A GENERAL MODEL OF THE ROLE OF ENVIRONMENTAL VARIABILITY IN COMMUNITIES OF COMPETING SPECIES

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ABSTRACT. This paper analyzes a general model of population dynamics for two species competing in a fluctuating environment. The model is a continuous state-space, discrete-time Markov process and is studied using the standard invasibility technique in conjunction with a small-effects approximation. This provides a general method of analyzing stochastic competition models and gives simple formulae for mean low-density growth rates in terms of mean environmental effects, mean competitive effects, and an interaction between environmental and competitive factors. Hence, the manner and strength with which environmental fluctuations affect coexistence is exhibited in a simple interpretable form.

1. INTRODUCTION. A central concern of community ecology is understanding the mechanisms determining community structure (the number and kinds of species that may live together in a particular locality). A

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classic essay of G. E. Hutchinson (1959) focused attention on the phenomenon of competition as a primary determinant of community structure. It is generally expected on the basis of mathematical models (see Roughgarden 1979, and May 1981) that a group of species will not be able to coexist if competition between species (interspecific competition), for resources that are in short supply, is too strong. It is known, for example, that interspecific competition will prevent a stable equilibrium coexistence when the per-capita growth rates of different species in a community are functions of the same factor (Armstrong and McGehee 1980). This single factor could, for example, be a common food source for which the organisms compete, or in plants it could be light, moisture or a nutrient.

The extent to which interspecific competition may be a factor in community structure has been the subject of intense debate recently (e.g. Den Boer 1986, Abrams 1986, Giller 1986, Roughgarden 1986). An important consideration is the fact that most populations in nature are subject to varying environmental conditions which may upset the predictions of equilibrium models based on competition alone.

Following the early work of May and MacArthur (1972), there have been a number of attempts to develop a theory of community structure accounting for the effects of environmental variability (Woodin and Yorke 1975, Armstrong and McGehee 1976, Levins 1979, Turelli 1981, Chesson and Warner 1981, Chesson 1983, 1984, Ellner 1984, Shmida and Ellner 1985, Abrams 1985). While this work has produced some striking general conclusions, there has been some confusion
about the circumstances under which environmental variability should promote coexistence or should do the opposite: promote competitive exclusion.

Moreover, most theoretical findings have been qualitative. The quantitative detail useful for checking the predictions of models in nature has been lacking.

It is the purpose of this article to continue the development of a general model put forward in Chesson (1987) that appears to provide a simple way of understanding the effects of environmental variability on community structure. Moreover, this model yields useful quantitative predictions. In Chesson (1987) it was necessary to assume that all of the species in the system would be biologically very similar. In this paper this assumption is removed, allowing consideration of the full range of possible ways in which species may differ from one another.

2. THE MODEL. The basic assumptions of the model are that the growth rate of a population can be expressed as a function of environmental and competitive factors. It is assumed that the major environmental effects can be summarized by a single population parameter such as a density-independent birth rate, survival rate or germination rate. This environmentally-dependent parameter will be denoted by $E_i(t)$, indicating that it is specific to species $i$ and varies with time $t$. It will always be defined so that larger values reflect more favorable conditions. Thus, $E$ will never be a mortality rate but could be a survival rate.

The effects of competition are also assumed representable by a single number $C_i(t)$ summarizing the
combined effects of intraspecific and interspecific competition on species $i$. For instance, competition might be measured by a comparison of the number of individuals competing for a limited amount of a critical resource and the supply of that resource. The precise form of $C_i(t)$ will depend on the circumstances, but in general it will be assumed to be a function of the population densities of the species in the system, $X_1(t), ..., X_n(t)$, and their environmentally-dependent parameters. Thus

$$C_i = c_i(E_1, X_1, E_2, X_2, ..., E_n, X_n),$$

where $c_i$ is some function of $2n$ variables. Time, $t$, is suppressed for notational simplicity.

Environmentally-dependent parameters can be expected to affect the amount of competition occurring through their effects on the abundances of competing forms. For instance, if the environmentally-dependent parameter is a germination rate, it will affect the abundance of seedlings competing as they grow, and thus will strongly influence the intensity of competition. The function $c_i$ is assumed to be monotonic in its arguments, and in particular it is assumed to increase as a function of population density. In general, if $X_j = 0$, i.e., species $j$ is absent from the system, $c_i$ is assumed to be constant in the argument $E_j$.

Population dynamics of the species in such a community will be represented in discrete-time form as

$$X_i(t+1) = G_i(E_i(t), C_i(t))X_i(t),$$

where the function $G_i$ combines the environmentally-dependent parameter and the competitive parameter to
obtain the finite rate of increase of the population from time \( t \) to time \( t+1 \). Generally, \( G_i \) will be an increasing function of \( E \), and a decreasing function of \( C \).

Analysis of models of populations in stochastic environments is facilitated by expressing population change on a log scale where we obtain

\[
(3) \quad \ln X_i(t+1) - \ln X_i(t) = g_i(E_i, C_i),
\]

with \( g_i = \ln Q_i \). Note that \( g_i \) is analogous to \( r \) in demography, and we shall refer to it simply as the growth rate. This growth rate is important because by summing it over any period of time we obtain the change in log population size for that period. Thus the average of the growth rate over any given period indicates whether the population increases or decreases over that period.

The important properties of the model are determined by the way in which \( E \) and \( C \) interact in their specification of the growth rate. In the case of no interaction (the additive case), the growth rate can be expressed in the form

\[
(4) \quad g_i(E_i, C_i) = A_i(E_i) + B_i(C_i),
\]

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

\[
(5) \quad \gamma_i = \frac{\partial^2 g_i}{\partial E_i \partial C_i}
\]

is equal to zero. When this quantity is negative, the growth rate is called subadditive; when positive the growth rate is called superadditive. The intuitive meanings of these different possibilities are
discussed in Chesson (1987). In brief, when $r$ is negative (the subadditive case), poorer environmental conditions make the growth rate less sensitive to competition: $g_1$ does not decline so quickly as a function of $C$. Essentially, the growth rate is buffered against simultaneous poor conditions such as a poor environment and high competition. As shown in Chesson (1987), simple yet common features of biology can produce these buffered growth rates.

When (5) is negative, the growth rate is called superadditive. In this case the growth rate is more sensitive to competition in a poorer environment: a poor environment in effect amplifies competition.

To expose the effects of the interaction between environment and competition, the parameters of the model can be transformed so that the model takes the following standard form:

$$g_1(E_1, C_1) = E_1 - C_1 + \Gamma_1(E_1, C_1)$$

(Chesson 1987). To see how to obtain this form, we designate the original parameters and growth rate function using the subscript $0$, and we then choose some particular value $E_1^*$ of the original environmentally-dependent parameter $E_{10}$, and a corresponding value $C_1^*$ of $C_{10}$ such that $g_{10}(E_1^*, C_1^*) = 0$. These define conditions that would constitute equilibrium in a constant environment. The new parameters and growth rate function are expressed in terms of the originals as

$$E_1 = g_{10}(E_{10}, C_{10}^*), \quad C_1 = -g_{10}(E_1^*, C_{10})$$

and
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\[ g_1(E_1, C_1) = g_{10}(E_{10}, C_{10}). \]

This standard form minimizes the differences between different models. In particular, it ensures that environmental and competitive factors have similar meanings in terms of their effects on the growth rate in all models. Indeed, near the values \((E_1, C_1) = (0, 0)\) (corresponding to \((E_1', C_1')\) in the old variables), the environmentally-dependent parameter and competitive parameter respectively represent the translation of environment and competition into the growth rate of the population. This standard form allows a unified treatment of the general class of models given by equation (2). Unless otherwise specified, we assume below that the model has been transformed to this standard form.

3. Analysis of the Model. To analyze the model, we restrict attention to the two-species situation and make the assumption that the environment process \(\{(E_1(t), E_2(t)), t = 0, 1, \ldots\}\) is an i.i.d. process, i.e., different times are independent and the bivariate distribution of \((E_1(t), E_2(t))\) is independent of \(t\). It follows that the community process \(\{(X_1(t), X_2(t)), t = 0, 1, \ldots\}\) is a homogeneous Markov process and can be analyzed using the standard invasibility analysis reviewed in Chesson (1987). This involves seeing if a species at low density (an "invader") can increase in the presence of the other species (the "resident"). The resident is minimally affected by the invader while the invader remains at low density. The Markov process describing the dynamics of the resident, with the invader density set
equal to 0, can usually be expected to converge on a stationary distribution (Ellner 1984). We let \( C_i^j \) be a random variable representing the competitive parameter of species \( i \) when \( j \) is at its stationary distribution and species \( i \) is at zero density. The law of large numbers implies that this invading species, \( i \), will have a trend to increase from low density if it has a positive value of

\[
\Lambda_i \overset{\text{def}}{=} \mathrm{Eg}_1(E_i, C_i^j).
\]

This quantity is the mean low-density growth rate, or "boundary" growth rate of species \( i \). A positive boundary growth rate is usually interpreted as implying that the species persists in the system. Thus, if the boundary growth rates of both species are positive, the species are interpreted as coexisting. Indeed, for a broad class of models there is strong mathematical justification for this assumption (Chesson and Ellner 1988). Moreover, there is good reason to expect the case \( \Lambda_i > 0, \Lambda_j < 0 \), to mean that species \( i \) persists in the system while species \( j \) converges to extinction.

The final case, defined by \( \Delta_1, \Delta_2 < 0 \), can be expected to imply that one of the species will become extinct while the other persists, with no certain predictability of which species does which. These assertions have only been proved for special classes of models within this general framework (Chesson and Ellner 1988), but are generally assumed to apply broadly. For the purposes of discussion, we shall assume that we are in situations where these assertions are valid. However, none of the mathematics
below depends on this assumption.

When a species is present alone, the assumptions of the model imply that there will generally be a unique equilibrium density, $X^*$, for any given constant value of the environmentally-dependent parameter. This equilibrium density is the solution of the equation $C_1 = 0$.

For the analysis, we introduce some additional assumptions.

(a) The fluctuations in $E_i(t)$ are concentrated in a finite range about 0, with length proportional to a small parameter $\sigma$.

(b) When the system is simplified to contain just a single species, a unique stationary distribution exists, and the corresponding equilibria, $X_1^*$, for constant-environment cases, are asymptotically exponentially stable.

(c) The mean values ($EE_i$) of the environmentally-dependent parameters are of order $\sigma^2$ ($O(\sigma^2)$).

(d) The function $c_1$ satisfies $c_1(0, 0, 0, X_j^*) = O(\sigma^2)$.

(e) The random variable $c_1(0, 0, E_j, X_j)$ can be written as a function of $c_j(E_j, X_j, 0, 0)$.

(f) The regression of $E_i$ on $E_j$ is linear to order $\sigma^2$, i.e. $E[E_i|E_j] = EE_i + b_e(E_j - EE_j) + O(\sigma^2)$, where $b_e$ is a constant.

Assumption (a) is simply the small fluctuation assumption. Assumption (b) insists on regular behavior for the single-species systems. Assumptions (c) and (d) imply that constant factors affecting the growth rates of the species, as represented by the means of the environmentally-dependent parameters and the competitive differences between species, have
similar strengths to the environmental variance, which is proportional to \( \sigma^2 \). This means that these constant factors are of smaller magnitude than the fluctuations in the environmentally-dependent parameter, which are of order \( \sigma \), by assumption (a).

Assumption (e) implies that the intraspecific and interspecific competitive effects caused by a species are determined by a common underlying function of its environmentally-dependent parameter and population size. For example if \( E_j \) is a birth rate and competition occurs among offspring, then \( E_j X_j \) will be the number of offspring of species \( j \), which will determine both the intraspecific and interspecific competitive effects of species \( j \).

Assumption (f) simply expresses the natural expectation of approximately linear relationships when fluctuations are restricted to small ranges. It is consistent with the other assumptions of the model.

Standard differentiability assumptions are introduced in the appendix where it is shown that the stationary distribution of the single-species system gives fluctuations in the competitive factors \( C_i \) that are concentrated in a finite range of order \( \sigma \) about 0. For the single-species system it follows that \( g_i \) has the second order Taylor approximation

\[
g_i(E_i, C_i) = E_i - C_i + \gamma_i E_i C_i,
\]

where \( \gamma_i = \frac{\partial^2 g_i}{\partial E_i \partial C_i} \), evaluated at \((0, 0)\), and "\( = \)" means that the difference between the LHS and RHS is \( o(\sigma^2) \). The appendix now shows that equation (10) continues to apply when species \( i \) is an invader (at zero density) and species \( j \) is a resident at its stationary distribution. These results also imply
that $E[C_j^i|C_j^i]$ is linear to $O(\sigma^2)$. The corresponding linear regression coefficient will be denoted by $b_c$.

To perform the invasibility analysis, we note that the expected value of (10) must be zero for a resident at its stationary distribution, because the expected value of $\ln X_i(t)$ cannot change once the stationary distribution has been reached. Defining $x_{jj}$ as the covariance between $C_j^i$ and $C_j^j$ and making use of the fact that $EE_jC_j^j = EE_jC_j^j + x_{jj} = o(\sigma^2) + x_{jj}$, we obtain

\begin{equation}
EC_j^j = EE_j + \gamma_j x_{jj}.
\end{equation}

Taking expected values in (10) under the assumption that species $i$ is at zero density, and species $j$ is a resident, we obtain

\begin{equation}
\Delta_i = EE_i - EE_i + \gamma_i EE_i C_i^j
\end{equation}

Now

\begin{equation}
x_{ij} = E(E_i C_i^j|E_j) = Eb_e E_j C_j^j = b_e b_c x_{jj},
\end{equation}

and so

\begin{equation}
\Delta_i = EE_i - EE_i + \gamma_i b_e b_c x_{jj}.
\end{equation}

Note that in this equation, $EC_j^j$ will likely be dependent on environmental variability, (c.f. equation [11] for the case of intraspecific competition), and so equation (13) may have environmental variability occurring twice but in ways that are in opposition. To overcome this problem, we substitute in (13) the quantity $\Delta C = EC_j^j - EC_j^j$, representing the difference
between average interspecific and average intraspecific competition. While this quantity may still depend on environmental variability, its dependence is likely to be less than the absolute average values of the these competitive parameters. Making this substitution in (13), using equation (11), defining $\theta = \gamma_i / \gamma_j$, and $\Delta E = EE_i - EE_j$, we obtain

$$\Delta \lambda = \Delta E - AC - \gamma_j (1 - \theta b_e b_c) x_{jj}.$$  

Thus the boundary growth rate is expressed in components that can be regarded as relatively independent. The first term represents mean environmental effects, the second term represents the mean excess of interspecific competition over intraspecific competition, and the last term represents the effects of the interaction between environment and competition.

Although expression (14) seems fairly clean, it is not always the best representation of the different effects because $\Delta C$ can be nonzero when different species respond to exactly the same competitive factor but have different magnitudes of response. In particular, $\Delta C$ can be nonzero when different species have growth rates that differ only by a positive proportionality constant, meaning that when one species increases, the other must also. In such cases the proper value of the difference in competitive effects should be 0. To make this the standard by which competitive differences between species are compared, one can define

$$\Delta C = EC_j^J - q EC_j^J,$$

where $q$ is some constant. A suitable choice for $q$ will often be $b_c$, because it measures the magnitude of
response of species $i$ to competition compared with the response of species $j$ to the same factor. Having done this, it is appropriate to redefine the environmental differences $\Delta E$ as $EE_i - qEE_j$. Equation (14) becomes

$$
\Delta _i = \Delta E - \Delta C - g_j(q - \theta b_e b_c) x_{jj}.
$$

Note however, that equation (14) is a special case of equation (16).

This equation shows that the boundary growth rate is simply the sum of three parts: (a) the mean environmental advantage that species $i$ has over the other species, (b) the mean excess of interspecific competition over intraspecific competition, and (c) an effect due to the interaction between environmental variability and competition. The covariance $x_{jj}$ is a reflection of variation in the environmentally-dependent parameter of the competitor species, not a direct reflection of the variability in the environmentally-dependent parameter of the species in question. As shown below, in the case of an i.i.d environment, this covariance is simply proportional to the variance in the competitor's environmentally-dependent parameter.

The term in parentheses contains a mixture of terms dealing with the asymmetry of the two species and the correlations between their environmentally-dependent parameters. To gain an appreciation of this term, it is helpful to consider a special case in which the species are similar enough that they have the same $g_i$, have $q = 1$ (reflecting the same magnitude of response to competitive conditions) and have equal variances for their environmentally-dependent parameters. In this case the term in parentheses reduces
to $1 - r$, where $r$ is the correlation between the environmentally-dependent parameters of the two species. Thus the term in parentheses will be positive unless the species respond in exactly the same way to the environment, in which case it will be 0.

In many cases the covariance $x_{ij}$ will be positive, for example when the environmental factor does not directly affect competitive processes (Chesson 1987). For simplicity, we will restrict discussion to this case. Assuming that asymmetry is not too strong (or that the correlation between the environmentally-dependent parameters is low), the term in parentheses will be positive too. This means that a negative interaction between environmental and competitive effects will lead to a positive addition to the boundary growth rate in the presence of environmental variability. This positive addition can make up for environmental and competitive disadvantages that a species may experience, and therefore can permit it to coexist with a superior competitor. In this setting environmental variability will promote species diversity.

In the opposite case, where the interaction term is positive, environmental variability will lead to a reduction in boundary growth rates and coexistence will be demoted. Indeed, species that could coexist in the absence of environmental variability may now both have negative boundary growth rates. This would mean that when either one of the species fluctuates to low density it will have a negative average growth rate, indicating an expected decline toward extinction. If the amount of environmental variability is of intermediate magnitude and there are asymmetries in
the competitive abilities of the two species, one species could have a negative boundary growth rate while that of the other remains positive. In this situation, environmental variability contributes to the competitive elimination of the inferior species, while the other species persists.

Scenarios other than those painted above are possible from this equation. The covariance could be negative in some settings, which would reverse the above conclusions. Alternatively, it might be negative for one species but positive for the other. Then environmental variability would have opposite effects on the two species, unless the interactions were also of opposite sign.

While each of the three terms constituting equation (16) can be regarded as conceptually distinct from the others, it will not always be possible to vary them independently. However, while we remain within a general framework where the $g_i$ and $C_i$ are not assumed to take particular forms, the different quantities in equation (16) can indeed be considered independent. In this case, the parameter space is infinite dimensional and there are no constraining relationships among the finite set of parameters appearing in equation (16). In specific applications, however, the model will often be defined in terms a finite number of underlying parameters. Indeed, sometimes the number of such parameters will be small. Whenever, the number of parameters defining the model is less than the number appearing in expression (16), there will necessarily be constraints among the latter. Indeed, it may not be possible to vary the three terms in this equation independently. See section 5
below.

4. THE COVARIANCE. To calculate the covariance, \( x_{jj} \), we simply express the resident's parameter in terms of its first-order Taylor expansion in \( E_j \) and \( X_j \) about \((0, X_j^*)\):

\[
  c_j = c_{j1}E_j + c_{j2}(X_j - X_j^*) + O(\sigma^2).
\]

It follows that

\[
  X_{jj} = c_{j1}V_{E_j}.
\]

This formula depends critically on the assumption that the environment process has no autocorrelation. This means that \( X_j(t) \) and \( E_j(t) \) are uncorrelated, and so the second term in (17) does not affect (18). In the autocorrelated case the formula is

\[
  X_{jj} = c_{j1}V_{E_j} + c_{j2}C(E_j, X_j),
\]

where the covariance \( C(E_j, X_j) \) is calculated using the joint stationary distribution of \( E_j \) and \( X_j \). In this autocorrelated case, expression (16) is not always correct and requires a slight modification. Expression (16) remains true, however, in a number of useful cases of autocorrelation, in particular, if the environment processes of the two species are independent of each other.

5. BACK TRANSFORMATION. Often it will be desired to know how the results of the model appear in terms of the original parameters, rather than just the standard parameters. In particular, this will facilitate the investigation of the constraints among the quantities in equation (16). In this section we derive formulae
that permit the results above to be expressed in terms of the original parameters.

To distinguish the standard parameters and the original parameters, the original parameters and all quantities associated with them will be given the subscript 0 for "original." We define

\[
\alpha_1^{(n)} = \left. \frac{\partial^n}{\partial E_{i0}^n} g_{i0}(E_{i0}, C_{i0}^*) \right|_{E_{i0} = E_{i0}^*}.
\]

A quantity \( \beta_i^{(n)} \) is defined similarly as the \( n \)th derivative of \(-g_{i0}\) in its second argument. In case of the first derivative, the superscript \( (n) \) will sometimes be dropped.

We can now obtain an approximation for the standard parameters in terms of the original parameters by using Taylor series expansion of \( g_{i0} \). This yields

\[
E_i \approx a_1^{(1)}(E_{i0} - E_{i0}^*) + \frac{1}{2} a_1^{(2)}(E_{i0} - E_{i0}^*)^2,
\]

with a corresponding expression for \( C_i \). It is easily seen that

\[
\tau_i = \tau_{i0}/a_i \beta_i,
\]

\[
\chi_jj = a_j^{(1)} \chi_{jj0}
\]

\[
b_e = (a_i/a_j) b_{eo}, \quad b_c = (\beta_i/\beta_j) b_{co}
\]

and

\[
\theta = \theta_0 (a_j^{(1)} \beta_j/a_i^{(1)} \beta_i).
\]

Although it will generally be possible to express \( q \) in terms of the original parameters, in general the quantity "\( q_0 \)" is not meaningful and is best considered undefined.
With these definitions, the components of equation (16) can be expressed in terms of the original parameters. In doing this we use the notation "\( \hat{\cdot} \)" to indicate the deviation from a \( * \)-value, e.g. \( \hat{E} = E - E^* \). We obtain

\[
\Delta E = a_i^{(1)} \hat{E}_{i0} - q a_j^{(1)} \hat{E}_{j0} \\
+ \kappa (a_i^{(2)} \hat{V}_{i0} - q a_j^{(2)} \hat{V}_{j0}),
\]

and

\[
\Delta C = \beta_i^{(1)} \hat{C}_{i0} - q \beta_j^{(1)} \hat{C}_{j0} \\
+ \kappa (\beta_i^{(2)} \hat{V}_{i0} - q \beta_j^{(2)} \hat{V}_{j0}).
\]

Finally

\[
\tau_j (q - \theta b e o) x_{jj} = \tau_{j0} (q - 0 e o) x_{j0}. 
\]

The first thing to note is that the interaction term, which is the main focus of this work, takes the same form in terms of the original parameters as it does in terms of the standard parameters. Thus choice of parameterization does not lead to ambiguity in the interpretation of this term. The other quantities, \( \Delta E \) and \( \Delta C \), take forms which will be different depending on the particular parameterization. For example, the variances of the parameters can appear here in terms of the original parameters, but are not present when standard parameters are used. Thus these terms can be sensitive to the variances of the original parameters to varying degrees and in varying ways depending on the particular situation. It is therefore important to consider what different parameterizations will mean.
before one attempts to interpret the results.

**Example: The Lottery Model.** For purposes of illustration we consider the application of these results to an especially well-studied model, the lottery model (Chesson and Warner 1981, Chesson 1982, Hatfield and Chesson 1988). The lottery model is a model of competition for space. We shall consider it in the form in which the environmentally-dependent parameter is the birth rate (which we take to include early juvenile mortality). The model can then be written as

\[ G_i(E_1, C_1) = 1 - \delta_i + E_1/C_1 \]

where \( \delta_i \) is the adult death, and is assumed constant here. Competition occurs only among juveniles as they seek sites for settlement among the places given up by adult death in the previous time period. Thus, the formula for \( C_i \) is

\[ C_i = (E_1 X_1 + C_2 X_2)/(\delta_1 X_1 + \delta_2 X_2), \]

which is equal to the amount of space opened up by adult death divided by the number of juveniles competing for this available space.

While this form of the model reveals its assumptions most clearly, simpler and more interpretable results are obtained if the birth rate is expressed on the natural log scale. In particular, this scale more clearly elucidates the constraints among the parameters that analysis of a specific model is intended to reveal. All that is changed by this transformation is the way the results are expressed, not the results themselves. A further transformation simplifies the analysis with no effect on the form of the results of
the model: the natural log of (24) multiplied by $\delta_1$ is used as the competitive factor. With these changes the model takes the form

\[(31)\quad G_{i0} = 1 - \delta_1 + \delta_1 e^{E_{i0}} - C_{i0}.\]

Simple calculations show that

\[(32)\quad a_1^{(1)} = \beta_1^{(1)} = \delta_1\]

and

\[(33)\quad a_1^{(2)} = -\beta_1^{(2)} = -\gamma_1 = \delta_1(1 - \delta_1).\]

Moreover,

\[(34)\quad C_{j0}^{c} = E_{j0}^{c} \quad \text{and} \quad C_{i0}^{c} = E_{j0}^{c} + \ln(\delta_1/\delta_j),\]

which implies the identical relationship among the means, equality of the variances and also that $\lambda_{j0} = \lambda_{j0}^{c}$ and $b_{co} = 1$.

The final quantity that we need is $q$, which we take here to be $b_c$. To get it we note that the standardized competition parameter takes the form

\[(35)\quad C_j^{c} = -\ln(1 - \delta_j + \delta_j e^{E_j} - E_{j0})\]

and

\[(36)\quad C_i^{c} = -\ln(1 - \delta_1 + \delta_1 e^{E_i} - E_{j0} - \ln \delta_1/\delta_j).\]

Using the fact that

\[(37)\quad E_i - E_j = \ln \delta_1/\delta_j\]

we deduce that $q = \delta_1/\delta_j$. Substituting in (23-24) and rearranging, we find that
(38) \[ \Delta E/\delta_1 = \hat{E}_{10} - \hat{E}_{j0} + \frac{\delta_1}{2} \{(1-\delta_1)VE_{10} - (1-\delta_j)VE_{j0}\} \]

(39) \[ \Delta C/\delta_1 = \frac{\delta_1}{2} \{(1-\delta_1) - (1-\delta_j)\}VE_{j0} \]

(40) \[ \gamma_j \{q - \delta_1 b_{eo} c_{co}\} x_{j0} = \delta_1 \{(1-\delta_1)b_{eo} - (1-\delta_j)\}VE_{j0} \]

This shows that the three components of the boundary growth rate involve common factors, and so varying any one of these common factors can lead to changes in each of the components of the boundary growth rate. For instance, increasing \( VE_{j0} \) by itself will increase \( \Delta E \), will increase or decrease \( \Delta C \) depending on the sign of \( (1-\delta_j) - (1-\delta_1) \), and increase or decrease the interaction term (37) depending on the sign of \( (1-\delta_1)b_{eo} - (1-\delta_j) \).

A significant question is whether the three terms (38-40) can vary independently as the environment is manipulated. The answer to this is clearly yes if the means, variances and covariances of the environmentally-dependent parameters can be varied arbitrarily, but the answer is generally no if only some of these quantities can be varied. For instance, if the correlation between the environmentally-dependent parameters of the two-species is held fixed, then the possible values of the interaction term are constrained by the value of the competition term. In particular, if the correlation is 0, and \( \delta_1 = \delta_j \), then the value of \( \Delta C \) determines the value of the interaction term. The fact that the competition term is not 0 implies that a variable environment introduces differences between interspecific and intraspecific competition that are absent when the environment is constant.

When expressions (38-40) are combined, one finds
that even though environmental variability possibly pushes different components of the boundary growth
rate in different directions, overall the effect is very simple. We obtain

$$\frac{\Lambda}{\delta_i} = E\hat{E}_{10} - E\hat{E}_{j0} + \frac{1}{2}(1-\delta_i)V(E_{10} - E_{j0}).$$

Thus we see that any disadvantage that species $i$ may have to species $j$, in terms of the mean of its
environmentally-dependent parameter, can be overcome by variance in the difference between the environ-
mentally-dependent parameters. It is interesting to note that (41) agrees closely with exact numerical
results for the lottery model given in Chesson and Warner (1981) for a broad range of parameter values.

6. DISCUSSION. The most important feature of the results obtained here is the ability to obtain quanti-
titative statements on the conditions for coexistence without making overly restrictive assumptions on the
relationships of the organisms to each other. The fact that the different species can have different
competitive factors permits the simultaneous consider-
aton several mechanisms of coexistence. The main
focus of this work has been on how the interaction
between environment and competition can alter average
growth rates in the presence of environmental vari-
bility. This present model allows other factors to be
operating through the difference between the mean
interspecific and intraspecific effects. For example,
the mean interspecific effects might tend to be
smaller than the mean intraspecific effects, and this
would be favorable to coexistence with or without
environmental variability. This case could arise
through differences in resource requirements of the different species ("resource partitioning") or could be a reflection of frequency-dependent predation (Roughgarden and Feldman 1974), even though the biological interpretation of these conditions is quite different.

The standard parameterization is responsible for the unity of the results even though the underlying models can differ arbitrarily and the environmentally-dependent parameters may represent different things in different circumstances. This standard parameterization permits the boundary growth rate (the mean growth rate at low density) to be expressed as a sum of three meaningful components, which clearly show how the different factors that affect a species appear in this boundary growth rate. It is important to note, however, that within the constraints imposed by the details of a specific system, it may not be possible to vary all three components independently. Moreover, depending on the scale on which environmental variability is measured, all of them may change with changes in the amount of environmental variability. Only the critical term involving the interaction between environment competition is independent of the scale of measurement. The form of the results obtained here suggests a standard scale of measurement removing the ambiguity inherent in models involving environmental variability when there is no rationale for measuring variability on any particular scale.

7. APPENDIX: SINGLE-SPECIES RESULTS. We need to show that the single-species iterations confine C to a finite range of order σ. As it causes no confusion,
we drop the subscript $i$ throughout. We assume that $g(E, C)$ and $C(E, X)$ ($= c(E, X, 0, 0)$) are jointly first differentiable in their arguments with first derivatives bounded in finite intervals. We define $Z(t) = \ln X(t)$ and $f(E, Z) = g(E, C(E, e^Z))$. For simplicity of notation we assume that $E^* = C^* = 0$, and $|E| < \sigma$.

Asymptotic exponential stability of the single-species case in a constant environment means that there is a symmetric neighborhood $(z_1, z_2)$ of $z^*$, and a positive number $\rho < 1$ such that

(a1) $|z - z^* + f(0, z)| < \rho |z - z^*|.$

Setting $z' = z + f(E, z)$ and substituting in (a1) we get

(a2) $|z' - z^*| < \rho |z - z^*| + |f(E, z) - f(0, z)|$

(a3) $< \rho |z - z^*| + \delta,$

where $\delta$ is the supremum over $|E| < \sigma$ and $z \in (z_1, z_2)$.

The differentiability assumptions mean that $\delta = O(\sigma)$ and so for $\sigma$ sufficiently small we have $z' \in (z_1, z_2)$. This means that

(a4) $Z(t) \in (z_1, z_2)$

whenever $Z(0) \in (z_1, z_2)$. Moreover,

(a5) $\limsup |Z(t) - z^*| < \frac{\delta}{1 - \rho}.$

As a consequence of (a5) and the bounded differentiability of $C$, it follows that

(a6) $\limsup |C(E(t), X(t))| \leq K\sigma$

for some constant $K$. Assumption (d) implies the identical result for the case where $C(E(t), X(t))$ is interspecific competition experienced by an invader with $E(t)$ and $X(t)$ referring to the resident.

The formulae for back transformation require that
$E_{j_{10}}^T$, $E_{j_{10}}^D$, and $E_{j_{10}}^D$ are each $O(\sigma^2)$. This can be
deduced easily by using the corresponding properties
of the standardized parameters. That $E_{j_{10}}^D = O(\sigma^2)$
follows from equation (11); and assumption (d) now
implies the same for $E_{j_{10}}^D$.

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