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 stoch-
astic 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 organ-
isms 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 sub-
ject of intense debate recently (e.g. Den Boer 1986,
Abrams 1986, Giller 1986, Roughgarden 1986). An
important consideration is the fact that most pop-
ulations in nature are subject to varying environ-
mental 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 dev-
elop 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 quali-
tative. 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 under-
standing 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 con-
sideration 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 denisty-independent birth rate,
survival rate or germination rate. This environ-
mentally-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 environ-
mentally-dependent parameters. Thus

(1) $C_i = c_i(E_1, X_1, E_2, X_2, \ldots, E_n, X_n)$,

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

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

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

with $g_i = \ln G_i$. 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) $g_i(E_i, C_i) = A_i(E_i) + B_i(C_i),$

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

(5) $\gamma_i \overset{def}{=} \dfrac{\partial^2 g_i}{\partial E_i \partial C_i}$

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 γ is negative (the subadditive case), poorer environmental conditions make the growth rate less sensitive to competition: g_i 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:

(6) $g_i(E_i, C_i) = E_i - C_i + \Gamma_i(E_i, C_i)$

(Chesson 1987). To see how to obtain this form, we designate the original parameters and growth rate function using the subscript o, and we then choose some particular value E_i^* of the original environmentally-dependent parameter E_{io}, and a corresponding value C_i^* of C_{io} such that $g_{io}(E_i^*, C_i^*) = 0$. 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

(7) $E_i = g_{io}(E_{io}, C_i^*), \quad C_i = -g_{io}(E_i^*, C_{io}),$

and

$$(8) \qquad g_i(E_i, \ C_i) \ = \ g_{io}(E_{io}, \ C_{io}).$$

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 $(E_i, \ C_i) =$ (0, 0) (corresponding to $(E_i^*, \ C_i^*)$ 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 speci-fied, we assume below that the model has been trans-formed 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 $\{(E_1(t), E_2(t)), \ t = 0, 1, \ ...\}$ is an i.i.d. process, i.e., different times are independent and the bi-variate distribution of $(E_1(t), E_2(t))$ is independent of t. It follows that the community process $\{(X_1(t), X_2(t)), \ t = 0, 1, \ ...\}$ is a homogeneous Markov process and can be analyzed using the standard invas-ibility 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

$$(9) \qquad \Delta_i \stackrel{\text{def}}{=} Eg_i(E_i, c_i^j).$$

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 imply-
ing 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 $\Delta_i > 0$, $\Delta_j < 0$, to mean that
species i persists in the system while species j
converges to extinction.

The final case, defined by Δ_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 asser-
tions 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 $C_i = 0$.

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 σ.

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

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

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

(e)   The random variable $c_i(0, 0, E_j, X_j)$ 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 σ^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 σ^2. This means that these constant
factors are of smaller magnitude than the fluctuations
in the environmentally-dependent parameter, which are
of order σ, 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 comp-
etition 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 ex-
pectation 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 intro-
duced 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 σ about 0.
For the single-species system it follows that g_i has
the second order Taylor approximation

(10) $g_i(E_i, C_i) \approx E_i - C_i + \gamma_i E_i C_i$,

where $\gamma_i = \partial^2 g_i / \partial E_i \partial C_i$, evaluated at (0, 0), and "$\approx$"
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 $E[c_i^j | c_j^j]$ 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 χ_{ij} as the
covariance between E_i and c_i^j and making use of the
fact that $EE_j c_j^j = EE_j Ec_j^j + \chi_{jj} = o(\sigma^2) + \chi_{jj}$, we
obtain

(11) $Ec_j^j \approx EE_j + \gamma_j \chi_{jj}.$

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

$$\Delta_i \approx EE_i - Ec_i^j + \gamma_i EE_i c_i^j$$

(12) $\approx EE_i - Ec_i^j + \gamma_i \chi_{ij}.$

Now

$$\chi_{ij} \approx E\{E[E_i c_i^j | E_j]\} \approx Eb_e E_j c_i^j \approx b_e b_c \chi_{jj},$$

and so

(13) $\Delta_i \approx EE_i - Ec_i^j + \gamma_i b_e b_c \chi_{jj}.$

Note that in this equation, Ec_i^j will likely be depen-
dent 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 $\Delta C = Ec_i^j - Ec_j^j$, representing the difference

between average interspecific and average intraspec-
ific 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 sub-
stitution in (13), using equation (11), defining $\theta =$
γ_i/γ_j, and $\Delta E = EE_i - EE_j$, we obtain

$$(14) \qquad \Delta_i \quad \approx \quad \Delta E - \Delta C - \gamma_j(1 - \theta b_e b_c)\chi_{jj}.$$

Thus the boundary growth rate is expressed in compo-
nents that can be regarded as relatively independent.
The first term represents mean environmental effects,
the second term represents the mean excess of inter-
specific competition over intraspecific competition,
and the last term represents the effects of the inter-
action between environment and competition.

   Although expression (14) seems fairly clean, it is
not always the best representation of the different
effects because ΔC can be nonzero when different
species respond to exactly the same competitive factor
but have different magnitudes of response. In par-
ticular, ΔC 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

$$(15) \qquad \Delta C = EC_i^j - qEC_j^j,$$

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 ΔE as $EE_i - qEE_j$. Equation (14) becomes

(16) $\Delta_i \approx \Delta E - \Delta C - \gamma_j(q - \theta b_e b_c) \chi_{jj}.$

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 en-
vironmental 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 χ_{jj} is a
reflection of variation in the environmentally-
dependent parameter of the competitor species, not a
direct reflection of the variability in the environ-
mentally-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 para-
meters. 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 pos-
itive unless the species respond in exactly the same
way to the environment, in which case it will be 0.

In many cases the covariance χ_{jj} 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 boun-
dary 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 divers-
ity.

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 extinc-
tion. 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 equ-
ation (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 quan-
tities 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 lat-
ter. 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, χ_{jj}, we simply express the resident's parameter in terms of its first-order Taylor expansion in E_j and X_j about $(0, X_j^*)$:

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

It follows that

(18) $\chi_{jj} \approx c_{j1}VE_j$.

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

(19) $\chi_{jj} \approx c_{j1}VE_j + c_{j2}C(E_j,X_j)$,

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 o for "original." We define

$$(20) \qquad \alpha_i^{(n)} = \left. \frac{\partial^n}{\partial E_{io}^n} \, g_{io}(E_{io}, \, C_{io}^*) \right|_{E_{io} = E_{io}^*}.$$

A quantity $\beta_i^{(n)}$ is defined similarly as the nth deriv-
ative of $-g_{io}$ 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 orginal parameters
by using Taylor series expansion of g_{io}. This yields

$$(21) \qquad E_i \approx \alpha_i^{(1)}(E_{io} - E_{io}^*) + \frac{1}{2}\alpha_i^{(2)}(E_{io} - E_{io}^*)^2,$$

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

$$(22) \qquad \gamma_i = \gamma_{io}/\alpha_i\beta_i,$$

$$(23) \qquad \chi_{jj} \approx \alpha_j\beta_j\chi_{jjo}$$

$$(24) \qquad b_e = (\alpha_i/\alpha_j)b_{eo}, \quad b_c = (\beta_i/\beta_j)b_{co}$$

and

$$(25) \qquad \theta = \theta_o(\alpha_j\beta_j/\alpha_i\beta_i).$$

Although it will generally be possible to express q in
terms of the original parameters, in general the
quantity "q_o" is not meaningful and is best considered
undefined.

With these definitions, the components of equation
(16) can be expressed in terms of the original para-
meters. In doing this we use the notation "$\hat{\ }$" to in-
dicate the deviation from a *-value, e.g. $\hat{E} = E - E^*$.
We obtain

$$(26) \quad \Delta E \approx \alpha_i^{(1)} E\hat{E}_{io} - q\alpha_j^{(1)} E\hat{E}_{jo}$$

$$+ \tfrac{1}{2}(\alpha_i^{(2)} VE_{io} - q\alpha_j^{(2)} VE_{jo}),$$

and

$$(27) \quad \Delta C \approx \beta_i^{(1)} E\hat{C}_{io}^j - q\beta_j^{(1)} E\hat{C}_{jo}^j$$

$$+ \tfrac{1}{2}(\beta_i^{(2)} VC_{io}^j - q\beta_j^{(2)} VC_{jo}^j).$$

Finally

$$(28) \quad \gamma_j(q - \theta b_e b_c)\chi_{jj} \approx \gamma_{jo}(q - \theta_o b_{eo} b_{co})\chi_{jjo}.$$

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, ΔE
and ΔC, 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 illus-
tration 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 com-
petition 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

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

where δ_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

(30) $C_i = (E_1 X_1 + C_2 X_2)/(\delta_1 X_1 + \delta_2 X_2),$

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 assump-
tions most clearly, simpler and more interpretable
results are abtained if the birth rate is expressed on
the natural log scale. In particular, this scale more
clearly elucidates the constraints among the param-
eters 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 δ_i is used as the competitive factor. With these changes the model takes the form

$$(31) \qquad G_{io} = 1 - \delta_i + \delta_i e^{E_{io} - C_{io}}.$$

Simple calculations show that

$$(32) \qquad \alpha_i^{(1)} = \beta_i^{(1)} = \delta_i$$

and

$$(33) \qquad \alpha_i^{(2)} = -\beta_i^{(2)} = -\tau_{io} = \delta_i(1 - \delta_i).$$

Moreover,

$$(34) \qquad c_{jo}^j = E_{jo} \quad \text{and} \quad c_{io}^j = E_{jo} + \ln(\delta_i/\delta_j),$$

which implies the identical relationship among the means, equality of the variances and also that $\chi_{jjo} = VE_{jo}$, 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

$$(35) \qquad c_j^j = -\ln(1 - \delta_j + \delta_j e^{E_j^*} - E_{jo})$$

and

$$(36) \qquad c_i^j = -\ln(1 - \delta_i + \delta_i e^{E_i^*} - E_{jo} - \ln \delta_i/\delta_j).$$

Using the fact that

$$(37) \qquad E_i^* - E_j^* = \ln \delta_i/\delta_j$$

we deduce that $q = \delta_i/\delta_j$. Substituting in (23-24) and rearranging, we find that

(38) $\Delta E/\delta_i = E\hat{E}_{io} - E\hat{E}_{jo} + \tfrac{1}{2}[(1-\delta_i)VE_{io} - (1-\delta_j)VE_{jo}]$

(39) $\Delta C/\delta_i = \tfrac{1}{2}[(1-\delta_j) - (1-\delta_i)]VE_{jo}$,

(40) $\gamma_{jo}(q-\theta b_{eo}b_{co})x_{jjo} = \delta_i[(1-\delta_i)b_{eo} - (1-\delta_j)]VE_{jo}$.

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_{jo} by itself will increase ΛE, will increase or decrease ΔC depending on the sign of $(1-\delta_j) - (1-\delta_i)$, and increase or decrease the interaction term (37) depending on the sign of $(1-\delta_i)b_{eo} - (1-\delta_j)$.

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 $\delta_i \leftrightarrow \delta_j$, then the value of ΔC 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

(41) $\Delta_i / \delta_i = E\hat{E}_{io} - E\hat{E}_{jo} + \frac{1}{2}(1-\delta_i)V(E_{io} - E_{jo})$.

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-
titive 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-
ation 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 varia-
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 bio-
logical 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 parameter-
ization 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 varia-
bility 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
$|E| \leqslant \sigma$.

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 postive number $\rho < 1$ such that

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

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

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

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

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

The differentiability assumptions mean that $\delta =$
$O(\sigma)$ and so for σ 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) $\limsup |Z(t) - z^*| < \dfrac{\delta}{1 - \rho}$.

As a consequence of (a5) and the bounded differen-
tiability of C, it follows that

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

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

$E\hat{E}_{io}$, $E\hat{c}_{jo}^{j}$, and $E\hat{c}_{io}^{j}$ are each $O(\sigma^2)$. This can be deduced easily by using the corresponding properties of the standardized parameters. That $E c_{j}^{j} = O(\sigma^2)$ follows from equation (11); and assumption (d) now implies the same for $E c_{i}^{j}$.

BIBLIOGRAPHY

1. Abrams, P. 1984. Variability in resource consumption rates and the coexistence of competing species. Theoret. Pop. Biol. 25: 106-124.

2. Abrams, P. 1986. Letter to the editor, Trends in Ecology and Evolution 1, 131-132.

3. Armstrong, R. A., and R. McGehee. 1976. Coexistence of species competing for shared resources. Theoret. Pop. Biol. 9: 317-328.

4. Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. Amer. Natur. 115: 151-170.

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

6. Chesson, P. L. 1983. Coexistence of competitors in a stochastic environment: the storage effect. In H. I. Freedman, and C. Strobeck, eds., Population Biology, Lecture Notes in Biomathematics No. 52, pp. 188-198.

7. Chesson, P. L. 1984. The storage effect in stochastic population models. In S. A. Levin and T. G. Hallam, eds., Mathematical Ecology: Trieste Proceedings, Lecture Notes in Biomathematics No. 54, pp. 76-89.

8. Chesson, P. L. 1987. Interactions between environment and competition: how fluctuations mediate coexistence and competitive exclusion. Lecture Notes in Biomathematics, in press.

9. Chesson, P. L., Ellner, S. P. 1988. Invasibility and stochastic boundedness in monotonic competition models. J. Math. Biol., in press.

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

11. Ellner, S. P. 1984. Asymptotic behavior of some difference equation population models. J. Math. Biol. 19: 169-200.

12. DenBoer, P. J. 1986. The present status of the competitive exclusion principle. Trends in Ecology and Evolution 1, 25-28.

13. Giller, P. 1986. Letter to the editor, Trends in Ecology and Evolution 1, 132.

14. Hatfield, J., Chesson, P. L. 1988. Diffusion approximation and stationary distribution for the lottery competition model. Manuscript.

15. Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Amer. Natur. 93, 145-159.

16. Levins, R. 1979. Coexistence in a variable environment. Amer. Natur. 114: 765-783.

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

18. May, R. M., ed. 1981. Theoretical Ecology, Sinauer Associates, Sunderland.

19. Roughgarden, J. 1979. Introduction to the Theory of Population Genetics and Evolutionary Ecology.

20. Roughgarden, J. 1986. Letter to the editor, Trends in Ecology and Evolution 1, 132.

21. Roughgarden, J., Feldman, M. W. 1974. Species packing and predation pressure. Ecology 56, 489-492.

22. Shmida, A., and S. P. Ellner. 1985. Coexistence of plant species with similar niches. Vegetatio 58, 29-55.

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

24. Woodin, S. A., and J. A. Yorke. 1975. Disturb-
ance, fluctuating rates of resource recruitment, and
increased diversity. In S. A. Levin ed., Ecosystem
ʼAnalysis and Prediction, Proceedings SIAM-SIMS Confer-
ence, Alta, Utah, 1974, pp. 38-41.

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