

chapter 14

Environmental Variation and the Coexistence of Species

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INTRODUCTION

Variation is a striking feature of many real populations and communities. Variation in both time and space occurs in the environment, in species densities, and in relative densities. The widespread occurrence of variation raises a number of important questions. Of what significance is variation to the dynamics of populations and communities? What note should ecologists take of variation? Are the effects of predictable variation, such as seasonal environmental variation, different from the effects of unpredictable variation, such as yearly rainfall or temperature? How is it possible to tell if the structure of a community depends on environmental variation?

Historically, ecologists' attitudes to variation have themselves been quite varied. Some, such as Andrewartha and Birch (1954), have focused on variation or fluctuations in population numbers and have sought the causes of such variation. Community ecologists usually have rather different questions in mind and view variation mainly in terms of how it affects community

structure or how it affects the study of community structure. Four different views of variation are set out below with a focus on stochastic variation, that is, variation that is not predictable with high confidence from one time to the next. The weather gives us many examples of stochastic environmental variation, but it must be remembered that stochastic variation still has its predictable aspects. For instance, yearly rainfall may be highly stochastic, while the average rainfall over a sufficient number of years is highly predictable.

Among the views of variation discussed here, view D is the one that is most strongly supported by models. Models of coexistence by means of recruitment variation are presented as a principal illustration of this view. Other models have not necessarily supported the idea that environmental variation promotes coexistence, but this chapter will show how the seemingly conflicting results of a variety of models can be understood within the context of a single general model. This general model suggests how certain kinds of life history traits may be generally favorable to coexistence in a temporally varying envi-

ronment. If the environment varies in space and time, then life history traits such as dispersal may also be important, and models incorporating dispersal in a spatially varying environment have strong similarities to models of recruitment variation in time.

It is often assumed that stochastic mechanisms of coexistence, such as those discussed here, will lead to population dynamics that are fundamentally different from those associated with deterministic mechanisms of coexistence. However, I shall argue that these two different sorts of mechanisms of coexistence may yield quite similar population dynamics in the real world.

FOUR VIEWS OF VARIATION

View A: Variation is noise, and it tends to obscure what is really happening in a system. This view makes no distinction between variation and sampling error. Sampling error is a common problem in ecological research. For instance, there are various methods one can use to try to determine the size of a small mammal population in a particular locality at a particular time (Seber 1982), but all entail sampling errors that can make it difficult to get an accurate result. However, there is nevertheless a true value for the population size for the particular place and time, and this value is potentially knowable.

Now consider a fish population. One may wish to know the number of juvenile fish maturing to adulthood, that is, the number of new recruits, in a particular year. This too has a true, potentially knowable value, but fisheries biologists often want more; they want to know the relationship between the size of the adult stock and the number of new recruits. One can measure the number of new recruits for different values of the adult stock, for the adult stock varies in time. Getting the relationship will certainly involve sampling error, but something else is going on also. Although two different years may have the same adult stock sizes, the actual numbers of recruits for these two years may be quite different (Cushing 1982). This has nothing to do with sampling error, for the numbers of recruits for the two different years are truly different, as would be seen if every individual in the population were

counted. Thus, if sampling error could be eliminated, there would still not be any precise relationship between stock and recruitment. Nevertheless, there will be a mean value for recruitment over many years with the same stock size, and view A treats the relationship between this mean value of recruitment and the stock size as the "true" relationship. Variation from this relationship is regarded as noise, or error, that need not be distinguished from errors resulting from the difficulties of sampling.

The remaining three views do make a distinction between sampling error and variation in the true population size and assume that variation in population size, and in environmental factors, is important to the workings of a population or the organization of a community.

View B: Variation is present and important. If the variation is stochastic, it is harmful in the sense that it increases the probability of extinction of a population and decreases the diversity of a community. This view pervades deterministic approaches to modeling. A stable equilibrium point, or a stable cycle, is regarded as necessary for community persistence. Stochastic variation causes displacements from equilibrium, and if sufficiently strong, it may cause some species to become extinct. For a community to persist in the face of strong stochastic variation, there must be strong deterministic forces opposing the displacements from equilibrium that are caused by the stochastic variation.

Many ideas and theories have developed in response to this view, including ideas on limiting similarity, multiple stable points, resilience, and vulnerability (May and MacArthur 1972, Holling 1973, May 1974b, Goh 1975, 1976, Leigh 1975, Beddington et al. 1976). As emphasized, this view mostly concerns stochastic variation because of its unpredictable properties.

View C: Variation leads to interruptions or reversals of biological interactions. It thereby slows down competitive exclusion and may prevent it from occurring on an ecologically relevant time scale. Hutchinson (1961) gave the first detailed discussion of this view. He suggested that competing species may coexist as a

result of changes in the environment that reverse the order of competitive superiority among the species. Hutchinson argued that if such environmental changes occur with a period roughly equal to the time for competitive exclusion of a species, then competitive exclusion would be prevented and a rich community might result. However, if the period between environmental changes is quite different from the time for competitive exclusion (either longer or shorter), then competitive exclusion would still occur.

Ideas on disturbance (Paine and Vadas 1969, Connell 1978, Caswell 1978, Fox 1979, Abugov 1982) usually involve the notion that environmental events or predators interrupt biological processes and prevent monopolization of resources (usually space) by a single species. Intuitively, interruption of biological processes, especially competition, should delay competitive exclusion. Theoretical support for this idea comes from Huston's (1979) model, in which disturbance leads to a reduction in the population sizes of all species and consequently a temporary reduction in competition. On the other hand, Caswell's (1978) analysis of a different model of disturbance assumes at the outset that the degree of delay of competitive exclusion is the appropriate focus of the analysis.

That environmental variation may primarily slow the rate at which competitive exclusion occurs is not an uncommon view, and although not stated explicitly in Hutchinson's original discussion, it is implicit in his arguments. In this view environmental variation is very different from mechanisms like resource partitioning that lead to stable equilibria in models and thereby eliminate trends toward extinction of one or more species. Variation is not seen as eliminating these trends; it merely slows them down. Often associated with this view is the idea that population dynamics should appear very unstable with large fluctuations in species relative abundances (Grossman 1982, Grossman et al. 1982).

View D: Variation not only slows processes like competitive exclusion, but changes trends as well. Species that cannot coexist in a constant environment may in the presence of variation all show positive average growth rates at low den-

sity. Each species would thus have an upward trend whenever its density is low. Moreover, in this view variation can lead to the creation of a central tendency for population fluctuations, analogous to the existence of a stable equilibrium point in a deterministic model. Variation is not greatly distinguished in its action from other forces in a community like competition or predation. Like these forces, variation may change average growth rates in a positive or a negative direction depending on the circumstances.

Levins (1979) gives perhaps the best expression to date of this view. He suggests that when a limiting resource varies in abundance, species may partition different aspects of resource variation. For example, some species may act like consumers of the resource variance, while others are consumers of the resource mean. By so partitioning resource variation, several species may coexist on a single limiting resource.

View D is also expressed implicitly in a number of models of disturbance in a patchy environment (Slatkin 1974, Crowley 1979, Hastings 1980). Disturbances are assumed to occur asynchronously in the different patches of a large (effectively infinite) habitat. These models all produce the result that disturbance can lead to an indefinite, stable coexistence, in the total habitat, of two or more strong competitors. Moreover, the coexisting species all have positive growth rates at low density. Crowley (1979) and Chesson (1981) argue that the sort of coexistence found in these models of infinite habitats is a reflection of tendencies that are present in more realistic models of finite habitats, but are more difficult to see there.

According to view D, it does not greatly matter whether environmental variation is regular (e.g., seasonal) or stochastic. With both kinds of variation the environment goes through a number of states, and both give a predictable frequency of different environmental states at least in the long term. These long-run frequencies of the different states are seen as one of the most important aspects of the environmental variation. Naturally, a regularly varying environment is predictable in the short term as well as in the long term, but this is not of overriding importance.

A considerable amount of evidence from sto-

chastic models has accumulated in support of view D, and the rest of this chapter is an elaboration of this view.

COEXISTENCE MEDIATED BY TEMPORAL VARIATION

An important role of environmental variation in population dynamics is suggested by the relative fragility of the juveniles of many organisms. Juvenile mortality rates are high and sensitive to environmental conditions. Thus, if the environment varies, juvenile survival varies widely. In contrast, adults may have higher survival rates that are relatively insensitive to environmental conditions. However, reproductive rates, like juvenile survival, may vary substantially with environmental factors. Indeed, since there is believed to be a trade-off between reproduction and adult survival (Murdoch 1966, Goodman 1974, Nichols et al. 1976, Schaffer 1979), some organisms may maintain high adult survival by varying their reproductive effort in response to the environment. Deferring reproduction in response to unfavorable environmental conditions may also permit deferring the use of resources that are allocated to reproduction (Harper 1977, Nichols et al. 1976, Tyler and Dunn 1976). A likely outcome of this deferral of resources is both a greater mean magnitude and a higher level of variability in recruitment. Extreme reproductive variation in some long-lived organisms, for example, some perennial plants, is believed to be not so much a response to environmental conditions, but a mechanism that thwarts predators (Silvertown 1982).

The characteristics of high and relatively unvarying adult survival coupled with highly variable juvenile survival or highly variable reproductive rates are not uncommon species properties, but are especially well documented for fishes (Gulland 1982, Cushing 1982) and perennial plants (Grubb 1977 and Chapter 12, Harper 1977, Hubbell 1980). These characteristics are also becoming increasingly apparent for sessile marine organisms (Butler and Keough 1981, Keough 1983, Underwood and Denley 1984, Caffey 1985). I now present models of communities having these features, for they provide an

especially valuable demonstration of the validity of view D.

Models of Communities

Consider a community of n species, each having the characteristics discussed above. An equation for the dynamics of the system is

$$X_i(t+1) = (1 - \delta_i)X_i(t) + R_i(t)X_i(t) \quad (14.1)$$

where $X_i(t)$ is the population of the i th species at time t , δ_i is the adult death rate, and $R_i(t)$ is the recruitment rate (the per capita number of new individuals entering the adult population). Equation 14.1 expresses the new population at time $t+1$ as the sum of adult survival and recruitment.

While adult survival is assumed not to vary in time, the recruitment rate varies as a function of both the environment and species densities. The recruitment rate is the product of the reproductive rate and the juvenile survival rate and reflects the effects of interactions within and between species, in addition to the effects of a varying environment. Thus, the recruitment rate can be expressed in the form

$$R_i(t) = f_i[E(t), X_1(t), \dots, X_n(t)] \quad (14.2)$$

where f_i is some function, $E(t)$ is a multidimensional variable representing the state of the environment at time t , and n is the number of species. The different dimensions of the environment can be things like temperature and moisture and can also include disturbances of different kinds. The involvement of a fluctuating environment in the recruitment rate means that regulation of recruitment may be density-vague (Chapter 15).

Because population growth is fundamentally a multiplicative process, we can best understand the consequences of equation 14.1 by taking logs. Then we see that the change in log population size is

$$\begin{aligned} \ln X_i(t+1) - \ln X_i(t) \\ = \ln[1 - \delta_i + R_i(t)] \end{aligned} \quad (14.3)$$

This change in log population over one time interval can be thought of as the instantaneous per capita growth rate applicable for that time period.

Since an adult lives an expected life time of

$(\delta_i)^{-1}$ time units (breeding seasons), it is helpful to divide this growth rate by δ_i to obtain a growth rate measured on a per generation time scale, a "scaled growth rate." This facilitates the comparison of species having different longevities. Expressing the recruitment rate on this same time scale as $\rho_i(t) = R_i(t)/\delta_i$, the "scaled recruitment rate," we obtain

$$\begin{aligned} \delta_i^{-1} [\ln X_i(t+1) - \ln X_i(t)] \\ &= \delta_i^{-1} \ln[1 - \delta_i + R_i(t)] \\ &= \delta_i^{-1} \ln\{1 + \delta_i[\rho_i(t) - 1]\} \quad (14.4) \end{aligned}$$

Notice that the population increases from one time to the next if $\rho_i(t) > 1$ and also that the change in log population from any time t_1 to some other time t_2 ($\ln X_i(t_2) - \ln X_i(t_1)$) can be obtained by summing equation 14.4 over the values $t = t_1$ to $t = t_2 - 1$, and multiplying by δ_i . In particular, the sign of the sum of the scaled growth rate over any period indicates whether the population has increased over that period.

The scaled growth rate is plotted as a function of scaled recruitment in Fig. 14.1. The ρ axis has a log scale, which means that the scaled growth rate for $\delta_i = 1$ plots as a straight line. The curve for $\delta_i = 0$ is the limit of the scaled growth rate as death rates are made small. The most important feature of these curves is that, except when $\delta_i = 1$ (nonoverlapping generations), the scaled growth rate has a lower bound equal to

$$\delta_i^{-1} \ln(1 - \delta_i) \quad (14.5)$$

which is achieved when recruitment fails completely ($\rho_i(t) = 0$). For small δ_i ($\delta_i \leq 1/3$), the lower bound given by equation 14.5 is reasonably approximated by -1 . Thus, when generations are overlapping, the scaled growth rate can never be less than the value of equation 14.5, which is the value determined by adult survival from the previous period. When $\delta_i = 1$, there is no adult survival, and it follows that when recruitment fails, the scaled growth rate is $-\infty$. Note that in no case is there an upper bound on the growth rate as a function of the recruitment rate; if a large recruitment occurs, the growth rate will be large. Notice also that the scaled growth rate curves up more strongly (is more convex in the mathematical sense) for smaller adult death rates.

These properties of the scaled growth rate are

explored in Fig. 14.2, where it is assumed that scaled recruitment fluctuates between the two values 1/5 and 5. If the scaled recruitment rate takes these values with equal frequency, then the average growth rate can be found as the midpoint of the line joining the two values of the scaled growth rate, for example, the point C joining A and B in Fig. 14.2. Although the figure illustrates only the case $\delta_i = 0.1$, this average value is positive for all values of δ_i except for $\delta_i = 1$, indicating that the population will show a net increase over all periods in which these two values for the scaled recruitment are equally frequent. The actual change in log population size is found by multiplying the average growth rate by the time period involved.

Values of the average growth rate for cases when the two values of the recruitment rate are not equally frequent are found in a similar manner. The points D and E are placed at 1/4 and 3/4 of the distance from $\rho = 1/5$ to $\rho = 5$, corresponding to cases where poor recruitment has a relative frequency of 3/4 and 1/4. The intersections of the vertical lines through D and E with the straight lines joining the values of the growth rates give the average growth rates with these recruitment frequencies.

With nonoverlapping generations the average growth rate is always negative whenever the poor recruitment is more frequent. However, with overlapping generations it is possible to have a positive average growth rate even though recruitment is poor much of the time. The smaller the adult death rate, the more likely it is that this will be so, for then the scaled growth rate is more strongly curved as a function of scaled recruitment. When adult death rates are small, survival from periods of strong recruitment can more than compensate for periods of poor recruitment, even when periods of poor recruitment are more frequent (provided such poor recruitments are not too frequent). This is reflected in the lower limit (equation 14.5) to the growth rate. Moreover, the average growth rate is relatively insensitive to the actual magnitude of poor recruitments (Fig. 14.3). Indeed, positive average growth is still possible in the face of complete recruitment failure ($\ln \rho = -\infty$), provided strong recruitments occur at other times.

These ideas extend beyond the case where re-

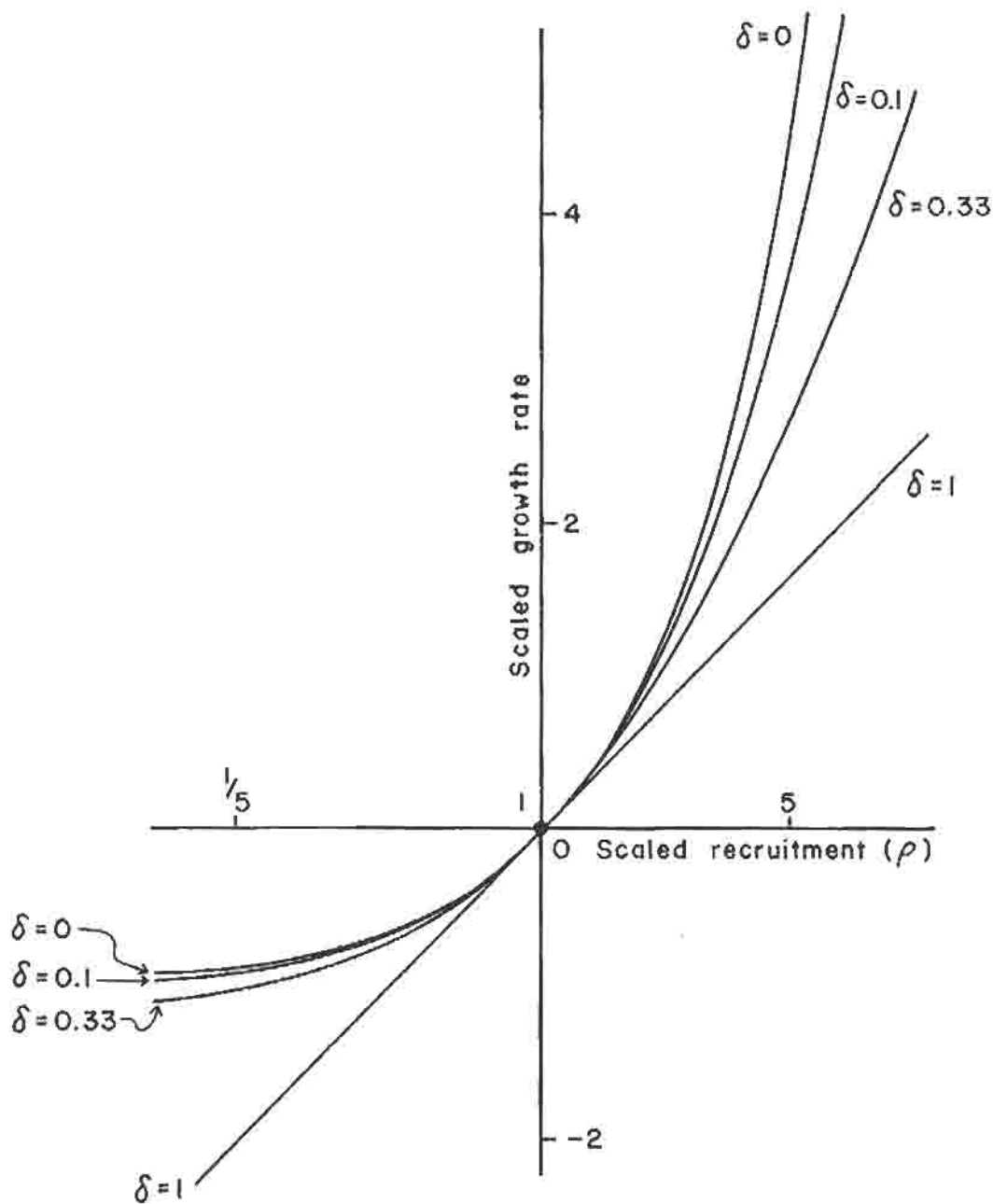


Fig. 14.1 Relationship between scaled growth rate (per capita growth rate scaled by the generation time) and scaled recruitment (per capita recruitment scaled by the generation time), for different values of the adult death rate, δ . Scaled recruitment is represented on a log scale. For $\delta = 1$ the relationship is linear, but for $\delta < 1$, the relationship is curved, with stronger curvature for smaller δ . Note that for all cases of $\delta < 1$ the scaled growth rate approaches a finite constant as scaled recruitment decreases.

recruitment takes on just two values to cases of arbitrary variation in recruitment (Chesson 1983). In particular, the simple idea that positive average growth is possible on the basis of periods of strong recruitments alone, when generations are overlapping, applies generally and has been termed the "storage effect" (Chesson 1983).

The interest here in the effects of variable recruitment and overlapping generations is not so

much for what they have to say about a single species, for that has been discussed at length by others (Murphy 1968, Schaffer and Gadgil 1975, Hastings and Caswell 1979, Goodman 1984), but for what they have to say about coexistence of a set of interacting species. For example, species in strong competition may depress each other's recruitment rates. The results above show that a species may still be able to have a positive aver-

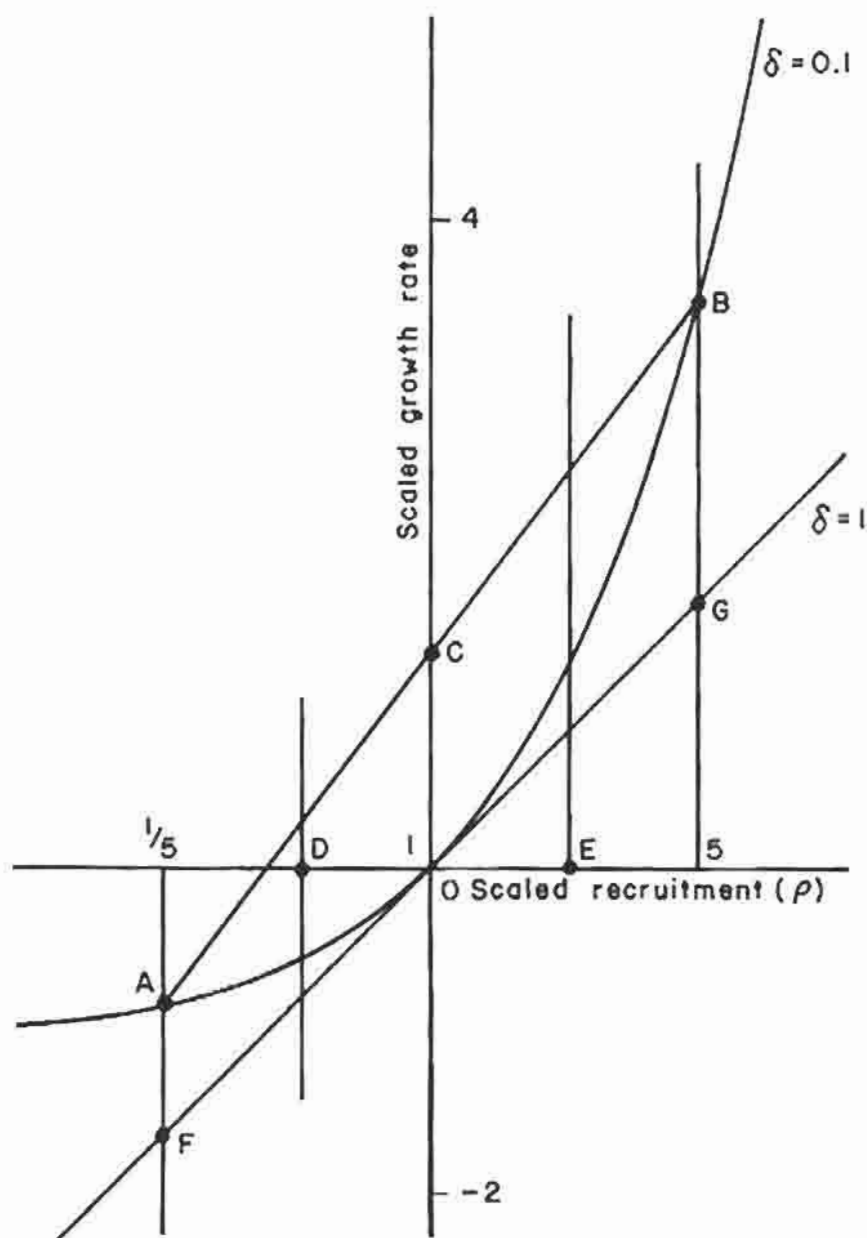


Fig. 14.2 Average growth rates in a fluctuating environment. If the scaled recruitment, ρ , fluctuates between 5 and $1/5$, then the scaled growth rate fluctuates between the values A and B ($\delta = 0.1$) or F and G ($\delta = 1$). The average growth rate lies on the straight line joining the two values of the scaled growth rate. For example, if ρ takes its two values equally frequently, then the average growth rate is at C ($\delta = 0.1$) or 0 ($\delta = 1$). If $\rho = 1/5$ occurs three times more often than $\rho = 5$, then the vertical line through D intersects lines AB and FG at the average growth rates. If $\rho = 5$ occurs three times more often than $\rho = 1/5$, then the line through E intersects at the average growth rates. Note that with $\delta = 0.1$ the average growth rate is positive in all of these cases, while for $\delta = 1$ (nonoverlapping generations) the average growth rate is positive only when the value $\rho = 5$ is more frequent.

age growth rate when faced with strong competition, provided it still has periods when it is able to recruit well. Moreover, it can do this even if much of the time it is at a disadvantage to other species and often recruits poorly. As suggested by Hutchinson (1961), variation in the environment may vary the relative competitive abilities of species, leading to strong recruitments for different species at different times.

A positive average growth rate at low density is important for persistence and, indeed, is a useful stochastic persistence criterion (Turelli 1978, 1981; Chesson 1982). At low density intraspecific competition will be minimal. Consequently, if the environment sometimes gives a species the edge in terms of interspecific competition, the

per capita number of recruits, $R_i(t)$, may be large. If such good recruitments are sufficiently strong, given their frequency, then the species will be able to recover from low density and hence persist in the system; its average growth at low density will be positive. In this way a number of negatively interacting species may be able to coexist as a result of varying recruitment rates.

The Lottery Model

The idea that varying recruitment can promote the coexistence of competing species is simply illustrated by the lottery model of competition (Chesson and Warner 1981). In this model competition is assumed to be for space. Although

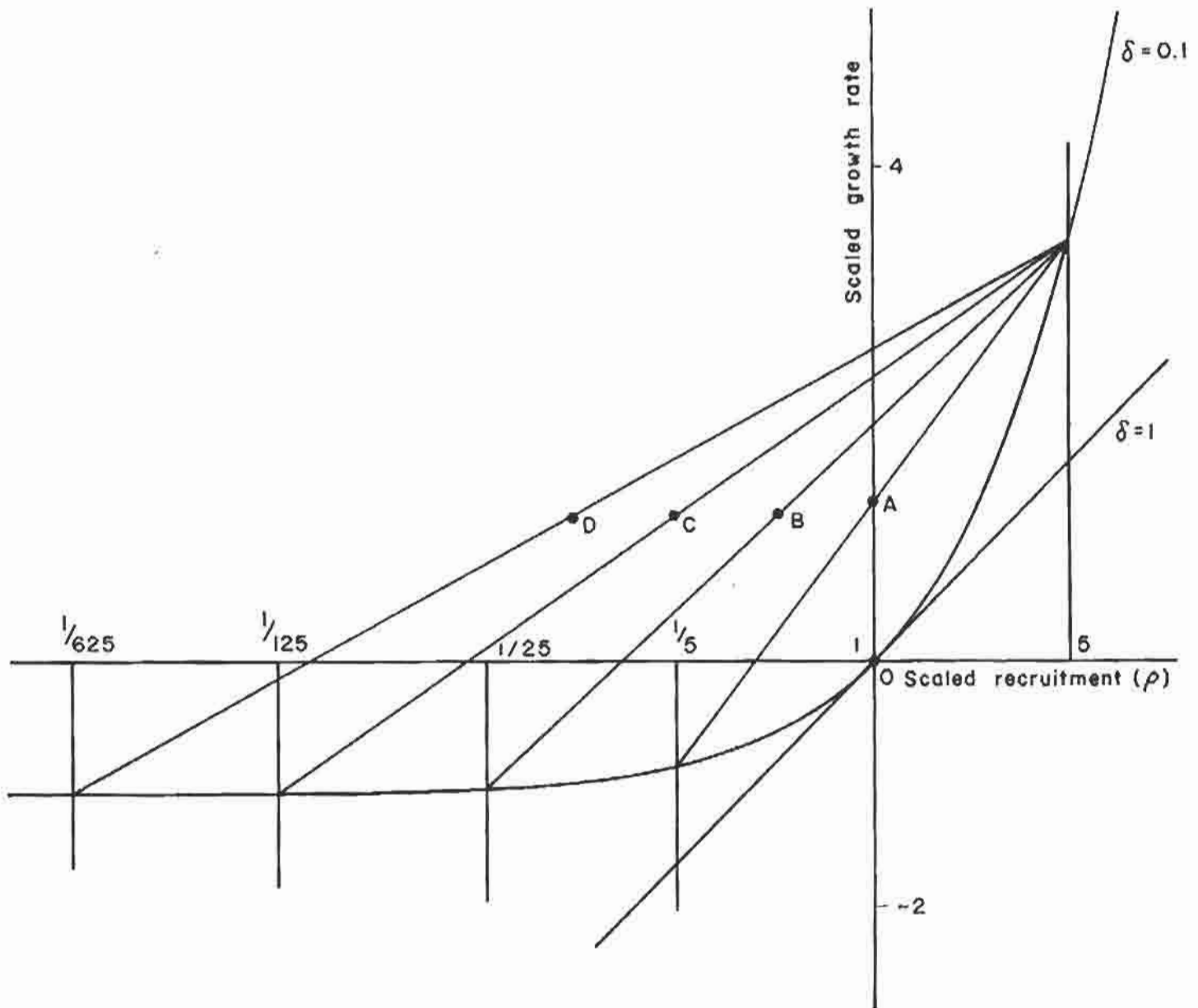


Fig. 14.3 Insensitivity of average growth rates to the magnitude of poor recruitment. The two values of recruitment are assumed equally frequent. The points A through D give the average growth rates when poor recruitment has the values $1/5$ through $1/625$, for $\delta = 0.1$. (A through D are the midpoints of the line segments.) For nonoverlapping generations ($\delta = 1$) the average growth rates are strongly negative when the poor recruitment is $1/25$ or less.

originally formulated to apply to territorial reef fishes, as discussed by Sale (1977), it is a useful model for other space-holding organisms as well. In particular, Comins and Noble (1985) have applied the model to forest trees, and Shmida and Ellner (1985) have suggested modifications of the model for other plant communities. Woodin and Yorke (1975) discussed a similar model for soft-bottomed benthic invertebrates, and the model is also closely related to Hubbell's (1979) model for tropical forests as discussed below.

In the lottery model potential recruits become adults by acquiring units of space, and space becomes available by death of adults. Thus, for a two-species system the amount of space becoming available is

$$\delta_1 X_1(t) + \delta_2 X_2(t) \quad (14.6)$$

because this is the number of adults that have died. The number of juveniles of species i seeking to settle in this space is assumed to be $\beta_i(t)X_i(t)$, where $\beta_i(t)$ is the product of the per

capita birth rate and the presettlement juvenile survival rate and is assumed to be a function of the environment, $E(t)$. In the forest example $\beta_i(t)$ might represent the average number of viable seeds produced by a tree in year t , and it may also include any density-independent mortality of seedlings. It can be thought of as representing the number of adult trees that would result from the average seed crop of a tree of species i , in year t , if the seedlings were grown in the absence of competition from other juveniles or adults. In the reef fish example $\beta_i(t)$ represents the product of the brood size of a female for year t and juvenile survival in the plankton for that year.

The lottery model assumes that space is allocated at random (by "lottery") to the juveniles of the two species. Thus, the fraction of the available space allocated to juveniles of species i is

$$\frac{\beta_i(t)X_i(t)}{\beta_1(t)X_1(t) + \beta_2(t)X_2(t)} \quad (14.7)$$

Multiplying equations 14.6 and 14.7 to get the number of new recruits and adding in adult survival, we find that the adult population at time $t + 1$ is

$$X_i(t + 1) = (1 - \delta_i)X_i(t) + [\delta_i X_1(t) + \delta_2 X_2(t)] \frac{\beta_i(t)X_i(t)}{\beta_1(t)X_1(t) + \beta_2(t)X_2(t)} \quad (14.8)$$

The formula for the recruitment rate is

$$R_i(t) = [\delta_i X_1(t) + \delta_2 X_2(t)] \frac{\beta_i(t)}{\beta_1(t)X_1(t) + \beta_2(t)X_2(t)} \quad (14.9)$$

It is important to note that in these equations the species densities sum to the total amount of space, so that when one species is at low density, the other species is at high density.

As noted above, the important values of the scaled recruitment rate are those occurring at low density. Setting $X_i(t) = 0$ in equation 14.9, these low-density values are found to be

$$\rho_1(t) = \frac{\beta_1(t)/\delta_1}{\beta_2(t)/\delta_2}$$

$$\rho_2(t) = \frac{1}{\rho_1(t)}$$

These expressions compare the ratio of β and δ for one species with the ratio for the other species. Although calculated for low density, a little algebra shows that these values for the $\rho_i(t)$ determine for all densities whether a species will be increasing. Thus, if $\rho_1(t) > 1$, then $\rho_2(t) < 1$, and species 1 increases at the expense of species 2. Since the $\rho_i(t)$ are determined entirely by the environment (in this system), there is no possibility of coexistence if the environment does not vary. (The best that can be achieved is a neutral equilibrium when $\rho_1(t) = \rho_2(t) = 1$.)

The reason for the failure of coexistence in a constant environment can be understood from the fact that among juveniles interspecific and intraspecific competition is equally intense, for only in this way can allocation of space be random. It follows that whichever species is at an advantage either reproductively or in adult survival will be able to displace the other species. However, when the environment varies, the advantage may shift between the two species. If generations are overlapping, this variation can lead to coexistence in the sense that each species shows upward trends from low density.

To see how coexistence occurs in variable environments, consider first a case where the species are equal on average, but the environment fluctuates so that the high value of ρ in Fig. 14.2 occurs half the time and the low value occurs the rest of the time. Note that when one species has the high value of ρ , the other has the low value of ρ . The average low-density growth rates for both species are then obtained at the intersection of the vertical axis with the line joining the values of the growth rates. Thus, the mean growth at low density is positive for both species. This is illustrated in Fig. 14.2 for the case $\delta_i = 0.1$, but positive average growth rates for both species occur in all cases except the case of non-overlapping generations ($\delta_i = 1$). When $\delta_i = 1$, the average growth rates are 0, and consequently a random walk occurs with one species eventually approaching extinction (Chesson and Warner 1981).

If the conditions are changed so that one species has an advantage over the other (for example, has three times as many favorable periods as the other), then the vertical lines D and E of Fig. 14.2 are used, instead of the vertical axis, to get

the average values of the growth rates. The average growth rate of the advantaged species is given by line E, while that of the disadvantaged species is given by line D. Note again that when generations are overlapping, both species can have positive average growth rates at low density and thus will tend to increase whenever their densities become low. With nonoverlapping generations, however, only one species can have a positive average growth rate at low density, and the other species therefore must become extinct. Overlapping generations have introduced an asymmetry between the effects of good periods and bad periods; poor recruitments can be made arbitrarily poor to the point of complete recruitment failure without a large change in the average growth rates.

Thus, when the environment varies in such a way that each species has times when it can have strong recruitments, the net effect is to favor positive growth rates at low density for both species. The fact that both species tend to increase from low density means that they will coexist in the system. More detail on the nature of the coexistence is given later, but the important thing to note at this stage is that both species show upward trends at low density. Without variation in the environment it is only possible to have one species with an upward trend at low density. Thus, the stochastic environment has changed the overall trends in population growth. It has not merely slowed down or delayed competitive exclusion.

GENERALIZATIONS OF THE LOTTERY MODEL

There are two critical requirements for coexistence in the lottery model, and these two requirements are found to lead to coexistence of competing species quite generally. First, environmental variation should permit each species to have periods when it has strong recruitment rates at low density. Second, generations must be overlapping, with adult death rates not greatly affected by competition. The second requirement places a lower bound on the growth rate and ensures that strong recruitments will have a greater effect on the average growth rate than poor recruitments.

These two requirements together favor positive average growth rates and promote coexist-

ence, given a broad variety of forms for the recruitment rate as a function of both the environment and species densities (Chesson 1983, 1984; Warner and Chesson 1985). For coexistence it is not necessary that recruitments of the two species should be strictly negatively related. The negative relationship in the lottery model is a result of the assumption that all space is filled and thus is an outcome of strong competition, not a requirement for coexistence. However, variation in the ratios of recruitment rates for different species in the system does seem to be a general requirement.

These ideas are not restricted to coexistence of just two species, but can apply to coexistence of an arbitrary number of species. Moreover, the variation in recruitment that is required for coexistence of two or many species does not have to be great if the species are similar to each other in average recruitment rates, mortality rates, and competitive abilities (Chesson 1984). Large variation in recruitment will be necessary for coexistence if there are big differences in these average properties of the species.

Overlapping generations are an essential part of coexistence achieved by temporal fluctuations in recruitment. However, overlapping generations can be achieved in ways other than through adult survival. For instance, annual plants with a seed bank have overlapping generations. Indeed, Ellner (1984) has discussed models that rely on variable recruitment to a seed bank and has demonstrated that coexistence results from variation and from overlapping generations. Both means of achieving coexistence are examples of the storage effect in action (Chesson 1983, 1984; Warner and Chesson 1985). The idea is that recruitments from different breeding periods become added together in the adult population or the seed bank; essentially, they are stored there subject to a rate of attrition equal to their death rates. These stored recruits are used every breeding season, but their use is most important during favorable periods, because then strong recruitments can replenish the store. That an adult population can be composed mostly of individuals from a few strong recruitments is well known for marine fishes, where good data are available (Gulland 1982, Cushing 1982). Such strong recruitments must be the major contributors to

future population growth. However, the main point here is that coexistence of competing species is promoted by such storage of recruitment. A species that normally recruits poorly because of competition with other species can nevertheless persist if it has occasional good periods when it recruits well and replenishes its store.

One can think of recruitment also in terms of acquisition of resources by the individuals in a population, especially if future reproduction is closely related to the total amount of resource that the population holds (Abrams 1984a, Warner and Chesson 1985). The storage of resource provides protection against periods when resource acquisition is poor. If the times that are favorable for acquisition of resources are different for different species, coexistence will be promoted.

Since fishes often have such obvious storage of recruitment in the adult population, they are candidates for coexistence by the storage effect, if competition can be shown to affect recruitment. Grubb (Chapter 12) discusses an assemblage of long-lived perennial herbs that have fluctuating recruitment rates. Although Grubb identifies a number of other possible explanations of coexistence, it seems likely that the storage effect at least contributes to coexistence. Other likely areas of application are perennial plants in general, long-lived benthic marine organisms, and annual plants with a seed bank (Shmida and Ellner 1984, Warner and Chesson 1985).

The lottery model and the generalizations discussed here all assume that the population is large enough for population size to be treated as a continuous variable. Moreover, demographic stochasticity (May 1973a) or within-individual variability (Chesson 1978) is ignored. This can be done only for large populations and only under certain conditions (Chesson 1981). These models, together with the majority of deterministic models in ecology, have been termed "infinite population models" (Chesson 1982) to correspond to the terminology of population genetics. Models that recognize within-individual variability and have discrete changes in population size are called "finite population models." As discussed by Chesson (1982), the results of most finite population models converge on those of their infinite population counterparts as population size is increased, and this is known to be true

for the finite version of the lottery model (Chesson 1982). Thus, such infinite population models can be validly taken to represent the properties of large, yet still finite populations.

GENERAL CONDITIONS FOR COEXISTENCE IN A TEMPORALLY VARYING ENVIRONMENT

We have seen how a temporally varying environment promotes the coexistence of competing species. However, such variation need not always be favorable to coexistence. In fact, depending on the circumstances, a temporally varying environment may do nothing or may even promote competitive exclusion (Turelli and Gillespie 1980, Turelli 1981, Chesson and Warner 1981). These different results can be understood in terms of how the effects of the environment on different species in the system interact.

To discuss the interaction of environmental effects, we first note that each species will have a response to the environment that will be expressed in quantities like the birth rate or death rate, which we normally use as parameters in a model. We shall now assume that just a single parameter varies with the environment, and this parameter will be denoted by E' for species 1 and E'' for species 2. For instance, in the lottery model $E' = \beta_1(t)$, the parameter giving the per capita rate of production of juveniles of species 1, and $E'' = \beta_2(t)$. We have seen previously that the instantaneous growth rate of a species at low density, which we shall call g here, is critical to persistence. This growth rate will often depend on both E' and E'' . For example, in the lottery model the value of g for species 1 is

$$g = \ln \left[(1 - \delta_1) + \frac{\delta_2 E'}{E''} \right] \quad (14.10)$$

where $1 - \delta_1$ represents adult survival and $\delta_2 E'/E''$ is per capita recruitment.

A general symmetrical model of two competing species, incorporating both E' and E'' in the growth rate of each, is analyzed in the appendix to this chapter. The symmetry of the model implies that the species have the same sorts of population dynamics, affect each other symmetrically, and experience the same frequencies of environ-

mental states, but usually at any one time E' will not equal E'' . Also, interspecific and intraspecific competition are equal in this model. In spite of these simplifications the model is in other respects very general, and it seems to indicate what is likely to occur in broad circumstances.

The symmetry properties of the model imply that in a constant environment a species at low density will have a 0 growth rate, that is, a 0 value of g , and will not be able to recover from that low density. However, when the environment varies, the average value of g can be different from 0, and this new value depends on the interaction between E' and E'' . The interaction between E' and E'' is said to be negative or antagonistic if a simultaneous increase in both E' and E'' leads to a change in g less than that accounted for by the sum of the changes due to each variable considered separately. This is the situation for g in the lottery model (equation 14.10), and in the general symmetrical model it leads to a positive average value of g for both species.

Thus, when E' and E'' are antagonistic, the two species will coexist; this result will apply regardless of the magnitude of the environmental variation, subject only to the condition that E' and E'' are not always equal, that is, the effects of the environment on the two species must sometimes be different.

Conversely, if E' and E'' are synergistic, the average values of g will be negative, and the stochastic environment will promote competitive exclusion.

Finally, if E' and E'' have just additive effects on g , the stochastic environment will yield 0 average values for g and will promote neither coexistence nor competitive exclusion.

Specific examples of antagonism between E' and E'' , and hence coexistence in a stochastic environment, include not only the lottery model but also the consumer-resource models of Abrams (1984a) and the seed bank model of Ellner (1984) with randomly varying germination rates. These examples include asymmetrical cases, suggesting that antagonism and a variable environment will generally promote coexistence in such cases as well. However, in asymmetrical cases g will not be 0 in a constant environment. Whether the average value of g is made positive for both species in a stochastic environment will

depend on both the degree of antagonism and on the magnitude of the environmental variability.

In the consumer resource models of Abrams (1984a) E' and E'' are the resource consumption rates of the two species. From these models Abrams notes that the storage effect is not the only way that coexistence can result from temporal variation in the environment. Indeed, the results above show that antagonism between E' and E'' is the key. However, this does not alter the fact that the storage effect is necessary in a number of specific models (Chesson 1983) and is operative in most of Abrams' specific examples. Moreover, the overlapping generations feature provides a general mechanism by which antagonism can occur. By giving a lower bound to the growth rate, overlap in generations means that a low value of E' and a high value of E'' will not be as harmful as suggested by the sum of their separate effects. Thus, it will lead to antagonism.

The failure of temporal variation to have interesting effects in the stochastic version of Lotka-Volterra competition analyzed by Turelli and Gillespie (1980) can be traced directly to considerations of this section. In their model the environmental variation is included in the per capita growth rate in an additive manner. Most important, the instantaneous growth rate of a species involves only the environmentally varying parameters of that species, that is, only E' is included in the growth rate of species 1 and only E'' in the growth rate of species 2. Thus, in the symmetrical cases studied by Turelli and Gillespie (1980) the environmental variation has no effect on coexistence. Asymmetrical cases studied by them give mixed results, but their essence is that environmental variation neither broadens nor narrows the conditions for coexistence. The discrete versions of stochastic Lotka-Volterra competition studied in some detail by Turelli (1981) similarly have each species' instantaneous growth rate depending only on its own environmentally varying parameters, and so these models also show minimal effects of environmental variation.

It is possible to build models involving the storage effect that do not include both E' and E'' in a species' growth rate, and then the storage effect does not promote coexistence. However, when both E' and E'' are included, the storage

effect is likely to promote coexistence as explained above. If environmental variation affects birth rates and juveniles compete, then both E' and E'' are necessarily included in the growth rates of both species. All published models of the storage effect have this feature.

The considerations of this section also allow us to examine cases of the lottery model in which death rates, rather than juvenile production rates (birth rates), vary. It is then easily checked that E' and E'' are synergistic and as a consequence promote negative growth rates at low density for both species, as discussed by Chesson and Warner (1981). The lottery model with variation in both birth rates and death rates involves a combination of two opposing effects. However, if death rates are generally small, birth rate variation is more important than death rate variation and continues to promote coexistence, but the quantitative details are modified by death rate variation and its correlation with birth rate variation.

COEXISTENCE MEDIATED BY VARIATION IN SPACE

That spatial variation in the environment or in species abundances can promote coexistence is an old idea, discussed in detail by numerous authors (Levin 1974, 1979; Yodzis 1978; Goh 1980; Dale 1978; Hastings 1980). The purpose of this section is to point out how spatial variation in recruitment, in particular, can promote coexistence in a manner that is closely related to coexistence promoted by temporal recruitment fluctuations. In a patchy environment recruitment can vary in space in two ways. First, there may be a fixed spatial pattern of heavy and light recruitment, that is, some places may always be superior sites for recruitment of a particular species. Second, the spatial pattern of heavy and light recruitment may change with time; that is, sites of heavy recruitment one year may be sites of light recruitment the next year and vice versa. If offspring disperse among patches, then coexistence of competing species is promoted by either kind of spatial variation in recruitment (Chapter 30; Chesson 1984, 1985; Comins and Noble 1985). The mechanism of coexistence is essentially the same as that for temporal variation, with dispersal taking the place of overlapping generations.

That coexistence can result from spatial variation in recruitment is important, because such spatial variation is found commonly in marine systems of space-holding organisms (see reviews in Chapter 30 and by Caffey 1984). Grubb (Fig. 12.6 and Table 12.5) demonstrates the same conclusion for a terrestrial plant community. Moreover, Hubbell and Foster (Chapter 19) point out that a spatially varying pattern of recruitment is to be expected in a tropical forest, because seedlings may remain in a suppressed state beneath the canopy until a canopy gap occurs above a particular group of seedlings. This effect reduces temporal variation in recruitment of a species for the forest as a whole, but introduces a temporally varying spatial pattern of recruitment, and this sort of recruitment variation can also promote coexistence.

Hubbell and Foster (Chapter 19) favor a different hypothesis for the diversity of tropical forests, suggesting that species abundances will be subject to drift in an area of forest through independent random processes of birth and death for individual trees (demographic stochasticity or within-individual variability) and that local diversity is maintained by immigration from neighboring areas. Hubbell's (1979) model for drift at a locality corresponds to the finite population version of the lottery model (Chesson 1982), but incorporates no environmental variability and therefore has no tendency to stabilize species numbers.

Yodzis (1978 and Chapter 29) also focuses on local community dynamics where migration is an important process in maintaining the community in an environmentally homogeneous setting. Unlike Hubbell, however, Yodzis assumes that deterministic processes are responsible for species extinction at a locality.

THE NATURE OF COEXISTENCE

The definition of persistence that has been used above is essentially the idea that a species should be regarded as persisting if it tends to increase from low density. We have seen how, under certain circumstances, environmental variation can change the trends in population growth so that all species tend to increase at low density, and we have regarded this as meaning that the species coexist. This definition of coexistence is usually

called "invasibility," and it is also used with deterministic models (e.g., MacArthur and Levins 1967, Armstrong and McGehee 1980).

It is now common to view coexistence in a deterministic model in terms of what it ought to mean when environmental variability is imposed. In this setting invasibility captures the essence of coexistence, for in the presence of environmental variability it is unreasonable to expect a community to remain at equilibrium, and stability of the equilibrium is then often seen as providing restoring forces back toward equilibrium and away from extinction of any of the species (Holling 1973; Goh 1975, 1976; Beddington et al. 1976). Thus, stability of the equilibrium creates trends in the direction of increase from population densities that are low relative to the equilibrium density. Of course, invasibility in a stochastic model involves a fluctuating increase about a mean trend. However, global stability of the equilibrium of a deterministic model is surely not to be viewed any differently when translated into its meaning for a community in the stochastic real world.

Although invasibility involves some key properties of coexistence and persistence, it is not regarded as a complete criterion for coexistence in either deterministic models or stochastic models. The reason is that although it guarantees positive trends at low density, it still does not eliminate the possibility of long periods of time being spent at low values (Armstrong and McGehee 1980, Chesson 1982). To prevent this, additional criteria are needed, and these can often be shown to apply to coexistence in stochastic models (Turelli and Gillespie 1980; Chesson 1982, 1983; Ellner 1984).

In some cases it is possible to get a detailed idea of the population fluctuations that are produced in a stochastic model. For instance, in the lottery model one can determine the probability distribution of population size when adult death rates are small. This probability distribution is approximately normal, with variance proportional to the adult death rate. This means that when adult death rates are small, population fluctuations will be small, regardless of the time scale on which the fluctuations are observed. Thus, if one used a time scale commensurate with the generation time, as recommended by Connell and Sousa (1983), one would judge a

system of long-lived species that coexist according to the lottery model to be a very stable assemblage.

These results appear to apply quite generally to models of recruitment variation Chesson (1984). They can be understood from the fact that in a long-lived species the adult population will be a sum over many seasons of recruitment, and thus the fluctuations at the level of recruitment will average out in the adult population. This phenomenon has been observed for real populations as well as for models (Chapter 12; Cushing 1982), and in models it permits the dynamics of the adult population to be described approximately, but not explained, by deterministic equations (Chesson 1984). However, the averaging out of recruitment fluctuations certainly does not mean that they are unimportant, for in some models (e.g., the lottery model) these fluctuations are necessary for coexistence, even though they do not cause large fluctuations in adult population densities. The resolution of this paradox involves the fact that the average of a nonlinear function is generally different from the nonlinear function of the average, $f(\bar{X}) \neq \bar{f(X)}$. The recruitment rate is generally a nonlinear function of more basic quantities like the β_i , and even though the variation in recruitment tends to average out, the average that is achieved reflects variation in the β_i . That is, it depends on the variances of the β_i , not just their means. Moreover, since the function that converts the β_i into recruitment rates depends on population densities, the effect of variation in the β_i on the average recruitment is density-dependent and has much to do with coexistence in models of recruitment variation.

The overall conclusion from this section is that the kind of coexistence that results from environmental variation is not fundamentally different from that found in deterministic models.

DETERMINISTIC VERSUS STOCHASTIC MECHANISMS OF COEXISTENCE

What is a stochastic mechanism of coexistence? The lottery model has the property that only one species can persist in the system in a constant environment. However, if the environment varies, coexistence of two or more species is possible. Thus, it seems appropriate to regard variation as the mechanism of coexistence. But if the

organisms are long-lived, little fluctuation in population density may be present, even on a time scale that is long compared to the generation times of the species. Thus, stochastic mechanisms of coexistence do not have to be associated with obvious stochastic variation in population densities.

As discussed previously, Turelli's and Gillespie's (1980) study of a stochastic version of the Lotka-Volterra model revealed essentially no overall effect of temporal variability on coexistence. Species may coexist in this model, but they do so because of factors that are unrelated to stochastic variation. For example, one such factor is resource partitioning; increased overlap in resource use will prevent coexistence. Such mechanisms that do not involve stochastic processes may be referred to as "deterministic." However, stochastic variation may cause large population fluctuations in this stochastic version of Lotka-Volterra competition, even though it has little effect on coexistence.

The mechanism of coexistence is determined by the effect that its addition or removal has on coexistence. It cannot generally be recognized by presence or absence of population fluctuations, for both deterministic and stochastic mechanisms are compatible with population fluctuations of any magnitude. Methods for determining the mechanism of coexistence on the basis of population fluctuations (Grossman 1982, Grossman et al. 1982) are therefore unreliable. The hypothesis that the mechanism of coexistence is stochastic is too general to be tested by crude population dynamics alone. However, specific forms of the hypothesis can be tested. For example, if the hypothesis is coexistence by the storage effect, then variation in recruitment rates should be observed. Moreover, the amount of recruitment variation can be compared with the contribution from other factors to see if it is a sufficient explanation of coexistence (Warner and Chesson 1985).

CONCLUSION

Stochastic models have revealed an enormous potential for stochastic mechanisms of coexistence. These mechanisms often involve the interaction of variation with the life history character-

istics of organisms. For example, the interaction of recruitment variation and overlapping generations leads to stochastic coexistence by the storage effect. In the case of the storage effect overlapping generations largely function in a manner that moderates the effect of unfavorable periods. An attractive hypothesis is that natural selection will often act in a manner that leads to life history traits with the effect of moderating unfavorable conditions. The results discussed above for the general symmetrical model of competition in a stochastic environment suggest a corollary to this hypothesis: Natural selection will often lead to life history traits that promote coexistence in a stochastic environment.

Coexistence under a stochastic mechanism can be just as strong and stable as that occurring under a deterministic mechanism. All species can show positive average growth rates at low density and may even give the appearance of tending toward a stable equilibrium point. Indeed, deterministic approximations can be found to some stochastic models that depend heavily for their properties on the presence of the stochastic components. Environmental variation can change the trends in population growth so that a positive central tendency, much like a stable equilibrium point, appears. Environmental variation need not always change the trends in a direction that favors coexistence; sometimes it may instead favor competitive exclusion. The important point is that the potential effects of variation are not just to increase population fluctuations or to slow down competitive exclusion, but to create new trends as well. In this sense variation is not very different from other sorts of factors affecting population and community dynamics.

SUMMARY

Ecologists have viewed stochastic temporal variation in a number of different ways: as noise that obscures the important features of a system, as a destabilizing factor that decreases diversity, and as a factor that interrupts or reverses the process of competitive exclusion and thus promotes diversity by slowing the trends to competitive exclusion. Models of stochastic environments have led to a fourth view: variation is a factor that changes trends by altering average population

growth rates. In particular, a stochastic environment can convert competitive exclusion into a situation in which all species have positive average growth rates at low density. Thus, variation reverses the trends toward competitive exclusion; it does not merely slow these trends down.

Models of recruitment variation illustrate this last view. These models are intended primarily for organisms, such as perennial plants, fishes, and sessile marine organisms, in which recruitment to the adult population is much more variable than adult survival. However, modifications of these models can apply to other communities, such as annual plants with seed banks.

A variable environment need not always change trends in a direction that promotes coexistence; trends in the direction of competitive exclusion can sometimes be created. The different circumstances for these different effects can be deduced from a general symmetrical model of competition in a variable environment.

Stochastic mechanisms of coexistence, such as recruitment variation, share many properties with traditional deterministic mechanisms of coexistence, such as resource partitioning or frequency-dependent predation. For both stochastic and deterministic mechanisms, coexistence involves positive average growth rates at low density for all species, and the actual population dynamics observed for the two sorts of mechanisms can be quite similar.

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APPENDIX

A general model of two-species competition in a stochastic environment is given by the following equation:

$$X_i(t+1) = X_i(t)G[E_i(t); E_1(t), X_1(t); E_2(t), X_2(t)] \quad (14.A1)$$

where the function G of five variables is the finite rate of increase of species i , and i can be either 1 or 2. $E_i(t)$ is a parameter giving the effect of the environment on species i , and it occurs in two places in equation 14.A1. Its function in the first place, before the first semicolon, is assumed to relate to the favorability of the environment of species i in the absence of competition. If the environment is favorable to species i , then it may contribute more competition to the system, for example, by producing more juveniles to compete, as in the lottery model. The second place that $E_i(t)$ occurs, as either $E_1(t)$ or $E_2(t)$, is assumed to relate to competition by species i . G is thus independent of the value of $E_i(t)$, in this second term, when $X_i(t)$ is equal to 0 (when species i cannot contribute any competition to the system).

Two symmetry assumptions are imposed on this model. The first is that

$$G[E_i(t); E_1(t), X_1(t); E_2(t), X_2(t)] = G[E_i(t); E_2(t), X_2(t); E_1(t), X_1(t)]$$

This assumption can be interpreted as meaning that the contribution of a species to the level of competition in the system does not depend on the species' identity. The second symmetry assumption is that the bivariate distribution of $[E_1(t), E_2(t)]$ is the same as that of $[E_2(t), E_1(t)]$. Thus, the two species will have the same frequencies of favorable periods, and the frequency of times when it is good for species 1 but bad for species 2 will equal the frequency of times when it is good for species 2 but bad for species 1.

Two additional assumptions have nothing to do with symmetry. First, the values of the environment are independent from one time to the next. (This is the standard random environment assumption.) Second, $E_1(t)$ is sometimes different from $E_2(t)$.

The analysis of this model is a standard invasibility analysis (Turelli 1978). If species 1 is absent from the system, then the resident species (species 2) is assumed to have an equilibrium probability distribution, and its mean instantaneous growth rate with respect to this distribution is 0, that is,

$$Eg[E_2(t); 0, 0; E_2(t), X_2(t)] = 0 \quad (14.A2)$$

where $g = \ln G$, and E means "theoretical mean" or "expected" value. The mean growth

rate of species 1 (the invader) while at low density will be

$$\mathbf{E}g[E_1(t); 0, 0; E_2(t), X_2(t)] \quad (14.A3)$$

and species 1 will be able to persist in the sense of invasibility if expression 14.A3 is positive. To identify the situations when this will be so, I define the environmentally dependent average growth rate, $h(E', E'')$, according to the formula

$$h(E', E'') = \mathbf{E}g[E'; 0, 0; E'', X_2(t)] \quad (14.A4)$$

where E' and E'' are treated as nonrandom values for the purpose of taking the average. Thus, the expected value in equation 14.A4 averages over the possible values of the resident density with the environment held fixed.

In terms of h , equations 14.A2 and 14.A3 become

$$\mathbf{E}h[E_2(t), E_2(t)] = 0 \quad (14.A5)$$

and

$$\mathbf{E}h[E_1(t), E_2(t)] \quad (14.A6)$$

The symmetry assumption on the environmental values now implies that

$$\mathbf{E}h[E_1(t), E_1(t)] = \mathbf{E}h[E_2(t), E_2(t)] \quad (14.A7)$$

and

$$\mathbf{E}h[E_1(t), E_2(t)] - \mathbf{E}h[E_2(t), E_1(t)] \quad (14.A8)$$

Symmetry thus implies that the question of whether species 1 can increase from low density in the presence of species 2 is the same as the question of whether species 2 can increase from low density in the presence of species 1. Using equations 14.A7 and 14.A8, it is clear that both species will be able to increase from low density if

$$\begin{aligned} \mathbf{E}h[E_1(t), E_2(t)] + \mathbf{E}h[E_2(t), E_1(t)] \\ > \\ \mathbf{E}h[E_1(t), E_1(t)] + \mathbf{E}h[E_2(t), E_2(t)] \end{aligned} \quad (14.A9)$$

Inequality 14.A9 will be true in general if the two arguments E' and E'' of the function $h(E', E'')$ are antagonistic, and then the two species will coexist. On the other hand, if E' and E'' are synergistic, both species will have negative mean instantaneous growth rates as invaders, and so competitive exclusion will be favored.

In the text antagonism and synergism are discussed for g rather than h , but since h is derived by averaging over g , antagonism or synergism for g implies the same for h . The analysis using h is, however, more general.