ENVIRONMENTAL VARIABILITY PROMOTES COEXISTENCE IN LOTTERY COMPETITIVE SYSTEMS

PETER L. CHESSON AND ROBERT R. WARNER

Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, California 93106

Can temporal environmental variability lead to coexistence of competing species? Conclusions from equilibrium theory tend to say no (May 1973, 1974a, 1974c). These conclusions are based on analysis of linearized versions of the Lotka-Volterra competition equations. The intuition behind the analysis can be paraphrased as: For two species to coexist there must be a stable equilibrium with both species present in positive numbers. Environmental variability prevents species numbers from remaining at equilibrium—the greater the variability the further from equilibrium these numbers can get and the greater the chance that one or more species will become extinct.

Hutchinson (1961) takes a different view: A stable equilibrium with all species present in positive numbers is not a prerequisite for coexistence provided environmental change is sufficiently frequent to change the order of competitive superiority before extinction of any species can occur. In this view environmental variability keeps species abundances away from equilibria in which one or more species are extinct. From both points of view environmental variability acts by keeping abundances away from equilibria. However, the equilibria are of different kinds and the role of environmental variability in maintaining species diversity is reversed.

In this paper we examine these two different points of view in relation to a model of competition for space in a lottery system. In its simplest form a lottery system requires that the available space is divided up randomly among the new recruits to the competing populations. Sale (1977, 1978) suggests that this kind of process might be operating in communities of coral reef fishes in which the species involved are generalists who have widely dispersing larvae and tenaciously territorial adults.

Sale argues that local diversity is maintained by random allocation of space. We agree that local diversity can be maintained in this way provided diversity is maintained on the large scale; but is random allocation of space sufficient to maintain diversity on the large scale? To explain large-scale maintenance of diversity Sale seems to rely again on random allocation of space, as it becomes available in an unpredictable fashion in both time and space. To aid this explana-

tion he observes that commercial fisheries statistics show little relationship be-
tween stock and recruitment to a fishery (but see Cushing 1975). As pointed out by
S. Levin (in Sale 1978, discussion), this latter observation is not an explanation for
species diversity, it is simply a possible outcome of the maintenance of species
diversity at the larval level.

A number of alternative suggestions for the maintenance of diversity in com-
munities of coral reef fishes have since appeared. Dale (1978) has suggested a
mechanism for maintenance of large-scale diversity that relies on different species
having exclusive habitats where only they survive—a possibility not allowed for
by Sale.

Anderson et al. (1981) question whether larval dispersal is a major factor in
these communities and they point to microhabitat and food specialization as a
possible alternative explanation for coexistence.

Our enquiry is not concerned with alternative explanations for coexistence, but
with the validity of the claim that random allocation of space can maintain species
diversity. Important considerations in our study are the effects of temporal envi-
ronmental variability and overlapping generations. In our models we assume no
microhabitat specialization or resource partitioning, but we do allow for differ-
ences between species in birth rates, death rates, and abilities of finding and
securing space.

MODELS FOR LOTTERY SYSTEMS

The essential features of Sale's lottery system can be stated as follows.

1. Larvae establish territories in suitable places on the coral reef. An individual
holds its territory for the rest of its life. Individuals that do not establish territories
do not survive to reproductive age.

2. Space is limiting: There are always far more larvae trying to establish
territories than the available space can hold.

3. Allocation of space is on a first-come first-served basis: The first individual to
arrive at a suitable site for a territory can establish a territory there.

4. Larvae are highly dispersive so that the number of larvae of any species
seeking territories in any one locality is not directly related to the number of
individuals already present at that locality.

We do not include the assumption that total recruitment for the entire range of
the species is independent of stock, because, as pointed out above, it is best
regarded as a possible consequence of coexistence, not a reason for coexistence.

For greater generality the discussion below uses the word *home* instead of
territory. A home is an area occupied by an individual to the exclusion of others;
unlike a territory it may not require defense. An individual with a home will be
called an "adult."

The lottery system is formulated mathematically as follows. Consider a suitable
homesite at a time when there are L_i larvae of species i ($i = 1, \ldots, k$) seeking a
home. The probability that this site is taken by an individual of species i is

$$L_i \bigg/ \sum_{j=1}^{k} L_j. \tag{1}$$

If the number of available homes is very large, then expression (1) is close to the actual proportion of available homes that become occupied by species i. We make the approximation throughout that expression (1) is actually equal to this proportion. In effect this assumes that there are infinitely many homes sought by infinitely many larvae. The implications of this assumption are discussed later. We shall also consider the situation in which individuals of different species are not equal in their abilities of finding and consolidating a home. In this case expression (1) is replaced by

$$c_i L_i \Big/ \sum_{j=1}^{k} c_j L_j, \qquad (2)$$

where the constants c_i indicate the relative competitive abilities of different species.

As Sale points out, island biogeography theory (MacArthur and Wilson 1967) and models of competition in patchy environments (Levins and Culver 1971; Horn and MacArthur 1972; Slatkin 1974) are similar to lottery systems in that randomness plays an important role in the processes being modeled. However, there are also very important distinctions. The focus in a lottery system is on space for an individual. The unit of space is exclusive: Only one individual can occupy a single unit at any one time. In the models and theory mentioned above the situation is quite different because the unit of space supports local populations of several species and does not allow the level of detail necessary for the consideration of the lottery mechanism. Thus we disagree with Sale's suggestion that the models of Horn and MacArthur (1972) and Slatkin (1974) provide a basis for the mathematical treatment of lottery systems. Useful information might be provided by considering patches made up of groups of homes with the competition parameters varying between patches, as this possibility is suggested by Sale's data (Sale 1978). However, in this paper attention is restricted to the case where there is no spatial variation in the competition parameters. Random migration and random allocation of space then make consideration of patches consisting of groups of homes unnecessary.

THE POPULATION MODEL

We need the following definitions:

1. $P_i(t)$ = total proportion of homes occupied by species i at the time t.

2. $\beta_i(t)$ = per capita net reproduction of species i during $(t, t + 1]$; i.e., for each adult at time t, $\beta_i(t)$ larvae reach the settling stage during $(t, t + 1]$. The value $\beta_i(t)$ is assumed to be positive, which prevents any species from reaching a zero population size in finite time. Most population models share this latter property (Chesson 1978). In such models one says that a species "becomes extinct" or "dies out" if $\lim_{t \to \infty} P_i(t) = 0$.

3. $\beta_i^*(t) = c_i \beta_i(t)$. This is the "birth-competition" parameter and can be thought of as an adjustment to the birth rate to take into account competitive differences between species.

4. $\delta_i(t)$ = proportion of adults of species i dying during $(t, t + 1]$.

5. K = total number of homes occupied by all species (assumed constant and effectively infinite).

During $(t, t + 1]$, $K\delta_i(t)P_i(t)$ adults of species i die and the total number of homes becoming available for new recruits is $K \sum_{j=1}^{k} \delta_j(t)P_j(t)$. Applying expression (1), recruits of species i take up the proportion $\beta_i(t)P_i(t)/\sum_{j=1}^{k} \beta_j(t)P_j(t)$ of this space. Putting this together we obtain

$$P_i(t + 1) = [1 - \delta_i(t)]P_i(t) + \left[\sum_{j=1}^{k} \delta_j(t)P_j(t)\right]\left[\frac{\beta_i(t)P_i(t)}{\sum_{j=1}^{k} \beta_j(t)P_j(t)}\right]. \qquad (3)$$

If we want to consider differences in competitive abilities between species we must base our model on expression (2), and this yields

$$P_i(t + 1) = [1 - \delta_i(t)]P_i(t) + \left[\sum_{j=1}^{k} \delta_j(t)P_j(t)\right]\left[\frac{\beta_i^*(t)P_i(t)}{\sum_{j=1}^{k} \beta_j^*(t)P_j(t)}\right]. \qquad (4)$$

Equation (4) is the same mathematical form as equation (3), and so it presents no greater difficulty in analysis. Since results for equation (4) are readily translated into results for (3) we base our analysis on equation (4).

As it stands equation (4) is very general, and it exhibits different behaviors depending on the assumptions made about the δ_i and β_i^*. We analyze equation (4) for four different sets of assumptions: overlapping or nonoverlapping generations together with constant or random environment. Generations are nonoverlapping when $\delta_i(t) \equiv 1$. When the environment is constant $\delta_i(t)$ and $\beta_i^*(t)$ are constants (δ_i and β_i^*) independent of t. For a random environment $\delta_i(t)$ and $\beta_i^*(t)$ are randomly varying. We define the vector $\sigma(t) = [\delta_1(t), \beta_1^*(t), \ldots, \delta_k(t), \beta_k^*(t)]$ and make the usual assumption that the random vectors $\sigma(0), \sigma(1), \sigma(2), \ldots$ all have the same probability distribution and are independent of each other. In a later section, where the environment process $(\sigma(t), t = 0, 1, \ldots)$ is discussed in more detail, it is shown that this assumption is not essential for some of our conclusions. However, our assumptions always imply that fecundity and death rates of adults are age independent.

We shall see below that the stochastic case (random environment) can give markedly different results from the deterministic case (constant environment). These differences depend on overlapping generations because only in that case does equation (4) have an important nonlinearity. We begin our investigation with the much simpler nonoverlapping generations situation.

Some mathematical detail is given in the Appendix, but for the most part the proofs of the mathematical results are too long and technical to be given here and only heuristic justifications are presented. Complete proofs can be found in Chesson (in press).

Nonoverlapping Generations

When generations are nonoverlapping equation (4) reduces to

$$P_i(t + 1) = \frac{P_i(t)\beta_i^*(t)}{\sum_{j=1}^{k} \beta_j^*(t)P_j(t)}. \qquad (5)$$

This equation corresponds to that in Dempster's (1955) haploid selection model, and our results parallel his. From equation (5) we deduce

$$\frac{P_i(t+1)}{P_j(t+1)} = \frac{\beta_i^*(t)}{\beta_j^*(t)} \cdot \frac{P_i(t)}{P_j(t)};$$ (6)

i.e., the ratios of species abundances change according to a linear equation.

The solution to equation (5) or (6) is easily seen to be

$$P_i(t) = \frac{P_i(0) \prod_{s=0}^{t-1} \beta_i^*(s)}{\sum_{j=1}^{k} P_j(0) \prod_{s=0}^{t-1} \beta_j^*(s)},$$ (7)

and in the deterministic case this reduces to

$$P_i(t) = \frac{P_i(0) \, (\beta_i^*)^t}{\sum_{j=1}^{k} P_j(0) \, (\beta_j^*)^t}.$$ (8)

To simplify our discussion we restrict attention to the two-species ($k = 2$) situation; the extension of our results to the more general case is trivial. We define $\rho(t) = \beta_1^*(t)/\beta_2^*(t)$. In the deterministic case the following conclusions are obvious from equation (8); if $\rho < 1$, species 1 dies out ($\lim_{t\to\infty} P_1(t) = 0$) and consequently species 2 increases in numbers to occupy all available space. If $\rho > 1$, species 2 dies out. Only when $\rho = 1$ do both species persist, and in this case their numbers do not change with time—all possible population densities are neutral equilibria. The $\rho = 1$ case represents an unlikely exact balancing of birth rates; moreover, it is an evolutionarily unstable situation, since any genetic change resulting in a change in ρ will lead to elimination of one species. For example, if species 1 increased its birth rate or its efficiency at finding homes then ρ would increase in species 1's favor and species 2 would be eliminated.

To analyze the stochastic model we note from equation (6) that $\log [P_1(t)/P_2(t)]$ undergoes a random walk (see Feller 1971, p. 389ff). The following conclusions are immediate (the symbol E is used to denote the expected or theoretical mean value of the random variable following E):

If E $\log \rho(t) < 0$ species 1 dies out.

If E $\log \rho(t) > 0$ species 2 dies out.

These two cases correspond to the deterministic cases $\rho < 1$ and $\rho > 1$. The qualitative results (extinction of one species) are the same as for the deterministic model but it is also instructive to note from random walk theory that

$$\log [P_1(t)/P_2(t)] = t\mu + Z(t),$$ (9)

where $\mu = $ E $\log \rho(t)$ and $Z(t)$ is an approximately normal random variable with zero mean and variance proportional to t. In the deterministic model

$$\log [P_1(t)/P_2(t)] = t\mu,$$ (10)

and so the population trajectories of the stochastic model are merely fluctuations about the trajectories of the deterministic model. This result is a special consequence of the fact that the model can be put in the linear form (6), and does not occur in the overlapping generations model where a transformation to linearity is not available (see below).

In the remaining case, where $\mu(= \mathrm{E} \log \rho(t))$ equals 0, the qualitative results are more complex. Random walk theory says that species proportions are subject to drift: $P_i(t)$ oscillates between 0 and 1. Although $P_i(t)$ never actually reaches 0 or 1 it becomes arbitrarily close to both at different times. In a sense both species appear to be persistent, but this persistence is very weak for two reasons. First, as t increases $P_i(t)$ will tend to be found near 0 or 1 with high probability; that is, $\lim_{t \to \infty} \mathrm{P}[P_i(t) \in (\epsilon, 1 - \epsilon)] = 0$ for all $\epsilon > 0$. Second, if $P_i(t)$ drops to some low level x then the expected waiting time for return to a higher level y is always infinite—the behavior of the process is highly unpredictable. In summary, most of the time one species will appear to dominate. Which species is dominant will change with time, but the timing of this change is highly unpredictable. Most of the time one of the species will be at very low population levels, and if one combines this with the stochastic effects of small population size (not included in this model) then extinction must occur. Thus, from the population dynamic point of view the situation $\mathrm{E} \log \rho(t) = 0$ does not give rise to a stable coexistence. From the evolutionary point of view it has the same instability that is present in the deterministic model with $\rho = 1$.

The conclusion from nonoverlapping generations models is that species diversity cannot be maintained in a lottery system. This conclusion is independent of environmental variability. As we shall see, the results from overlapping generations models are quite different.

Overlapping Generations

Again we restrict attention to the two-species case ($k = 2$), but here the extension to the more general case is not a simple matter. When $k = 2$ we have $P_2(t) = 1 - P_1(t)$ and equation (4) reduces to

$$P_1(t + 1) = [1 - \delta_1(t)]P_1(t) + \frac{\{\delta_1(t)P_1(t) + \delta_2(t)[1 - P_1(t)]\}\beta_1^*(t)P_1(t)}{\beta_1^*(t)P_1(t) + \beta_2^*(t)[1 - P_1(t)]}$$

$$= P_1(t)\left\{1 + \frac{[1 - P_1(t)][\beta_1^*(t)\delta_2(t) - \beta_2^*(t)\delta_1(t)]}{\beta_1^*(t)P_1(t) + \beta_2^*(t)[1 - P_1(t)]}\right\}. \tag{11}$$

By inspection it is clear that P_1 increases or decreases depending on the sign of $\beta_1^*(t)\delta_2(t) - \beta_2^*(t)\delta_1(t)$, or equivalently, depending on the sign of $\rho(t) - 1$, where we define $\rho(t) = \beta_1^*(t)\delta_2(t)/\beta_2^*(t)\delta_1(t)$.

In the deterministic case there are three possible outcomes. (a) If $\rho = 1$ then $P_1(t) = P_1(0)$ for all t. (b) If $\rho > 1$ then $P_2(t) \to 0$ as $t \to \infty$ (i.e., species 2 dies out). (c) If $\rho < 1$ then $P_1(t) \to 0$ as $t \to \infty$ (i.e., species 1 dies out). Since $P_1(t) + P_2(t) = 1$, when one species dies out the other species increases to occupy all available space.

These results are the same as for the deterministic model with nonoverlapping

generations. In particular, coexistence only occurs when $\rho = 1$, which requires an unlikely and evolutionarily unstable exact balancing of birth, competition, and deaths for the two species.

A rigorous analysis of the stochastic model is given in Chesson (in press), but here we give a heuristic analysis based on the standard invasibility criterion for stochastic population models (Turelli 1978b). According to the invasibility criterion a species persists or becomes extinct depending on whether the mean instantaneous growth rate, at low population levels, is positive or negative. The invasibility criterion is not completely satisfactory because it may say that a species persists in situations where the probability of observing an arbitrarily small population size at time t increases to 1 as $t \to \infty$ (Chesson, in press). However in the present model this problem does not arise. Here persistence according to the invasibility criterion ensures that small population sizes have correspondingly small probabilities of occurring at any given time. (See the section below on the meaning of persistence.)

To see how the invasibility criterion works here, we note from equation (11) that

$$P_1(t + 1)/P_1(t) \simeq 1 + \delta_1(t) [\rho(t) - 1] \tag{12}$$

for small $P_1(t)$, and this shows that $1 + \delta_1(t) [\rho(t) - 1]$ is the approximate finite growth rate for small $P_1(t)$. Thus when $P_1(t)$ is small it will increase or decrease depending on whether the geometric mean of (12) is greater than 1 or less than 1. Equivalently $P_1(t)$ will increase or decrease depending on whether the arithmetic mean of log $\{1 + \delta_1(t) [\rho(t) - 1]\}$, the instantaneous growth rate, is positive or negative. This result heuristically justifies the invasibility criterion for our model. To see its implications let Δ_i be the mean instantaneous growth rate of species i when low in numbers, i.e.,

$$\Delta_1 = E \log \{1 + \delta_1(t) [\rho(t) - 1]\}, \quad \text{and}$$

$$\Delta_2 = E \log\{1 + \delta_2(t) [\rho^{-1}(t) - 1]\}.$$

The invasibility criterion now gives the following four possible behaviors of the model. (a) Both species persist ($\Delta_1 > 0, \Delta_2 > 0$). (b) Species 2 dies out ($\Delta_1 > 0, \Delta_2 < 0$). (c) Species 1 dies out ($\Delta_1 < 0, \Delta_2 > 0$). (d) One of the two species dies out, but which one is a matter of chance ($\Delta_1 < 0, \Delta_2 < 0$).

Situations b and c occur for the deterministic model, but d is unique to stochastic models. Furthermore, in contrast to the deterministic model, case a occurs here for a broad range of evolutionarily stable situations. We now discuss the conditions favoring each of these four possible cases of the stochastic model. The A-prefixed references below are to Appendix results.

Case a (coexistence).—Case a is favored by a tendency for ρ to take on both small values (less than 1) and large values (greater than 1); that is, values of birth-competition and death parameters that allow one species to be favored sometimes and the other species at other times. In almost any situation it is possible to make both Δ_1 and Δ_2 positive—indeed, arbitrarily large—by increasing variability in ρ (AI). For example, we can increase the variance of log ρ, V log ρ, while keeping the mean constant, by defining

$$\beta_{ni}^* = n(\log \beta_i^* - E \log \beta_i^*) + E \log \beta_i^*, \quad i = 1, 2,$$

where the quantity n defines the level of variability. The value $V \log \rho_n$ is asymptomatically equal to $n^2 V \log \beta_1^*/\beta_2^*$ while $E \log \rho_n = E \log \rho$. As n increases both $\Delta_{n1} = E \log[1 + \delta_1(\rho_n - 1)]$ and $\Delta_{n2} = E \log[1 + \delta_2(\rho_n^{-1} - 1)]$ tend to $+ \infty$ (AI). In particular there is a level of variability (value of n) above which both Δ_{n1} and Δ_{n2} are positive and the two species will coexist.

The example above increases variability in ρ by increasing variability in the birth-competition parameters. Variability in ρ can also be increased by increasing variability in the death rates. However, increasing variability in death rates need not increase the values of the Δ_i. When the δ_i's are small we can make the following statements (AII): If the δ's are independent of the β^*'s then variability in the δ's has no effect on the chance of coexistence. If δ_i is positively correlated with β_i^*/β_j^* then an increase in variability in δ_j will increase Δ_i, making persistence of species i more likely without affecting the value of Δ_j. Thus, in a situation in which one species tends to have relatively good birth-competition periods when the other species has a high death rate, an increase in variability of death rates favors coexistence. On the other hand, if the correlation between δ_j and β_i^*/β_j^* is negative then exclusion is favored by an increase in variability in the death rates.

Recall that in the deterministic model coexistence cannot occur if $\log \rho \neq 0$. In contrast, in the stochastic model coexistence is possible with any value for $E \log \rho$ provided variability is great enough. That is, the deterministic tendency for one species to be driven out by another is overridden by variability.

We consider variability about the mean of $\log \rho$ because ρ is a ratio quantity and only on the log scale do the numerator and denominator contribute to the mean in an equitable manner. $E \log \rho$ measures the mean advantage that species 1 has over species 2 as a result of its relative birth, death, and competition parameters. (If $E \log \rho$ is negative then species 2 has a mean advantage over species 1.)

The discussion above says that for any mean advantage there is a level of variability giving coexistence but does not say what this level is. When $E \log \rho = 0$, i.e., when neither species has a mean advantage, any variability in ρ is sufficient to give coexistence provided the δ_i are not too variable (AIII).

If $E \log \rho \neq 0$, then the magnitudes of the δ_i become important. Coexistence is favored by small values of δ_i (AII); that is, coexistence is more likely to occur if only a small proportion of the individuals are replaced each year. By letting $\delta_i \rightarrow 0$ we can find threshold levels of variability such that coexistence occurs for sufficiently small but positive values of the δ_i. This threshold is sufficient variability so that both $E\rho$ and $E\rho^{-1}$ are greater than 1 (AII). In the special case that $\log \rho$ has a normal distribution with mean μ and variance σ^2 this condition can be expressed as $\sigma^2 > 2|\mu|$. Note that μ is the mean advantage that species 1 has over species 2.

To see how much variability is necessary when the δ_i are not necessarily small we have calculated a chart (fig. 1) by numerical evaluation of Δ_i assuming that $\log \rho$ is normal. For simplicity we have considered only the case where $\delta_1 = \delta_2$. The curves give threshold relationships between $|\mu|$ and σ^2 for given δ_i. Coexistence occurs for $(|\mu|, \sigma^2)$ points above the curve for a given value of δ_i. As can be seen, there exist broad ranges of variability in which coexistence can occur.

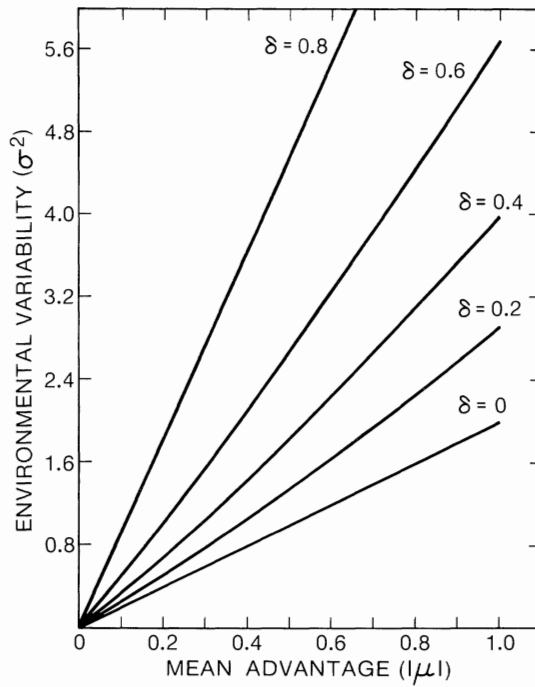Figure 2 plots Δ_i as a function of μ for $\delta_i = .1$ and various values of σ^2. The case

FIG. 1.—Thresholds of variability giving coexistence.

$\sigma^2 = 0$ gives the boundary growth rates (Δ_1) for the deterministic model, which are a direct reflection of the mean advantage of species 1. For positive σ^2, species 1 can have a positive growth rate at low relative abundance even though it has a mean disadvantage ($\mu < 0$). Furthermore, the range of negative μ values for which Δ_1 is positive increases with σ^2.

Figure 2 yields Δ_2 values when δ_1 and μ are read as δ_2 and $-\mu$, respectively. The corresponding curves for different δ values can be found from the given curves as explained in the Appendix (AV).

Case d (random exclusion).—In case d one species, determined by chance, dies out. This situation is favored by a tendency for (δ_1, δ_2) to take on values near $(0, 1)$ and $(1, 0)$ at different times; that is, the death rates of the two species are variable and negatively correlated. To demonstrate this we show (AIV) that the Δ_i decrease as functions of how near (δ_1, δ_2) comes to $(0, 1)$ and $(1, 0)$. If (δ_1, δ_2) comes sufficiently close to $(0, 1)$ and $(1, 0)$, with some fixed probability, the Δ_i will be negative and can be arbitrarily large and negative. The special case where $\beta_1^* = \beta_2^*$ and $\delta_1 - \delta_2$ has a distribution symmetrical about 0 provides an explicit example of case d. Here any variability in the δ's combined with any correlation less than $+1$ gives random exclusion. Negative correlation between the δ's and high variability give rise to large negative values of Δ_1 and Δ_2, meaning that rapid extinction can be expected.

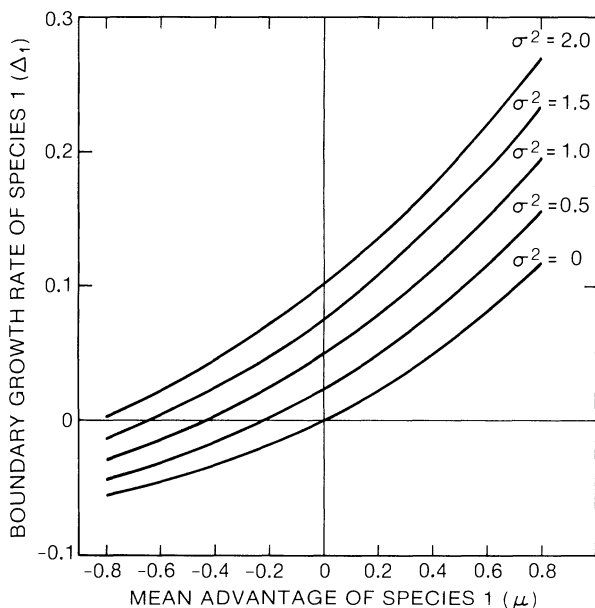*Cases b and c (exclusion of a particular species).*—The remaining cases occur

Fɪɢ. 2—Growth rates at low relative density as a function of mean advantage and environmental variance (σ^2).

whenever one species has a sufficiently strong mean advantage over the other species to override the effect of environmental variability. For example, if both Δ_1 and Δ_2 are finite it is easy to see that by increasing the mean of log $\rho(t)$ (the mean advantage of species 1) while keeping the shape of the distribution constant, then eventually Δ_1 will become positive and Δ_2 negative, producing case b. Similarly, decreasing the mean of log $\rho(t)$ can result in case c.

In these cases of competitive exclusion the population trajectories cannot simply be described as fluctuations about the trajectories of the deterministic model. To see this note that Δ_1 is the average rate at which species 1 declines at low population levels, and figure 2 illustrates the dependence of this rate on the variance of log ρ. (It was explained earlier that the variance of log ρ is the natural variance to consider.) Population decline is slower with higher variance, and so the average rate of competitive exclusion is slower in the stochastic model. By contrast we have seen that increasing the variance of log ρ has no effect on the average rate of population decline in the nonoverlapping generations model because it can be put in the linear form (6).

Summary of Model Results

In the nonoverlapping generations model, randomness in the environment has very little effect on the conclusions. This is not surprising because in this case the model can be transformed to a simple linear model. When generations are

nonoverlapping coexistence of two species can only occur in very special and evolutionarily unstable circumstances.

When generations are overlapping, randomness in the environment has marked effects because the model has important nonlinearities. With a constant environment the model gives essentially the same results as the nonoverlapping generations model. When the environment is random, coexistence of two species is possible under broad and evolutionarily stable conditions. Coexistence is favored by increased variability in the birth-death-competition parameter ρ. Extinction of a randomly determined species can occur in situations where the death rates (δ_1 and δ_2) are negatively correlated.

MEANING OF PERSISTENCE

In a deterministic model one is willing to say that a species persists if the population size never gets below some positive lower limit L ($P_1(t) \geq L$ for all t). This definition of persistence is not very useful in stochastic models because in most cases there is no lower bound on population size; in most stochastic models, given enough time, fluctuations to arbitrarily small population sizes will be seen. This is not a weakness of stochastic models, for it is a highly plausible though unfalsifiable hypothesis for real populations; but it does lead to difficulties in defining persistence for stochastic models. There has been much discussion on this problem (Botkin and Sobel 1975; Ludwig 1976; Chesson 1978, in press; Turelli 1978a, 1980a). Chesson (1978) suggested calling a population persistent if it is stochastically bounded from below.

Stochastic boundedness is most easily understood in terms of the quantiles $\zeta_p(t)$ of the probability distribution of population size. By definition of $\zeta_p(t)$, the population size at time t will be greater than $\zeta_p(t)$ with probability $1 - p$ or, equivalently, the population will be less than $\zeta_p(t)$ with probability p. Thus $\zeta_p(t)$ essentially provides a lower ''confidence'' limit or probability limit on the population size at time t. The population is said to be stochastically bounded from below if there is a positive lower bound L_p on these probability limits, i.e., if $\zeta_p(t) \geq L_p$ for all t. Thus the probability limits on population size are kept away from zero just as the actual population size is kept away from 0 in the deterministic notion of persistence. $\zeta_p(t)$ can only be arbitrarily small for arbitrarily small p; that is, small population sizes have correspondingly small probabilities.

The kind of persistence found in case a of the overlapping generations model is indeed persistence in the sense of stochastic boundedness (Chesson, in press) but even more can be said: Not only are the probability limits $\zeta_p(t)$ bounded away from 0, but as $t \to \infty$ the $\zeta_p(t)$ converge to definite numbers ζ_p; i.e., the probability distribution of $P(t)$ converges to a stationary or ''equilibrium'' probability distribution. This convergence to an ''equilibrium'' probability distribution is the stochastic analogue of global stability of a positive equilibrium in a deterministic model and is sufficient to ensure stochastic boundedness in the same way that global stability of an equilibrium point ensures persistence in a deterministic model.

In the nonoverlapping generations model with E log ρ = 0 we observed that

$P_1(t)$ does not converge to 0 as $t \to \infty$. Nevertheless it is found near 0 with probability approaching $\frac{1}{2}$, and we explained earlier that this situation does not deserve to be called persistence. The criterion of stochastic boundedness supports this earlier conclusion, for $\zeta_p(t) \to 0$ as $t \to \infty$ for any $p < \frac{1}{2}$, and so the probability of observing a small population at time t is not correspondingly small. Indeed this probability approaches 50%.

In most cases it is not possible to calculate the quantiles $\zeta_p(t)$ explicitly; however, some approximations are available in special cases (Chesson, in press). As an illustration assume that $P_1(0) = \xi$ and is nonrandom, death rates are equal and nonrandom, and variability in birth rates is high. In this situation $P_1(t)$ is approximately normally distributed with mean $\frac{1}{2} + e^{-\delta t}(\xi - \frac{1}{2})$ and variance $\delta(1 - e^{-2\delta t})/8$. Taking $p = .025$ and using tables of the normal distribution we find that

$$\zeta_{.025}(t) \approx \tfrac{1}{2} + e^{-\delta t}(\xi - \tfrac{1}{2}) - 1.96\sqrt{\delta(1 - e^{-2\delta t})/8}.$$

Note that as $t \to \infty$, $\zeta_{.025}(t) \to \frac{1}{2} - 1.96\sqrt{\delta/8}$, which is therefore the quantile $\zeta_{.025}$ of the equilibrium distribution discussed above. Notice also that $\zeta_{.025}(t) \geq \min(\xi, \frac{1}{2})$ $- 1.96\sqrt{\delta/8}$. This latter quantity is thus $L_{.025}$. Clearly the same exercise can be carried out for any value of p to give approximate numerical values for the quantities involved in the concept of stochastic boundedness.

THE ENVIRONMENT

In our stochastic models we define $\sigma(t) = [\delta_1(t), \beta_1(t), \delta_2(t), \beta_2(t)]$ and made the assumption that $\sigma(0)$, $\sigma(1)$, $\sigma(2)$, . . . are independent of each other and all have the same multivariate probability distribution. We do not make any assumption about the distribution that $\sigma(t)$ has for fixed t; we do not assume, for example, that $\delta_1(t)$ and $\beta_2(t)$ are independent. We do assume that the value that $\sigma(t)$ takes at one time has no influence on its value for the next time, or any later time. This independence assumption is unlikely to be satisfied in the real world. However, since our models are discrete time, we do not have to assume that the environment takes on an independent value at every instant as is commonly done in continuous time stochastic models. Models of this latter kind use the Gaussian white noise environment process, whose interpretation is ambiguous and controversial (Turelli 1977). We have at least avoided these difficulties.

An environment process more general than the kind we have considered is a stationary environment process (Doob 1953). It is a model for the situation in which there is no trend in the environment through time. A stationary process is defined mathematically as a process σ such that for every n the joint distribution of $\sigma(t)$, $\sigma(t + 1)$, . . ., $\sigma(t + n)$ does not depend on t. Note that it is the distribution that does not depend on t; the actual values taken by the environment will certainly change with t. The effect of a periodic environment can also be studied conveniently using a stationary process: When observation begins at a random time a periodic environment becomes a stationary one.

In practical problems stationary processes have a property called ergodicity (Breiman 1969) which entails that the sample average $t^{-1}\sum_{s=1}^{t} f[\sigma(s)]$ converges to the theoretical mean $Ef[\sigma(s)]$ for functions f such that the theoretical mean

exists. For ergodic stationary environment processes the conditions $\Delta_1 > 0$, $\Delta_2 > 0$ are still sufficient for coexistence; indeed, the heuristic argument given here for these conditions is applicable to this more general case, and so our conclusions concerning the role of environmental variability in promoting coexistence are still valid. Hutchinson's (1961) original discussion of the effect of environmental variability was motivated by coexistence of planktonic species in lakes where this variability has a strong seasonal component. Our results on coexistence do remain valid with this kind of environmental variability.

INFINITE POPULATIONS AND SPACE FILLING ASSUMPTIONS

Our models assume that there are effectively infinitely many homes available and that total reproduction always exceeds total death. From the latter it follows that all homes are occupied at the end of each time period. As the number of homes becomes large, these models are justified as limiting cases of fully stochastic models with finitely many homes and individuals having finite capacities of reproduction (Chesson, in press). To ensure that the limiting model will always have all homes filled one has to impose the condition that $\beta_i(t) \geq \delta_i(t)$; i.e., for every species, births always exceed deaths of adults. This will be satisfied if $\beta_i(t) \geq 1$, that is, the adults of each species produce an average of at least one potential recruit each in each time period.

The major difference between the finite and infinite models is that the finite models allow extinction in finite time; when $P_i(t) \to 0$ as $t \to \infty$ then there is a time $\tau < \infty$ such that $P_i(t) = 0$ for $t \geq \tau$. This is never so in the infinite models—extinction is always asymptotic as it is in most models in population biology (Chesson 1978). In spite of this qualitative difference the infinite models are still capable of yielding useful information about the behavior of finite models with many homes. The probability distributions for most random variables of interest in the finite model are well approximated by the corresponding probability distributions given by the infinite model, provided the finite model has a large number of homes (Chesson, in press). Examples of such random variables are $P_i(t)$, $n^{-1}\sum_{j=1}^{n} P_j(t)$, and the number of times $P_i(t)$ drops below some level during the first n time intervals.

An important question is, How much need our conclusions be modified to apply to the finite model? For the infinite model we know that increased environmental variability in birth-competition promotes coexistence. Can we validly draw the same conclusion for the finite model? The answer is "yes" provided the number of homes is large enough for the infinite approximation to hold for the range of variability under consideration. This raises the question of whether, for a fixed number of homes, the approximation of the finite model by the infinite model breaks down as variability is increased. This would be true if increased environmental variability results in a corresponding increase in population fluctuation so that low population levels become more frequent with increasing environmental variability. We are able to demonstrate that this is not so (Chesson, in press). There is a definite upper limit on how much the population can fluctuate even when environmental variability in birth-competition is arbitrarily large. For example, if the death rates are equal and nonrandom then increasing variability in birth-

competition, with the mean advantage fixed, produces a limiting model in which $P_1(t)$ has a mean of .5 and a variance of $\frac{1}{4}\delta_1/(2 - \delta_1)$. Nonoverlapping generations means that infinite variability in birth-competition does not lead to infinite variability in population numbers (infinite variability corresponds to a variance of $\frac{1}{4}$); indeed, variability is strictly limited by the degree of overlap in generations. Thus we can conclude that increased environmental variability will not lead to a divergence between the finite and infinite models. In other words, for some fixed but large number of homes, the infinite model will provide a good approximation to the finite model over the entire infinite range of possible environmental variability. Hence, provided the number of homes is large, we can conclude that increased environmental variability in birth-competition promotes coexistence.

CONCLUSION

The deterministic models say that two species cannot coexist in a lottery system unless the ratio of the birth-competition and death parameters are the same for both species. This case is an unlikely, evolutionarily unstable situation and so it appears that random allocation of space alone cannot maintain large-scale species diversity. The deterministic model either has no stable equilibria with both species having positive numbers or is evolutionarily unstable and has only neutrally stable equilibria. The standard equilibrium approach to modeling would see no point in proceeding further because of the assumption that the addition of environmental variability can only lead to further instability and therefore would not alter the conclusions. However we proceeded further to investigate Hutchinson's idea that environmental variability can lead to coexistence by keeping species abundances away from equilibria in which one species is extinct.

If the stochastic analysis involved only the nonoverlapping generations model, one would conclude that Hutchinson's explanation does not work for this system. In these models Hutchinson's idea breaks down for intuitive reasons: Unless the logarithms of the birth-competition parameters have equal means for different species, the superior species will tend to make greater gains during its favorable periods than the other species do during their favorable periods. These gains will add up over time, which means that the superior species comes to dominate the system.

The stochastic analysis of the overlapping generations model completely changes these conclusions, and since most organisms do have overlapping generations we are inclined to regard this model as the more generally applicable. In this model the actual magnitude of the gains made by a species when favored by the environment depends on its relative density. The gains are higher when it is in low abundance and lower when in high abundance. This occurs as follows.

When a species is in high abundance it cannot increase much in an absolute sense, because space is limiting, but it can increase relative to the other species by an arbitrarily large amount if the other species decreases sufficiently. This is exactly what happens in the nonoverlapping generations model where $P_i(t + 1)/P_j(t + 1) = [\beta_i^*(t)/\beta_j^*(t)]P_i(t)/P_j(t)$, which means that the change in the ratio of population sizes is directly proportional to the ratio of the birth-competition

parameters for the two species. Here, if species i occupies most of the space and if it experiences a relatively favorable period, then most of its relative increase is the result of a decline in the other population. In the overlapping generations model things happen differently because during each time period there are survivors from the previous time period. Regardless of how unfavorable birth and competition is for a particular species, its new population must be at least equal to survivorship from the previous period. This puts an upper limit on the relative gains that can be made by a species in high abundance during a favorable period. However, a species in low abundance has virtually unlimited opportunity to increase and therefore can take full advantage of its favorable periods. Mathematically this represents an essential nonlinearity in the overlapping generations model that is absent when generations are nonoverlapping.

In this model the effect of increasing variability in the birth-competition parameter is to increase the gains made by the species, while at low density, during its favorable periods. The losses will also be increased, but by a relatively smaller amount. Hence environmental variability in the birth-competition parameter does promote stability. Moreover, any mean advantage that one species may appear to have can be overcome by environmental variability; that is, there is always a level of variability in the birth-competition parameters which results in coexistence.

If the death parameters, δ_i, are small and δ_j is positively correlated with β_i^*/β_j^* (i.e., a relatively favorable period for species i corresponds to a higher death rate for species j) then increased variability in death rates also promotes coexistence. High values (near 1) of the δ_i do not favor coexistence because then the model is close to the nonoverlapping generations model. If δ_i values can be both high and low but δ_1 and δ_2 are negatively correlated, then extinction of one species can occur, but which species becomes extinct is unpredictable. This situation is favored by increased environmental variability in the death rates.

Our results are in general agreement with Hutchinson's idea that environmental variability can promote species diversity. Environmental variability can increase the chance of coexistence, and in this sense environmental variability can be stabilizing. The idea that environmental variability can destabilize a previously stable equilibrium is borne out by our analysis; however, in our models, destabilization occurs for equilibria in which one species is extinct. The result is coexistence.

Although not part of Hutchinson's original idea, nonlinearity is an essential ingredient in our results; it acts by making the effect of the environment density dependent. In our models nonlinearity has a mitigating effect on environmentally unfavorable periods at low density. However, there are some subtleties involved: What matters is not simply whether a model is linear or nonlinear but whether it is possible to transform the model so that it is linear. For example, the nonoverlapping generations model is described by the nonlinear equation (5), and yet we observe agreement between the results of the deterministic and stochastic versions. On the other hand, if relative densities are expressed as ratios instead of proportions, precisely the same model can be written in the linear form (6), and it is clear that the existence of this linear form is responsible for the close agreement between the deterministic and stochastic versions of the model. There is no such

transformation to linearity for the overlapping generations model (Chesson, in press), and so we say it has an essential nonlinearity. It is the presence of this essential nonlinearity that causes the environment to act in a density-dependent way.

In May's analysis of stochastic Lotka-Volterra models (May and MacArthur 1972; May 1973, 1974a, 1974b, 1974c) nonlinear effects are ignored and the analysis is based on linear approximation to the model about an internal equilibrium, and so there is no opportunity for the environment to operate in a density-dependent manner. In this setting environmental variability does little more than keep species abundances away from equilibrium, and May concludes that environmental variability is generally detrimental to species coexistence. Moreover, he suggests that a small amount of environmental variability may have a large effect.

Turelli (1978a) has pointed out that one needs to examine the behavior of the model near boundary equilibria (where one species is in low abundance) in order to answer questions of persistence and coexistence. Turelli's analysis of difference equation analogues to the stochastic Lotka-Volterra equations (Turelli 1978b, 1980, 1981) shows much milder effects of small amounts of environmental variability: A small amount of environmental variability has at most a small effect which can be either favorable or unfavorable to coexistence. Turelli and Gillespie (1980) provide an exact analysis of the stochastic Lotka-Volterra equations for the case of two competing species with any magnitude of environmental variability. They find that environmental variability has no overall effect on the ability of species to coexist because, in contrast to our model, the range of parameter values permitting coexistence is no broader or narrower than in the deterministic model.

May's approach involving linearization about an internal equilibrium inevitably leads to the conclusion that environmental variability is destabilizing. The analyses of Turelli and Gillespie have emphasized the deficiencies in May's approach, but they do not reveal a strong coexistence promoting role for environmental variability.

The present model gives an example of coexistence without the benefit of a stable equilibrium point. Thus it may be thought of as a case of nonequilibrium coexistence as recently emphasized by Armstrong and McGehee (1980) and Levins (1979). Stewart and Levin (1973) and Koch (1974) have discussed examples of nonequilibrium coexistence which, like ours, depend on temporal variation in the environment, but these examples differ from ours in a number of essential ways. First they emphasize deterministic population cycling, and the nature of the environmental change is fundamentally different. In our models environmental change is incorporated simply by making the parameters of the model functions of time, while in these previous models environmental change involves fundamental changes in the equations governing the species. For example, in Koch's paper the major effect of the environment is a periodic reduction in population size which necessitates an extra equation to define the model. This reduction in population size produces a reduction in competition, a condition which never occurs in our models. Yet contrary to Koch's expectations we obtain a strong coexistence. A

reduction in competition also occurs in Stewart's and Levin's model but it is achieved in a more complex way.

When Sale put forward his lottery idea (Sale 1977) he made two predictions. The first of these is that selective removal of one species of a guild at any site should not be followed rapidly by recovery of the original species composition to that site. This prediction does agree with our model, but we can make a more precise statement: If n individuals from each of two species are simultaneously removed from the same site, then the vacated territories should be refilled independently of the species formerly occupying the territory. This is not so much a prediction from our model as a testable proposition upon which it is based.

The second prediction of Sale is that the diversity of reef communities should be directly correlated with the rate of small scale unpredictable disturbances (including predation) to the supply of living space. This prediction seems more in keeping with the disturbance hypothesis (Paine and Vadas 1969; Connell 1978; Fox 1979) than with the lottery idea. Our analysis suggests that if the death rate increases with disturbance then diversity should decrease. However if disturbance has other effects such as increasing variability in birth rates, then no clear prediction is available because the outcome depends on a combination of factors working in opposition.

The clearest prediction from our model is that diversity should be positively related to variability in birth rate. This might be tested by comparing different regions or different guilds, but unfortunately the difficulty of measuring birth rates precludes such comparisons at the present time.

SUMMARY

In deterministic approaches to modeling, two species are generally regarded as capable of coexistence if the model has a stable equilibrium with both species in positive numbers. Temporal environmental variability is assumed to reduce the likelihood of coexistence by keeping species abundances away from equilibrium.

Here we present a contrasting view based on a model of competition for space among coral reef fishes, or any similarly territorial animals. The model has no stable equilibrium point with both species in positive abundance, yet both species persist in the system provided environmental variability in birth rates is sufficiently high. In general the higher the environmental variability the more likely it is that coexistence will occur. This conclusion is not affected by one species having a mean advantage over the other. Not all kinds of environmental variability necessarily lead to coexistence, however, for when the death rates of the two species are highly variable and negatively correlated, the extinction of one species, determined by chance, is likely to occur.

The results in this paper are shown to depend on the nonlinearity of the dynamics of the system. This nonlinearity arises from the simple fact that the animals have overlapping generations.

When applied to the coral reef fish setting, our analysis confirms the view that coexistence can occur in a system where space is allocated largely at random,

provided environmental variability is sufficiently great (Sale 1977); but our explanations and predictions differ in detail with those of Sale.

APPENDIX

I. *The effect of increasing variability in ρ.*—Coexistence occurs if Δ_1 and Δ_2 are both positive. Note that

$$\Delta_1 = E \log (1 - \delta_1) + E \log [1 + \delta_1(1 - \delta_1)^{-1}\rho]$$

and there is a corresponding expression for Δ_2. Clearly both Δ_1 and Δ_2 will be positive when ρ varies in a manner that allows both $\delta_1\rho$ and $\delta_2\rho^{-1}$ to take on sufficiently large values with some given positive probability. We can be more precise about this as follows. Let ϵ, M, and K be positive numbers and suppose

$$P(\delta_1\rho > M) \geq \epsilon$$

$$P(\delta_2\rho^{-1} > M) \geq \epsilon$$

and

$$E \log (1 - \delta_i) \geq -K, \qquad i = 1, 2;$$

then

$$\Delta_i \geq \epsilon \log M - K, \qquad i = 1, 2. \tag{A1}$$

Clearly the Δ_i will both be positive if M is sufficiently large, indeed $\Delta_i \to \infty$ as $M \to \infty$. To see from this that increasing variability in ρ must eventually give rise to positive Δ_i's we start with a random vector $(\delta_1, \beta_1^*, \delta_2, \beta_2^*)$ and modify it so that variability is increased as follows.

Assume that δ_1 and δ_2 are strictly positive random variables and β_1^*/β_2^* is nondegenerate (not a constant). Then there are positive numbers ϵ, γ, and ζ such that

$$P(\delta_2 > \gamma, \log \beta_1^*/\beta_2^* - E \log \beta_1^*/\beta_2^* > \zeta) \geq \epsilon$$

and

$$P(\delta_1 > \gamma, \log \beta_2^*/\beta_1^* - E \log \beta_2^*/\beta_1^* > \zeta) \geq \epsilon.$$

To increase variability we define $\log \beta_{in}^* = n(\log \beta_i^* - E \log \beta_i^*) + E \log \beta_i^*$, $i = 1, 2$. The variance of $\log \beta_{in}^*$ is an increasing function of n but the mean is fixed. Now

$$P(\delta_2 > \gamma, \log \beta_{1n}^*/\beta_{2n}^* - E \log \beta_{1n}^*/\beta_{2n}^* > n\zeta) \geq \epsilon,$$

and defining $\theta = \exp(E \log \beta_1/\beta_2)$ we have

$$P(\delta_1\rho_n > \theta\gamma e^{n\zeta}) \geq \epsilon.$$

Similarly

$$P(\delta_2\rho_n > \theta^{-1}\gamma e^{nz}) \geq \epsilon.$$

It follows that inequality (A1) applies here with $M = \gamma e^{n\zeta} \min(\theta, \theta^{-1})$ and $K = -\min(E \log |1 - \delta_1|, E \log |1 - \delta_2|)$. Clearly as $n \to \infty, \Delta_{in} \to \infty, i = 1, 2$. In particular, for values of n above some minimum level both Δ_{1n} and Δ_{2n} will be positive.

II. *Small death rates.*—Coexistence is also favored by small values of the δ_i. To see this we again start with some given $(\delta_1, \beta_1^*, \delta_2, \beta_2^*)$. We define $\delta_{in} = (1/n)\delta_i, i = 1, 2$, but do not modify the β^*. This leaves ρ unchanged also. Note that $n \log [1 + \delta_{1n}(\rho - 1)]$ is an increasing function of n with limiting value $\delta_1(\rho - 1)$. Applying the monotone convergence theorem we see that

$$n\,E \log [1 + \delta_{1n}(\rho - 1)] \uparrow E\delta_1(\rho - 1)$$

as $n \to \infty$, i.e., $n\Delta_{in} \uparrow E\delta_1 (\rho - 1)$ as $n \uparrow \infty$. Similarly $n\Delta_{2n} \uparrow E\delta_2(\rho^{-1}-1)$ as $n \uparrow \infty$. This shows that small death rates favor positivity. Indeed if

$$E\delta_1(\rho - 1) > 0 \tag{A2}$$

and

$$E\delta_2(\rho^{-1}-1) > 0, \tag{A3}$$

then both Δ_{1n} and Δ_{2n} will be positive for n sufficiently large. The LHS's of A2 and A3 can be considered approximate expressions for Δ_1 and Δ_2 when δ_1 and δ_2 are small. If δ_1 and δ_2 are nonrandom the approximate coexistence criteria become $E\rho > 1$ and $E\rho^{-1} > 1$.

The approximate coexistence criteria (A2) and (A3) can be used to see how variability in the δ_i affects coexistence when the δ_i are small. Write θ_1 for the correlation between β_1^*/β_2^* and δ_2, and θ_2 for the correlation between β_2^*/β_1^* and δ_1. We have

$$E\delta_1(\rho - 1) = E\delta_2(\beta_1^*/\beta_2^*) - E\delta_1$$

$$= \theta_1(V\delta_2)^{\frac{1}{2}}(V\beta_1^*/\beta_2^*)^{\frac{1}{2}} + (E\delta_2)(E\beta_1^*/\beta_2^*) - E\delta_1. \tag{A4}$$

First of all note that variability in δ_1 has no effect on $E\delta_1(\rho - 1)$, which means also that variability in δ_2 has no effect on $E\delta_2(\rho^{-1}-1)$. Second, if $\theta_1 = 0$ then variability in δ_2 also has no effect on $E\delta_1(\rho - 1)$. However, if θ_1 is positive $E\delta_1(\rho - 1)$ increases as a function of $V\delta_2$ and if θ_1 is negative $E\delta_1(\rho - 1)$ decreases as a function of $V\delta_2$.

Hence we can conclude that coexistence is favored by positive θ's and variable δ's and exclusion is favored by one or two negative θ's and variable δ's.

III. *Zero mean advantage.*—When $E \log \rho = 0$ it is possible to have Δ_1 and Δ_2 positive with arbitrarily small variability in ρ. To see this note that since log is a strictly concave function with $\log 1 = 0$,

$$\log(1 - \delta_1 + \delta_1\rho) \geq \delta_1\log \rho \tag{A5}$$

with strict inequality whenever $\rho \neq 1$. It follows that any variability at all in ρ must give

$$\Delta_1 > E\delta_1\log \rho. \tag{A6}$$

If δ_1 were nonrandom we would have $E\delta_1\log \rho = \delta_1 E \log \rho = 0$ and hence $\Delta_1 > 0$. Similarly $\Delta_2 > 0$ whenever δ_2 is nonrandom. The same results hold if the δ_i and $\log \rho$ are uncorrelated or δ_1 and δ_2 have, respectively, positive and negative correlations with $\log \rho$. In other cases Δ_1 could be negative or zero. However if β_1^*/β_2^* is random then it can be shown that there is a positive lower bound to the difference $\Delta_1 - E\delta_1\log \rho$ when the distribution of β_1^*/β_2^* is held constant, $E\delta_1$ and $E\delta_2$ are bounded above 0 and the variability in the δ_i is allowed to decrease to 0. Since $E\delta_1\log \rho \to 0$ as $V\delta_i \to 0$ it is clear that the Δ_i will be positive for $V\delta_i$ sufficiently small.

IV. *Random exclusion.*—Here we show how variable and negatively correlated death rates can result in case d, random exclusion.

Define $K = \max \{E \log(1 + \beta_i^*/\beta_j^*) \,|\, i = 1, 2, j = 1, 2\}$ and assume that there are positive numbers γ and ϵ such that

$$P(\delta_i < \gamma, \delta_j > 1 - \gamma) \geq \epsilon$$

for $i \neq j$. Small γ and high ϵ imply that δ_1 and δ_2 are highly variable and negatively correlated.

Now

$$\Delta_1 = E \log(1 - \delta_1 + \delta_2 \beta_1^*/\beta_2^*)$$

and when $\delta_2 < \gamma$ and $\delta_1 > 1 - \gamma$ we have $\log(1 - \delta_1 + \delta_2\beta_1^*/\beta_2^*) \leq \log \gamma + \log(1 + \beta_1^*/\beta_2^*)$. It is always true that $\log(1 - \delta_1 + \delta_2\beta_1^*/\beta_2^*) < \log(1 + \beta_1^*/\beta_2^*)$ and it follows that

$$\Delta_1 \leq \epsilon \log \gamma + E \log(1 + \beta_1^*/\beta_2^*)$$

$$\leq \epsilon \log \gamma + K.$$

The same inequality applies for Δ_2, i.e., we have

$$\Delta_i \leq \epsilon \log \gamma + K$$

for $i = 1, 2$. Thus if γ is small enough both Δ_1 and Δ_2 will be negative. Indeed $\Delta_i \rightarrow -\infty$ as $\gamma \rightarrow 0$.

It is instructive to consider a more specific example of random exclusion. Assume that $\beta_1^* = \beta_2^*$ and that the distribution of $\delta_1 - \delta_2$ is symmetric about 0. We have

$$\Delta_1 + \Delta_2 = E \log(1 - \delta_1 + \delta_2) + E \log(1 - \delta_2 + \delta_1)$$
$$= E \log [1 - (\delta_1 - \delta_2)^2].$$

Provided $V(\delta_1 - \delta_2) \neq 0$ then $\Delta_1 + \Delta_2 < 0$. But here $\Delta_1 = \Delta_2$ and so both Δ_1 and Δ_2 are negative. In this case "sufficient" variability is any variability and a sufficiently "negative" correlation is any correlation less than $+1$.

V. *The relationship between Δ's based on different δ's.*—The Δ_i generally have to be calculated by numerical integration. Here we show how a special identity can be used to save computation and make the graphs given in the text more useful.

In the text Δ values are calculated for lognormal ρ and nonrandom δ's. In this case $\log \rho = \sigma X + \mu$ where X is normal with mean 0 and variance 1. Writing Δ_1 as a function of δ_1, μ and σ^2 the following identity is easily derived.

$$\Delta_1(\delta_1', \mu + \log[(1 - \delta_1')\delta_1(1 - \delta_1)^{-1}\delta_1'^{-1}], \sigma^2)$$

$$= \Delta_1(\delta_1, \mu, \sigma^2) + \log[(1 - \delta_1')(1 - \delta_1)^{-1}].$$

Using this identity, the curves given in the text for Δ_1 as a function of μ for $\delta_1 = .1$ can be converted into the corresponding curves for any value of δ_1.

LITERATURE CITED

Anderson, G. R. V., A. H. Ehrlich, P. R. Ehrlich, J. D. Roughgarden, B. C. Russell, and F. H. Talbot. 1981. The community structure of coral reef fishes. Am. Nat. 117:476–495.
Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. Am. Nat. 115:151–170.
Botkin, D. B., and M. J. Sobel. 1975. Stability in time-varying ecosystems. Am. Nat. 109:625–646.
Breiman, L. 1969. Probability and stochastic processes: with a view toward applications. Houghton Mifflin, Boston.
Chesson, P. L. 1978. Predator-prey theory and variability. Annu. Rev. Ecol. Syst. 9:323–347.
———. In press. The stabilizing effect of a random environment. J. Math. Biol.
Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.
Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge.
Dale, G. 1978. Money in the bank: a model for coral reef fish coexistence. Environ. Biol. Fishes 3:103–108.
Dempster, E. R. 1955. Maintenance of genetic heterogeneity. Cold Spring Harbor Symp. Quant. Biol. 20:25–32.
Doob, J. L. 1953. Stochastic processes. Wiley, New York.

Feller, W. 1971. An introduction to probability theory and its applications. 2d ed. Wiley, New York.

Fox, J. F. 1979. Intermediate-disturbance hypothesis. Science 204:1344–1345.

Horn, H. A., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53:749–752.

Hutchinson, G. E. 1961. The paradox of the plankton. Am. Nat. 95:137–145.

Koch, A. L. 1974. Coexistence resulting from an alteration of density dependent and density independent growth. J. Theor. Biol. 44:373–386.

Levins, R. 1979. Coexistence in a variable environment. Am. Nat. 114:765–783.

Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. Proc. Natl. Acad. Sci. USA 68:1246–1248.

Ludwig, D. 1976. A singular perturbation problem in the theory of population extinction. Soc. Ind. Appl. Math. Am. Math. Soc. Proc. 10:87–104.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. Am. Nat. 107:621–650.

———. 1974a. Ecosystem patterns in randomly fluctuating environments. Pages 1–50 in R. Rosen and F. Snell, eds. Progress in theoretical biology. Academic Press, New York.

———. 1974b. On the theory of niche overlap. Theor. Popul. Biol. 5:297–332.

———. 1974c. Stability and complexity in model ecosystems. 2d ed. Princeton University Press, Princeton, N.J.

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

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanogr. 14:710–719.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337–359.

———. 1978. Coexistence of coral reef fishes—a lottery for living space. Environ. Biol. Fishes 3:85–102.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128–134.

Stewart, F. M. and B. R. Levin. 1973. Partitioning of resources and the outcome of interspecific competition: a model and some general considerations. Am. Nat. 107:171–198.

Turelli, M. 1977. Random environments and stochastic calculus. Theor. Popul. Biol. 12:140–178.

Turelli, M. 1978a. A reexamination of stability in randomly fluctuating versus deterministic environments. Theor. Popul. Biol. 13:244–267.

———. 1978b. Does environmental variability limit niche overlap? Proc. Natl. Acad. Sci. USA 75:5085–5089.

———. 1980. Niche overlap and invasion of competitors in random environments II. The effects of demographic stochasticity. Pages 119–129 in W. Jäger et al., eds. Biological growth and spread: mathematical theories and application. Lecture notes in biomathematics. Vol. 38. Springer-Verlag, New York.

———. 1981. Niche overlap and invasion of competitors in random environments I. Models without demographic stochasticity. Theor. Popul. Biol. (in press).

Turelli, M., and J. H. Gillespie. 1980. Conditions for the existence of asymptotic densities for some two-dimensional diffusion processes with applications in population biology. Theor. Popul. Biol. 17:167–189.