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Community consequences of life-history traits in a variable environment

Peter L. Chesson & Nancy Huntly

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Models of interspecific competition in a stochastic environment show that the effects of environmental fluctuations on species coexistence can be expected to vary from community to community. However, by taking account of some basic properties of the species in a community it is possible to predict whether environmental fluctuations should promote coexistence, promote competitive exclusion or have no effect on species coexistence. One such property is the way the growth rates of the species respond to the joint effects of environment and competition. In simple (additive) models the joint effect of environment and competition is the sum of their separate effects. Deviations from additivity, in either the direction of subadditivity or superadditivity, are important determinants of species coexistence in a fluctuating environment. Such nonadditive growth rates are predicted on the basis of life-history traits, heterogeneity within a population and heterogeneity in space. Nonadditive growth rates have intuitive interpretations in terms of buffers and amplifiers of the joint effects of environment and competition.

A second property concerns the way fluctuations in the strength of competition are related to environmental fluctuations. We argue that favorable environmental conditions at some stage in the life cycle of an organism may lead to more competition for resources needed at a later stage, and hence positive covariance between environment and competition. In the presence of positive covariance, subadditive growth rates promote coexistence in a fluctuating environment, while superadditive growth rates promote competitive exclusion. Negative covariance between environment and competition reverses these conclusions.

Peter L. Chesson, Department of Zoology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210, USA.
Nancy Huntly, Department of Biological Sciences, Idaho State University, Campus Box 8007, Pocatello, Idaho 83209, USA.

1. Variability, disequilibrium and competition

Field biologists are often impressed by variability in natural populations and communities. Population parameters, such as fecundity, mortality and germination may show marked fluctuations in response to variation in environmental factors. Population densities also may vary greatly through time. As emphasized by many authors over many years, such environmental and populational variability implies that communities are usually not at equilibria determined by current environmental conditions and suggests that nonequilibrial processes may be important in community organization (Andrewartha & Birch 1954, 1984, Hutchinson 1951, 1961, Sale 1977, Connell 1978, Connell & Sousa 1983, Sale & Douglas 1984, Grubb 1977, 1986, Wiens 1977, 1986, Hubbell 1979, 1980, Murdoch 1979, Strong 1984, 1986, Underwood & Denley 1984, Murdoch et al. 1985). In response, there has been steady growth of verbal theories in which nonequilibrial phenomena are central (Andrewartha & Birch 1954, 1984, Hutchinson 1951, 1961, Paine & Vadas 1969, Sale 1977, Grubb 1977, Wiens 1977, Connell 1978, Strong 1986). These nonequilibrium ideas have been bolstered by the recent debate on the extent to which community patterns in nature are consistent with the predictions of equilibrium theory (see Simberloff 1984, Schoener 1984).

Doubts about equilibrium theory suggested that interspecific competition might not be an important force in nature (Schoener 1983). However, reviews of field experiments by Connell (1983) and Schoener (1983) show that interspecific competition is in fact widespread. Thus we are led to an important question: If competition, variability and disequilibrium all are common, what patterns of community organization are predicted? Such predictions are available from recent mathematical theories, as reviewed by Chesson & Case (1986). Here we discuss in detail the predictions that come from one well-developed theory, the theory of interspecific competition in an environment that varies stochastically through time.

2. Models of community dynamics in a temporally stochastic environment

The intuition of field biologists often has been that unpredictable environmental fluctuations should promote the coexistence of competing species (e.g. Hutchinson 1951, 1961, Grubb 1977, Sale 1977, Wiens 1977, Connell 1978). While some mathematical models support this conclusion, others do not, and this disagreement among models contains some important lessons. Detailed examination of Lotka-Volterra competition in a stochastic environment (May & MacArthur 1972, May 1974, Turelli 1981) led ultimately to the conclusion that environmental fluctuations have little effect on coexistence when the different species in the community have equal mean carrying capacities and intrinsic rates of increase. If mean carrying capacities or intrinsic rates of increase may differ between species (Turelli & Gillespie 1980), environmental variability appears to promote coexistence in some circumstances but demote it in others. In contrast to the field biologist's intuition, environmental variability produces no broadening or diminishing of the conditions for coexistence in these stochastic versions of the Lotka-Volterra model.

The lottery model of Chesson & Warner (1981), agrees with the conclusion that environmental variability has little effect on coexistence in the case where generations do not overlap. In other cases, however, the lottery model gives strikingly different results. The lottery model assumes that competition occurs among juveniles for space that they retain as adults. When adult death rates are relatively constant, fluctuations in recruitment rates, caused by a fluctuating environment, lead to coexistence in situations where no equilibrium coexistence is possible. This same result was found in the related models of Ågren & Fagerström (1984) and Shmida & Ellner (1985), and in a variety of significantly different models (Chesson 1983, 1984, Abrams 1984, Ellner 1984).

The idea that environmental variability may promote competitive exclusion is also supported by models. In the lottery model, variability in adult death rates can promote competitive exclusion (Chesson & Warner 1981). Environmental variability is also found to promote competitive exclusion in a model of fluctuating resource uptake rates (Chesson 1988a).

The diversity of results from these stochastic models looks confusing. Is there something general that one can say about the effect of a stochastic environment? The answer is yes, if one takes into account the life-history traits of the organisms.

3. Life-history traits and community dynamics

Organisms are frequently observed to possess life-history traits that buffer them against adverse conditions of the biotic or physical environment. These traits can act as buffers against unfavorable combinations of events such as simultaneous negative effects of competitors and poor environmental conditions. Other traits amplify the effects of unfavorable combinations of events. The models reviewed above conform to the following pattern: Models in which environmental variability promotes coexistence incorporate traits that function as buffering mechanisms. Those in which environmental variability promotes competitive exclusion incorporate traits that tend to amplify. Models in which environmental variability has no effect on coexistence include no buffering or amplifying traits.

Below we consider a general model permitting the effects of different kinds of life-history traits to be studied. This model reveals that buffering and amplifying mechanisms are central to the effect of environmental variability on species coexistence, but the model shows also that there is another important ingredient, viz the covariance between environment and competition, which is defined and discussed in Section 6, below. While this covariance may often be positive, we shall see that a negative covariance reverses the effects of buffering and amplifying mechanisms on the outcome of interspecific competition in a variable environment.

Before defining the general model, we consider how buffering and amplifying mechanisms can result from certain kinds of life-history traits that species may possess. While we can observe these traits, we do not make an argument for their evolutionary significance. Our purpose is to consider how they affect the outcomes of competitive interactions between species.

The long-lived seed bank of many annual plant species has long been recognized as a buffer (Harper 1977). Of interest here is the way in which a seed bank can buffer the joint effects of an unfavorable environment and competition. Many co-occurring plant species differ in their germination responses to environmental conditions (Went 1949, Juhren et al. 1956, Harper & Benton 1966, Mott 1972, Oomes & Elberse 1976, Grubb 1977, Shmida & Ellner 1985, Chesson & Huntly, unpublished data). Thus, a species may have poor germination in a year in which its competitors perform relatively better. In such years, it will produce few seeds. Without survival from one year to the next in the seed bank a species could suffer a major setback; however, the seed bank provides a buffer against strong competition and a poor environment because the seeds in any cohort can germinate over a number of years, diminishing the effect of failure in any given year.

Other stages in the life-cycle, such as the adults of iteroparous plants and sessile marine organisms, can buffer by participating in reproduction over a number of years (see reviews in Harper 1977, Warner & Chesson 1985, Chesson 1986). Semelparous species can experience these buffering effects if the offspring of an individual mature over a range of years (Inouye & Taylor 1980). Buffering can also occur as a consequence of such adaptations as diapause (Hanski, this issue) and storage of resources (Chapin 1980, Chapin and Shaver 1985, Gray & Schlesinger 1983, Nobel 1985, Mooney & Miller 1985). The roots and rhizomes of long-lived perennial plants may buffer species against poor environmental and competitive conditions (Coupland 1958, Miles 1979) because they store energy and nutrients gained in good years, which tide over bad years.

The evolutionary importance of life-history traits that buffer single-species populations has been discussed at length in the literature. In this context, such traits are often associated with bet-hedging strategies (Murphy 1968, Schaffer & Gadgil 1975, Hastings & Caswell 1979, Goodman 1984, Brown & Venable 1986, Bulmer 1985, Ellner 1985a,b). As emphasized above our focus is not at the single species level: we argue that such buffering traits are part of a mechanism of maintenance of species diversity. This mechanism is a generalization of the storage effect of Warner & Chesson (1985).

In the examples above, the buffering role of high survival in either adult or seed stages depends on its relative insensitivity to environmental and competitive factors. It therefore should not be too surprising that the converse trait, sensitivity of survival in these stages to environment or competition, can be an amplifying mechanism (Chesson 1988a). This is easy to see in cases where adult survival is sensitive to the environment, and competition occurs at the juvenile phase, for then a poor environment (low adult survival) combined with strong competition will lead to a precipitous population decline.

Another trait that can be an amplifier is environmental sensitivity of resource uptake, which commonly occurs in plants (Chabot & Mooney 1985). Such sensitivity may often take place in the presence of resource storage, which creates an overall buffering effect (Abrams 1984). However, without such storage, sensitivity of resource uptake to environmental conditions can amplify the joint effects of competition and an unfavorable environment (Chesson 1988a).

4. A general model

To develop a general mathematical theory incorporating the above ideas, we need to define buffers and amplifiers in precise mathematical ways, and show that they do indeed promote coexistence and competitive exclusion, respectively. The general model of Chesson (1986, 1988a, b) shows how this can be done. For a system of n species, this model can be written in the form

$$X_i(t+1) = X_i(t)\, G_i(E_i, C_i), \tag{1}$$

where $X_i(t+1)$ and $X_i(t)$ are respectively the population sizes of species i at times $t+1$ and t, and $G_i(E_i, C_i)$ is the multiple by which the population changes from one time to the next. The arguments E_i and C_i of the function $G_i(E_i, C_i)$ are respectively an environmentally-dependent parameter of the population (e.g. a density-independent birth rate, juvenile survival rate, or germination fraction), and a factor measuring the amount of competition experienced by species i. Both E_i and C_i are assumed to vary in time. The amount of competition, C_i, depends on the den-

Table 1. The lottery model.

The Lottery Model:

$$X_i(t+1) = (1-\delta_i)\,X_i(t) + [\delta_1 x_1(t) + \delta_2 x_2(t)]\,\frac{E_i\,X_i(t)}{E_1X_1(t) + E_2X_2(t)}$$

$X_i(t)$: adult population size of species i at time t.

δ_i : adult death rate of species i.

E_i : birth rate of species i (varies with time t).

$(1-\delta_i)\,X_i(t)$: number of adults of species i surviving from time t to time t+1.

$[\delta_1 X_1(t) + \delta_2 X_2(t)]$: total adult death (= total space opened) between t and t+1.

$E_1X_1(t) + E_2X_2(t)$: total number of juveniles seeking space between t and t+1.

$E_iX_i(t)\,/\,[E_1X_1(t) + E_2X_2(t)]$: fraction of available space captured by juveniles of species i. (This represents random allocation of space.)

The Lottery Model expressed in terms of the General Model:

$$G_i(E_i, C_i) = 1 - \delta_i + E_i/C_i$$

$$C_i = [E_1X_1(t) + E_2X_2(t)]\,/\,[\delta_1X_1(t) + \delta_2X_2(t)]$$

$$g_i(E_i, C_i) = \ln(1 - \delta_i + E_i/C_i)$$

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sities of the species in the system and also on the environmentally-dependent parameters, $E_1, E_2, \ldots, E_n$, of the n species.

While there may be correlations among the environmentally-dependent parameters of the different species, it is assumed that these correlations are less than 1, i.e. there must be some asynchrony in the fluctuations of the environmentally-dependent parameters of different species.

As an example of a model within this framework, in Table 1 we have defined the two-species form of the lottery model (Chesson & Warner 1981), which is a model of competition for space. In the lottery model, E_i is the product of the per-capita birth rate and early juvenile mortality rate, and C_i is the number of juveniles in the system divided by the total amount of space for which they are competing in order to mature to adulthood. The lottery model was originally developed to describe the coexistence of territorial reef fishes (Chesson & Warner 1981). It has been suggested also as explaining the diversity of tropical forests (Leigh 1982), *Eucalyptus* forests (Comins & Noble 1985), and some aspects of coexistence of perennial plants in the chalk grasslands (Grubb 1986).

It is important to keep in mind that the environmentally-dependent parameter, E_i, is assumed to affect population growth in the absence, as well as in the presence, of competition. It is thus a direct environmental effect, not one that simply modifies the effects of interactions with other species or individuals. In contrast, some of Turelli's (1981) models assume that the environment affects only the carrying capacity of a species. It thus has little effect on population growth when the densities of all species in the system are low.

The multiplicative nature of population growth means that the properties of the general model are determined by population growth rates on the log scale. Thus we define $g_i(E_i, C_i) = \ln G_i(E_i, C_i)$ to give

$$\ln X_i(t+1) - \ln X_i(t) = g_i(E_i, C_i). \qquad (2)$$

Changes in log population size are obtained by summing $g_i(E_i, C_i)$ over time. We shall refer to $g_i(E_i, C_i)$ simply as the "growth rate" of species i. Using this growth rate we can define buffering, amplifying and neutrality. These definitions are given graphically in Fig. 1, where the growth rate is plotted as a function of competition for two different values of the environmentally-dependent parameter. The situations depicted in Fig. 1 are (a) additive (neutral), (b) subadditive (buffering), and (c) superadditive (amplifying). Case (a) is additive because the effect of competition, which is given by the slope of $g_i(E_i, C_i)$ as a function of C_i, does not change with environmental factors E_i. Therefore the total effect of

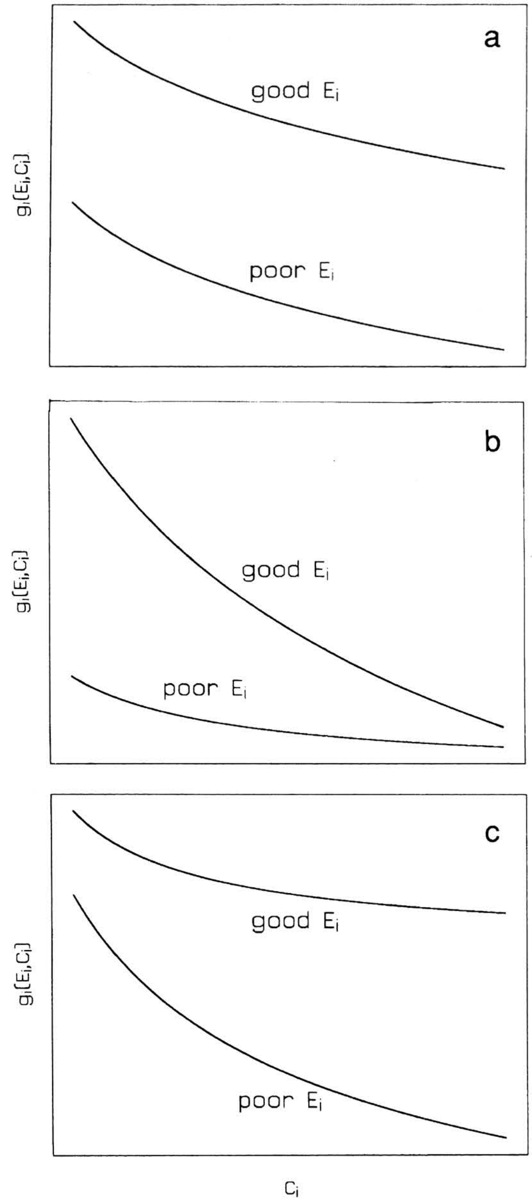

Fig. 1. The growth rate $g_i(E_i, C_i)$ as a function of the amount of competition C_i for two different values of the environmentally-dependent parameter, E_i. — (a) Additive (neutral); (b) subadditive (buffering); (c) Superadditive (amplifying).

environment and competition is merely the sum of their separate effects.

In case (b) the decline in the growth rate as competition increases is less steep in the poor environment. This case is the buffered situation: the joint effect of a poor environment and competition is less than the sum of their separate effects. In the superadditive case (c), when environmental conditions are poor, the effect of competition is stronger than when environmental conditions are good. This case gives amplification of the unfavorable effects of competitive and environmental factors.

Models such as some of Turelli's (1981), with variable carrying capacity, in essence have variability only in the competitive parameter, with no direct effect of environmental variability on population growth. Such situations can be viewed within our framework as additive.

Mathematically, it is easy to decide whether the contributions to the growth rate of competition and direct environmental effects are additive, subadditive or superadditive. One just takes the cross partial derivative:

$$\gamma = \frac{\partial^2 g}{\partial E\, \partial C}, \tag{3}$$

where the subscript i has been dropped for notational simplicity. This indicates how the slope of the population growth rate, $\partial g/\partial C$, changes as E is varied. Thus, if γ is 0, the slope of g as a function of C does not change with E and the additive or neutral situation of Fig. 1(a) prevails. If γ is negative, then $\partial g/\partial C$ becomes more negative as E is increased, i.e. the subadditive situation (b) occurs. Finally, if γ is positive, the superadditive or amplifying case occurs.

The published stochastic models cited in the previous section can all be seen as special forms of the general model given here. The classification into additive, subadditive, or superadditive corresponds to no effect, a positive effect, or a negative effect of environmental fluctuations on coexistence, in these models. As we shall see below, these effects of nonadditive growth rates can be reversed by negative covariance between environment and competition (Section 6), but nonadditivity *per se* remains critical.

5. The occurrence of nonadditive growth rates: covariance of sensitivity

We can see generally how life-history traits can be associated with nonadditive growth rates using the following model. Assume that the population of a species consists of a number of different classes, e.g. age classes, different phenotypes, or individuals in particular microenvironments. Then, the function G_i, which gives the multiple by which the population changes from one time to the next, can be written as the sum of the contributions to population growth of the k classes that make up the population:

$$G_i(E_i, C_i) = \sum_{l=1}^{k} [K_l A_l(E_i)/B_l(C_i)]. \tag{4}$$

In this formula, K_l represents the contribution that the lth class would make to population growth when unmodified by the environment and competition, while $A_l(E_i)$ and $B_l(C_i)$ represent the modifications in this contribution due to environment and competition.

The environmental effects, given by $A_l(E_i)$, imply that each class is sensitive to basically the same environmental factors, as summarized by some quantity E_i, but the function $A_l(E_i)$ of E_i gives the particular pattern of sensitivity for class l. For instance, if the classes represent different phenotypes in the population, E_i might represent the average change in percapita reproduction in all classes due to environmental effects in the current reproductive season. The functions $A_1(E_i), A_2(E_i), \ldots, A_n(E_i)$ would then express reproduction in each phenotypic class as a function of these current average reproductive conditions. In a similar way, the competitive factors $B_l(C_i)$, represent sensitivity of each class to some common underlying competitive factor C_i, for species i.

While this model may represent the contributions of different phenotypes within a population, it might also represent the contributions of individuals in different patches. In addition, it can apply simply to different processes that contribute to population growth rather than to different classes of individuals within the population. For example, the lottery model explained in Table 1 is of this form. It has two processes contributing to population growth: adult survival (a process that is insensitive to environmental and competitive factors giving $A_1(E_i) = B_1(C_i) = 1$) and reproduction ($A_2(E_i) = E_i$, $B_2(C_i) = C_i$).

A similar example comes from a model of fluctuating germination rates in annual plants with seed banks (Ellner 1984). In this case we measure population size as the number of seeds in the seed bank. The multiple by which this population changes from one time to the next can then be represented as follows:

$$G_i(E_i, C_i) = s_i(1 - E_i) + Y_i E_i / C_i, \tag{5}$$

where E_i represents the germination fraction, s_i is the survival rate of ungerminated seeds, and Y_i is the yield of seeds at the end of the growing season in the absence of competition. The two processes contributing to population growth are seed survival, $s_i(1 - E_i)$, and production of new seeds, $Y_i E_i / C_i$. Here $s_i = K_1$, $A_1(E_i) = 1 - E_i$, $B_1(C_i) = 1$, $Y_i = K_2$, $A_2(E_i) = E_i$ and $B_2(C_i) = C_i$.

Equation (4) expresses the contribution to population growth of each class or process as a ratio of environmental and competitive effects. As discussed in Chesson (1988a), it is quite natural to expect homogeneous units or single processes contributing to population growth to take this ratio form, although there are important exceptions (Chesson 1988a). The ratio form means that in isolation each of these classes or processes would produce an additive growth rate. When these potentially additive contributions are combined, however, the result can be nonadditive.

To see how these nonadditive growth rates arise we note that the population growth rate is

$$g_i(E_i, C_i) = \ln \left[\sum_{l=1}^{k} K_l A_l(E_i)/B_l(C_i)\right], \tag{6}$$

and we define $W_l = K_l A_l(E_i)/B_l(C_i)$ (the contribution to population growth from the lth class), $\alpha_l = d \ln A_l(E_i)/dE_i$ (the sensitivity of the lth population class to the environment), and $\beta_l = d \ln B_l(C_i)/dC_i$ (the sensitivity of the lth class to competition). Taking the cross partial derivative of g_i, we find that

$$-\gamma = -\frac{\partial^2 g}{\partial E\, \partial C} = \frac{\sum_{l=1}^{k} W_l(\alpha_l - \bar{\alpha})(\beta_l - \bar{\beta})}{\sum_{l=1}^{k} W_l}, \tag{7}$$

which is the weighted covariance of α_l and β_l, with weights equal to the contributions, W_l, to population growth from the different classes. ($\bar{\alpha}$ and $\bar{\beta}$ are the corresponding weighted means.) Thus, the ways in which sensitivity to environment and competition covary within a population determine whether the growth rate will be additive, subadditive, or superadditive. In particular, if sensitivity to environment tends to occur together with sensitivity to competition, then the growth rate is subadditive (γ is negative), i.e. it incorporates a buffer against simultaneously unfavorable competitive and environmental conditions.

This representation of γ in terms of a covariance allows us to see immediately that the lottery model and the seed-bank model produce buffered growth rates because of the positive covariation in sensitivity to environment and competition of the different processes contributing to population growth. For example, in the lottery model, and other models of recruitment variation (Chesson 1984), adult survival is insensitive to both environment and competition, while recruitment of new adults is sensitive to both. In addition it is clear that a buffer will be present whenever a population has some phenotypes that are less sensitive to environment and competition than others. Patches that expose individuals to lesser rigours of environment and competition than other patches also should act as buffers.

This covariance in sensitivity to environment and competition relates to the *potential* of different individuals or processes to respond to environment and competition. It makes no assumptions about the magnitude of environmental variation, the magnitude of competitive effects, or the tendency of particular sorts of environmental and competitive conditions to occur together in time. Covariance of sensitivity is a property of a population that applies within a year. Because it determines nonadditivity of growth rates, it affects the reponse of a population to the particular combination of environmental and competitive conditions that prevail in a given year. The sorts of combinations of environmental and competitive conditions that tend to occur is determined by the covariance of environment and competition over time, a between-year measure, which we discuss next.

6. The covariance between environment and competition

The results of published models appear to be explained by classifying their growth rates as additive, subadditive, or superadditive. However, these models also share the assumption that environmental and competitive effects covary. In all nonadditive cases C is assumed to increase as E increases, which means that environment and competition have positive covariance.

Surprisingly, such positive covariances are most likely to occur in the common situation where environmental influences act in a density-independent way and have no direct effect on competition. Positive covariance occurs because such density-independent factors can nevertheless cause large changes in density, size or vigour of organisms, in turn affecting the intensity of competition that may occur at a later stage. Thus higher survival, reproduction, germination, or growth promoted by environmental conditions that have nothing to do with resource supply can lead to stronger competition for limiting resources. In this way we expect positive covariance between environment and competition to be common.

The opportunities for positive covariance are illustrated by the two specific examples of the general model given here. In the lottery model (Table 1), juveniles are assumed to compete for space that permits them to mature as adults. Reproduction and juvenile survival have no effect on the total resource supply, but these factors, which may be environmentally dependent, have a strong influence on the amount of competition through their effect on the total number of juveniles seeking this limited resource. Thus, the competitive parameter in the lottery model is an increasing function of the environmentally-dependent parameters, giving positive covariance between environment and competition.

The second example is the seed-bank model, Eq. (5). In that model the fraction of seeds germinating is the environmentally-dependent parameter. If the weather causes a high germination fraction, there will be more seedlings and adult plants to compete for water, light and nutrients. Therefore, unless the resources available for survival, growth and seed set of the plant are closely linked to germination cues, the increased density that results from a higher germination fraction can cause more competition. Again the covariance between environment and competition will be positive.

Negative covariance between environment and competition is only likely in the restricted situation where favorable environmental factors directly increase resource supply. Even then, the ultimate effect can be a positive covariance if the greater resource supply early in a season leads to higher survival or growth of individuals who will, as a consequence of greater number or size, deplete resources sufficiently that the net effect is stronger competition.

Once the covariance between environment and competition are specified, conclusions are available from the general model. These are summarized for the case of positive covariance in Table 2. For the case of negative covariance between environment and competition, the conclusions are simply reversed. The case of zero covariance, like the case of no interaction between environment and competition, implies no effects of environmental variability on coexistence.

The results in Table 2 were first demonstrated for two-species systems in Chesson (1986) under the as-

Table 2. Results of the general model with positive covariance between environment and competition.

Growth rate properties		Effect of environmental fluctuations	
Type	Sign of $\partial^2 g/(\partial E\,\partial C)$	Mean low-density growth rates	Coexistence
Subadditive (buffering)	negative	Increased	Promoted
Additive (neutral)	zero	Unchanged	Unaffected
Superadditive (amplifying)	positive	Decreased	Demoted

sumption of symmetry, i.e. that the species have the same function g converting E and C into changes in log population size, and the same mean and variance of the environmental variables. This result is generalized for symmetric multispecies models in Chesson (1988a). In Chesson (1988a, b) these results are extended to asymmetric two-species models under the assumption that variability in the environment is small, and that deterministic effects operating in the model are of correspondingly small magnitude. In this case the symmetry assumptions can be removed completely and the results of Table 2 hold whether or not the species have the same g, different means and variances of their environmentally-dependent parameters, E, and different competitive factors, C.

While the general asymmetric multispecies model has not been analyzed by these methods, we emphasize that the conclusions of Table 2 have been upheld for important multispecies models that are special cases of the general model. Examples are models of recruitment variation (Chesson 1984), which are subadditive, general additive multispecies models (Chesson 1988a), and stochastic versions of Lotka-Volterra models (Turelli, 1981), which are additive.

7. Quantitative results

The amount of variation necessary to see the effects described above has been determined for the lottery model (Chesson & Warner 1981, Warner & Chesson 1986) and the general model (Chesson 1988a, b). In the two-species case, the results can be stated quite simply under the assumption that the amount of variation is small. In that case a species i will able to persist in the presence of a competitor species j if

$$\Delta E - \Delta C - \gamma \chi\, b_c(1 - \theta b_e) > 0. \qquad (8)$$

This quantity represents the long-term average growth rate of species i while at low density in the presence of its competitor species j. Here ΔE measures the average degree to which the environment favors species i over species j, ΔC measures the average excess of interspecific competition (the effect of species j on species i) over intraspecific competition (the effect of species j on species j), γ is expression (3) and measures the strength of the interaction between environment and competition, and χ is the covariance between environment and competition for species j. The term $b_c(1-\theta b_e)$ will usually be positive, except in cases of strong asymmetry between the species, and high correlations among the environmental fluctuations of different species. Here b_e and b_c are regression coefficients, respectively, of the environmentally-dependent parameter of species i on species j, and the competitive parameter of species i on species j. The quantity θ is the ratio of the γ's for species i and species j.

Environmental variability enters primarily through the covariance χ, which can be shown to be approximately proportional to the variance of the environmentally-dependent parameter (Chesson 1988b). Thus, as environmental variability increases, χ will increase in absolute value. If the product of γ and χ is negative, the formula implies that environmental variability promotes coexistence, because it means that $\Delta E - \Delta C$ can be negative (species i can be at an average environmental and competitive disadvantage to species j) and yet species i still persists in the system. Thus, if growth rates are subadditive and C is positively correlated with E (as justified above) then environmental variability will be favorable to coexistence. The regression coefficient b_e takes into account the correlations in the environmental fluctuations of different species. It will be near 1 if the two species respond to the environment in almost the same way, and then opportunities for coexistence by this mechanism are substantially reduced. Situations where the species responses to the environment are independent ($b_e = 0$), or negatively correlated ($b_e < 0$), are much more favorable to coexistence.

Formula (8) shows in a simple quantitative way how different factors contribute to coexistence, with few assumptions beyond small environmental variance. Restricting attention to small variance means that the formula is useful for understanding the first effects of environmental variability that appear in a model as variance is increased. In some models such as the lottery model, the formula is known to give accurate results even when variances are quite large (Chesson 1988b). The simplicity of the formula is, however, deceptive because the term ΔC can be complicated. In particular, if competitive effects experienced by the two species cannot be linearly related to one another, ΔC will itself be affected by environmental variability (Chesson, unpublished). This means that in addition to effects of environmental variability stemming from nonadditive growth rates, other effects, including other mechanisms of coexistence and competitive exclusion, may result from relative nonlinearity of the competitive effects experienced by two species.

8. The nature of coexistence and competitive exclusion in these models

It is commonly believed that communities dependent on stochastic environmental fluctuations are inherently loose, unstable assemblages. Theory implies that this need not be so (Chesson 1986). As discussed above, nonadditive interactions between the environmental and competitive effects may oppose competitive exclusion when the environment fluctuates. In such cases, populations at low density have an advantage over populations at high density. Paradoxically, environmental variability creates a central tendency to population fluctuations that tends to stabilize competitors at intermediate relative abundances. For example, Chesson (1984, 1985) has shown that in models of recruitment variation (e.g. the lottery model) the probability distribution of population size is approximately normal with variance proportional to the adult death rate. Examples of these approximately normal curves are depicted in Fig. 2. The figure shows that population fluctuations have strong central tendencies in the presence of environmental variability.

While quantitative results on population fluctuations are not yet available for the general model, it appears from the lottery model (Hatfield & Chesson 1988) that, once there is sufficient environmental variability for coexistence, the magnitude of population fluctuations is determined primarily by the quantity γ, which measures the strength of the buffering effects of life-history traits. Environmental variability has less effect on the magnitude of population fluctuations because it has two opposing effects that tend to cancel: it creates a tendency for species to grow toward intermediate densities and a tendency for species to fluctuate away from intermediate densities.

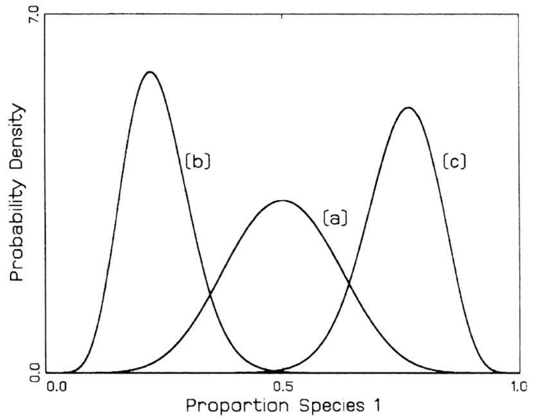

Fig. 2. Probability densities summarizing the population fluctuations in the two-species lottery model. Species abundances are expressed as the proportion of the available space occupied by species 1. Species 2 occupies one minus this amount. To define these curves, let μ = mean of $\ln(E_1/E_2) - \ln(d_1/d_2)$ (a measure of average competitive superiority of species 1 over species 2), and σ^2 = variance of $\ln(E_1/E_2)$ (a measure of environmental variability). The parameter values defining the curves are then (a) $\delta_1 = \delta_2 = 0.1$, $\mu = 0$, $\sigma^2 > 0$; (b) $\delta_1 = \delta_2 = 0.05$, $\mu = -0.5$, $\sigma^2 = 2$; (c) $\delta_1 = 0.04$, $\delta_2 = 0.12$, $\mu = 0$, $\sigma^2 > 0$. Calculations are based on Hatfield & Chesson (1988).

9. Discussion

Den Boer (1968) introduced the concept of spreading-of-risk to explain how species living in a variable environment avoid rapid extinction in the situation where density-dependent stabilizing mechanisms are weak or act only infrequently. His reasoning implies that, on a sufficiently large temporal or spatial scale, the average effect of uncertain environmental influences will be small and population fluctuations will be dampened. Part of his idea involves dispersal among patches that may experience different environmental conditions, but it also involves the spreading of risk through time by a population subdivided into different age classes. These situations have been considered in theories of life-history evolution (Murphy 1968, Schaffer & Gadgil

1975, Hastings & Caswell 1979, Goodman 1984, Bulmer 1985, Ellner 1985a, b) with the conclusion that life-history traits leading to risk spreading can be favored by natural selection. Den Boer points out that phenotypic variation within a population also can result in risk spreading.

The kinds of life-history phenomena that den Boer considered are critically important in the models of community dynamics presented here. However, the reduction in population fluctuations as a result of risk spreading, which does occur in these models, is of secondary interest. In general, we have found that risk-spreading life-history traits can provide a buffer to the joint effects of unfavorable environmental and competitive conditions. In the cases where environmental influences and competitive effects are positively correlated, this buffer creates an average advantage to a species at low density and, thus, opposes competitive exclusion. While all species involved in a competitive interaction may benefit from buffers or risk spreading, these models imply that the benefit is greatest for low-density species, which explains why competitive exclusion is opposed.

Grubb's (1977, 1986) concept of the regeneration niche of plant species involves many ideas that are important to our models. Grubb emphasizes that there are many ways in which production of seeds, dispersal, germination, establishment of seedlings and onward growth of the plant can be sensitive to the environment. He argues that these regeneration requirements are a legitimate part of the niche of an organism, and may be the component most strongly differentiated among species. In Grubb's view, environmental variation provides different species opportunities for population increase at different times or in different places, and that in certain circumstances this can maintain species diversity. We have dealt here only with variation in time, but elsewhere it has been shown that these sorts of mathematical models extend to the consideration of spatial variation (Chesson 1984, 1985, Comins & Noble 1985). By expressing the ideas involved in the regeneration niche in terms of a mathematical model we are able to quantify the effects, and elucidate the important components such as nonadditivity (buffers and amplifiers) and covariance between environment and competition.

The results of the model illustrate, in particular, that the effect of environmental variability may differ among communities. The quantitative deviation from additive growth rates, as measured by γ, is important in determining the magnitude of the effect of environmental variability. The sign of γ determines the nature of the effect, i.e whether competitive exclusion is opposed or promoted by environmental fluctuations. If the deviation from additivity is weak, only a weak coexistence-promoting effect can be expected. In this regard, coexistence conditions for the lottery model (Chesson & Warner 1981, Warner & Chesson 1985, Hatfield & Chesson 1988) are instructive. In that model (Table 1), birth rates are the environmentally-dependent parameter and adult survival causes the deviation from additivity. If only a small proportion of the adults survive from one year to the next, the coexistence-promoting effect of environmental variability will be weak, and conclusions about coexistence derived from the analogous deterministic model remain valid even in the presence of large environmental and population fluctuations. On the other hand, 90% survival yields close to the maximum coexistence promoting effect available from this model.

An appreciation of this maximum coexistence-promoting effect can be obtained by comparing the amount of environmental variability necessary for coexistence in this model with the amount of habitat segregation necessary for coexistence according to equilibrium theory (Chesson 1985). To do this, one relates the variance over time in relative birth rates of species in the lottery model to the variance in space of relative abundances of species in the corresponding equilibrium model of habitat segregation. One finds that the maximum coexistence-promoting effect available from the lottery model is exactly equal to the coexistence-promoting effect of habitat segregation.

This sort of detailed analysis is not yet available for other special cases of our general model, but the formula (8) for the mean low density growth rate provides the means by which this can be done. Moreover, through the term $\Delta E - \Delta C$, it permits classical "equilibrium" mechanisms to be evaluated in the same model as "nonequilibrium" mechanisms involving a stochastic environment. This formula shows that deviation from equilibrium, due to environmental fluctuations, need not prevent the expression of classical mechanisms of coexistence or competitive exclusion. This is true even if environmental fluctuations make competition infrequent (Chesson 1988a). Rather, both classical mechanisms and mechanisms dependent on environmental fluctuations need to be considered together. The model presented here provides a theoretical means by which this can be done. The challenge now is to measure the components of formula (8) to deduce the contributions of different mechanisms to coexistence or competitive exclusion in nature.

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