Stochastic models in ecology and evolution

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Introduction

- **huge** topic (Ulam's analogy: the study of nonlinear systems as the study of "non-elephant animals". Ditto for deterministic systems.)
- stochasticity generally not covered thoroughly in math biology classes (but see Allen (2003), Kot (2001)); harder math, (?) less clear-cut results (?)
- stochasticity in a model: *epistemological* rather than an *ontological* purpose
- analysis harder . . . especially for nonlinear systems (most of the interesting ones, although there are interesting linear approximations, e.g. during invasions)
- definitions can be a bit tricky: is a diffusion model a "stochastic" model or not? Not explicitly . . . but implicitly based on a "random walk" or Brownian motion process (movement of individuals in space, or of populations in state space)
- well-posed stochastic models typically converge to deterministic ones in *some* limit (e.g. Kurtz (1970)), either in a large-population case or as the expected solution of an ensemble of realizations
- defs: *endogenous* ($\approx$ demographic) vs. *exogenous* ($\approx$ environmental) stochasticity
- state space can get very large (e.g. metapopulation models)

Examples

- discrete-state populations (Markov chains, etc.) easier than continuous populations (stochastic differential equations)
- discrete time easier than continuous time

Simple population models: analogues of logistic equation. Mortality = binomial ($\mu+\alpha N$). Fecundity = Poisson(fN). (Different from SI model, which has infection binomial with probability $(1-\exp(-\beta I \Delta t))$ — maximum value = 1.)

(Discrete models have their own issues: results may be sensitive to the order of events — fecundity before mortality, or vice versa? Problems go away as $\Delta t \to 0$.)

Continuous-time model: use *master equation* $\begin{array}{lll} \text{birth} & N \to N+1 & fN\Delta t \\ \text{death} & N \to N-1 & (\mu+\alpha N)\Delta t \end{array}$

(**note** $r = f - \mu$, $K = (f-\mu)/\alpha$; $R = f/\mu$ disappears from deterministic analogue but not in stochastic case

Analytical techniques

- branching processes
- moment generating functions
- Kolmogorov (Fokker-Planck) "forward equation"), diffusion approximations
- (quasi-)stationary distributions (Keeling and Ross, 2008)
- moment equations/moment closure (e.g. Isham (2005))

Numerical techniques

- Gillespie model
- exact solutions of Kolmogorov forward equations (leading eigenvectors)
- moment equations

Phenomena

Are stochastic models just "deterministic models with added noise"?

- Jensen's inequality (static, not dynamic, but important): e.g. geometric mean in exponential growth
- extinction and fixation: absorbing boundaries in population genetics and ecology (first passage times etc.)
- neutral theories of population genetics (Ewens) and ecology (Hubbell): related to classical "urn problems"
- interaction of nonlinearity with noise: fractal basin-hopping, (de)stabilization of attractors by noise (stochastic repellors) (Coulson et al., 2004) Rand & Keeling

See also

Some talks by Rick Durrett (applied probability, Cornell): `http://www.math.cornell.edu/~durrett/Talks/Talks.html`, and the corresponding paper `http://www.math.cornell.edu/~durrett/Talks/waldpaper.pdf`

Lecture notes: `http://www.amath.washington.edu/courses/423-winter-2007/outline.pdf`

Bailey (1990); Renshaw (1993); Lande, Engen, and Sther (2003)

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