

Lecture Notes in Biomathematics 54, 76-89

THE STORAGE EFFECT IN STOCHASTIC POPULATION MODELS

Peter L. Chesson
Department of Zoology
The Ohio State University
1735 Neil Avenue
Columbus, Ohio 43210 U.S.A.

Introduction

Many populations occur in environments that vary substantially in time. Some of this variation is regular, for example, seasonal variation, and some of it is stochastic, i.e., has a strong element of randomness. Although I shall focus mainly on this stochastic variation there are many parallels between the effects of regular and stochastic variation and some of the mathematics below holds equally well for both kinds of temporal environmental variation.

The presence of significant stochastic variation suggests that stochastic models, not deterministic models, should be used to describe population dynamics. Yet they rarely are. The lack of emphasis on stochastic models seems in part due to the difficulty in analyzing stochastic models and in part due to the feeling that either stochasticity is mostly noise obscuring a deterministic signal or its effect is one that destabilizes systems. Discussions of these views are to be found in Goh (1976), Turelli (1978a), Murdoch (1979), Chesson and Warner (1981), and Chesson (1982). The perception that environmental variability is destabilizing might well have encouraged the use of stochastic models; instead it has led to an emphasis on features in deterministic models that ought to prevent destabilization by stochasticity (Beddington et al. 1976, Goh 1976). However, if destabilization is equated with the likely extinction of one or more species, then the conclusion that stochasticity is generally destabilizing is not correct. Recently there have appeared a number of models in which the effect of stochasticity is to promote coexistence of competing species (Chesson and Warner 1981, Chesson 1982, Chesson, in press, Ellner, in press, Shmida and Ellner, in press, Abrams, ms). Indeed, stochastic models have a variety of interesting and important behaviors that cannot be guessed from their deterministic counterparts. Thus no longer is there any good justification for the low emphasis on stochastic models.

There is a particular broad class of models where a stochastic environment seems especially likely to promote coexistence of competing species. Models in this class contain a feature that has been called the storage effect (Chesson, in press, Warner and Chesson, ms).

The Storage Effect

For many organisms the life cycle is naturally divisible into pre-reproductive individuals (juveniles) and reproductive individuals (adults). Maturation to an adult is called recruitment and the per capita number of new adults appearing in a unit of time is called the recruitment rate. The environment can affect adults and juveniles quite differently. In many organisms, highly variable birth rates and juvenile survivorship rates lead to highly variable recruitment rates. On the other hand, adult survivorship may be relatively constant and much higher than juvenile survivorship (Chesson, in press, Warner and Chesson, ms). These features are especially well documented for fish populations (Gulland 1982) and perennial plant populations (Grubb 1977, Harper 1977, Hubbell 1980).

To model the consequences of variable recruitment rates and low, less variable, adult death rates, let $X_1(t)$ be the adult population size of species 1 at time t , δ_1 the death rate of adults, and $R_1(t)$ the recruitment rate. With these definitions

$$X_1(t+1) = (1-\delta_1)X_1(t) + R_1(t)X_1(t). \quad (1)$$

The recruitment rate is assumed to take the form

$$R_1(t) = f_1(\xi(t), X_1(t), X_2(t), \dots, X_n(t)) \quad (2)$$

where f_1 is some function of the randomly varying environment, $\xi(t)$, and the adult densities of the n species in the system. For simplicity, the death rate is constant in this system. However, provided adult death rates are small, the results of Chesson and Warner (1981) and Chesson (1982) extend to show that moderate adult death rate variation does not qualitatively affect the results we obtain below. For definiteness we shall generally assume that the environment process $\xi(0), \xi(1), \dots$ is an independent and identically distributed (i.i.d.) sequence, but many features of our analysis hold more generally.

To investigate the consequences of this model for population growth, we define $\rho_i(t) = R_i(t)/\delta_i$ so that

$$X_i(t+1)/X_i(t) = 1 + \delta_i(\rho_i(t)-1). \quad (3)$$

Thus species i increases or decreases depending on whether $\rho_i(t) > 1$ or < 1 . Such situations of population increase and decrease will be referred to respectively as favorable and unfavorable periods. According to the invasibility criterion (Turelli 1978b) species i will persist in the system if

$$E \log\{1 + \delta_i(\rho_i(t) - 1)\} > 0 \quad (4)$$

when this expression is evaluated at 0 density for species i . (It is usually assumed that the system has a unique stationary distribution in the absence of species i and (4) is evaluated for this stationary distribution.)

The LHS of (4) is essentially the mean instantaneous growth rate of species i at low density and it has some quite remarkable properties. For example, a sufficient, but by no means necessary condition for (4), and hence for persistence is

$$E[\log \rho_i | \rho_i > 1] > c(\delta_i)P(\rho_i < 1)/P(\rho_i > 1) \quad (5)$$

(Chesson, in press), where $c(\delta_i) = -\delta_i^{-1} \log(1-\delta_i) \approx 1$ for small δ_i . This sufficient condition involves only the magnitude of ρ_i during favorable periods: no account is taken of what happens during unfavorable periods. In other words, for a given frequency of occurrence of favorable periods, a species can persist provided sufficient benefit in terms of recruitment is derived during favorable periods, independently of the magnitude of the recruitment costs that are incurred during unfavorable periods. This is not to say that the costs during unfavorable periods are unimportant, but simply that they are less important than the benefits gained during favorable periods.

Some idea of the effect of unfavorable periods can be gained from the approximation

$$E \log\{1 + \delta_i(\rho_i(t) - 1)\} \approx \delta_i\{E\rho_i - 1\} \quad (6)$$

which holds for small δ_i or situations where ρ_i takes only values near 1. Recalling that $E[X;A] = E[X|A]P(A)$, the persistence criterion becomes

$$E[\rho_i; \rho_i < 1] + E[\rho_i; \rho_i > 1] > P(\rho_i \neq 1). \quad (7)$$

Clearly both favorable and unfavorable periods contribute to this inequality. In particular, values of ρ_i near 1 during unfavorable periods mean that favorable periods do not have to be strongly favorable for the persistence criterion to be satisfied. However, it is equally clear that favorable periods have a potentially larger effect: while 0 is a lower limit to ρ_i , so that $E[\rho_i; \rho_i < 1] \geq 0$, in general there is no reason for any particular upper limit to ρ_i . Thus $E[\rho_i; \rho_i > 1]$ has the potential to be large, and will be large if strong recruitments are not too infrequent.

What we have seen is that in populations with small adult death rates and variable recruitment rates, there is a definite asymmetry in the effects of favorable versus unfavorable periods. Strong recruitments contribute quite significantly to population growth while poor recruitments can be made arbitrarily poor without causing much decline in the mean growth rate of the population. This asymmetry between the effects of favorable versus unfavorable periods is called the storage effect because it comes about by summation or "storage" of recruitment in the adult population: the adult population consists of the sum of past recruitments, each being discounted every time unit by the adult death rate. The fact that the adult population is essentially a sum over a number of periods of recruitment diminishes the harm that occurs whenever recruitment fails. The storage effect is present whenever generations are overlapping, i.e., whenever $\delta_i < 1$, but it is strongest when adult death rates are small, for then the effects of favorable periods of recruitment persist for a long time.

The Storage Effect as a Mechanism of Coexistence

Consider a group of species that compete quite strongly, but assume that this competition mostly affects recruitment of juveniles to the adult population. Then if adults are competing, the number and vigor of their offspring are affected by competition, while competition among juveniles affects their chances of surviving

to adulthood. If competitive dominance varies through time from species to species, each species is able to have periods of strong recruitment and the asymmetry imparted by the storage effect means that periods of poor recruitment, when a species is competitively inferior, need not cancel out the effects of these favorable periods. In this way the storage effect favors coexistence.

To demonstrate the potential role of the storage effect in promoting coexistence in a variety of competition models we take a conservative approach using

$$R'_i(t) = \inf_{X|X_i=0} f_i(\mathcal{E}(t), X) \quad (8)$$

which is the minimum value of the recruitment rate that will occur for a given state of the environment with species i at 0 density. We are considering a worst case situation for the possible effects of the other species.

If $R'_i(t)$ can be made arbitrarily large by a suitable choice of values of the environment $\mathcal{E}(t)$, then $\rho_i(t)$ can take on arbitrarily large values, and if there are such values of $\mathcal{E}(t)$ for each species, then there are probability distributions for $\mathcal{E}(t)$ such that the species coexist. For example, if the δ_i are small, condition (7) says that coexistence will occur if $P(\rho_i > n) = 1/n$ for each species. However, since the storage effect diminishes the harm to population growth during unfavorable periods, there is clearly a broad variety of probability distributions for $\mathcal{E}(t)$ that permit coexistence.

This analysis gives merely sufficient conditions for coexistence, and because of its conservatism these sufficient conditions themselves may not be very useful. Thus the analysis is best viewed as demonstrating the trend toward coexistence as variation in the environment is increased in certain broad directions. It gives little indication of the actual magnitude of variation necessary for coexistence. However, the strength of the analysis is its generality as illustrated by the examples below. Moreover, the analysis above is not restricted to the case where the environment is i.i.d. Indeed it demonstrates invasibility with very general kinds of environment processes including both stationary ergodic processes and regular environment processes in which $\mathcal{E}(t)$ is a periodic function of time. On the

other hand, retaining the assumption that the environment is i.i.d. allows us to conclude that each species persists in the strong sense of stochastic boundedness (Chesson, in press).

Example 1. The multispecies lottery model.

This model involves competition for space. Each adult holds a unit of space and thus death of adults releases $\sum \delta_j X_j(t)$ units of space in the time interval $(t, t+1)$. The $\beta_i(t)X_i(t)$ offspring of species i compete for this space with the $\beta_j(t)X_j(t)$ offspring from all species. Under the assumption that space is allocated at random, the proportion of available space taken by species i is $\beta_i(t)X_i(t) / \sum \beta_j(t)X_j(t)$. This involves also the assumption that the number of offspring always exceeds adult deaths, so that space is always in short supply. It now follows that

$$R_i(t) = (\sum \delta_j X_j(t)) \frac{\beta_i(t)}{\sum \beta_j(t)X_j(t)} \quad (9)$$

In the simplest case the "birth rates" $\beta_i(t)$ (which include density independent juvenile mortality) are simply functions of the environment and we deduce

$$R_i'(t) = \delta_i \frac{\beta_i(t)/\delta_i}{\max_{j \neq i} \beta_j(t)/\delta_j} \quad (10)$$

The ratio $\beta_i(t)/\delta_i$ is a natural measure of the competitive ability of a species. Thus expression (10) says that all species can coexist in the system if each species experiences periods when it is sufficiently competitively superior to all of the other species. This will be achieved with appropriate variation in the environment.

This simplest form of the lottery model does not permit coexistence in a constant environment, nor in an environment with non-overlapping generations (Chesson and Warner 1981). It follows that the storage effect is essential to coexistence.

The storage effect can also be shown to promote coexistence in a variety of more complex versions of the lottery model (Chesson, in press, in prep.). These models allow for such features as density dependence in the $\beta_i(t)$, spatial heterogeneity, and the possibility that fecundity is not always sufficiently high

to fill all of the available space.

Example 2. Generalized Lotka-Volterra Competition.

To obtain examples that are analogous with the more usual sorts of competition models, consider first the case of just two competing species and let $L_i(t)$ be the number of juveniles of species i produced in time $(t, t+1)$. The model for $L_i(t)$ is

$$L_i(t) = B_i(t)X_i(t)f_i(X_i(t), X_j(t)) \quad (11)$$

where the environmentally varying parameter $B_i(t)$ is the per capita birth rate in the absence of competition, and the function f_i represents the proportionate reduction in the birth rate due to competition among adults. The function f_i is thus assumed decreasing in both arguments.

Competition may also occur among juveniles affecting their survivorship to adulthood. Thus we have

$$R_i(t)X_i(t) = \theta_i L_i(t)g_i(L_i(t), L_j(t)), \quad (12)$$

where θ_i is survivorship without competition and g_i is the reduction in survivorship due to competition; g_i also is decreasing in both arguments.

Equations (11) and (12) may represent discrete forms of Lotka-Volterra competition as suggested by Chesson (in press) or they may represent some arbitrary generalization of Lotka-Volterra competition.

Under the assumption that $g_i(x, 0)$ has a finite maximum M_i we see that

$$X_i(t+1) \leq (1-\delta_i)X_i(t) + \theta_i M_i \quad (13)$$

and so $X_i(t)$ is bounded above by $\kappa_i = \theta_i M_i / \delta_i$ if it starts below this value. Thus we obtain

$$R_i'(t) \geq \theta_i B_i(t) g_i(0, B_j(t)\kappa_j) f_i(0, \kappa_j). \quad (14)$$

The monotonicity of g_i now implies that $R_i'(t)$ will be large whenever $B_i(t)$ is large provided that $B_j(t)$ is not simultaneously large. It follows that the two species will coexist provided only that the density independent components of their birth rates (the $B_i(t)$) take on sufficiently large values at different times. This

particular example generalizes quite trivially to cover the case of an arbitrary number of species. Coexistence occurs by the storage effect in the multispecies case if each species has large values of $B_i(t)$ while the values for the other species are small or moderate.

Without specifying the g_i and f_i , it is quite possible that coexistence occurs without the storage effect, either without a stochastic environment or without overlapping generations, but the important point is that the storage effect can lead to coexistence regardless of the specific form of the f_i and g_i , and so there is no doubt that it broadens the range of situations in which coexistence can occur.

Comparison with a spatial model

We have seen that the storage effect promotes coexistence in a variety of circumstances but the analysis gives little indication of how much variation is necessary for coexistence to occur nor does it say how effective the storage mechanism is relative to other mechanisms of coexistence. Some idea of the necessary amount of variation can be obtained from the two-species lottery model where this has been well-documented (Chesson and Warner 1981). A comparison with spatial heterogeneity lets us judge the relative efficacy of the storage mechanism. This is especially interesting because spatial heterogeneity is commonly regarded as a strong promoter of coexistence.

To make the comparison we construct an analogous spatial model which applies to a planktonic larval situation. Local populations of adults are assumed to exist on discrete patches, their offspring enter a pool of plankton which are then redistributed to the patches where the larvae may or may not mature as adults depending on the outcome of larval competitive interactions. The number of patches in the system, k , is assumed to be effectively infinite, and this assumption is justified by the usual convergence of the dynamics of finite systems of patches to those of infinite systems (Chesson 1981). The equation describing the dynamics of species i on patch j is

$$X_{ij}(t+1) = (1-\delta_i)X_{ij}(t) + R_{ij}(t)\bar{X}_i(t) \quad (15)$$

In this equation $X_{ij}(t)$ is the number of adults of species i on patch j , $\bar{X}_i(t) = \frac{1}{k} \sum_{j=1}^k X_{ij}(t)$ (the spatial average of adult numbers), and $R_{ij}(t) \bar{X}_i(t)$ is the number of new recruits to the adult population on patch j . Adults do not migrate: the only connection between patches is through the larval pool. The local recruitment rate $R_{ij}(t)$ takes the form

$$R_{ij}(t) = f_i(\mathcal{E}_j(t), \bar{X}_1(t), \dots, \bar{X}_n(t)) \quad (16)$$

which essentially embodies the idea that the total density of adults of each species in the system determines the size of the larval pool of each species. The local environment $\mathcal{E}_j(t)$ affects both the relative rates of migration of larvae to different patches, and the outcomes of the interactions among larvae on individual patches. Certainly more complex spatial models are possible but then they must be compared with models more complex than (1) for the storage effect. However for spatial versions of the lottery model it is best to have

$$R_{ij}(t) = \left(\sum_l \delta_{lj} X_{lj}(t) \right) \frac{\beta_{ij}(t) \bar{X}_i(t)}{\sum_l \beta_{lj}(t) \bar{X}_l(t)} \quad (17)$$

so that local recruitment depends on the local amount of space becoming available. But, because the $X_{lj}(t)$ enter (17) linearly, $\bar{X}_l(t)$ can be substituted for $X_{lj}(t)$ without altering the results we obtain (Chesson, in prep.). Thus it is sufficient to work with the general form (16).

To model spatial heterogeneity it is assumed that $\mathcal{E}_1(t), \mathcal{E}_2(t), \dots$ are i.i.d. for fixed t , and that the distribution of the $\mathcal{E}_j(t)$ does not depend on t . These assumptions provide spatial variation, and permit temporal variation locally in space, but do not allow any temporal variation that is correlated over all patches.

With these assumptions the dynamics of the spatial averages of population numbers are given by the equation

$$\bar{X}_i(t+1) = (1-\delta_i) \bar{X}_i(t) + \phi_i(\bar{X}_1(t), \dots, \bar{X}_n(t)) \bar{X}_i(t) \quad (18)$$

where

$$\phi_i(x_1, \dots, x_n) = Ef_i(\mathcal{E}_j(t), x_1, \dots, x_n). \quad (19)$$

Note that (18) is a simple difference equation and so the \bar{X}_i will behave deterministically but this deterministic behavior depends on spatial heterogeneity through its effects on the ϕ_i .

If $\mathcal{E}(t)$ is substituted for $\mathcal{E}_j(t)$ in (16), the subdivision of the total population into local populations becomes irrelevant and equation (18) no longer holds, at least not exactly; instead, the $\bar{X}_i(t)$ satisfy the storage model (1). With this observation the assumption that $\mathcal{E}(t)$ and $\mathcal{E}_j(t)$ have the same probability distribution establishes a one-one correspondence between the storage model and the spatial model. However, the correspondence goes beyond a mere formal relationship for the two models actually converge to each other numerically as the death rates are made small. To see how this happens let $\delta_i = h\delta'_i$, $f_i = hf'_i$, $\phi_i = h\phi'_i$. Decreasing h decreases death rates and lengthens the lives of individuals. The recruitment rate also decreases with h . In general this is necessary to prevent unbounded growth in the total reproductive output of an individual in its lifetime, but in the lottery models it is an automatic consequence of decreasing the δ_i with h .

Defining $\bar{X}_h(t) = (\bar{X}_1(t/h), \dots, \bar{X}_n(t/h))$ for the spatial process, and $X_h(t) = (X_1(t/h), \dots, X_n(t/h))$ for the storage model, we can view these models, appropriately, on a time scale commensurate with the life expectancy of an adult. A general theorem of M.F. Norman applies. In the presence of mild regularity conditions (Norman 1975) the difference $X_h(t) - \bar{X}_h(t)$ converges in probability to 0, provided $X_h(0) = \bar{X}_h(0)$. Thus the storage model and the spatial model are essentially indistinguishable for long-lived organisms: at least for long-lived organisms, the storage effect promotes coexistence just as effectively as does spatial heterogeneity.

The results of Norman (1975) are actually stronger than this simple convergence in probability for he shows that the rate of convergence is of order $h^{1/2}$: specifically,

$$h^{-k} [\underline{X}_h(\cdot) - \bar{X}_h(\cdot)] \quad (20)$$

converges weakly in distribution to a diffusion process $\underline{Z}(t)$. If $\bar{X}_h(0) = \underline{x}^*$ is an equilibrium point for the spatial process (such points do not depend on h), then $\underline{Z}(t)$ has an especially simple structure. It is a multivariate Ornstein-Uhlenbeck process and the distribution of $\underline{Z}(t+s)$ given $\underline{Z}(t)$ is

$$N(e^{As} \underline{Z}(t), \int_0^s e^{Au} \Sigma_0 e^{A^T u} du) \quad (21)$$

where $N(\underline{\mu}, \Sigma)$ means multinormal with mean $\underline{\mu}$ and variance matrix Σ ,

$$A = \left(x_i^* \frac{\partial \phi_i'}{\partial x_j}(\underline{x}^*) \right), \quad \Sigma_0 = \left(x_i^* x_j^* \mathcal{C} \{ f_i'(\underline{E}(t), \underline{x}^*), f_j'(\underline{E}(t), \underline{x}^*) \} \right) \text{ and } \mathcal{C} \text{ means covariance.}$$

In the event that the eigenvalues of A have negative real parts so that the spatial model is locally stable at \underline{x}^* for small h , the process $\underline{Z}(t)$ converges as $t \rightarrow \infty$ to a stationary stochastic process with mean 0 and variance

$\Sigma = \int_0^\infty \exp(Au) \Sigma_0 \exp(A^T u) du$. Thus for large t and small h , $\underline{X}_h(t)$ will be approximately a stationary process with distribution

$$N(\underline{x}^*, h\Sigma). \quad (22)$$

This means that for long-lived organisms the storage model will give us small fluctuations about the spatial equilibrium, with the variance of these fluctuations being proportional to the adult death rates.

On the other hand, if any eigenvalue of A has a positive real part, the spatial model will be locally unstable at \underline{x}^* and the storage model will show increasingly severe fluctuations about the value \underline{x}^* . This close link between stability in the two sorts of model further strengthens our conclusion that the stabilizing effects of spatial heterogeneity are matched in the analogous models of the storage effect.

Example: The multispecies lottery model.

The spatial version of the lottery model (Chesson, in prep.) has

$$\phi_1(\underline{x}) = (\Sigma \delta_{\ell} x_{\ell}) E \frac{B_{1j}}{\Sigma_{\ell} B_{\ell j} x_{\ell}} \quad (23)$$

Equilibrium points satisfy the equation

$$E \frac{\Gamma_i}{\sum_l \Gamma_l u_l^*} = 1 \quad (24)$$

where $\Gamma_i = \beta_{ij}/\delta_i$ and $u_i^* = x_i^* \delta_i / \sum_l \delta_l x_l^*$. In the lottery model, A has a 0 eigenvalue because $\sum X_i(t) = \text{a constant}$ (the total amount of space in the system). However if the distribution of $(\Gamma_1, \dots, \Gamma_n)$ is n-dimensional, i.e., cannot be supported by a linear space of fewer than n dimensions, then 0 is a simple root of the characteristic equation of A while the other eigenvalues have negative real parts. It follows that small h and feasibility of the solution to (24) give stability of the spatial model at x^* , and they give small fluctuations about this value in the storage model.

An instructive special case is obtained by assuming that $(\Gamma_1, \dots, \Gamma_n)$ has an exchangeable distribution, i.e., $(\Gamma_{\pi_1}, \dots, \Gamma_{\pi_n})$ has the same joint distribution for all permutations (π_1, \dots, π_n) of $(1, \dots, n)$. An exchangeable distribution gives a model of similar species, and for this model (24) has the feasible solution $x_i^* = \delta_i^{-1} / \sum_l \delta_l^{-1}$. If the distribution of $(\Gamma_1, \dots, \Gamma_n)$ is also n-dimensional, the storage effect leads to coexistence with small fluctuations about x^* , for small h. An n-dimensional and exchangeable distribution for $(\Gamma_1, \dots, \Gamma_n)$ is consistent with arbitrarily small but positive variances for the Γ_i . Thus this particular example provides an important complement to our previous results for it shows that in the lottery model similar species can coexist by the storage effect with arbitrarily small amounts of temporal environmental variability.

Summary

In many organisms the product of the birth rate and the juvenile mortality rate (the recruitment rate) is highly variable while the adult death rate is low and relatively less variable. These conditions lead to an asymmetry between the contributions of favorable and unfavorable periods to population growth. This asymmetry is called the storage effect and it can permit a species to persist provided favorable periods convey sufficient benefit regardless of the costs incurred during unfavorable periods. The storage effect is a stochastic mechanism of coexistence capable of acting in a broad variety of situations. For long-lived

organisms its efficacy appears comparable to that of spatial heterogeneity.

Acknowledgements

I am grateful for comments on the manuscript by Jerry Downhower, Stephen Ellner and Michael Turelli.

Literature Cited

- Abrams, P.A. (manuscript). Variability in resource consumption rates and the coexistence of competing species.
- Beddington, J.R., Free, C.A. and Lawton, J.H. (1976). Concepts of stability and resilience in predator-prey models. J. Anim. Ecol. 45:791-816.
- Chesson, P.L. (1981). Models for spatially distributed populations: the effect of within-patch variability. Theoret. 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. (in press). Coexistence of competitors in a stochastic environment: the storage effect. Proc. International Conference on Population Biology. Edmonton, Alberta 1982. Lecture Notes in Biomathematics.
- Chesson, P.L. (in prep.). A stochastic model of competition in a patchy environment.
- Chesson, P.L. and Warner, R.R. (1981). Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. 117:923-943.
- Ellner, S.P. (in press). Asymptotic behavior of some stochastic difference equation population models. J. Math. Biol.
- Goh, B.S. (1976). Nonvulnerability of ecosystems in unpredictable environments. Theoret. Pop. Biol. 10:83-95.
- Grubb, P.J. (1977). The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52:107-145.
- Gulland, J.A. (1982). Why do fish numbers vary? J. Theoret. Biol. 97:69-75.
- Harper, J.L. (1977). Population Biology of Plants. Academic Press, New York. 892pp.
- Hubbell, S.P. (1980). Seed predation and the coexistence of tree species in

- tropical forests. Oikos 35:214-229.
- Murdoch, W.W. (1979). Predation and the dynamics of prey populations. Fortschr. Zool. 25:245-310.
- Norman, M.F. (1975). Approximation of stochastic processes by Gaussian diffusions, and applications to Wright-Fisher genetic models. SIAM J. Appl. Math. 29:225-242.
- Shmida, A. and Ellner, S.P. (in press). Coexistence of plant species with similar niches. Vegetatio.
- Turelli, M. (1978a). A reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity. Theoret. Pop. Biol. 13:244-266.
- Turelli, M. (1978b). Does environmental variability limit niche overlap? Proc. Natl. Acad. Sci. USA. 75:5085-5089.
- Warner, R.R. and Chesson, P.L. (manuscript). Coexistence mediated by environmental fluctuations: a field guide to the storage effect.