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INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
34100 TRIESTE (ITALY) - P.O.B. 586 - MIRAMARE - STRADA COSTIERA 11 - TELEPHONES: 224281/2/3/4/5/6
CABLE: CENTRATOM - TELEX 460392-I

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STOCHASTIC COMMUNITY THEORY:
A PARTIALLY GUIDED TOUR

Michael TURELLI

Department of Genetics
University of California
Davis, California 95616
U.S.A.

Stochastic Community Theory: A Partially Guided Tour

Michael Turelli
Department of Genetics
University of California
Davis, California 95616
U.S.A.

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I. Introduction and Overview

These notes are intended as an introduction to the biological questions, mathematical analyses, and biological conclusions of stochastic models for multispecies assemblages. Little attention will be devoted to detailed analysis of particular models. Instead, I will attempt a survey of the key ideas and provide references for further study. The presentation will be organized according to the mechanism(s) creating the probabilistic effects. The three classes to be considered are:

1. Demographic stochasticity (or "within individual stochasticity", Chesson, 1978) - Whether or not God plays dice, apparently identical individuals have different life lengths and produce different numbers of offspring. Integer-valued stochastic models are typically used to investigate the consequences of this variation.

2. Environmental stochasticity - Environments vary unpredictably through time in ways that affect all individuals equally. Most analyses of the consequences begin by introducing random variation into the parameters of a standard deterministic model.

3. Joint effects of demographic and environmental stochasticity.

For a more thorough classification see the excellent review by Chesson (1978).

In addition to reciting some standard results, I would like to convey one key idea. The qualitative answers to broad questions like, "Does environmental variability limit the similarity of competitors?" can depend critically on both the model analyzed and the method of analysis used. Hence it behooves the modeller to carefully suit the analysis to the biological question addressed and to determine the robustness of conclusions to the details of the model considered. All modellers should read Pielou's (1981) critical assessment of the field.

The references given are a very limited and uneven sample of those available. Emphasis is placed on references that are biologically well-motivated or mathematically elegant, provide extensive bibliographies, or were written by me. References to parallel work in population genetics are provided at random.

II. Demographic Stochasticity.

Both continuous-time and discrete-time models have been analyzed. Essentially all are stochastic generalizations of standard deterministic models and, therefore, have natural "deterministic analogs". The random variation is essentially always Markovian, i.e. the future is independent of the past once present conditions are specified. No attempt will be made to describe the models or analyses in detail; most of the key mathematical ideas will reappear in the discussion of environmental stochasticity. The central conclusion is that demographic stochasticity produces little departure from deterministic dynamics if initial population sizes are large and the deterministic analog treats a collection of homogeneously interacting populations (see Chesson, 1978, 1981) whose joint deterministic dynamics possess a globally stable equilibrium at which all populations remain large. Conversely, if initial population sizes or equilibria are small, the populations are subdivided, or there are several or no deterministically stable equilibria, demographic stochasticity plays a central role in population dynamics and community structure. Slight elaborations of each of these items and references follow.

A. Demographic stochasticity is mathematically interesting (i.e. relatively tractable) but biologically fairly boring if all populations are initially large, individuals interact homogeneously (i.e. each individual experiences the total population density, rather than only local density), and the deterministic analog has a globally stable equilibrium with all populations large. There is a large body of mathematically sophisticated analyses that demonstrate this. The basic idea is that the populations tend to settle into long-term "quasi-stationary" fluctuations about the deterministic equilibrium. These fluctuations can be nicely approximated by Ornstein-Uhlenbeck processes and the coefficient of variation (variance/(mean)^2) for each species is roughly proportional to the inverse of its equilibrium population size. The fluctuations are only "quasi-stationary" because ultimate extinction for each species is certain in the absence of recurrent immigration. However, the expected extinction time due to demographic stochasticity will be of geological proportions for large populations and thus ecologically irrelevant.

References: Barbour, 1976; Bartlett, 1960; Kurtz, 1981; May, 1973, Ch. 2; McNeil and Schach, 1973; Nisbet and Gurney, 1982; Wang, 1975.

B. If initial population sizes are small or species have low equilibrium abundances (on the order of 10), relatively rapid extinction due to demographic stochasticity becomes likely. This represents a qualitative departure from deterministic results. Most analyses concern the dynamics of colonizing species. The likelihood of successful invasion and long-term persistence are sensitive to the presence of competitors that slow growth rates and lower equilibrium population sizes. Typical multispecies analyses involve heuristic applications of single-species results obtained from birth and death processes or branching processes. The basic theme is reminiscent of the classic observation by Fisher, Haldane, and Wright that selectively advantageous, rare mutations are often eliminated by chance (see Ewens, 1979, Ch. 1).

References: Becker, 1973; Goel and Richter-Dyn, 1974, Ch. 4; Ludwig, 1976; MacArthur, 1972, Ch. 5 Appendix; Turelli, 1980.

C. Demographic stochasticity can play a decisive role in determining to which of multiple stable equilibria a population is attracted. Park's classical competition experiments with Tribolium, in which apparently identical replicates gave different outcomes, are the standard paradigm. The fate of communities near a deterministic separatrix is subject to chance fluctuations in abundances.

References: Barbour, 1976; Bartlett, 1960, Ch. 5; Mangel and Ludwig, 1977.

D. If deterministic mechanisms of species interaction are ignored or assumed to be relatively weak, demographic fluctuations (interpreted here as random replacement processes) become key determinants of relative abundances. Caswell (1976) exploited the elaborate machinery of the "neutral theory" of protein evolution (see Ewens, 1979) to analyze a "neutral" model of community structure that ignores biological interactions. This analysis is philosophically closely allied to the new wave hypothesis-testing school of ecology championed by the so-called Florida State Mafia (see, for instance, Simberloff and Connor, 1981). Horn (1975) and Hubbell (1979) analyzed mathematically related models of forest communities. Unlike much of stochastic community theory, this area is dominated by analyses tailored to specific ecosystems (principally those governed by competition for space) and empirically motivated questions concerning the role of disturbance (Horn, 1975; Hubbell, 1979) and particular sorts of interactions (Karlson and Jackson, 1981). Depending on whether immigration is allowed from a species pool of invariant composition, either transient or steady-state patterns of diversity are investigated.

E. Like much of mathematical ecology, the analyses above assume that all individuals respond to the total numbers of their population and the populations with which they interact. Real populations exhibit spatial structure and the *local* density experienced by an individual can differ appreciably from the *average* density of the entire population. Chesson (1978) catalogs this as "within patch variability". When local densities rather than average densities govern dynamics, the effects of demographic stochasticity can persist even in infinitely large populations if *local* densities remain small. Within-patch variability induced by local demographic effects can qualitatively alter the outcome of interspecific interactions (e.g. Hastings, 1977) and natural selection (e.g. Wilson, 1980).

References: Caswell, 1978; Chesson, 1981; Crowley, 1978; Slatkin, 1974.

III. Environmental Stochasticity

A. Sample Questions

1. A quantum leap in the mathematical sophistication of ecological modelling occurred when May (May and MacArthur, 1972; May, 1974) introduced stochastic differential equations (SDEs) to investigate limits to niche overlap in randomly fluctuating environments. This question has now been addressed with a wide range of models and mathematical techniques. Interestingly, the supposedly widespread pattern that the original papers sought to explain may not exist (Simberloff and Boecklen, 1981).

2. Environmental fluctuations ineluctably produce fluctuations in population levels. A general question is to determine how species dynamics and interactions translate environmental fluctuations into temporal and spatial patterns. For "low levels" of noise, stochastic linearization procedures suffice (see Roughgarden, 1979, Ch. 20; Nisbet and Gurney, 1982, Ch. 7).

B. A central obstacle in stochastic community theory is the general intractability of nonlinear multidimensional stochastic processes. A critical problem then is to incorporate noise into a deterministic model in a way that is biologically meaningful yet mathematically tractable. Because mathematical ecology was traditionally phrased in differential equations and Markov processes are relatively "nice", SDEs, which represent multidimensional diffusion processes, appear as natural candidates for study. Unfortunately, they impose artificial biological constraints (e.g. noise can only be easily introduced into parameters that enter linearly) and are mathematically treacherous (see Feldman and Roughgarden, 1975; Turelli, 1977). Difference equations provide more latitutde (and realism) but their stochastic analogs are less well characterized, even when Markovian (see Chesson, 1982; Ellner, 1982).

C. A critical step in mathematically unravelling the consequences of environmental stochasticity is determining whether or not a local analysis will suffice (see Turelli, 1978). If it will, you're in luck.

1. Local analysis of fluctuations about a deterministically stable equilibrium is straightforward, at least in principle, for both SDE and discrete-time stochastic models (see May, 1973, Ch. 5; Bartlett et al., 1960). SDE applications produce Ornstein-Uhlenbeck processes, i.e. diffusion processes with infinitesimal mean and variance-covariance structures of the form

$$M_i(x_1,\ldots,x_n)=\sum_{i=1}^{n} a_{ij}x_j \quad \text{for } i=1,\ldots,n,$$

with negative real parts for all the eigenvalues of $A=(a_{ij})$, and

$$V_{ij}(x_1,\ldots,x_n)=b_{ij} \qquad \text{for } i,j=1,\ldots,n$$

with $B=(b_{ij})$ symmetric and positive definite. Here x_i measures departures from the deterministic equilibrium $\hat{X}_i$, e.g. $x_i(t)=(X_i(t)-\hat{X}_i)/\hat{X}_i$.

The stationary distribution for this process is multivariate normal with mean vector $\underline{0}$ and variance-covariance matrix Σ satisfying

$$\Sigma A + A^T\Sigma = -2B.$$

In the discrete case, one arrives at a first order autoregressive process, i.e.

$$\underline{x}_{t+1} = A\underline{x}_t + B\underline{z}_t$$

where $\underline{z}_t$ denotes the introduced noise processes. In either case, the mathematics reduces to (possibly horrendous) linear algebra.

In general, local analyses about internal deterministic equilibria cannot be relied on to provide conditions for species coexistence, which unavoidably involves global dynamic behavior (Turelli, 1978). When dealing with specific models, such as Lotka-Volterra systems, the interaction observed between deterministic parameters and stochastic fluctuations will depend on the way noise is incorporated. Generalizations based on specific models are unlikely to be valid. An unavoidable consequence of interior (as opposed to boundary point) linearizations is that environmental stochasticity is viewed as a destabilizing factor which jostles populations away from their deterministic equilibria (May, 1973, Ch. 5). For additional applications of linearization and refinements thereof see Bulmer (1976), Nisbet and Gurney (1982, Ch. 7), Poole (1978), and topic 2b below.

2. Global analyses are much more delicate. The key problem is that incorporating environmental stochasticity in a meaningful way usually eliminates all internal equilibrium *points* (or cycles). Hence stochastic convergence concepts that generalize the standard deterministic convergence-to-point-equilibria ideas are generally inapplicable. One is forced to apply persistence and coexistence criteria that allow populations to undergo undiminishing fluctuations without extinction. All criteria have some weaknesses, either biological or mathematical.

a) An extremely appealing stochastic analog of deterministic global convergence is the existence of a unique nondegenerate stationary distribution that describes persistent long-term fluctuations. Unfortunately, very little machinery is available for disctete-time models, even Markovian ones. (See Chesson (1982) and Ellner (1982) for particular one-dimensional examples.) The situation is only slightly better for SDEs. Turelli and Gillespie (1980) provide heuristic conditions for two-dimensional processes that look like exponential growth in a random environment near the extinction boundaries. Kushner (1972) has shown that Liapunov-like functions can yield sufficient conditions. Applications of this technique appear in Polansky (1979), Turelli and Gillespie (1980), and Turelli (1981a). On rare circumstances, one can guess the functional form of the stationary density by generalizing results from one-dimension or symmetric models (e.g., Turelli, 1981b).

b) In desperation, one can ignore mathematical rigor, devise a heuristic criterion, then do simulations and hope for the best. One example is the heuristic invasion analysis applied in Turelli (1981a) and Turelli and Petry (1980). This criterion is based on the conjecture that a stationary distribution is likely to exist if each species can invade when rare and the remaining species are fluctuating at steady-state. The weaknesses of this approach are described in Turelli (1981a) and a one-dimensional counterexample is provided by Chesson (1982). Nevertheless, the technique appears to be useful for analyzing stochastic models built by injecting small amounts of possibly autocorrelated noise (e.g., $CV \leq .1$) into difference equations. Like local linearization, this technique is built on Taylor series approximations, but it takes into account both linear and quadratic terms. The necessity of complementing this sort of analysis with computer simulations cannot be overemphasized.

c) Chesson (1978) has proposed a stochastic persistence criterion that is weaker than the existence of a nondegenerate stationary distribution but retains its biological content by requiring that stochastic fluctuations lead to neither population extinction nor explosion. A population X(t) is said to be <u>stochastically bounded</u> if for every $\varepsilon>0$, there exist time independent constants $L_\varepsilon>0$ and $U_\varepsilon<\infty$ such that

$$P(L_\varepsilon<X(t)<U_\varepsilon)>1-\varepsilon$$

for all t. Unlike the hack heuristic approaches, application of this criterion requires some mathematical talent and training and is extremely difficult in multiple dimensions.

d) Recognizing that ultimate extinction is certain in the presence of demographic fluctuations, Ludwig (1975) proposed calculating the mean extinction time (measured as the mean time to reach a low population threshold) as a measure of persistence. This general approach is also supported by Nisbet and Gurney (1982). Here again the mathematical difficulty of applying the criterion is formidable, even for multidimensional diffusions. Chesson (1982) and Turelli (1980, 1981a) discuss relationships among the persistence criteria and the nontrivial difficulties associated with their application to ecological problems. (See Hanson and Tuckwell (1978) for a discussion of persistence times under large random perturbations.)

D. Sample applications. Three approaches to understanding the consequences of environmental stochasticity on the coexistence of competitors will be reviewed: i) May and MacArthur's (1972) original linearization analysis; ii) Turelli's (1981) invasion analysis; and iii) Chesson and Warner's (1981) analysis of "lottery competition".

IV. Joint Effects of Demographic and Environmental Stochasticity

Clearly in the real world both demographic and environmental stochasticity are unavoidable. Given the difficulties of analyzing each separately, it should come as no surprise that relatively few multispecies analyses have been performed.

A. Invasion analyses have relied on the machinery available for branching processes in random environments.

References: Keiding, 1975, 1976; Turelli, 1980.

B. Persistence time analyses typically start with diffusion approximations and are carried out via asymptotic expansions.

References: Chesson, 1982; Hanson and Tier, 1981; Ludwig, 1976; Tier and Hanson, 1981.

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Bibliography

Barbour, A. D. 1976. Quasi-stationary distributions in Markov population processes. Adv. Appl. Probab. 8:296-314.

Bartlett, M. S. 1960. "Stochastic Population Models in Ecology and Epidemiology." Methuen, London.

Bartlett, M. S., Gower, J. C., and Leslie, P. H. 1960. A comparison of theoretical and empirical results for some stochastic population models. Biometrika 47:1-11.

Becker, N. G. 1973. Interactions between species: some comparisons between deterministic and stochastic models. Rocky Mount. J. Math. 3:53-68.

Bulmer, M. G. 1976. The theory of predator-prey oscillations. Theor. Pop. Biol. 9:137-150.

Caswell, H. 1976. Community structure: A neutral model analysis. Ecol. Monographs 46:327-354.

Caswell, H. 1978. Predator-mediated coexistence: A nonequilibrium model. Am. Nat. 112:127-154.

Chesson, P. 1978. Predator-prey theory and variability. Ann. Rev. Ecol. Syst. 9:323-347.

Chesson, P. L. 1981. Models for spatially distributed populations: The effect of within-patch variability. Theor. Pop. Biol. 19:288-325.

Chesson, P. L. 1982. The stabilizing effect of a random environment. J. Math. Biol. 15:1-36.

Chesson, P. L. and Warner, R. R. 1981. Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. 117:923-943.

Crowley, P. H. 1978. Effective size and the persistence of ecosystems. Oecologia 35:185-195.

Ellner, S. P. 1982. Stationary distributions for some stochastic difference equation population models. To appear in J. Math. Biol.

Ewens, W. J. 1979. "Mathematical Population Genetics." Springer-Verlag, Berlin.

Feldman, M. W. and Roughgarden, J. 1975. A population's stationary distribution and chance of extinction in a stochastic environment with remarks on the theory of species packing. Theor. Pop. Biol. 7:197-207.

Goel, N. S. and Richter-Dyn, N. 1974. "Stochastic Models in Biology." Academic Press, New York.

Hanson, F. B. and Tier, C. 1981. An asymptotic solution of the first passage problem for singular diffusion in population biology. SIAM J. Appl. Math. 40:113-132.

Hanson, F. B. and Tuckwell, H. C. 1978. Persistence times of populations with large random fluctuations. Theor. Pop. Biol. 14:46-61.

Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. Theor. Pop. Biol. 12:37-48.

Horn, H. 1975. Markovian models of forest succession. In "Ecology and Evolution of Communities" (Cody, M. L. and Diamond, J. G., Eds.), pp. 196-211.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299-1309.

Karlson, R. H. and Jackson, J. B. C. 1981. Competitive networks and community structure: A simulation study. Ecology 63:670-678.

Keiding, N. 1975. Extinction and exponential growth in random environments. Theor. Pop. Biol. 8:49-63.

Keiding, N. 1976. "Population Growth and Branching Processes in Random Environments." Preprint No. 9, Institute of Mathematical Statistics, University of Copenhagen.

Kurtz, T. G. 1981. "Approximation of Population Processes." SIAM, Philadelphia.

Kushner, H. J. 1972. Stability and existence of diffusions with discontinuous or rapidly growing drift terms. J. Differentials Equations 11:156-168.

Leigh, E. G. 1981. The average lifetime of a population in a varying environment. J. Theor. Biol. 90:213-239.

Ludwig, D. 1975. Persistence of dynamic systems under random perturbations. SIAM Rev. 17:605-640.

Ludwig, D. 1976. A singular perturbation problem in the theory of population extinction. SIAM-AMS Proc. 10:87-104.

MacArthur, R. H. 1972. "Geographical Ecology." Harper & Row, New York.

Mangel, M. and Ludwig, D. 1977. Probability of extinction in a stochastic competition. SIAM J. Appl. Math. 33:256-266.

May, R. M. 1973. "Stability and Complexity in Model Ecosystems." Princeton University Press, Princeton.

May, R. M. 1974. On the theory of niche overlap. Theor. Pop. Biol. 5:297-332.

May, R. M. and MacArthur, R. H. 1972. Niche overlap as a function of environmental variability. Proc. Natl. Acad. Sci. USA 69:1109-1113.

McNeil, D. R. and Schach, S. 1973. Central limit analogues for Markov population processes. J. R. Stat. Soc. B 35:1-23.

Nisbet, R. M. and Gurney, W. S. C. 1982. "Modelling Fluctuating Populations." Wiley, Chichester.

Pielou, E. C. 1981. The usefulness of ecological models: A stock-taking. Quart Rev. Biol. 56:17-31.

Polansky, P. 1979. Invariant distributions for multi-population models in random environments. Theor. Pop. Biol. 16:25-34.

Poole, R. W. 1978. The statistical prediction of population fluctuations. Ann. Rev. Ecol. Syst. 9:427-448.

Roughgarden, J. 1979. "Theory of Population Genetics and Ecology: An Introduction." MacMillan, New York.

Simberloff, D. and Boecklen, W. 1981. Santa Rosalia reconsidered: Size ratios and competition. Evolution 35:1206-1228.

Simberloff, D. and Connor, E. F. 1981. Missing species combinations. Am. Nat. 118:215-239.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128-134.

Tier, C. and Hanson, F. B. 1981. Persistence in density dependent stochastic populations. Math. Biosciences 53:89-117.

Turelli, M. 1977. Random environments and stochastic calculus. Theor. Pop. Biol. 12:140-178.

Turelli, M. 1978. A reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity. Theor. Pop. Biol. 13:244-267.

Turelli, M. 1980. Niche overlap and invasion of competitors in random environments. II. The effects of demographic stochasticty. In "Biological Growth and Spread, Mathematical Theories and Applications" (Jäger et al., Eds.), pp. 119-129.

Turelli, M. 1981a. Niche overlap and invasion of competitors in random environments. I. Models without demographic stochasticity. Theor. Pop. Biol. 20:1-56.

Turelli, M. 1981b. Temporally varying selection on multiple alleles: A diffusion analysis. J. Math. Biol. 13:115-129.

Turelli, M. and Gillespie, J. H. 1980. Conditions for the existence of stationary densities for some two-dimensional diffusion processes with applications in population biology. Theor. Pop. Biol. 17:167-189.

Turelli, M. and Petry, D. 1980. Density-dependent selection in a random environment: An evolutionary process that can maintain stable population dynamics. Proc. Natl. Acad. Sci. USA 77:7501-7505.

Wang, F. J. S. 1975. Limit theorems for age and density dependent stochastic population models. J. Math. Biol. 2:373-400.

Wilson, D. S. 1980. "The Natural Selection of Populations and Communities." Benjamin/Cummings, Menlo Park.