Coexistence of Competitors in Spatially and Temporally Varying Environments: A Look at the Combined Effects of Different Sorts of Variability

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A stochastic model is developed for competition among organisms living in a patchy and varying environment. The model is designed to be suitable for species with sedentary adults and widely dispersing larvae or propagules, and applies best to marine systems but may also be adequate for some terrestrial systems. Three kinds of environmental variation are incorporated simultaneously in the model. These are pure spatial variation, pure temporal variation, and the space × time interaction. All three kinds of variation can promote coexistence, and when variation is restricted to immigration rates, all three kinds act very similarly. Moreover, for long-lived organisms their action is nearly identical, and their effects, when present together, combine equivalently. For short-lived organisms, however, pure temporal variation is a less effective promoter of coexistence. Variation in death rates acts quite differently from variation in birth rates for it may demote coexistence in some circumstances, while promoting coexistence in other circumstances. Furthermore, pure spatial variation in death rates has quite different effects than other kinds of death-rate variation. In addition to conditions for coexistence, information is given on population fluctuations, convergence to stationary distributions, and asymptotic distributions for long-lived organisms. While the model is presented as an ecological model, a genetical interpretation is also possible. This leads to new suggested mechanisms for the maintenance of polymorphisms in populations. © 1985 Academic Press, Inc.

INTRODUCTION

Environmental variation has often been suggested as an important factor in the dynamics of real populations and communities (Andrewartha and Birch, 1954; Hutchinson, 1961; Wiens, 1977; Grubb, 1977; Sale, 1977; Connell, 1978; Strong, 1985). The ways in which environmental variation might affect community dynamics have been examined in a variety of models (see reviews by Chesson, 1985; and Chesson and Case, 1985); and many of

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these models give the conclusion that environmental variation promotes coexistence of competitors. However, environmental variation need not always have this effect (Chesson, 1985).

The environment can vary both in space and in time, but it can also fluctuate asynchronously at different spatial locations. Thus there are basically three different ways in which the environment can vary, as discussed in more detail below. These three different kinds of environmental variation have all been incorporated in models, but generally in different models, or incorporated in rather different ways. These modeling differences have complicated the comparison of the effects of different sorts of environmental variation. In this paper, all three kinds of environmental variation are considered simultaneously in a single model. Thus their effects can be compared and studied in combination.

The model presented here is the patchy environment lottery, or PEL, model, and is a generalization of the lottery model of Chesson and Warner (1981). It is most suitable for organisms with sedentary adults and widely dispersing larvae or propagules, and applies best for marine systems, but may also be adequate for some terrestrial communities, as discussed in the section below on applications.

KINDS OF ENVIRONMENTAL VARIATION

My review (Chesson, 1978) classified the different kinds of variation of relevance to population dynamics. However, my terminology was not easily committed to memory and caused confusion. Thus I use here a new and better terminology.

The environment can vary purely in space. Some places are permanently better for a species than others, and so there can be fixed a spatial pattern of environmental variation. Previously I called this "between-patch variation," but here I shall use the term "spatial environmental variation," or when emphasis is necessary, "pure spatial environmental variation."

The environment varies purely in time if all spatial locations experience the same environmental changes. I shall call this "temporal environmental variation" or "pure temporal environmental variation."

Finally, different spatial locations may show statistically independent fluctuations through time in environmental variables. When this is so, the spatial averages of the environmental variables show no fluctuation through time, and the temporal averages show no differences in space. I shall call this kind of environmental variation "spatiotemporal environmental variation" or "pure spatiotemporal environmental variation." It is a component of what I have called "within-patch variability" (Chesson, 1978, 1981).

There is abundant evidence for the importance of all three kinds of variation in the real world, especially with regard to several important features of the model developed here, *viz.* reproduction, settlement, and juvenile mortality (Grubb, 1977; Harper, 1977; Hubbell, 1980; Butler and Keough, 1981; Gulland, 1982; Doherty, 1983; Keough, 1983; Underwood and Denley, 1984; Caffey, 1985; Swarbrick, 1984). Most real-world systems will experience all three kinds of variation in combination. Standard analysis of variance techniques can be used to partition the total variation into the spatial variance, the temporal variance and the space × time interaction.

The PEL Model

Consider a system of many patches supporting local populations of two species. For a general patch model, it is known that the dynamics of an infinite system of patches provides a good approximation to those of a large yet finite system (Chesson, 1981). Similar justifications apply to the present case and so we shall assume that the system of patches is effectively infinite.

In this system, $Z_{ij}(t)$ represents the adult population size of species i on patch j at time t. Each adult occupies a unit of space or "home" (*sensu* Chesson and Warner, 1981) which may be a defended territory. Patch j can support K_j adults. The density of adults of species i, $P_i(t)$, in the entire system, is the defined as the number of adults per unit space, i.e.,

$$P_i(t) = \lim_{n \to \infty} \sum_{j=1}^{n} Z_{ij}(t) \Big/ \sum_{j=1}^{n} K_j. \tag{1}$$

Given the environmental conditions on patch j at time t, adults are assumed to die in the next unit of time independently and with probability $\delta_{ij}(t)$. Since the total amount of space on a patch is assumed completely occupied at time t, if follows that the mean amount of space becoming available during the time interval $(t, t+1)$, for these given probabilities of death, is

$$Z_{1j}(t)\,\delta_{1j}(t) + Z_{2j}(t)\,\delta_{2j}(t). \tag{2}$$

The adults on each patch reproduce and their offspring are assumed to disperse from the patch and enter a pool of juveniles (larvae, seeds, etc.) that are redistributed to the individual patches when they have reached the settling stage. The total number of juveniles of species i in the pool is assumed to be proportional to $P_i(t)$, the density of adults of species i in the system; and the number of juveniles arriving at patch j and seeking to settle there is $\beta_{ij}(t)\,P_i(t)$, where the quantity $\beta_{ij}(t)$ depends on the total birth rate

of species i in the system and the rate of migration of juveniles from the pool to patch j during $(t, t+1)$. This quantity reflects both the environmental conditions in the total system and the specific conditions applying to patch j.

The total number of juveniles arriving at a patch in one unit of time is assumed to exceed the available space there, and the juveniles are assumed to compete for this space in a preemptive fashion: the first juvenile to find a unit of space establishes there and can hold that space against others. Thus if space is discovered completely randomly by the individuals in the population, the mean proportion of the space on patch j that becomes allocated to species i is given by

$$\frac{\beta_{ij}(t)\, P_i(t)}{\beta_{1j}(t)\, P_1(t) + \beta_{2j}(t)\, P_2(t)}. \tag{3}$$

The lottery aspect of the model comes from this random allocation of space. As in Chesson and Warner (1981), a modification of the $\beta_{ij}(t)$ allows space allocation to be biased toward one species or the other. Other interpretations of the formula that might apply where juveniles exclude one another as they grow after settlement is discussed below in the section on applications.

The death rate, $\delta_{ij}(t)$, and immigration rate, $\beta_{ij}(t)$, are assumed to be functions of the state of the local environment on patch j at time t, which is designated $\mathscr{E}_j(t)$. However, the patch size, K_j, is assumed to be independent of the local environmental conditions. Dependence of K_j on $\mathscr{E}_j(t)$ can be taken account of simply, as explained in Appendix 1, and does not affect any of our conclusions here.

MODELS FOR THE ENVIRONMENT

To analyze the PEL model, we need to consider the components of the environment and the relationships among these components. The local environment on patch j at time t, $\mathscr{E}_j(t)$, is a logical sum of (i.e., is a combination of) three components:

$$\mathscr{E}_j(t) = T(t) + S_j + I_j(t). \tag{4}$$

In this expression, the first component represents temporal variation, the second is spatial variation, and the third is the interaction of space and time, $viz.$, spatiotemporal variation. These three components are assumed independent and also it is assumed that each of the sequences $\{T(t), t = 0, 1, ...\}$, $\{S_j, j = 1, 2, ...\}$, $\{I_j(t), j = 1, 2, ..., t = 0, 1, ...\}$ consists of independent and identically distributed random variables or vectors. While

independence in time is for mathematical convenience, the other indepen-
dences serve to separate and define the different components of variation.
Given the absence of distance effects in larval dispersal, very general
environments can be accommodated by this framework. However, an
important restriction is placed on this: for most of the discussion the $\delta_{ij}(t)$
are assumed not to vary with S_j, i.e., there are no fixed components of the
environmental differences between death rates on different patches; such
fixed components are restricted to the $\beta_{ij}(t)$. In addition, technical con-
ditions must occasionally be imposed on the distributions of the $\delta_{ij}(t)$ to
rule out some odd distributions with peculiar behavior. The details are
given in Appendix 2.

While in general the representation of the environment (4) is a logical
rather than an arithmetical summation, arithmetic sums may be used in
particular models. I shall occasionally refer to the following "log-additive"
model in which the combination of parameters

$$\rho_{1j}(t) = \frac{\beta_{1j}(t)/\delta_{1j}(t)}{\beta_{2j}(t)/\delta_{2j}(t)} \tag{5}$$

has the form

$$\ln \rho_{1j}(t) = \mu + T(t) + S_j + I_j(t), \tag{6}$$

where μ is a constant, and $T(t)$, S_j, and $I_j(t)$ are independent normal ran-
dom variables with mean zero. This log-additive model is a simple and
natural way of combining the different sorts of environmental variation.
The parameter $\rho_{1j}(t)$ compares the ratio of the juvenile immigration rate
and the adult death rate of species 1 with the corresponding ratio for
species 2, in patch j at time t. It thus compares the relative advantage that
species 1 has over species 2, for that place and time, and is very important
in the overall dynamics of the system. Because $\rho_{1j}(t)$ is a nonnegative quan-
tity, the lognormal distribution is a natural candidate for its probability
distribution, i.e., its natural log may be normal as implied by (6). The
additivity of the components of the environment on a log scale in (6) is to
be expected if the different factors affecting immigration rates act indepen-
dently of one another. The parameter μ is important for it can be thought
of as measuring the mean competitive advantage that species 1 has over
species 2. A negative value of μ means that species 1 is disadvantaged on
average.

The log-additive model is completed by assuming that the death rates,
$\delta_{ij}(t)$, do not vary with the environment, but are possibly different for the
two species in the system, i.e., are possibly different for different i.

Conditions for Coexistence

The description of the system implies the following equation for the conditional mean number of adults on patch j at time t, given past population sizes and environmental conditions:

$$E[Z_{ij}(t+1)|Z_{lk}(u), \mathscr{E}_k(u), u \leqslant t, l = 1,2, k = 1,2,...]$$

$$= [1 - \delta_{ij}(t)] Z_{ij}(t) + [\delta_{1j}(t) Z_{1j}(t) + \delta_{2j}(t) Z_{2j}(t)]$$

$$\times \frac{\beta_{ij}(t) P_i(t)}{\beta_{1j}(t) P_1(t) + \beta_{2j}(t) P_2(t)} \tag{7}$$

The first term on the RHS of (7) represents the conditional mean number of adults of species i surviving from time t to time $t+1$ on patch j, while the second term is the product of the conditional mean amount of space becoming available and the mean proportion of this space allocated to new recruits of species i.

Appendix 1 now shows that the general assumptions about the environment lead to the following equations for the average densities of the species:

$$P_i(t+1) = P_i(t) E[1 - \delta_{ij}(t)|T(t)] + E\left[\left\{\delta_{1j}(t)\frac{Z_{1j}(t)}{EK_j} + \delta_{2j}(t)\frac{Z_{2j}(t)}{EK_j}\right\}\right.$$

$$\times \frac{\beta_{ij}(t) P_i(t)}{\beta_{1j}(t) P_1(t) + \beta_{2j}(t) P_2(t)} \left| P_i(t), T(t)\right]. \tag{8}$$

The assumption that the death rates, $\delta_{ij}(t)$, do not depend on S_j (pure spatial variation) enters at this point, for if pure spatial variation did affect the $\delta_{ij}(t)$ then the first term in (8) would have to be replaced by

$$E[Z_{ij}(t)(1 - \delta_{ij}(t))|T(t)]/EK_j.$$

To see that the PEL model is a direct extension of the lottery model, note that when $S_j \equiv I_j(t) \equiv 0$, Equation (8) reduces to the equation governing the lottery model. If in addition $T(t) \equiv 0$, we have the lottery model in a constant environment for which coexistence is impossible. Therefore coexistence in the PEL model requires at least some variation of some kind.

To see if species i will persist in the system, we note that at low density (low $P_i(t)$), $Z_{ij}(t) = 0$ with high probability, and it follows (Appendix 1) that

$$P_i(t+1)/P_i(t) \simeq 1 + E[\delta_{ij}(t)(\rho_{ij}(t) - 1)|T(t)], \tag{9}$$

where $\rho_{1j}(t)$ is the ratio of immigration rates and death rates given by (5) and $\rho_{2j}(t) = 1/\rho_{1j}(t)$. For species i to persist in the sense of invasibility (Turelli, 1978), its mean instantaneous growth rate at low density must be positive. From (9) this mean rate is

$$\Delta_i = E \log\{1 + E[\delta_{ij}(t)(\rho_{ij}(t) - 1) \mid T(t)]\}, \tag{10}$$

and for coexistence both Δ_1 and Δ_2 must be positive. Applying Jensen's inequality we see that

$$E \log\{1 + \delta_{ij}(t)[\rho_{ij}(t) - 1]\} < \Delta_i < \log\{1 + E[\delta_{ij}(t)(\rho_{ij}(t) - 1)]\}. \tag{11}$$

The lower limit in (11) is achieved when all variation is temporal, in which case the PEL model reduces to the lottery model. Thus coexistence must occur in the PEL model with at least the same set of probability distributions for $(\delta_{1j}(t), \delta_{2j}(t), \beta_{1j}(t), \beta_{2j}(t))$ as it does in the lottery model, regardless of the origin of the variation as temporal, spatial, or spatiotemporal. Consequently, for given death-rate distributions, coexistence will occur provided only that $\rho_{1j}(t)$ $(= 1/\rho_{2j}(t))$ varies sufficiently on either side of one. Details are given in Chesson and Warner (1981), but it is important to note that since death-rate distributions are being held fixed, this sufficient variation in $\rho_{1j}(t)$ comes from variation in $\beta_{1j}(t)/\beta_{2j}(t)$.

The upper limit in (11) is achieved when there is no pure temporal variation. This means that for given joint distributions of the $\beta_{ij}(t)$ and $\delta_{ij}(t)$, coexistence is most likely to occur when all variation is some combination of spatiotemporal and spatial variation: pure temporal variation promotes coexistence less effectively than these other two forms of variation. In particular, temporal variation can only lead to coexistence in the presence of overlapping generations, but overlapping generations are not required when the variation is spatiotemporal or spatial. With non-overlapping generations $(\delta_{ij}(t) \equiv 1)$ and the absence of pure temporal variation, the conditions for coexistence derived from the upper limit in (11) are $E\rho_{1j}(t) > 1$ and $E\rho_{2j}(t) > 1$. Again, these conditions will be met with sufficient variation of $\rho_{1j}(t)$ on either side of one. In the log-additive model, this sufficient variation is specified by the inequality $|\mu| < \frac{1}{2}(VS_j + VI_j(t))$, i.e., that the mean competitive difference between the species, on the log scale, is less than half the sum of the two environmental variances. (This result is a consequence of the standard formula $Ee^U = e^{a + \frac{1}{2}b}$, for U normal with mean a and variance b.)

Although the conditions for coexistence do distinguish temporal variation from the other two kinds of environmental variation, no distinction is made between the latter, for in (10) no distinction is made between them. Spatial and spatiotemporal variation enter (10) only to the extent that they determine the conditional distribution of $\delta_{ij}(t)(\rho_{ij}(t) - 1)$

given $T(t)$. The result will be the same regardless of the origin of this conditional distribution as spatial variation, spatiotemporal variation, or a combination of both. Moreover, in the log-additive model, the sum of the variances $(VS_j + VI_j(t))$ is all that matters; their separate magnitudes are unimportant. However, it must be remembered that (10) is derived on the assumption that no pure spatial variation enters into the $\delta_{ij}(t)$. Indeed, spatial variation and spatiotemporal variation can affect coexistence differently through their effects on adult death rates, as discussed below.

The difference between the effects of temporal variation and the other kinds of variation is highly dependent on the overlap of generations. To see this we write $\delta_{ij}(t) = h\delta'_{ij}(t)$, where h is a nonrandom scaling factor and $\delta'_{ij}(t)$ is a positive random variable not dependent on h. Decreasing h decreases the adult death rates. Thus it increases the mean life time of an adult and consequently the overlap of generations. On a time scale commensurate with the generation time, the mean instantaneous growth rate of species i, at low density, is Δ_i/h. As $h \to 0$ the monotone convergence theorem implies that

$$\Delta_i/h \to E[\delta'_{ij}(t)(\rho_{ij}(t) - 1)]. \tag{12}$$

In this limiting expression no distincion at all is made between the three kinds of variation and so they can have equivalent effects on coexistence. Moreover, in the log-additive model, only the total variance $(VT(t) + VS_j + VI_j(t))$ is important, not how it is partitioned into different sources. In the log-additive model the condition for coexistence reduces to

$$|\mu| < \tfrac{1}{2}(VT(t) + VS_j + VI_j(t)).$$

Both the log-additive model and the general case lead to the conclusion that pure temporal variation promotes coexistence just as effectively as do spatial and spatiotemporal variation, when the organisms are long-lived.

Pure Spatial Variation in Adult Death Rates

No attempt is made here to study in detail the consequences of pure spatial variation in adult rates. However, a very revealing special case is presented in Appendix 4. There it is assumed that only in some patches do adults of a species survive for more than one reproductive period. Moreover, the patches that favor adult survival are different for the two species. Immigration rates, however, are assumed to be the same for all patches and to be constant also in time. From this special case it is concluded that if survival in the favored patches is sufficiently high, given the

frequency of these patches and the immigration rates of the two species, then the species will coexist. Thus coexistence occurs there purely from variation in adult death rates.

In contrast, adult death-rate variation alone does not promote coexistence if the variation is temporal or spatiotemporal. Spatiotemporal variation in adult death rates alone has no effect on coexistence, while pure temporal variation in adult death rates alone is harmful to coexistence (Chesson and Warner, 1981). However, if immigration rates (the $\beta_{ij}(t)$) also vary, then the effect of adult death-rate variation depends on its correlations with the $\beta_{ij}(t)$. Indeed, when appropriately correlated with immigration rate variation, pure temporal variation in adult death rates can promote coexistence also. Details are given in Chesson and Warner (1981), where it should be noted that the case of long-lived organisms and temporal variation gives identical results to the case of spatiotemporal variation with organisms of any longevity.

THE NATURE OF COEXISTENCE

So far we have been concerned with conditions under which both species will tend to increase from low density, i.e., will coexist in the sense invasibility. However, this analysis says little about the nature of the population fluctuations of the coexisting species. It is known that wild population fluctuations are compatible with invasibility (Chesson, 1982), but, in the examples that have been investigated, only mild restrictions have been found necessary to ensure that unacceptable fluctuations do not occur, i.e., that the species persist in the sense that they are stochastically boundedly persistent (Chesson, 1982). Stochastically bounded persistence means that the population densities $P_i(t)$ are uniformly stochastically larger than some positive random variable U_i, i.e., for all x and t

$$P(P_i(t) > x) \geqslant P(U_i > x). \tag{13}$$

Chesson (1982) has shown that invasibility implies stochastically bounded persistence in the lottery model. Moreover, $P_i(t)$ approaches a unique positive stationary distribution as $t \to \infty$. Similar results can be proved for the PEL model under appropriate assumptions. For example, if adult death rates are equal $(\delta_{1j}(t) = \delta_{2j}(t))$, Equation (8) reduces to

$$P_i(t+1) = P_i(t)\, E[1 - \delta_{ij}(t) \mid T(t)]$$

$$+ E\left[\delta_{ij}(t)\, \frac{\beta_{ij}(t)\, P_i(t)}{\beta_{1j}(t)\, P_1(t) + \beta_{2j}(t)\, P_2(t)} \,\middle|\, P_i(t),\, T(t) \right], \tag{14}$$

which is a simple difference equation with stochastically varying parameters. Appendix 2 now shows that invasibility implies that $P_i(t)$ converges to a unique stationary distribution as $t \to \infty$.

If there is no pure temporal variation in the system, Equation (14) is a difference equation with constant coefficients, and so the stationary distribution reduces to a globally stable equilibrium point, p^*, which is given for species 1 as the unique solution less than 1 to the equation

$$-E\delta_{ij}(t) + E\left[\delta_{ij}(t)\frac{\beta_{1j}(t)}{\beta_{1j}(t)\,p^* + \beta_{2j}(t)(1-p^*)}\right] = 0. \tag{15}$$

It is important to keep in mind that the existence of this equilibrium is dependent on the presence of environmental variation. Without it the only equilibria are $p^* = 0$ and $p^* = 1$, i.e., equilibria with one species extinct.

In the presence of a pure temporal component of environmental variation, quantitative detail about population dynamics . is generally extremely difficult to obtain. However, for long-lived organisms the solution of the stochastic Equation (14) converges to the difference equation that applies when there is no pure temporal component to the environmental variation (Appendix 3). Thus for long-lived organisms, not only are the conditions for coexistence independent of the origin of the variation, but the actual population dynamics are also asymptotically independent of the constitution of the environmental variation.

Because of the assumption of effectively an infinity of patches, there is no stochastic fluctuation in the $P_i(t)$ as a result of spatiotemporal environmental variation. The lack of dependence of dynamics on the source of the variation, for long-lived organisms, implies little stochastic fluctuation as a result of temporal variation also. We can be more precise about this: if $P_i(t) = p^*$, i.e., the process starts at equilibrium, then the stochastic fluctuations in $P_i(t)$ are approximately normal, they are centered about p^*, and have variance proportional to h (Appendix 3). Thus these fluctuations will be small for small h. Although environmental variation is necessary for coexistence in the PEL model, it need not lead to large fluctuations in population density, even when environmental fluctuations are perfectly synchronized across space as they are with pure temporal variation.

DISCUSSION

(a) Effects of Environmental Variation

We have seen that three different basic kinds of environmental variation can promote coexistence of competing species. They each do this when present alone, and when present in combination with the other kinds of

variation. A way in which pure temporal variation can promote coexistence has been studied in detail for the lottery model and related models, and depends critically on overlapping generations and iteroparity (Chesson, 1983, 1984). The overlap of generations means that the adult population is composed of cohorts from a number periods of recruitment. If recruitment varies through time, it can be shown that the growth rate of population is much more sensitive to the magnitude of recruitment when recruitment is good than when it is poor (Chesson, 1982, 1983). Indeed, a population can sustain positive average growth even when recruitment often fails provided strong recruitments occur at other times.

These results have been termed the storage effect because they depend on contributions to the adult population from different periods of recruitment. The adult population can be regarded as storing strong year classes, subject to a discount equal to the adult death rate, permitting these year classes to contribute to reproduction in a number of different breeding seasons of varying favorability to the species. This leads to a greater probability that a strong year class is able to reproduce during a favorable period, so producing another strong year class.

This storage effect promotes coexistence because it buffers a species against poor recruitments that occur during periods when the other species has a competitive advantage. Coexistence by means of spatial and spatiotemporal variation, and dispersal in space, can be understood in a similar manner to coexistence by means of the storage effect. The total population for the entire system is the sum over all patches and the finite (i.e., discrete time) per capita growth rate for species i is therefore equal to

$$\left(\sum_j Z_{ij}(t+1) - \sum_j Z_{ij}(t) \right) \Big/ \sum_j Z_{ij}(t). \tag{16}$$

The assumption of a large number of patches, however, allows the total population at time t, $\sum_j Z_{ij}(t)$, to be approximated by its theoretical mean, $kEZ_{ij}(t)$, where k is the total number of patches. Defining $G_{ij}(t) = (Z_{ij}(t+1) - EZ_{ij}(t))/EZ_{ij}(t)$, the per capita growth rate can be rewritten as

$$\frac{1}{k} \sum_{j=1}^{k} G_{ij}(t), \tag{17}$$

i.e., the per capita growth rate is the average over space of the $G_{ij}(t)$. The quantity $G_{ij}(t)$ is the local contribution to the growth rate coming from patch j. It is not strictly the local per capita growth rate but the relative deviation of the local population size at time $t+1$ from the mean local population size at time t.

To look at conditions for coexistence, the values of $G_{ij}(t)$ for low-density situations are the most important. For species 1 at low density in the PEL model we find that

$$G_{1j}(t) = \frac{(1 - \delta_{1j}(t))Z_{1j}(t)}{P_1(t)EK_j} - 1 + \delta_{2j}(t)\frac{\beta_{1j}(t)}{\beta_{2j}(t)}, \tag{18}$$

with an exactly analogous expression for $G_{2j}(t)$ when species 2 is at low density. Note that species 1 will increase from low density if the average of $G_{1j}(t)$ over all patches is positive. Inspection of (18) shows that $G_{1j}(t)$ is bounded below: it can never be less than -1. However, $G_{1j}(t)$ has no upper bound and will be large if species 1 has a large immigration rate (relative to species 2) into patch j at time t, i.e., if $\beta_{1j}(t)/\beta_{2j}(t)$ is large. This ratio is dependent simply on the environment and not at all on species densities. Thus $G_{1j}(t)$ will be large if species 1 is favored by the environment at that time, but no matter how bad environmental conditions are in a patch, the growth rate contribution there, $G_{1j}(t)$, cannot be less than -1. It follows that the average of these growth rate contributions (the growth rate for the whole system of patches) will be positive simply if species 1 is favored sufficiently by the environment in some patches, regardless of how poorly it is favored in other patches.

Species 1 and 2 cannot be favored simultaneously in a patch because the space-filling assumption entails that an increase for one species is necessarily a decrease for the other. However, in a varying environment the two species can be favored in different patches, and because the growth rate is more sensitive to the magnitude of the favorability in the patches where a species is favored, it is not difficult for the growth rates of both species to be positive at low density. Thus variation in the ratios of the immigration rates will favor coexistence of the species.

These results apply whether the variation is pure spatial or spatiotemporal. The lack of a distinction between these two kinds of variation involves two properties of the model. The first property is the assumption of many patches. Consequently the law of large numbers holds for both kinds of variation when they are averaged over space. Even though spatiotemporal variation involves fluctuations in time, its average over many patches, by virtue of the law of large numbers, does not show much variation in time. Thus one important distinction between pure spatial variation and spatiotemporal variation disappears when one looks at the spatial average of local populations. However, this property by itself is not enough to remove all of the important differences between the two types of variation. To see that it is not we must look more closely at the assumptions of the model.

In setting up the model it was assumed that pure spatial variation does not enter the adult death rates, the $\delta_{ij}(t)$. If this assumption is not made,

the dynamical equation (8) does not apply. Indeed, as discussed in the section above on pure spatial variation in adult death rates, pure spatial variation can have quite different effects than spatiotemporal variation when they are included in the $\delta_{ij}(t)$. The reason for this difference is that pure spatial variation leads to a correlation between $\delta_{ij}(t)$ and $\delta_{ij}(t-1)$. As a consequence of this correlation, there is a correlation between $\delta_{ij}(t)$ and $Z_{ij}(t)$. No such correlation is caused by pure spatiotemporal variation, and it follows that the average of $\delta_{ij}(t)Z_{ij}(t)$ over space is different in the presence of pure spatial variation compared with pure spatiotemporal variation. Consequently the average number of adult deaths per patch is different with the two different types of variation.

When pure spatial variation is excluded from the $\delta_{ij}(t)$, the only opportunity for correlations over time to affect local dynamics occurs in the relationship between the amount of space becoming available and the number of larvae migrating to a patch. At low density of a species (species 1, say), which is the important case for questions of persistence, even this opportunity disappears. Then the local proportion of space becoming available has conditional mean value approximately equal to $\delta_{2j}(t)$, which, by assumption, involves no correlations over time. Consequently the correlation over time that is imparted by pure spatial variation is not expressed when the mean growth rates, $\varDelta_i$, are evaluated. Thus pure spatial variation and pure spatiotemporal variation are not distinguished. Any combination of the two giving the same overall variation in the local environment will give the same answers to questions of coexistence.

Some caution is necessary, for the conclusion above does not apply when extended to consideration of the dynamical behavior of the system. This is because the temporal correlations imparted by spatial variation become important away from low densities, except when special assumptions, such as equality of adult death rates, are made. On the other hand, for questions of coexistence the considerations above show that the strict independence over time assumed for spatiotemporal variation can be replaced by some autocorrelation without changing the results.

While averaging the local growth contributions over space is sufficient in the absence of any component of pure temporal variation, when pure temporal variation is added multiplication over time is necessary also. To see this define $G_i(t)$ to be the average over space of the $G_{ij}(t)$ and then $P_i(t+1) = \{1 + G_i(t)\} P_i(t)$, which means that the general tendency for population increase of decrease is determined by the product of the $\{1 + G_i(t)\}$ over time.

When the adult death rate is small, the actual population changes taking place during any period of time are small, for the adult death rate not only determines how many individuals die, but also how much space is available for new recruits; indeed, $G_i(t)$ is proportional to h, the scaling factor in the

adult death rates. When the $G_i(t)$ are small, the product of the $\{1 + G_i(t)\}$ over time is close to 1 + the sum of the $G_i(t)$ over time. It follows that the general tendency for population increase or decrease is determined by the time average of the $G_i(t)$. In the absence of spatial or spatiotemporal variation this amounts to averaging the $G_{ij}(t)$ over time, for then the subscript j has no effect. Thus for long-lived organisms, spatial and temporal variation are dealt with similarly: they both amount to averaging the growth rate contributions, $G_{ij}(t)$, in one case in time and in the other case in space.

When variation occurs both in space and time, the average must be taken over both. At low density of species i, this average over space and time reduces to $E\delta_{ij}(t)(\rho_{ij}(t) - 1)$, which is approximately equal to Δ_i, the mean instantaneous growth rate at low density. The fact that spatial and temporal variation are dealt with by simple averaging explains the equality of their effect on coexistence of long-lived organisms. Moreover, it explains why partitioning of variation into its components is unimportant for long-lived organisms.

When organisms are not long-lived, the effect of pure temporal variation cannot be deduced from the simple average of the $G_i(t)$ over time, but is determined by the average of $\log(1 + G_i(t))$, the instantaneous growth rate. Although pure temporal variation can still promote coexistence in organisms that are not long-lived, but still have overlapping generations, it is not as effective as pure spatial or spatiotemporal variation.

(b) Implications for Field Methodology

The PEL model provides explanations for coexistence that rely on stochastic processes. These stochastic processes can quite reasonably be regarded as the "regulators" of the community, for without them just a single species would be present. Grossman (1982) and Grossman et al. (1982) have suggested field methods to determine the relative importance of stochastic versus deterministic modes of community regulation in the real world. The basic method consists of sampling populations over time and seeing if relative abundances of different species fluctuate. However, the results obtained here and elsewhere (summarized by Warner and Chesson, 1985) cast considerable doubt on this procedure, for we have found that long-lived organisms will show little fluctuation over time, even if the time scales involved are very long compared with the life of an individual. This follows from our finding that the population will fluctuate about the value p^* with variance proportional to h.

In certain circumstances, Grossman's methodology would also fail to reveal stochastic regulation of short-lived organisms. For instance, if local patchiness is on a spatial scale that is small relative to the sampled area, then stochastic regulation by means of spatiotemporal variation would not

be revealed because the population density estimates would tend to average out the asynchronous local population fluctuations that are necessary for coexistence.

(c) *A Comparison with Other Ecological Models*

The PEL model extends existing models of competition in a patchy environment in two distinct directions. First, analytical models that emphasize local stochastic events have tended to model simply species presence and absence at the local population level (e.g., Slatkin, 1974; Hastings, 1980; Hanski, 1983). Consequently the precise assumptions being made at this local population level have not been clear. Moreover, the lack of quantitative detail about local populations makes these models difficult to test empirically. In contrast, in the PEL model actual local population sizes are modeled, and so it has been possible to give explicit quantitative details of both local population interactions and the effects of environmental variation on these local populations. Moreover, the simple but plausible local dynamics built into the model do appear amenable to empirical verification. For instance, studies of larval settlement could in principle test the lottery assumption of the model. The assumption that adult death rates do not depend on local species composition, or the ages of the adults, is also in principle testable. Recently, Comins and Noble (1985) have independently developed an extension of the lottery model to a patchy environment. Their model differs from the PEL model by not including overlapping generations but incorporates the possibility that a fraction of an adult's propagules do not disperse to other patches. Using simulation, Comins and Noble also investigated stepping stone dispersal, where propagules disperse to neighboring patches. The additional finding of interest there is that the conditions for coexistence are relatively insensitive to the migration assumption imposed.

Previous models involving actual population sizes, that are closest in spirit to the PEL model, are those of Yodzis (1978) and Atkinson and Shorrocks (1981). Yodzis given an interesting though somewhat complex discussion of founder effects, while Atkinson and Shorrocks present simulation results for the effects of independent aggregation of competitors. Neither model explicitly considers environmental variation as discussed here.

The second direction in which the PEL model extends existing models involves the inclusion of several different sorts of variability simultaneously in the one model. It is a feature that is also likely to aid in the empirical testing of the model, for in real systems several different kinds of variation are indeed likely to be present. Thus it is important to know how these different kinds of variation should combine. More generally, many ecological communities are likely to require a number of different factors to explain

their structure (Connell, 1978). Although the PEL model explains community structure mostly through the effects of environmental variation, it can be modified to incorporate other factors such as presettlement competition among larvae, or postsettlement competition among adults, without becoming so complicated that it cannot be analyzed. How these modifications are made is illustrated by the several variations on the lottery model that have appeared (Chesson, 1983; Shmida and Ellner, 1984). The likelihood that multiple factors are necessary to explain a community means that it is especially important to have a model containing them all if their mutual necessity and relative contributions are to be assessed.

(d) Applications of the PEL Model

The assumption of random migration means that marine organisms with planktonic larval phases are the most obvious candidates for the application of the PEL model. However, the results of Comins and Noble discussed above suggest that the model may be at least a qualitatively good approximation for organisms such as terrestrial plants in which dispersal of larvae or propagules is far from random.

The details involved in the second assumption, lottery competition for space, have been discussed elsewhere (Chesson and Warner, 1981); briefly, it is most easily seen to apply if the first individual that settles in a particular site can usually prevent other individuals from establishing there. Sale (1977) claims this to be true for some territorial coral reef fishes. It may also be true of solitary sessile organisms that can grow quickly upon settlement. For terrestrial plants, however, many juveniles will often begin growing in a site and may compete actively as they grow. This situation still fits the lottery formula if the two species have similar juvenile mortality rates as functions of total density of juveniles in a site. However, the case where the mortality rates are different for the two species is not to simple and may require the more complex variations on the lottery formula discussed in Chesson (1983).

Data on coral reef fishes (Sale, 1980; Doherty, 1982) suggest that spatiotemporal environmental variation might be an important factor in recruitment, which would make it difficult to find any relationship between local stock and local recruitment. Sale (1982), in his model of a coral reef fish community, did not, however, include any spatiotemporal environmental variation, but just modeled a single patch with no immigration or emigration. Sale's model has been the subject of a detailed criticism by Abrams (1984), who points out that it implies something like intraspecific competition among larvae before settlement but no interspecific competition. Intraspecific competition among adults is also consistent with Sale's model. Since these species have been argued to be essentially ecologically equivalent at all stages in their life cycle (Sale, 1977)

intraspecific competition, without interspecific competition, seems very unlikely.

The PEL model, which uses larval dispersal and stochastic immigration processes to achieve a relative independence of local stock and local recruitment, seems a much more appropriate expression of the ideas on reef fish communities that Sale addresses. However, experimental evidence discussed by Doherty (1983) and Sale (1984) suggests that the space-filling assumption of the PEL model needs to be removed before a reasonably accurate description of the system is achieved. This has been done for the lottery model (Chesson, 1983), without a substantial change in the conclusions, but has not been extended to the PEL model.

(e) *Relationship to Models in Population Genetics*

Without overlapping generations the PEL model is very similar to some models in population genetics. To interpret the PEL model in a population genetical context, $Z_{ij}(t)$ is equated with abundance of allele i in local population j at time t. In cases of asexual reproduction, $Z_{ij}(t)$ may refer to the abundance of genotype i rather than allele i.

The genetical model that bears the greatest similarity to the PEL model is that of Gillespie (1974). Indeed, essentially the same model is obtained if the PEL model is specialized to nonoverlapping generations ($\delta_{ij}(t) \equiv 1$) and Gillespie's model is specialized to the case of haploid or asexually reproducing organisms. Gillespie does not analyze his model exactly, but uses a diffusion approximation that quite naturally corresponds to the log-additive model considered here. The variances and mean differences of fitnesses in Gillespie's diffusion approximation are comparable to the variances and mean differences of the $\log \beta_{ij}(t)$, and when this correspondence is recognized, the results obtained here agree with Gillespie's.

Gillespie's results can be used to extend special cases of the PEL model to the case of a finite number of patches. On the other hand, the results here for the PEL model can be used to extend Gillespie's model. First, I have discussed exact results for general distributions of the $\beta_{ij}(t)$, not just for the log-additive case. Secondly, these results apply also to the case of overlapping generations ($\delta_{ij}(t) < 1$). This second extension is important for it gives something quite new. Gillespie's model in the haploid or asexual form does not allow a polymorphism as a result of pure temporal environmental variation. Indeed, this fact is a reexpression of the result of Dempster that a polymorphism cannot be maintained in haploid organisms by random temporal fluctuations in relative fitnesses. However, the PEL model shows that pure temporal variation can be responsible for a polymorphism in a haploid or asexual population provided generations are overlapping. This is also true for the original lottery model of Chesson and Warner (1981).

Maintenance of a polymorphism by temporal variation and overlapping generations involves fluctuating selection intensities at the juvenile stage, so that the $\beta_{ij}(t)$ must vary through time. Selection at the adult stage can be measured by the relative values of the adult death rate, $\delta_{ij}(t)$, but for a polymorphism to be maintained these $\delta_{ij}(t)$ must not fluctuate proportionately to the $\beta_{ij}(t)$; i.e., $\beta_{ij}(t)/\delta_{ij}(t)$ must not be a constant, it must vary in time. Precise results for the types of covariation in the $\beta_{ij}(t)$ and $\delta_{ij}(t)$ that are favorable to a polymorphism are given in Chesson and Warner (1981) for the case of small adult death rates. We note here simply that fluctuating selection intensities at the juvenile stage are of primary importance for a polymorphism to occur.

Although overlapping generations are necessary for a haploid polymorphism to result from pure temporal variation, in n-ploid populations with $n > 1$ pure temporal variation does lead to polymorphisms without overlapping generations. Indeed an elaborate theory of maintenance of genetic variability by means of temporal variation has been developed for diploid organisms (see Gillespie, 1978; and Turelli, 1981b, where futher references can be found). A simple extension of our model to cover the n-ploid cases in Gillespie (1974) shows that a polymorphism is easier to obtain if generations are overlapping. Indeed, genetical reinterpretation of the results of Chesson (1983, 1984) suggests that overlapping generations, combined with fluctuating selection intensities at the juvenile stage, are quite generally favourable to the maintenance of polymorphisms in populations.

APPENDIX 1

Equation (3) for the conditional mean population size, given past densities and environmental conditions, holds regardless of independence of K_j (patch size) and $\mathscr{E}_j(t)$ (local environmental conditions). Allowing for dependence between K_j and $\mathscr{E}_j(t)$ and defining $\zeta_i(t) = E[Z_{ij}(t)| T(t)]$, we see that

$$\zeta_i(t+1) = \zeta_i(t)\, E[1 - \delta_{ij}(t)|\, T(t)]$$

$$+ E\left[\{\delta_{1j}(t)\, Z_{1j}(t) + \delta_{2j}(t)\, Z_{2j}(t)\} \right.$$

$$\left. \times \frac{\beta_{ij}(t)\, P_i(t)}{\beta_{1j}(t)\, P_1(t) + \beta_{2j}(t)\, P_2(t)} \right|\, P_i(t),\, T(t) \right], \qquad \text{(A1)}$$

where in the first term on the RHS I have used the assumption that $\delta_{ij}(t)$

does not depend on S_j (pure spatial variation) or K_j. Applying the law of large numbers to the system we see that

$$\zeta_i(t) = \lim_{n \to \infty} \frac{1}{n} \sum_{j=1}^{n} Z_{ij}(t) \quad \text{and} \quad EK_j = \lim_{n \to \infty} \frac{1}{n} \sum_{j=1}^{n} K_j.$$

Since $P_i(t)$ is the ratio of these two limits, the following equation applies

$$P_i(t+1) = P_i(t)\, E[1 - \delta_{ij}(t) \mid T(t)]$$

$$+ E\left[\left\{ \delta_{1j}(t) \frac{Z_{1j}(t)}{EK_j} + \delta_{2j}(t) \frac{Z_{2j}(t)}{EK_j} \right\} \right.$$

$$\left. \times \frac{\beta_{ij}(t)\, P_i(t)}{\beta_{1j}(t)\, P_1(t) + \beta_{2j}(t)\, P_2(t)} \,\middle|\, P_i(t),\, T(t) \right], \qquad \text{(A2)}$$

which is Equation (8) in the text.

To obtain low-density approximations to this equation, we need to evaluate the limit as $P_i(t) \to 0$ of $P_i(t+1)/P_i(t)$. Using the well-known inequality $P(Z_{ij}(t) > \varepsilon) < EZ_{1j}(t)/\varepsilon = P_1(t)\, EK_j/\varepsilon$, we see that $Z_{1j}(t) \to^P 0$ as $P_1(t) \to 0$. It follows that

$$[\delta_{1j}(t)\, Z_{1j}(t) + \delta_{2j}(t)\, Z_{2j}(t)] \frac{\beta_{1j}(t)}{\beta_{1j}(t)\, P_1(t) + \beta_{2j}(t)\, P_2(t)}$$

$$\xrightarrow{P} \delta_{2j}(t)\, K_j \frac{\beta_{1j}(t)}{\beta_{2j}(t)} \quad \text{as} \quad P_1(t) \to 0.$$

This means that as $P_1(t) \to 0$,

$$P_1(t+1)/P_1(t) \xrightarrow{P} E[1 - \delta_{1j}(t) + \delta_{2j}(t)\, K_j\, \beta_{1j}(t)/\beta_{2j}(t)\, EK_j \mid T(t)]$$

$$= 1 + E\,[\delta_{1j}(t)(\rho_{1j}(t)\, K_j/EK_j - 1) \mid T(t)]$$

$$= 1 + E\,[(K_j/EK_j)\, \delta_{1j}(t)(\rho_{1j}(t) - 1) \mid T(t)], \qquad \text{(A3)}$$

where this last step uses the fact that $\delta_{1j}(t)$ is assumed to be independent of S_j or K_j. (Actually the application here removes the effect of the previous application of this assumption above.) If K_j varies independently of the local environment, $\mathscr{E}_j(t)$, then K_j/EK_j cancels out of (A3) to yield (9) in the text. Otherwise the distribution of $\mathscr{E}_j(t)$ (and hence the distributions of $\delta_{ij}(t)$ and $\beta_{ij}(t)$) must be weighted by K_j to give the correct result, as shown in (A3). Indeed, if all the expected values in the text are assumed weighted in this way, then the results in the text are extended to the case where patch size and patch quality are statistically dependent.

APPENDIX 2

To show that the Δ_i become positive as variation in the $\beta_{ij}(t)$ is increased, it is necessary to impose the condition

$$E \log(1 - \delta_{ij}(t)) > -\infty, \tag{A4}$$

i.e., that adult death rates do not approach 1 too often. To prove convergence to a stationary distribution, the following stronger condition, with the same intuitive interpretation, must be imposed:

$$E(1 - \delta_{ij}(t))^{-\varepsilon} < \infty. \tag{A5}$$

To prove now that the process given by (14) converges to a unique stationary distribution, when $\Delta_1, \Delta_2 > 0$, we modify theorems 5.1 and 5.2 of Chesson (1982).
Define

$$Y_c = E[1 - \delta_{ij}(t) \mid T(t)]$$

$$+ \inf_{0 < p < c} E\left[\delta_{ij}(t) \frac{\beta_{1j}(t)}{\beta_{1j}(t) p + \beta_{2j}(t)(1 - p)} \,\Big|\, T(t)\right]. \tag{A6}$$

Now

$$E \log Y_c > E \log E[1 - \delta_{ij}(t) \mid T(t)]$$

$$> E \log(1 - \delta_{ij}(t)) \quad \text{(by Jensen's inequality)}$$

$$> \varepsilon^{-1}\{1 - E(1 - \delta_{ij}(t))^{-\varepsilon}\}$$

$$> -\infty \quad \text{(by assumption A5)}.$$

Thus $\log Y_c$ is bounded below by a random variable with finite expected value. The monotone convergence theorem now applies and we see that $E \log Y_c \to \Delta_1$ as $c \to 0$ and therefore that $E \log Y_c > 0$, for sufficiently small c. The proofs of theorems 5.1 and 5.2 of Chesson (1982) continue without further modification to show that P_1 converges to a unique stationary distribution on $(0, 1)$ as $t \to \infty$.

APPENDIX 3

With the substitution $\delta_{ij}(t) = h\delta'_{ij}(t)$, the stochastic difference equation (14) takes the form

$$P_i(t + 1) = P_i(t)\{1 + hf(P_i(t), T(t))\}. \tag{A7}$$

Similar to Chesson (1984), various theorems of Norman (1975) apply. Defining

$$\varphi(p) = Ef(p, T(t)) \tag{A8}$$

and

$$p(t+1) = p(t)\{1 + h\varphi(p(t))\}, \tag{A9}$$

with $p(0) = P_i(0)$, it follows that $P_i(t/h) - p(t/h)$ converges in probability to 0 as $h \to 0$. Note that the process $p(t)$ describes population dynamics in the situation where none of the environmental variation is pure temporal. Also, h^{-1} is proportional to the mean life of an adult, and so consideration of t/h involves a time scale commensurate with the generation time.

If $P_i(0) = p^*$, the results of Norman (1975) also imply that $h^{-\frac{1}{2}}(P_i(t/h) - p^*)$ converges to a normal distribution with mean 0 and variance equal to

$$(1 - e^{-\alpha t}) \sigma_0^2/\alpha, \tag{A10}$$

where

$$\tfrac{1}{2}\alpha = -p^* \varphi'(p^*)$$

$$= \rho^* E \, \delta_{ij}'(t) \frac{\beta_{1j}(t) [\beta_{1j}(t) - \beta_{2j}(t)]}{[\beta_{1j}(t) p^* + \beta_{2j}(t)(1 - p^*)]^2} \tag{A11}$$

and

$$\sigma_0^2 = p^{*2} \, Vf(p^*, T(t))$$

$$= p^{*2} V \left\{ E \left[\delta_{ij}'(t) \left(\frac{\beta_{1j}(t)}{\beta_{1j}(t) p^* + \beta_{2j}(t)(1 - p^*)} - 1 \right) \,\middle|\, T(t) \right] \right\}. \tag{A12}$$

It is not difficult to show that $\varphi'(p^*)$ is negative, and hence that for small h and large t, $P_i(t/h)$ is approximately normal with mean p^* and variance $h\sigma_0^2/\alpha$.

APPENDIX 4

To see the potential interesting consequences of pure spatial variation in adult death rates, let θ_1 and θ_2 be positive constants less than 1, and assume $P(\delta_{ij}(t) = \theta_i) = 1 - P(\delta_{ij}(t) = 1) = p_i$ with $\delta_{1j}(t)$ or $\delta_{2j}(t) = 1$, a.s. If

the variation in the $\delta_{ij}(t)$ is due to pure spatial variation alone, then these assumptions mean that a given patch has $100(1 - \theta_i)\%$ survival of species i, for $i = 1$ or 2, and 0% survival of the other species. Assume also that $\beta_{ij}(t) \equiv \beta_i$, i.e., that the $\beta_{ij}(t)$ do not vary in time or space. Define $P_i^{(j)}(t)$ to be the average proportion of species i over patches for which species j has adult death rate equal to θ_j, then

$$P_1^{(1)}(t+1) = (1 - \theta_1) P_1^{(1)}(t) + [1 - (1 - \theta_1) P_1^{(1)}(t)] \frac{\beta_1 P_1(t)}{\beta_1 P_1(t) + \beta_2 P_2(t)}$$

$$\geqslant (1 - \theta_1) P_1^{(1)}(t) + [1 - (1 - \theta_1) P_1^{(1)}(t)] \frac{p_1 \beta_1 P_1^{(1)}(t)}{p_1 \beta_1 P_1^{(1)}(t) + \beta_2}$$

It follows that $P_1^{(1)}(t+1) > P_1^{(1)}(t)$ whenever

$$\theta_1 < [1 - (1 - \theta_1) P_1^{(1)}(t)] p_1 \beta_1 / (p_1 \beta_1 P_1^{(1)}(t) + \beta_2), \qquad (A13)$$

and substituting 0 for $P_1^{(1)}(t)$ in (A13) gives the following sufficient condition for $P_1^{(1)}(t)$ to increase from small positive values:

$$\theta_1 < p_1 \beta_1 / \beta_2.$$

When this is true species 1 will remain in the system. It will be present in every patch, but individuals will not survive more than time period in the proportion $1 - p_1$ of the patches. It follows that a sufficient condition for coexistence of the two species is

$$\theta_i < p_i \beta_i / \beta_j, \qquad i = 1, 2, \qquad j \neq i,$$

which can easily be satisfied by having the θ_i small. Thus pure spatial variation in death rates alone is capable of leading to coexistence, while spatiotemporal variation can never do this, for if the only variation is spatiotemporal variation in adult rates then the condition for coexistence $(\Delta_i > 0, i = 1, 2)$ reduces to $\beta_1/\beta_2 > E\,\delta_{1j}(t)/E\,\delta_{2j}(t)$ and $\beta_2/\beta_1 > E\,\delta_{2j}(t)/E\,\delta_{1j}(t)$, which is never satisfied.

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