

CHAPTER 5

Interactions Between Environment and Competition:

How Fluctuations Mediate Coexistence and

Competitive Exclusion.

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1. INTRODUCTION

One of the major theoretical and empirical challenges in ecology today is elucidating the role of various kinds of heterogeneity, such as environmental fluctuations, in the dynamics of populations and the organization of communities. There is substantial evidence that stochastic environmental fluctuations have a strong role in population and community processes (Andrewartha and Birch 1954, 1984, Hutchinson 1961, Sale 1977, Connell and Sousa 1983, Sale and Douglas 1984, Grubb 1977, Wiens 1977, 1986, Murdoch 1979, Underwood and Denley 1984, Simberloff 1984, Murdoch et al 1985, Strong 1986, Victor 1986), and as a consequence, a variety of verbal theories of community structure in a stochastic environment have been developed (Hutchinson 1951, 1961, Paine and Vadas 1969, Sale 1977, Grubb 1977, Wiens 1977, Connell 1978). However, the mathematical theories of stochastic environments have not provided an adequate alternative to the classical theory based on deterministic models. There seem to be two reasons for this. First, the existing stochastic models have generally not provided the sort of simple quantitative results that often follow from deterministic models. Second, there is a widespread perception that models incorporating temporal variability may give unfathomable or inconsistent results (Hastings and Caswell 1979, Levin et al 1984). Indeed, an examination of models of communities of competitors reveals that a stochastic environment can have essentially any effect depending on the specific model involved and the assumptions that are made about it. Some models say that environmental variability promotes coexistence (Chesson and Warner 1981, Abrams 1984, Ellner 1984, Shmida and Ellner 1985), others say that environmental variability has little effect on coexistence (Turelli 1981, Chesson and Warner 1981), while others say that environmental variability promotes competitive exclusion (Chesson and Warner 1981).

Using a general model, Chesson (1986) shows that much of the confusion surrounding stochastic models is related to different implicit assumptions about the life-history traits of the species. It is our purpose here to consider a more interpretable formulation of the model

of Chesson (1986), and to extend its results. With this new formulation of the general model, it is possible to show how the effects of environmental fluctuations follow from qualitative features of biology. In particular, the life-history traits of model organisms will often dictate an interaction between environmental and competitive effects that determines how environmental variability influences competitive interactions and their outcomes. Moreover, within this framework simple interpretable results are available.

2. The Model

Consider a community of n competing species. To describe their dynamics in discrete time we use the equation

$$X_i(t+1) = G_i(\mathcal{E}_i, C_i)X_i(t), \quad (1)$$

where $X_i(t)$ is the population size of species i at time t , \mathcal{E}_i is an environmentally-dependent parameter of the population of species i , C_i measures the amount of competition that the population is exposed to, and the function G_i converts the environmental and competitive conditions, as measured by the quantities \mathcal{E}_i and C_i , into the finite rate of increase for the time interval $(t, t+1)$. The environmentally-dependent parameter will often be something like a density-independent birth rate, survival rate, or seed germination rate. We will assume that the environment fluctuates over time, which means that \mathcal{E}_i fluctuates over time also and can be written as $\mathcal{E}_i(t)$ to emphasize this.

The competitive factor will measure shortage of a critical resource. Sometimes, for instance, it will be density of individuals competing for this resource. In general, C_i will be a function of the species densities in the system and also of their environmentally-dependent parameters, i.e, it will be written in the form

$$C_i = c_i(\mathcal{E}_1, X_1, \mathcal{E}_2, X_2, \dots, \mathcal{E}_n, X_n), \quad (2)$$

where c_i is some function. Since the \mathcal{E}_i 's and the X_i 's will be functions of time, so will C_i . Moreover, C_i and \mathcal{E}_i will be correlated. If a species is at zero density, it will be assumed that its environmentally-dependent parameter does not contribute to any of the C_i 's.

Generally \mathcal{E}_i will be defined so that a larger value reflects more favorable environmental conditions for a species. For example, when the environment causes fluctuating mortality rates, \mathcal{E}_i will be defined as the survival rate. The competitive factor will often increase as the environmentally-dependent parameters increase. For example, if an environmental change increases seed germination then there will be more seedlings around later to compete for moisture, light and nutrients. In some cases an increase in the environmentally-dependent parameter may be a consequence of a greater availability of

limiting resources, in which case this assumption is inapplicable and the reverse assumption is more appropriate. However, in all that follows we shall assume that the competitive parameters increase as the environmentally-dependent parameters increase.

Models of population dynamics in a temporally variable environment are best viewed on a log scale for which changes in population size can be written

$$\ln X_i(t+1) - \ln X_i(t) = g_i(\mathcal{E}_i, C_i), \quad (3)$$

where $g_i = \ln G_i$. Note that changes in log population size are found by summing g_i over time, i.e., they are additive in g_i . The function g_i can be thought of as an instantaneous per-capita growth rate applicable for the period $(t, t+1)$. We shall refer to it simply as the growth rate.

While change in log population size is additive over the growth rate, g_i , the growth rate itself can be additive or nonadditive in its arguments. In the additive case

$$g_i(\mathcal{E}_i, C_i) = A_i(\mathcal{E}_i) + B_i(C_i), \quad (4)$$

for some functions A_i and B_i . This additive form applies whenever the quantity

$$\gamma \stackrel{\text{def}}{=} \frac{\partial^2 g_i}{\partial \mathcal{E}_i \partial C_i} \quad (5)$$

is equal to zero. When this quantity is negative, the growth rate is called subadditive, and when positive it is superadditive. These different possibilities for the growth rate are illustrated in figure 1.* In the subadditive case, the slope of g_i as a function of C_i is less in a poorer environment, i.e., when the environment is bad the additional effect of competition is slight. Essentially, the growth rate is buffered against simultaneous poor conditions such as a poor environment and high competition. As we shall see later, simple features of biology can produce these buffered growth rates and they are likely to be widespread in nature. The superadditive case is the opposite of a buffer. There the additional effect of competition is worse in the poor environment. The poor environment amplifies the effect of competition.

To analyze the model, we need to introduce some assumptions. We first consider a case where the species have similar biology (we shall call it the symmetric case). The advantage of this case is that results can be obtained for general g_i , and general \mathcal{E}_i , and it appears to indicate the sort of results to expect in asymmetric settings. We then go on to approximations that allow direct conclusions about asymmetric situations.

II.1 SYMMETRIC CASE

The first of the symmetry assumptions is that the species have the same competitive factors ($C_1 = C_2 = \dots = C_n = C$, say), and the same functions G_i and g_i converting environmental and competitive effects into growth rates. The competitive factor C will

* SEE PAGE 71

depend symmetrically on the different species in the system, and we assume that the environmental parameters undergo fluctuations of a similar sort: we assume that the probability distribution of $(\mathcal{E}_1, \mathcal{E}_2, \dots, \mathcal{E}_n)$ is exchangeable, i.e., invariant under arbitrary permutation of subscripts. We will, however, assume that the environmentally-dependent parameters do not exhibit perfectly synchronous fluctuations: $P(\mathcal{E}_i = \mathcal{E}_j) < 1$. Justification for such assumptions comes from the fact that some ecologically similar species nevertheless exhibit marked relative fluctuations in their environmentally-dependent parameters. For example, this is the case with tropical trees (Leigh 1982, Connell, unpublished data), and desert annuals (Shmida and Ellner 1984). The final assumption we make is that the vector of environmentally-dependent parameters satisfies the standard random environment assumption: the sequence $[\mathcal{E}_1(0), \mathcal{E}_2(0), \dots, \mathcal{E}_n(0)], [\mathcal{E}_1(1), \mathcal{E}_2(1), \dots, \mathcal{E}_n(1)], \dots$ is an independent and identically distributed sequence of random vectors.

Before analyzing the stochastic case of this model, it is instructive to examine its behavior in a constant environment. The symmetry assumptions imply that in a constant environment there is a neutral equilibrium. To see this, we define the equilibrium amount of competition, C^* , by the equation

$$g(\mathcal{E}, C^*) = 0, \quad (6)$$

where \mathcal{E} is the common constant value of the environmentally-dependent parameter. In terms of C^* , the set of neutrally stable equilibrium densities is the set N of all points (X_1, \dots, X_n) such that

$$c(\mathcal{E}, X_1, \dots, \mathcal{E}, X_n) = C^*. \quad (7)$$

This set N will often be a global attractor of the system, but in cases where $g(\mathcal{E}, C)$ can be too large in absolute magnitude, the system will not approach N but will oscillate about it as a consequence of the timelags inherent in this discrete-time formulation.

Except for unlikely functions c , the set N will include points on all faces and edges of the positive cone, $[0, \infty) \times [0, \infty) \times \dots \times [0, \infty)$, excluding the origin. Thus N contains points for which $1, 2, \dots, n-1$ of the species are extinct in all possible species combinations. Moreover, N will in most cases be a connected set and the equilibria will form a continuum between these states of extinction. Classically, when faced with a deterministic model of this sort ecologists have concluded that only one species can persist when the likely effects of a stochastic environment are taken into account. The reason for this conclusion is the argument that environmental perturbations will cause a random walk to take place in which eventually all but one species becomes extinct. Our analysis below supports this conclusion in only a narrow range of circumstances.

To analyze the model in a stochastic environment we use the invasibility criterion Turelli (1978). The idea is to examine the mean low-density growth rate of each species in the system to see whether species tend to increase or decrease at low density. The mean

low-density growth rate of species i is defined as

$$\Delta_i = \text{E}g_i(\mathcal{E}_i, C_i), \quad (8)$$

where the expectation is evaluated under the assumption that $X_i(t) = 0$, and that the remaining species in the system have converged to a unique stationary distribution. The method breaks down if the other species do not converge to a unique stationary distribution. Such convergence is to be expected in regular cases (Revuz 1975), but there are few practical results that can identify when this is true in population models (Ellner 1984). Positive values of the quantity Δ_i mean that species i tends to increase from low density. Indeed, the strong law of large numbers can generally be invoked to show that $X_i(t)$ will increase, in a fluctuating manner, at least until the approximation (8) to the mean growth rate breaks down (see Chesson 1982, Ellner 1984, Chesson and Ellner 1988). In broad two-species settings it has been shown that positive Δ_i 's imply coexistence in the sense that both species are stochastically boundedly persistent (Chesson and Ellner 1988).

Cases where the Δ_i are negative mean that a species at low density will have a tendency to converge to extinction. In the general two-species model of Chesson and Ellner (1988) and in the lottery model (Chesson 1982), clear conclusions are available: If Δ_1 and $\Delta_2 < 0$, there is probability 1 that exactly one of the species converges to extinction. If $\Delta_i > 0$, but $\Delta_j < 0$, species j will converge to extinction, and species i will persist in the system.

To apply the invasibility criterion to the general model in this article we focus on a pair of species i and j and define

$$h(\mathcal{E}_i, \mathcal{E}_j) = \text{E}[g(\mathcal{E}_i, C) \mid \mathcal{E}_1, \dots, \mathcal{E}_n], \quad (9)$$

where species i is at zero density and the other species are at their joint stationary distribution. Expression (9) depends on the environmentally-dependent parameters of all species in the community, but for simplicity of notation only the dependence on the critical pair \mathcal{E}_i and \mathcal{E}_j is represented on the LHS. Note that expression (9) is an average of the growth rate over the species densities in the community for fixed values of the environmentally-dependent parameters. This average is performed using the conditional distribution of $(X_1(t), \dots, X_n(t))$ given $(\mathcal{E}_1(t), \dots, \mathcal{E}_n(t))$. However, independence of the environment over time implies that $(X_1(t), \dots, X_n(t))$ and $(\mathcal{E}_1(t), \dots, \mathcal{E}_n(t))$ are independent, and therefore the conditional distribution is the same as the unconditional (marginal) distribution.

The function h itself can be classified as additive, subadditive or superadditive on the basis of the sign of

$$\gamma^*(\mathcal{E}_i, \mathcal{E}_j) \stackrel{\text{def}}{=} \frac{\partial^2 h}{\partial \mathcal{E}_i \partial \mathcal{E}_j} . \quad (10)$$

(Note that γ^* depends on $\mathcal{E}_1, \dots, \mathcal{E}_n$, even though only the two focal parameters are represented explicitly as arguments.) Moreover, additivity, subadditivity and superadditivity are properties of h that are inherited directly from g . Under the assumption C is increasing in all of its arguments, the sign of $\partial^2 g / \partial \mathcal{E}_i \partial \mathcal{E}_j$ is the same as the sign of $\gamma (= \partial^2 g / \partial \mathcal{E}_i \partial C)$. Since γ^* is simply an average of $\partial^2 g / \partial \mathcal{E}_i \partial \mathcal{E}_j$ over the species densities, γ^* inherits the sign of $\partial^2 g / \partial \mathcal{E}_i \partial \mathcal{E}_j$ provided the sign of the latter is constant. Otherwise γ^* inherits the average sign of $\partial^2 g / \partial \mathcal{E}_i \partial \mathcal{E}_j$. Thus, when we speak of additivity, subadditivity, or superadditivity, it does not matter greatly whether it is defined in terms of g or h .

In terms of h , the mean low-density growth rate of species i can be evaluated by the formula

$$\Delta_i = E h(\mathcal{E}_i, \mathcal{E}_j) . \quad (11)$$

In addition, note that $h(\mathcal{E}_j, \mathcal{E}_j) = E[g(\mathcal{E}_j, C_j) \mid \mathcal{E}_1, \dots, \mathcal{E}_n]$, for the community at its stationary distribution in the absence of species i . In this situation, $E \ln X_j(t+1) = E \ln X_j(t)$, and so

$$E h(\mathcal{E}_j, \mathcal{E}_j) = 0 . \quad (12)$$

These results can now be used to decide coexistence using the relationship

$$\begin{aligned} & h(\mathcal{E}_i, \mathcal{E}_i) + h(\mathcal{E}_j, \mathcal{E}_j) - h(\mathcal{E}_i, \mathcal{E}_j) - h(\mathcal{E}_j, \mathcal{E}_i) \\ &= \int_{\mathcal{E}_j}^{\mathcal{E}_i} \int_{\mathcal{E}_j}^{\mathcal{E}_i} \gamma^*(e_1, e_2) de_1 de_2 . \end{aligned} \quad (13)$$

Taking expected values in (13), and using (11), (12) and the symmetry assumptions, we get

$$\Delta_i = -\frac{1}{2} E \int_{\mathcal{E}_j}^{\mathcal{E}_i} \int_{\mathcal{E}_j}^{\mathcal{E}_i} \gamma^*(e_1, e_2) de_1 de_2 . \quad (14)$$

If γ^* is constant in sign it follows that Δ_i has the opposite sign. Thus, in the subadditive case, the Δ 's of all species in the system will be positive, and the species will coexist by the invasibility criterion. Clearly the value of Δ_i will tend to be greater for distributions in which \mathcal{E}_i and \mathcal{E}_j have greater probability of being far apart. Thus large values of Δ_i should be associated with distributions having large variances and negative correlations between \mathcal{E}_i and

\mathcal{E}_j . However, Δ_j will still be positive in all situations where the correlation between \mathcal{E}_i and \mathcal{E}_j is any value less than +1. Thus coexistence by this mechanism can still occur even when the environmentally-dependent parameters of the species have strong positive correlations.

In the superadditive case, the opposite sorts of result occur: the Δ 's will be negative and a species at low density will have an average tendency to decrease to extinction. Although there is as yet no general proof, this sort of situation tends to imply that all but one species will ultimately converge to extinction, and the identity of the surviving species will be a matter of chance. Chesson and Ellner (1988) show that this is so for a class of two-species models.

In the remaining case (additive growth rates) all the mean low-density growth rates are zero. The invasibility criterion implies that they have neither an average tendency to increase or decrease at low density. In this case, the growth rates must take the form

$$g_i(\mathcal{E}_i, C_i) = A(\mathcal{E}_i) + B(C), \quad (15)$$

which means that the change in $(\ln X_i - \ln X_j)$ from time t to time $t + 1$ is equal to $A(\mathcal{E}_i) - A(\mathcal{E}_j)$, i.e. it is simply a random variable with mean 0. Thus $\ln X_i - \ln X_j$ undergoes a mean-zero random walk, with no density or frequency dependent effects. Thus, over time, the relative abundances of different species approach extreme values. And in particular, recovery from a state of very low relative abundance is an event with infinite expected waiting time, according to the theory of random walks (Feller 1971). It is reasonable to assume that competition prevents any species from spending correspondingly large periods of time at absolute abundances that are extremely high, and this means that the predicted long periods of time at arbitrarily low relative abundances imply long periods of time at low absolute abundances. As explained for the lottery model (Chesson and Warner 1981), this must be interpreted in the real-world as meaning that the system simplifies to a single species.

In this additive case it is easy to see the consequence of removing some of the symmetry assumptions. We need not assume any symmetry for the distribution of the environmentally-dependent parameters, and we can modify the growth rate (15) so that it takes the form

$$g_i(\mathcal{E}_i, C_i) = A_i(\mathcal{E}_i) + b_i B(C). \quad (16)$$

In this form, competition affects different species to different degrees, but the effects of competition are proportional, reflecting a single underlying competitive factor C . It follows that changes in $(\ln X_i)/b_i - (\ln X_j)/b_j$ from t to $t + 1$ are given by the random variable $A_i(\mathcal{E}_i)/b_i - A_j(\mathcal{E}_j)/b_j$. If this random variable always has mean 0, then a mean-zero random walk occurs once more, and the system must be interpreted as simplifying to a single-species. On the other hand, if one species has a larger value of $EA_i(\mathcal{E}_i)/b_i$ than other species, the

strong law of large numbers implies that $(\ln X_i)/b_i - (\ln X_j)/b_j$ must converge to ∞ for all $j \neq i$. This means of course that species i drives all the other species asymptotically to extinction, with probability 1.

In summary, the analyses in this section show that environmental variability should promote coexistence when growth rates are subadditive, should promote competitive exclusion when growth rates are superadditive, and in the additive case environmental variability should not alter the conclusion of equilibrium models that different species cannot stably coexist when limited by a common competitive factor.

II.2 ASYMMETRIC CASES

In nonadditive cases, deviations from the strict symmetry assumptions present complex problems for analysis. It is clear, however, that the conclusions will not collapse with small deviations from strict symmetry because given enough smoothness in the growth rates g , stationary distributions of residents, and mean low-density growth rates, Δ_i , will vary continuously with the joint distribution of the environmentally-dependent parameters. It follows that small asymmetries in the distributions of the environmentally-dependent parameters (favoring some species over others) will not alter the sign of the mean growth rates, except in the additive case for which the effects of asymmetry are well understood, as discussed above.

In general, however, it can be expected that sufficiently large departures from symmetry, in directions that give average advantages to some species over others, will destroy the conclusions of the symmetric case. In particular, in the subadditive case, it can be expected that there will be a relationship between the amount of environmental variability needed for coexistence and the extent to which the environment confers average advantages on some species.

For the subadditive case, expression (14) suggests that the mean low-density growth rates should be increasing functions of the variation in the environmentally-dependent parameters. Hence we would expect that the degree of asymmetry possible before the signs of the Δ_i disagree with the predictions of the symmetric case, should increase with the amount of variation in the environmentally-dependent parameters. Can we verify these speculations and obtain a quantitative assessment of the joint action of variability and asymmetry? We can do this in the case where the amount of variation is small.

Let \mathcal{E}^* be any particular value of the environmentally-dependent parameter. We consider the effects of environmental variation in the vicinity of this arbitrary fixed value. Since $g(\mathcal{E}, C)$ is a decreasing function of C , there will be a unique value C^* of C such that $g(\mathcal{E}^*, C^*) = 0$. To obtain general results on the effects of environmental variability we introduce a standard parameterization of the model, which involves transforming the scales of measurement of the environmentally-dependent and competitive parameters. The standard

parameters replacing the original parameters \mathcal{E} and C are

$$\mathcal{E}_s = g(\mathcal{E}, C^*) \quad \text{and} \quad C_s = -g(\mathcal{E}^*, C). \quad (17)$$

The formula for the growth rate in terms of the new parameters is defined implicitly by the equation

$$g_s(\mathcal{E}_s, C_s) = g(\mathcal{E}, C). \quad (18)$$

Note that this parameterization of the model is characterized by the property that

$$g_s(\mathcal{E}_s, C_s) = \mathcal{E}_s - C_s + \Gamma(\mathcal{E}_s, C_s) \quad (19)$$

where the function Γ satisfies the equations $\Gamma(0,0) = \partial\Gamma(\mathcal{E}_s,0)/\partial\mathcal{E}_s = \partial\Gamma(0,C_s)/\partial C_s = 0$.

The standard parameterization thus enables the model to be expressed simply in terms of its additive and interactive components. It is important to note that the type of interaction (additive, subadditive or superadditive) is unaffected by this reparameterization because the sign of the cross-partial derivative, γ , is not altered. From now on we will assume that the transformation of the model to standard form has been done, and so we will drop the subscript s . Note that in standard form \mathcal{E}^* and C^* are both 0.

Equation (19) implies that a model in standard form can be approximated about the value $\mathcal{E} = C = 0$ by the second-order Taylor expansion

$$g(\mathcal{E}, C) = \mathcal{E} - C + \gamma_0 \mathcal{E}C, \quad (20)$$

where $\gamma_0 = \gamma(0,0) = \partial^2 g / \partial \mathcal{E} \partial C$, at $\mathcal{E} = C = 0$.

Now consider the usual resident-invader situation with two species. The species will be assumed to have the same growth rate function g and the same competitive factor, but the distributions of the environmentally-dependent parameters will be assumed different. In particular, it will be assumed that they have different means. However, in order to use the approximation (20) we must assume that these distributions are both concentrated near the value 0.

Applying (20) to a resident at its stationary distribution gives

$$E\mathcal{E}_j - EC^j + \gamma_0 E\mathcal{E}_j C^j = 0 \quad (21)$$

where C^j is random variable representing the competition variable C for the resident at its stationary distribution. It follows from this that

$$E\mathcal{E}_j - EC^j + \gamma_0 (E\mathcal{E}_j)(EC^j) = -\gamma_0 \chi, \quad (22)$$

where χ is the covariance between \mathcal{E}_j and C^j . This can be rearranged to give the following formula for EC^j :

$$EC^j = \frac{E\mathcal{E}_j + \gamma_0 \chi}{1 - \gamma_0 E\mathcal{E}_j}. \quad (23)$$

The mean growth rate of an invader is

$$\Delta_i = E\mathcal{E}_i - EC^j + \gamma_0 E\mathcal{E}_i C^j. \quad (24)$$

To go beyond this formula we need to relate \mathcal{E}_i and \mathcal{E}_j , and it turns out that all we need is the regression of \mathcal{E}_i on \mathcal{E}_j , i.e. the function $E[\mathcal{E}_i | \mathcal{E}_j]$. Provided this regression function is differentiable, we can use the first order Taylor approximation

$$E[\mathcal{E}_i | \mathcal{E}_j] = E\mathcal{E}_i + b(\mathcal{E}_j - E\mathcal{E}_j), \quad (25)$$

where b is a constant. This first order approximation is all that is needed to retain the second order character of our approximation for Δ_i . This implies that $E\mathcal{E}_i C^j = E\{E[\mathcal{E}_i | \mathcal{E}_j] C^j\} = (E\mathcal{E}_i)(EC^j) + b\chi$. Substituting this and (23) in (24) we obtain

$$\Delta_i = E\mathcal{E}_i - (E\mathcal{E}_j + \gamma_0\chi) \frac{1 - \gamma_0 E\mathcal{E}_i}{1 - \gamma_0 E\mathcal{E}_j} + \gamma_0 b\chi \quad (26)$$

Eliminating terms of order higher than 2 (the limit of accuracy of these approximations) this reduces to

$$\Delta_i = (\Delta E\mathcal{E}) (1 + \gamma_0 E\mathcal{E}_j) - \gamma_0 (1-b)\chi, \quad (27)$$

where $\Delta E\mathcal{E} = E\mathcal{E}_i - E\mathcal{E}_j$.

This mean growth-rate formula is most easily interpreted when converted into a condition for Δ_i to be positive, allowing invasion to occur. The condition is

$$E\mathcal{E}_i > E\mathcal{E}_j + \frac{\gamma_0 (1-b)\chi}{1 + \gamma_0 E\mathcal{E}_j}. \quad (28)$$

Note that the regression coefficient b can be written as the product of the correlation coefficient between \mathcal{E}_i and \mathcal{E}_j and the ratio of their standard deviations. In most cases the value of b will be less than 1. It follows that in subadditive situations (negative γ_0) the invader can increase from low density even though it is at a disadvantage to the resident (has a smaller mean environmental parameter). The disadvantage that species i has to species j can be measured by $E\mathcal{E}_j - E\mathcal{E}_i$, and the supremum of values of this quantity permitting invasion is, by (28), $|\gamma_0| (1-b)\chi / (1 + \gamma_0 E\mathcal{E}_j)$. Thus, species i can invade at a greater disadvantage for larger values of $|\gamma_0|$ (the degree of subadditivity), larger values of χ (the covariance between the environment and competition), and smaller values of the coefficient of regression of the environmental parameter of the invader on that of the resident.

The invader can always successfully invade in this subadditive case if it has an advantage over the resident ($E\mathcal{E}_i > E\mathcal{E}_j$), and so these conditions for invasion of a weaker species are also conditions for coexistence. A multispecies extension of these results is possible but is deferred to a subsequent article.

If γ_0 is 0 (the additive case), invasion can only occur if the invader is superior on average to the resident, as the earlier exact results demonstrate. With positive γ_0 (superadditivity), negative mean low-density growth rates are favored by environmental variability for both species of a two-species system. This means that whichever species first fluctuates to low-density is likely to become extinct. However, with enough asymmetry in the system, it is possible for one species to have a positive mean low-density growth rate, while that for other species is negative. Thus, there is a specific winner and loser in competition. To have a positive mean low-density growth rate, species i must be superior to species j by at least a little more than $\gamma_0(1-b)\chi/(1+\gamma_0E\mathcal{E}_j)$. Thus conditions unfavorable to invasion by species i are defined by a large interaction, γ_0 , a large covariance, χ , or a small regression coefficient, b .

The covariance, χ , in these results, will vary with the details of the specific situation. It is possible, however, to get some feeling for it by considering the case of strong competition for a resource such as space. If this strong competition tends to lead to all space being filled, then in a single-species system the growth rate, $g(\mathcal{E}, C)$, will approach 0. Thus in two-species space-filling models a resident will satisfy the equation $0 = g(\mathcal{E}_j, C^j)$. It follows that $(\mathcal{E}_j)^2 = (C^j)^2 + \text{terms of order higher than 2}$. Hence

$V\mathcal{E}_j = VC^j = \chi$, to second order, where V means variance. Thus, in such space filling situations, χ can be approximated by the variance of the environmentally-dependent parameter. In other situations this will not be true. In particular the variance of C^j will have components of variation due to fluctuations in species densities as well as variation in the environmentally-dependent parameter. Thus VC^j may often be larger than $V\mathcal{E}_j$.

Nevertheless, the covariance, χ , is still likely to be closely related to $V\mathcal{E}_j$.

The results that we have obtained here extend those of the symmetric model to asymmetric distributions of the environmental parameters. Moreover, here we have obtained explicit quantitative results defining conditions for coexistence and competitive exclusion showing how they are affected by different factors in the system. Assumptions that are retained in this analysis are equality of the competition variables C_i and equality of the function g_i converting the environmental and competitive effects into the growth rate.

However, these remaining assumptions also can be removed (Chesson, in prep.)

III. HOW ADDITIVITY AND NONADDITIVITY ARISE

Mathematical models using difference equations have focused on organisms with strictly nonoverlapping generations. The best examples of such organisms are univoltine insects and annual plants without a seed bank. In such organisms there will usually be a

period of reproduction followed by a period of juvenile growth, mortality, and final maturation to adulthood before the next breeding season. The per-capita number of adults at the next breeding season can be represented as the product of the per-capita birth rate B , for adults alive at the beginning of the breeding season, and the juvenile survival rate Θ , giving the fraction of births that ultimately yield an adult at the beginning of the next breeding season. Both stages may be affected by environment and competition, but consider for the moment an environmental factor that affects only the birth rate B . The quantity B is then an environmentally-dependent parameter, i.e., $\mathcal{E}_i = B$. If juveniles compete, then Θ is dependent on C_i , the competitive factor for the species, and so we have

$$G_i(\mathcal{E}_i, C_i) = \mathcal{E}_i \Theta(C_i). \quad (29)$$

Since this is a product, $g_i(\mathcal{E}_i, C_i)$ is necessarily additive. Note that it is quite reasonable in this case for C_i to be an increasing function of the environmentally-dependent parameters of the species in the community because a higher birth rate will lead to a larger number of juveniles and therefore more competition among those juveniles. If the factor causing the high birth rate persists during the period of juvenile competition and in some way is able to more than make up for the increased number of juveniles, then the reverse assumption that C_i is a decreasing function of \mathcal{E}_i must be made. Nevertheless, both $g_i(\mathcal{E}_i, C_i)$ and $h(\mathcal{E}_i, \mathcal{E}_j)$ remain additive.

Other variations on the arrangement above retain the same additive property. Instead of the birth rate being variable, or in addition to this, early juvenile mortality could be environmentally-dependent, but later juvenile mortality could depend on competition. Or the birth rates might be affected by competition among adults while the juvenile survival rates are environmentally-dependent. In all cases g_i remains additive.

Another important case is where the environmental factor and the competitive factor operate simultaneously. For example, suppose they operate during a mortality phase. The environmentally-dependent parameter could then be an instantaneous contribution to survival due to the environment while the competitive factor would be the instantaneous contribution to mortality due to competition. The latter could be called C_i' , because it would not be equivalent to the total competitive factor for the relevant period. The change in population size during the juvenile period could then be represented as

$$\frac{1}{X_i} \frac{dX_i}{dt} = -C_i' + \mathcal{E}_i. \quad (30)$$

Note that \mathcal{E}_i is a negative number. Letting h be the length of the relevant juvenile period, it follows that the fraction of the population surviving over the juvenile period is

$$e^{-C_i + h\mathcal{E}_i}, \quad (31)$$

where

$$C_i = \int_0^h C_i'(u) du. \quad (32)$$

Note that $C_i'(u)$ will be dependent on the environment and the species densities in the system at the time u and even possibly at previous points in time. However, species densities at time u are functions of what they were at time 0. It follows that the representation (2) for C_i is still applicable.

These results show that organisms with very simple life histories will often have additive growth rates if the environmentally-dependent parameter is something like a birth rate or survival rate. More complex features of biology are necessary before we find nonadditive growth rates and interesting conclusions. It turns out that seemingly minor perturbations of the model can have large effects on these conclusions: additivity is not a structurally stable feature of a model.

Organisms with nonoverlapping generations

Suppose now that we are dealing with organisms that are iteroparous, i.e., the adults may remain reproductive for several seasons. In many such organisms, reproduction, juvenile survival, and maturation are processes that are much more environmentally and competitively sensitive than adult survival (Chesson 1986). Thus we shall represent adult survival as a constant s . The net per-capita number of new adults produced in a year can be represented as a function $G_i'(\mathcal{E}_i, C_i)$, where $\ln G_i'(\mathcal{E}_i, C_i)$

(= $g_i'(\mathcal{E}_i, C_i)$) is additive. It follows that

$$g_i(\mathcal{E}_i, C_i) = \ln\{s + G_i'(\mathcal{E}_i, C_i)\}. \quad (33)$$

Elementary calculus shows that

$$\gamma = s\alpha\beta G_i' / G_i'^2, \quad (34)$$

where $\alpha = \partial g_i' / \partial \mathcal{E}_i$ and $\beta = \partial g_i' / \partial C_i$. Since β is negative, while all other factors in (34) are positive, we see that γ is negative and therefore g_i is subadditive. It follows that overlapping generations and iteroparity promote coexistence in a variable environment. It must be kept in mind, however, that we assume positive covariance between environmentally-dependent parameters and competition, and that adult survival is insensitive to environmental and competitive factors.

The discussion above assumes that generations overlap in the adult phase of the life cycle. However, the results apply also to annual plants with seed banks by interpreting s as the fraction of seeds that remain viable but do not germinate. This representation is

satisfactory provided germination itself is not the environmentally-dependent parameter. When germination is the environmentally-dependent parameter we obtain the equation

$$g_i(\mathcal{E}_i, C_i) = \ln\{s(1 - \mathcal{E}_i) + G_i'(\mathcal{E}_i, C_i)\}. \quad (35)$$

For this model, we obtain

$$\gamma = s[(1 - \mathcal{E}_i)\alpha + 1]\beta G_i' / G_i^2. \quad (36)$$

Again γ is negative, showing that growth rates are subadditive and that coexistence will be promoted in a variable environment, as first demonstrated in a specific seed-bank model by Ellner (1984).

The superadditive situation is also easily seen in these models. To obtain that case, one can make the survival rate in (33) and (35) the environmentally-dependent parameter. These growth rates become respectively

$$g_i(\mathcal{E}_i, C_i) = \ln\{\mathcal{E}_i + G_i'(\mathcal{E}_i, C_i)\} \quad (37)$$

and

$$g_i(\mathcal{E}_i, C_i) = \ln\{\mathcal{E}_i(1 - \theta) + G_i'(\mathcal{E}_i, C_i)\}, \quad (38)$$

where the germination rate is now θ . In both cases, simple calculus shows that γ has the same sign as

$$1 - \alpha\mathcal{E}_i. \quad (39)$$

The quantity α measures the dependence of reproduction and juvenile survival on adult or seed survival, at a fixed level of competition. The existence of tradeoffs between adult survival and reproduction in some organisms (Nur 1984) suggests that α may be negative. In any case, large positive values of α seem unlikely. Thus it appears that (39) will often be positive indicating superadditivity, and competitive exclusion will be promoted by environmental fluctuations.

A model with poor alternative resources.

In foraging theory it is recognized that species may change their selection of resources as the abundances of the resources change. However, classical theories of resource consumption, which receive their most detailed expression in MacArthur's (1970) consumer-resource model, do not allow for this possibility. Consider a situation in which there are good resources that the organisms need to sustain a positive growth rate and poor resources that are able to prevent precipitous decline of the population but are not able provide positive growth. For example, Scott (1980), and Scott and Murdoch (1983) have found that *Notonecta* populations show markedly different growth responses to different prey species. Moreover, the relative availabilities of these species vary over time. In classical resource competition theories, limiting resources allow population increase when these resources are sufficiently abundant. Population increase causes decline in availability of

limiting resources by increased consumption, which eventually halts population growth. This scenario does not apply to poor resources that merely moderate the rate of decline of a species, because population increase cannot occur in response to such resources. Thus, we will regard availability of the poor alternative resources as insensitive to consumer species density.

Let s (< 1) be the finite rate of increase when a species is concentrating on poor resources. These resources set a minimum growth rate for a population and therefore the finite rate of increase of the population might be represented as

$$G_1(\mathcal{E}_1, C_1) = \max\{s, G_1^!(\mathcal{E}_1, C_1)\}, \quad (40)$$

where $G_1^!(\mathcal{E}_1, C_1)$ is the finite rate of increase applicable in the absence of these poor alternative resources. This equation assumes that the growth rate on the good resources is environmentally sensitive, reflecting possibly environmental dependence in ability to use the good resources. It assumes also a complete switch from good to poor resources at the point where poor resources actually become more profitable. Such a complete switch is unlikely unless the species change habitat or foraging mode to use the poor resources. However, as we shall see it represents the worst case situation for nonadditive growth rates, and so our analysis of this model is conservative.

If $g_1^!(\mathcal{E}_1, C_1)$ is additive, it follows that γ is zero everywhere except on the set M of \mathcal{E}_1 and C_1 values for which $G_1^!(\mathcal{E}_1, C_1) = s$. On M , γ does not exist. It follows that γ cannot characterize the joint dependence of $g_1(\mathcal{E}_1, C_1)$ on \mathcal{E}_1 and C_1 when (\mathcal{E}_1, C_1) can cross from one side to the other of the set M . However, this problem can be got around using the following finite difference definition of subadditivity:

$$g(\mathcal{E}', C') - g(\mathcal{E}, C) \leq [g(\mathcal{E}', C) - g(\mathcal{E}, C)] + [g(\mathcal{E}, C') - g(\mathcal{E}, C)] \quad (41)$$

for $\mathcal{E}' > \mathcal{E}$ and $C' > C$. The growth rate $g_1(\mathcal{E}_1, C_1)$ satisfies (41), and the inequality is strict whenever (\mathcal{E}', C') and (\mathcal{E}, C) are on opposite sides of the curve M in (\mathcal{E}_1, C_1) -space. Thus, our model of poor alternative resources is subadditive in this finite-difference sense. It is easy to see using the finite-difference methods of Chesson (1986) that coexistence will be promoted in a fluctuating environment provided the (\mathcal{E}_1, C_1) values of the invader fluctuate on either side of M .

Other versions of this model in which there is a smooth change over from one resource to another, will have γ existing everywhere. Generally, γ will be negative in the region where both resources are being utilized, and therefore the model will show subadditivity in this range. Coexistence will thus be promoted by environmental fluctuations.

Fluctuating resource uptake rates.

Abrams (1984) put forward a model in which the resource uptake rates of a species are

the environmentally-dependent parameters. He showed that under a variety of conditions these fluctuating uptake rates promoted coexistence. In all cases where coexistence occurred, however, he assumed either overlapping generations or nonlinear conversion of resource into consumer biomass. Here we seek the effects of the fluctuating uptake rates alone without these other complications. Thus we consider the following formula for the finite rate of increase of the population:

$$G_i(\mathcal{E}_i, C) = f(\mathcal{E}_i R(C)) - m_i \quad (42)$$

Here $R(C)$ is the amount of resource present in the environment as a function of the level of competition C for the resource. The environmentally-dependent parameter \mathcal{E}_i is a measure of relative availability of the resource to consumer species i : it alters the effective abundance of the resource to consumer species i . The functional response f gives the actual per-capita resource consumption as a function of resource availability, $\mathcal{E}_i R(C)$. Finally, m_i represents a minimum amount of resource that must be consumed before any individuals are produced in the next time period. This minimum amount of resource would be 0 if all resource consumption resulted directly in the production of new individuals. For example, this occurs in parasitoids in which the resource is a host population that provides food for developing larvae alone. Note that the model assumes nonoverlapping generations.

In the case where $m_i = 0$, routine calculations show that

$$\gamma = R'(C)\phi'(\mathcal{E}_i R(C)) + \mathcal{E}_i R(C)R'(C)\phi''(\mathcal{E}_i R(C)), \quad (43)$$

where $\phi = \ln f$ and the primes indicate derivatives. Since $R'(C)$ is necessarily negative, it follows that the sign of γ is opposite to the sign of $\phi' + x\phi''$, where $x = \mathcal{E}_i R$. By solving the differential equation $\phi' + x\phi'' = 0$, one obtains the following formula for a functional response that will yield additive growth rates:

$$f(x) = f(1)x^{f'(1)/f(1)}. \quad (44)$$

It is not difficult to see that in the subadditive case, $f(x)$ will be greater than the RHS of (44) for all x except $x = 1$; and in the superadditive case, $f(x)$ will be less than the RHS of (44) everywhere except $x = 1$. Functional responses generally approach a constant value as x increases, which means that they generally do not satisfy the power law relationship implied by (44). Indeed, at least for large x , they will be less than (44). Functional responses may satisfy a power law at low x but since they saturate they may often follow a law that can be approximated by the formula

$$f(x) = \frac{ax^b}{c + ax^b} \quad (45)$$

It is a simple calculus exercise to show that this functional response always gives superadditive growth rates. Moreover, the fact that functional responses generally saturate will invariably add an element of superadditivity to the model even if the formula (45) is not

a good approximation.

When the value of m_1 is positive, simple calculus shows that the sign of γ is opposite the sign of

$$\phi' + x\phi'' - x(\phi')^2 \frac{m_1}{f - m_1} . \quad (46)$$

Hence the maintenance requirement itself is a factor that promotes superadditivity. Indeed, it will lead to superadditivity in instances where the functional response by itself would not, for instance, in cases where the functional response is linear with no upper limit on the consumption rate. In general, this model implies that fluctuating resource consumption rates should favor competitive exclusion, unless there are other factors in the model that oppose this tendency.

Abrams' (1984) model differs from this one in that in all cases he assumed a linear functional response. The presence of a maintenance requirement would imply superadditivity from the results above; however, Abrams is able to get subadditivity by adding overlapping generations or accelerating conversion of resource into consumer biomass. Thus he finds that fluctuating resource-uptake rates promote coexistence. Finally, it should be kept in mind that here consumption rates are assumed to vary as a consequence of fluctuations in the availability of fixed abundances of resource to consumer species. This means that environmental factors not tied to resource abundance interfere with the ability of the species to consume the resource. Different biological assumptions about the nature of variability could lead to different results.

CONCLUSION

An interaction between the environment and competition is necessary before environmental fluctuations have any overall effect on community structure. In many ways this is hardly surprising: if the environment does not interact with competitive processes then their long-term effect should be moot because the fluctuations should just average out to the equivalence of a constant value. The additive case (no interaction) confirms this intuitive expectation. With negative or subadditive interactions, competitive exclusion is opposed, while with positive or superadditive interactions competitive exclusion is promoted. Within this framework the results are clear and unambiguous. Ambiguity often arises in stochastic models because the space of probability distributions is infinite dimensional, yet discussions of the effects of random variables often focus on just two dimensions, the mean and variance alone. The effects of the neglected parameters are responsible for the ambiguous results. In the investigations here, the results are clear because in the symmetric case the symmetry itself prevented the infinite dimensionality from being expressed. Symmetry in essence led to cancellation of the effects of parameters other than a measure of variation. In the asymmetric analysis, the standard parameterization concentrated all the important effects in the means

and covariances. Thus ambiguities due to the action of other parameters did not arise.

While these results are simple and interpretable mathematically, it is important that they are also interpretable biologically in terms of buffers, amplifiers and neutral traits. The subadditive case can be interpreted as the presence of biological properties that buffer unfavorable combinations of events. When the environment is poor for a species, the additional effect of competition is slight. Thus the form of the growth rate provides a buffer against simultaneously having a poor environment and strong competition. Biologically, such buffers can result from overlapping generations or the availability of alternative resources.

The superadditive case involves amplification of unfavorable combinations of events: when environmental conditions are poor the additional effect of competition is strong. Amplification can occur when a feature that would buffer when it is itself insensitive to the environment, is made the environmentally-dependent parameter. For example, competition among juveniles or seedlings will have more effect on the growth rate at times of poor adult or seed survival, and so environmental sensitivity of adult and seed survival is a feature that leads to amplification of the combined effects of a poor environment and strong competition. We found also that the shape of the functional response can lead to superadditivity when resource uptake rates fluctuate.

Additive growth rates result from neutral traits. But we found that neutral traits can easily be overcome by other traits that act as buffers or amplifiers. Thus, strictly additive growth rates must be regarded as idealizations that may be approximated in nature but are probably never actually achieved. Neutrality seems to arise generally as a result of sequential action of environmental and competitive effects in organisms that have strictly nonoverlapping generations. Simple modeling approaches often treat events as taking place sequentially, not interacting simultaneously, and these approaches often lead to additive growth rates. While such approaches have been adequate for consideration of equilibrium situations, our results show that the addition of just a little more reality can markedly change the conclusions in nonequilibrium settings.

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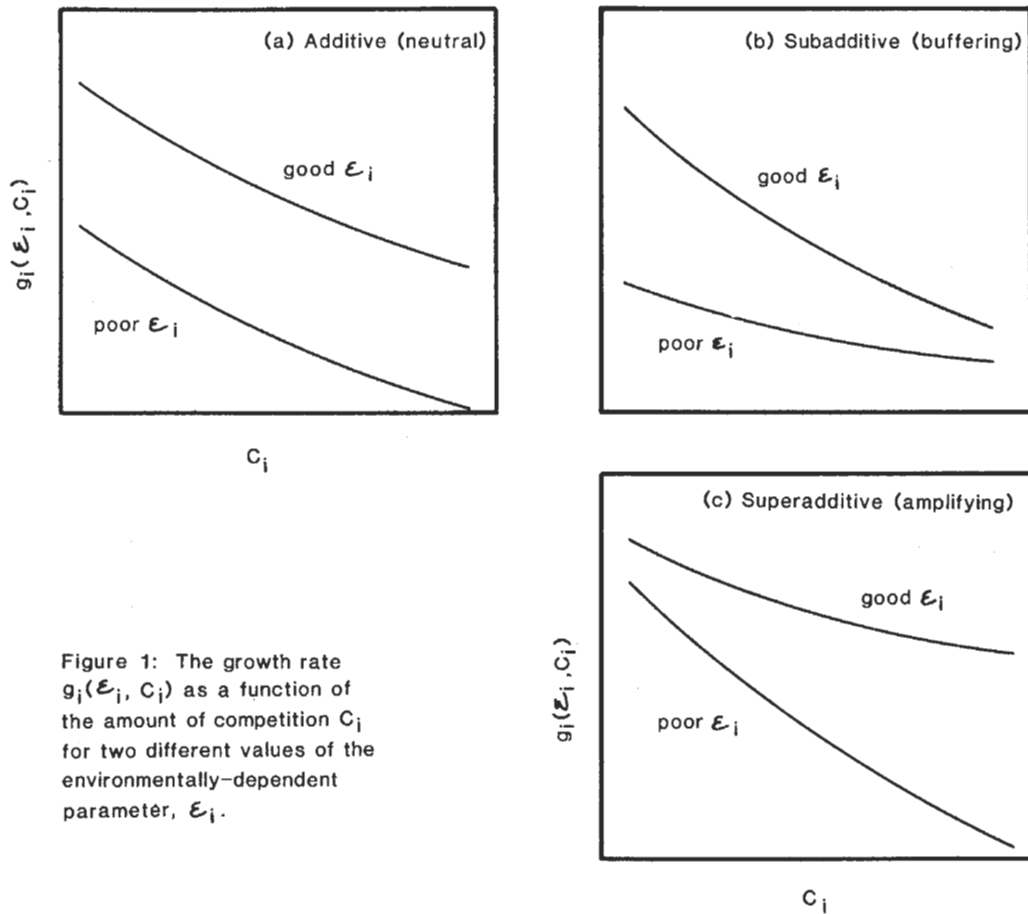


Figure 1: The growth rate $g_i(E_i, C_i)$ as a function of the amount of competition C_i for two different values of the environmentally-dependent parameter, E_i .