhibits cycles superimposed on long-term trends. The complex power spectrum results directly from the 'echoing' of the stochasticity by the life-cycle interactions -- according to $r'_t + cr'_{t-1}$ ('the cohort resonance effect').

Stochastic divergence

As reviewed in the text, ecological systems have the potential to exhibit chaotic dynamics and *sensitivity to initial conditions* (*15, 16*). Theoretically, initially nearby trajectories will diverge exponentially until they are no more correlated than expected from the invariant distribution of the dynamical process. Deterministic systems that exhibit sensitivity to initial conditions have the 'stochastic property' that forecasting ability is very restricted, since the prediction error increases with prediction interval, closely mimicking the prediction profiles of truly stochastic models (Fig 2). The sensitivity to initial conditions of determinsitic systems is usually measured by the dominant Lyapunov exponent (*16*). LE quantifies the average divergence/convergence of nearby trajectories across the deterministic attractor. Ellner and co-workers (*16-18*) developed a nonparametric method to estimate the LE directly on the basis of time series of abundance. When applied to stochastic systems, this will measure the average divergence in two nearby trajectories exposed to the same realization of the stochastic term. However, since real populations are not subject to the same perturbation, and the phase-space may contain multiple interacting attractors, saddles, and repellors, the current focus is on using local Lyapunov exponents to understand the interaction between noise and nonlinearity at particular locations in phase-space (*19, 20*).

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