

# General Theory of Competitive Coexistence in Spatially-Varying Environments

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Received October 15, 1999

**A general model of competitive and apparent competitive interactions in a spatially-variable environment is developed and analyzed to extend findings on coexistence in a temporally-variable environment to the spatial case and to elucidate new principles. In particular, coexistence mechanisms are divided into variation-dependent and variation-independent mechanisms with variation-dependent mechanisms including spatial generalizations of relative nonlinearity and the storage effect. Although directly analogous to the corresponding temporal mechanisms, these spatial mechanisms involve different life history traits which suggest that the spatial storage effect should arise more commonly than the temporal storage effect and spatial relative nonlinearity should arise less commonly than temporal relative nonlinearity. Additional mechanisms occur in the spatial case due to spatial covariance between the finite rate of increase of a local population and its local abundance, which has no clear temporal analogue. A limited analysis of these additional mechanisms shows that they have similar properties to the storage effect and relative nonlinearity and potentially may be considered as enlargements of the earlier mechanisms. The rate of increase of a species perturbed to low density is used to quantify coexistence. A general quadratic approximation, which is exact in some important cases, divides this rate of increase into contributions from the various mechanisms above and admits no other mechanisms, suggesting that opportunities for coexistence in a spatially-variable environment are fully characterized by these mechanisms within this general model. Three spatially-implicit models are analyzed as illustrations of the general findings and of techniques using small variance approximations. The contributions to coexistence of the various mechanisms are expressed in terms of simple interpretable formulae. These spatially-implicit models include a model of an annual plant community, a spatial multispecies version of the lottery model, and a multispecies model of an insect community competing for spatially-patchy and ephemeral food.** © 2000 Academic Press

## INTRODUCTION

Heterogeneity of populations in space is an important topic in ecology: spatial heterogeneity potentially has major roles in the persistence of species, the stability of populations, and the coexistence of interacting species (Hanski and Gilpin, 1997; Tilman, Lehman, *et al.*, 1997; Bascompte and Sole, 1998). In particular, recent results for plant communities from both theoretical (Tilman, 1994; Pacala and Levin, 1997; Bolker and Pacala, 1999; Neuhauser and Pacala, 1999) and empirical studies

(Rees, Grubb, *et al.*, 1996) imply that an understanding of the effects of spatially local interactions is essential for a proper appreciation of competitive interactions between species. Spatial environmental variation should have a major influence on the outcome of local interactions and their regional effect according to specific models for a variety of systems (Tilman, 1982; Holt, 1984; Shigesada, 1984; Shmida and Ellner, 1984; Iwasa and Roughgarden, 1986; Roughgarden and Iwasa, 1986; Pacala, 1987; Ives, 1988; Holt, 1997; Klopfer and Ives, 1997). The majority of attention in models of spatial dynamics, however, has been concerned with homogeneous physical environments or

metapopulation models in which presence–absence variables are the spatially-local state variables. The structure of the physical environment is represented poorly if at all. Hence, understanding the role of environmental variation in space remains a major challenge in spatial ecology (Thomas and Hanski, 1997). In contrast, competitive interactions between species subject to temporal environmental variation (Armstrong and McGehee, 1976; Chesson and Warner, 1981; Abrams, 1984; Namba, 1984; Ebenhoh, 1991; Loreau, 1992) are well understood theoretically (Chesson, 1994; Chesson and Huntly, 1997). It is the purpose of this article to present a parallel theory for competitive and apparent competitive interactions in space, in the presence of spatial and spatio-temporal environmental variation.

A defining feature of models of temporal variation is multiplication over time. In discrete time, population dynamics may be expressed simply by the equation

$$N_i(t+1) = \lambda_i(t) N_i(t)$$

which means that the fate of the population is determined by the product of  $\lambda_i(t)$  over time, which in many important situations can be approximated adequately by the  $t$ th power of the geometric mean of  $\lambda_i(t)$  over time. The key to understanding temporal models is how variation over time affects this temporal product. In the presence of spatial variation, local populations are summed over space to give the total population, and the dynamics of the total population involve averaging  $\lambda_i(t)$  over space weighted by local population density (Hassell, May, *et al.*, 1991). In the case of uniform dispersal in space, this weighted average is equal to the unweighted average, and the difference between space and time comes down to the difference between the arithmetic mean over space and the geometric mean over time of  $\lambda_i(t)$  or, equivalently, the difference between the behavior of the arithmetic mean of  $\lambda_i(t)$  over space and the behavior of the arithmetic mean of  $\ln \lambda_i(t)$  over time. With more general dispersal scenarios, the difference between the weighted average in space of  $\lambda_i(t)$  and the unweighted average must be taken into account. These facts mean that the study of spatial variation can proceed by comparing the properties of different sorts of averages. Many results for temporal variation translate into the spatial context by relating the appropriate spatial and temporal averages. Indeed, much of the present work involves translating prior results for the temporal context (Chesson, 1994) into the spatial context. Differences between spatial and temporal contexts emerge quite simply in terms of the ways these different sorts of averages interact with population processes.

The theory developed here is set out in terms of competition between a set of species that I shall refer to as a *guild* (Root, 1967) in an ecological community. The essential feature of the guild is that the members have mutually negative interactions with each other. They may do this because they share resources and experience competition or they may share predators or pathogens and experience apparent competition (Holt and Lawton, 1994). Also they may interfere with each other through various behaviors affecting feeding or survival. Such mutually negative interactions will be lumped together in the term *competition*.

Although the emphasis is on spatially implicit models, where explicit representations of regional population dynamics are available, the effects of limited dispersal are studied also, and the general theory applies to arbitrary modes of dispersal. Several different particular spatial models are considered and simple multispecies coexistence criteria are obtained by a quadratic approximation method. These particular models are the lottery model in space, insect aggregation models, and an annual plant model.

## THE GENERAL MODEL

Individual organisms in the species under consideration are assumed affected by the physical environment and competition (or a generalization of competition as discussed above). Variables  $E_{jx}$  and  $C_{jx}$  are assumed to quantify the effects of environment and competition specifically for the species  $j$ , location  $x$ , and time  $t$  (a variable that will only be explicitly represented in the notation when needed for emphasis). For each individual of each species and each location  $x$  and time  $t$  these variables are assumed to define a probability of survival to time  $t+1$  and an expected number of offspring surviving to time  $t+1$ , which together define an individual-level finite rate of increase,

$$\lambda_{jx} = G_j(E_{jx}, C_{jx}), \quad (1)$$

where  $G_j$  is a function that combines the effects of these two factors. The quantity  $E_{jx}$  is called an environmentally-dependent parameter and is not a direct measure of the physical environment, but a population parameter that depends on the physical environment, such as a survival probability, a germination probability, or an expected number of offspring. For this reason, it may also be called an *environmental response* (Chesson and Huntly, 1997). In most cases, it is defined so that larger

values of  $E_{jx}$  mean more favorable environments, i.e., so that  $G_j$  is an increasing function of  $E_{jx}$ .

The competition parameter  $C_{jx}$  measures the total effect of competition on  $\lambda_{jx}$  in some well-defined way, and normally  $G_j$  decreases in  $C_{jx}$ . Note that  $\lambda_{jx}(t)$  is the expected contribution of an individual to the population in the system at time  $t + 1$ , given  $E_{jx}$  and  $C_{jx}$ . Thus the expected output from the location  $x$  at time  $t + 1$ , given  $E_{jx}$ ,  $C_{jx}$ , and  $N_{jx}(t)$ , is  $\lambda_{jx}(t) N_{jx}(t)$ . In general,  $\lambda_{jx}(t) N_{jx}(t)$  differs from  $N_{jx}(t + 1)$ , which takes account of dispersal also. However, mortality during dispersal is assumed to be factored into  $\lambda_{jx}(t)$ .

The location  $x$ , depending on the situation, could be a particular patch or cell in the landscape supporting a local population, a particular point in continuous space, or a point on a lattice able to support just a single individual organism. The development here is general although the worked examples are all cell-based or its equivalents. Two spatial scales are considered explicitly: the scale of a single location and the scale of the whole population, which is a scale at which the system is effectively closed (Chesson, 1996) and will be referred to for convenience as the regional scale following (Slatkin, 1974). In models, this regional scale may actually include an infinite amount of space, such as an infinite number of patches or the entire real plane,  $R^2$ . Such infinite systems may be considered large system limits that simplify modeling. The following example motivates the general model.

### Model of an Annual Plant Community

Consider an annual plant with a seed bank. An individual seed is assumed to have a particular germination probability,  $E_{jx}$ , as a function of the environmental conditions that it experiences. If it germinates, then it grows and has seed yield

$$Y_j/C_{jx},$$

where  $Y_j$  is seed yield in the absence of competition, i.e., with competition parameter equal to one. The competition parameter,  $C_{jx}$ , is then the amount by which yield is reduced by the presence of neighbors.

If the seed does not germinate, it has some survival probability  $s_j$ . Putting this information together gives

$$\lambda_{jx} = G_j(E_{jx}, C_{jx}) = s_j(1 - E_{jx}) + E_{jx} Y_j/C_{jx}. \quad (2)$$

Note that this formula describes the *mean* contribution to the total seed population of species  $j$  at time  $t + 1$  from an individual seed experiencing  $E_{jx}$  and  $C_{jx}$ , at time  $t$ .

What an individual actually does naturally shows chance variation from this mean, leading to demographic stochasticity; but (2) defines the mean for an individual experiencing these conditions. We can imagine that the germination probability  $E_{jx}(t)$  is defined by physical conditions at location  $x$  and time  $t$ . Indeed, those physical conditions prescribe a particular value for the vector of germination probabilities  $(E_{1x}, E_{2x}, \dots, E_{nx})$  for the  $n$  species guild. Hence there are likely to be correlations between the germination probabilities of different species due to a common physical environment.

Equation (2) does not define the full dynamics of the system. At the very least,  $C_{jx}$  needs to be defined. Plausibly, it depends on the number of other seeds germinating in a defined neighborhood of the given seed. For example,

$$C_{jx} = 1 + \sum_{l=1}^n \alpha_l E_{lx} \eta_{lx}, \quad (3)$$

where  $\eta_{lx}$  is a measure of the number of seeds of species  $l$  present in a neighborhood of location  $x$  and  $\alpha_l$  is the competitive effect of an individual of species  $l$ . A very simple assumption, uniform dispersal, in which seeds produced at any location are dispersed equally to all locations, would give  $\eta_{lx} = \bar{N}_l(t)$ , the average density in space of the species in the system. In that case, given the probability distribution of  $(E_{1x}, E_{2x}, \dots, E_{nx})$ , the dynamics of seed densities in the system are fully defined. However, more complex dispersal scenarios are realistic, and in general  $\eta_{lx}$  will not be available from a simple formula.

In the above example, the competition parameter (Eq. 3) does not depend on  $j$ , the species; and for this reason, we can say that there is only one *competitive factor* in this system. We can write  $C_{jx} = 1 + F_x$ , where the competitive factor  $F_x$  is the weighted sum of the seedling densities in the neighborhood of  $x$ , the weights being the competitive effects of the different species. Summarizing competition in this way in terms of competitive factors allows the competitive relationships between species to be better understood. In a system that is homogeneous in space and time, for example, this representation leads to the immediate conclusion that only one species would be able to persist in the long run (Levin, 1970; Armstrong and McGehee, 1980; Chesson and Huntly, 1997). In general, we shall think of the competition parameter  $C_{jx}$  as some function  $\phi'_j(\mathbf{F})$  of a vector of  $p$  competitive factors  $\mathbf{F} = (F_{1x}, \dots, F_{px})'$ . There is no loss of generality in this assumption because the definition  $F_{jx} = C_{jx}$  is always possible, although uninformative.

Another property of the formula (3) for  $C_{jx}$  in the above example is that it is explicitly a function of the environmentally-dependent parameters of the species: the competitive factor, seedling density, is dependent on the local germination rates. Thus, the environmentally-dependent and competition parameters covary; i.e., there is *covariance between environment and competition*. Even without explicit representation of competition in terms of environment, such covariance arises when there is limited dispersal in space and there are correlations over time in the environment, for then the local density  $N_{jx}(t)$  is correlated with the environmentally-dependent parameter,  $E_{jx}(t)$ . If the spatial locations,  $x$ , are cells within which density-dependent interactions are confined, competition may be represented explicitly as a function  $f_j$  of local environmentally-dependent parameters and local density; i.e.,

$$C_{jx}(t) = f_j(E_{1x}(t), E_{2x}(t), \dots, E_{nx}(t), N_{1x}(t), N_{2x}(t), \dots, N_{nx}(t)). \quad (4)$$

However, with more general assumptions about space, such a tidy representation of competition would not apply.

### Population Dynamics at the Regional Scale

On the regional scale, where the system as a whole is assumed closed, the total number of individuals of species  $j$  at time  $t + 1$  is approximately equal to the sum of  $\lambda_{jx}$  over all individuals in the population. The actual total population at time  $t + 1$  will differ randomly from this, but for large populations this random deviation can be ignored. Demographic stochasticity occurring locally in space, and interacting with nonlinear dynamics locally in space, potentially has systematic effects on the sum of the  $\lambda_{jx}$  (Chesson, 1981; Durrett and Levin, 1994; Bolker and Pacala, 1997; Chesson, 1998; Bolker and Pacala, 1999) and in general should not be ignored because in some cases it has major effects on species coexistence (Durrett and Levin, 1994; Bolker and Pacala, 1999; Neuhauser and Pacala, 1999).

From this approximation to the total population at time  $t + 1$ , it follows that the dynamics of the density of species  $j$  for the whole system are given by the equation

$$\bar{N}_j(t + 1) = \tilde{\lambda}_j \bar{N}_j(t), \quad (5)$$

where  $\tilde{\lambda}_j$  is the average of  $\lambda_{jx}$  over all individuals in the population of species  $j$ , and  $\bar{N}_j$  is the average density of species  $j$  in the system, i.e., the total population of species

$j$  in the system divided by the area for a system with finite area or an appropriate limit of such a ratio for a system with infinite area.

Equation (5) importantly contains two different sorts of averages: an average of  $\lambda_{jx}$  over individuals and an average of population density over space. The average over individuals can also be expressed as an average over space if we define the *local relative density* to be

$$v_{jx} = N_{jx} / \bar{N}_j, \quad (6)$$

where  $N_{jx}$  is the population density of species  $j$  at location  $x$ . Then the average of  $\lambda_{jx}$  over all individuals can be written as

$$\tilde{\lambda}_j = \overline{\lambda_j v_j} = \bar{\lambda}_j + \text{Cov}(\lambda_j, v_j), \quad (7)$$

which expresses the average over individuals first as a spatial average weighted by density of individuals at a locality and then as a spatial average plus the covariance in space of  $\lambda_{jx}$  and local relative density,  $v_{jx}$ . Because the system is large enough that fluctuations due to demographic stochasticity at the regional scale can be ignored, these averages can be written as theoretical mean or expected values; and the covariance can be written as the theoretical spatial covariance. In particular, we can write

$$\bar{\lambda}_j = E[G_j(E_j, C_j)], \quad (8)$$

where the expected value is over space, and the symbols  $E_j$  and  $C_j$  refer to random variables that take the particular values  $E_{jx}(t)$  and  $C_{jx}(t)$  when the location  $x$  and time  $t$  are specified; i.e.,  $E_j$  and  $C_j$  are functions of  $x$  and  $t$  whose variation with  $x$  and  $t$  can be described by probability distributions.  $E_{jx}(t)$  and  $C_{jx}(t)$  are the realized values of  $E_j$  and  $C_j$ . Similarly,  $N_j$  will be a random variable representing the local densities, which takes the value  $N_{jx}(t)$  for given  $x$  and  $t$ , and  $E[N_j(t)] = \bar{N}_j(t)$ , to an adequate approximation in large systems—a probability theory perspective on this is given in Appendix I.

In general, the vector of environmentally-dependent parameters ( $E_1, E_2, \dots, E_n$ ), for the  $n$  species has a joint  $n$ -dimensional probability distribution describing the joint variation in space of these parameters. This distribution will be assumed not to vary in time, which means there is no overall temporal variation in the system, but there may well be spatio-temporal variation. Thus, although the distribution of the values of ( $E_1, E_2, \dots, E_n$ ) over all space is the same at every time, it is quite possible that the value of ( $E_1, E_2, \dots, E_n$ ) at any given location

varies with time. *Pure spatio-temporal variation* (Chesson, 1985) is the case where  $(E_1, E_2, \dots, E_n)$  varies independently over time at each spatial location,  $x$ , and conversely varies independently over space for each time,  $t$ . *Pure spatial variation* is the case where  $(E_1, E_2, \dots, E_n)$  does not vary with time and hence only varies in space. In general, it is assumed here that some mixture of these two sorts of variation applies. The role of *pure temporal variation* has been investigated at length in Chesson (1994) and will not be considered in this article. The spatial patterns of  $E_j$  may be correlated between species. However, realistically, it must also be expected that species do not have perfectly correlated spatial patterns of variation; i.e., there are likely to be *species-specific responses to the environment*.

The variation in space of the competition parameter,  $C_j$ , can be expected to depend on or be correlated with the environmentally-dependent parameters of the species, as illustrated in Eq. (3) and discussed at length elsewhere in the context of temporal variation (Chesson and Huntly, 1988). Thus, in general it can be expected that  $E_j$  and  $C_j$  will covary over space; i.e., there will be *covariance between environment and competition*. Naturally,  $C_j$  also varies with local abundances.

How organisms migrate, disperse, or otherwise move in space is not specified in the formulation above. The finite rate of increase is assumed to take into account any mortality that takes place during dispersal, but dispersal should have major effects on relative local densities,  $v_{jx}$ . Note that because of dispersal,  $N_{jx}(t+1) \neq \lambda_{jx}(t) N_{jx}(t)$ . The  $\lambda_{jx}(t) N_{jx}(t)$  individuals at time  $t+1$  arising from the  $N_{jx}(t)$  individuals at location  $x$  and time  $t$  are dispersed by some rule, which, for the most general developments here, need not be specified. The outcome of dispersal registers in the variables  $v_{jx}$ , and it is the properties of  $v_{jx}$ , not the underlying cause of these properties, that figures in these general developments. Very simple migration assumptions, however, lead to spatially-implicit models, which we consider next as one particularly tractable class that illustrates in simple form the general principles to be derived here.

### **Spatially-Implicit Models**

The general model presented above can be very complicated to analyze from the fact that the probability distribution for relative local density,  $v_{jx}$ , changes with time in a manner that is difficult to determine in general. In certain models, sometimes called *spatially implicit* or *pseudo-spatial*, the probability distribution for relative local density can be written as a function of regional average densities,  $(\bar{N}_1(t), \bar{N}_2(t), \dots, \bar{N}_n(t))$ . Such spatially-implicit models are most clearly applicable to the situation

where local populations are ephemeral, dispersing widely in space every unit of time. In such cases, dispersing organisms can be regarded as forming a common pool from which they are redistributed. Populations do not build up over time in particular localities, although they need not be randomly distributed in space. Random dispersal would lead to a Poisson distribution in space with mean  $\bar{N}_j(t)$ , which at high local densities is approximated by uniform dispersal in which the emigrants from any locality are equally distributed over all localities. Nonrandom dispersal may occur with widespread dispersal because organisms may be clumped in space by aggregation in relation to local environmental conditions or in relation to chance prior immigration at a locality. The negative binomial distribution with mean  $\bar{N}_j(t)$  and constant clumping parameter  $k$  is a model representing aggregation of widely dispersive organisms to particular local environmental conditions (Chesson, 1998). In this scenario, immigration to a locality from the pool of dispersing individuals may be explicitly represented as a function of the environmentally-dependent parameter  $E_j$  (Chesson, 1985). These various instances of widespread dispersal are justifications for spatially-implicit models of population dynamics; they may be good approximations for some systems such as insects feeding on ephemeral resource patches (Atkinson and Shorrocks, 1981; Ives, 1988), marine systems with widely dispersing larvae (Chesson, 1985; Comins and Noble, 1985), and even annual plant communities when dispersal is large compared with the mean spacing between individual organisms (Pacala and Silander, 1985).

In these circumstances it is often possible to write  $\tilde{\lambda}_j(t)$  in a similar form to Eq. (8) for  $\tilde{\lambda}_j(t)$ ; i.e., there is a function  $H_j$  such that

$$\tilde{\lambda}_j = E[H_j(E_j, C_j)]. \quad (9)$$

Thus, the function  $H_j$  combines  $G_j$  and  $v_j$ , but is not always simply the product, but more generally, the conditional expectation

$$H_j(E_j, C_j) = E[\lambda_j v_j | E_1, \dots, E_n], \quad (10)$$

in which  $C_{jx}$  may have a slightly different definition than would naturally apply. The example below illustrates this idea.

### **Model of Insects Laying Eggs in Ephemeral Patches of Food**

Some insects, especially Dipterans, lay their eggs in ephemeral patches of food, such as fruit, fungi, or the

dead bodies of animals, in which their larvae develop (Atkinson and Shorrocks, 1981; Ives, 1988). As these patches last for just one generation, to lay their eggs, the flies emerging from these food patches must disperse to new food patches. Common models for this situation take forms equivalent, for the purposes of studying species coexistence, to

$$\lambda_{jx} = e^{r_j(1 - C_{jx})}, \quad (11)$$

where

$$C_{jx} = \sum_{l=1}^n \alpha_{jl} N_{lx}, \quad (12)$$

$N_{lx}$  is the number of eggs deposited in food patch  $x$  of species  $l$ , and the  $\alpha_{jl}$  are competition coefficients. A simple model of dispersal is  $N_{jx}(t) = E_{jx}(t) \bar{N}_{jx}(t)$ , i.e., the total pool of eggs, is divided up over patches according to some environmental characteristic of the food patches such as attractiveness or accessibility of a food patch to adults of the species. In this particular instance,  $v_{jx} = E_{jx}$ , and we see that

$$H_j(E_{jx}, C_{jx}) = \lambda_{jx} v_{jx} = E_{jx} e^{r_j(1 - C_{jx})}. \quad (13)$$

An alternative interpretation of this formula is that dispersal is uniform in space, meaning that  $v_{jx} = 1$ , and  $E_{jx}$  is a patch and species-specific survival rate from egg to larva due to the physical conditions of the particular patch. With this latter interpretation, expression (13) equals  $G_j$  as well as  $H_j$ .

Following the first scenario where the number of individuals arriving at a patch depends on the environment of the patch, it is common in the literature to have a negative binomial for the distribution of eggs over patches. To cover that case,  $E_{lx} \bar{N}_l(t)$  can be considered to be the conditional mean number of eggs of species  $l$  in the patch with the conditional distribution of  $N_{lx}(t)$ ,  $l = 1, \dots, n$ , being independent Poisson given  $E_{lx}$ ,  $l = 1, \dots, n$ . If the marginal (i.e., ordinary or unconditional) distributions of the  $E_{lx}$  are gamma, it follows that the marginal distributions of the  $N_{lx}(t)$  are negative binomial—this is in fact the approach used by (Ives, 1988). In this case, formula (13) for  $H_j$  still applies, with the following changes.  $H_j(E_j, C_j)$  is now interpreted as the conditional expectation,  $E[\lambda_{jx} v_{jx} | E_j, l = 1, \dots, n]$ ;  $r_j$  and the  $\alpha_{jl}$  are replaced by

$$r'_j = r_j(1 - \alpha_{jj}) \quad \text{and} \quad \alpha'_{jl} = \frac{1 - e^{-r_j \alpha_{jl}}}{r_j(1 - \alpha_{jj})}. \quad (14)$$

The competition parameter is replaced by the average value of (12) for the given environmental conditions, viz.

$$C_{jx} = \sum_{l=1}^n \alpha_{jl} E_{lx} \bar{N}_l. \quad (15)$$

It is worthwhile noting also that the Poisson component has a small effect if the competition coefficients are small. As  $1/\alpha_{jj}$  is the local carrying capacity in terms of egg number, moderately large average local egg numbers remove any appreciable effect of the Poisson component of negative binomial variation, and the gamma distribution based just on variation in  $E_{jx}$  can be used instead. A similar remark applies to the annual plant model for large dispersal distances. Although a Poisson distribution is certainly more realistic than no variation in space in seed densities, which arises from the assumption of uniform dispersal, moderately large local neighborhoods mean that the Poisson distribution would have negligible effects and important effects of space would continue to arise from spatial variation in seed germination (attributed here to an environmental effect), not seed abundance. Naturally, other dispersal assumptions, such as environmentally-dependent dispersal, or short distance dispersal could lead to important effects of spatial variation in seed abundance, as demonstrated by Bolker and Pacala (1999).

## MODEL ANALYSIS

Having established the equation  $\bar{N}_j(t+1) = \tilde{\lambda}_j \bar{N}_j(t)$  as defining the regional dynamics of a large population, how do we analyze it? In spatially-implicit models as discussed above,  $\tilde{\lambda}_j(t)$  can be expressed as a function of  $(\bar{N}_1(t), \bar{N}_2(t), \dots, \bar{N}_n(t))$  alone, and therefore the dynamics of average population density are simply defined by autonomous difference equations. Standard methods apply. In other cases, a full analysis of the system is potentially extremely complex. However, for a broad subset of cases, necessary conditions for coexistence are available with important general information about coexistence in a spatially variable environment. In many situations, it seems likely that these conditions are also sufficient, but at present there is no general approach demonstrating sufficiency.

When it is possible for species to be perturbed to arbitrarily low densities, a necessary condition for stable coexistence is that each species increases from such low densities in the presence of its competitors (*mutual invasibility*). Additional conditions are necessary to specify

sufficient conditions for stable coexistence (Chesson, 1982; Hutson and Law, 1985; Chesson and Ellner, 1989; Ellner, 1989; Law and Morton, 1996), but an increase from low density is an essential feature of stable species coexistence and provides a means of quantifying coexistence. In an invasibility analysis, species perturbed to low density are termed *invaders* and will be denoted here by the species label  $i$ . The rest of the community, which has not been perturbed to low density, is given species labels  $r$  and  $s$ , and is termed *the residents*. If  $\tilde{\lambda}_i$  is greater than 1, species  $i$  is assumed to be able to persist in the presence of its competitors (the residents) and the actual value of  $\tilde{\lambda}_i$  can be used to quantify coexistence and therefore to measure quantitatively the contributions of different coexistence mechanisms. Indeed, this ability to quantify coexistence is an important attribute of the invasibility criterion.

Calculating the invader growth rate,  $\tilde{\lambda}_i$ , is far from straightforward in general spatial models. First,  $\tilde{\lambda}_i$  might fluctuate over time, in which case, invasion is determined by the mean of over time of  $\ln \tilde{\lambda}_i(t)$  (Turelli, 1981; Chesson and Ellner, 1989). However, most spatial models of competitive interactions that do not involve pure temporal environmental variation (Chesson, 1985) do not lead to important temporal fluctuations in  $\tilde{\lambda}_i$  for large regional populations; that situation will be assumed here because the purpose is to focus on the effects of variation in space. Indeed, consideration will be restricted here to the common case where the residents converge on constant regional densities, i.e., where the vector of resident densities  $\{\bar{N}_r(t), r \neq i\}$  converges with time on a constant value, with the invader constrained to low density. This convergence of resident regional densities is associated with convergence over time of the probability distribution describing the joint variation in space of  $\{E_{rx}(t), C_{rx}(t) \text{ and } N_{rx}(t), r \neq i\}$ . When these conditions have been satisfied, the residents are said to be at their stationary distribution.

Under the above scenario, the invader rate of increase is a function of the stationary statistical properties of the resident population, the invader's environmentally-dependent parameters, and the invader's distribution in space. To understand the key features of the invader's distribution in space, note that when local population densities are modeled as continuous variables, low regional densities will normally also mean that local densities are mostly small. It follows that effects of species  $i$ 's density on itself and on the residents will become negligible as the regional density,  $\bar{N}_i(t)$ , of species  $i$  is made arbitrarily small. The dynamics of invader species  $i$  will therefore be asymptotically linear its own local densities, as  $\bar{N}_i(t) \rightarrow 0$ , which means that the dynamics of relative densities,  $\{v_{ix}(t), \text{ all locations, } x\}$ , will not

depend on the invader regional density, which can therefore be set equal to 0. The probability distribution describing spatial variation in  $(v_{ix}(t), \lambda_{ix}(t))$  should converge with time to a unique limiting distribution with  $\tilde{\lambda}_i$  being the spatial average of  $\lambda_{ix}(t) v_{ix}(t)$  for this limiting distribution.

The above described convergence of the invader's spatial distribution will be assumed here. In addition to common applicability to models where local population sizes are continuous variables, such convergence is also commonly applicable to spatially-implicit models with integer local population sizes. Spatially-explicit models with integer local population sizes and local dispersal pose thorny issues with respect to the existence of the various limits implying a unique well-defined value of  $\tilde{\lambda}_i$ , which I shall not attempt to solve here. I simply ask the reader to be satisfied that the invasion analysis applies to a broad enough class of models to make the development that follows worthwhile.

In studies of invasions of alien species (e.g., Shigesada and Kawasaki, 1997) it is common to study invasion from a single point in space. However, the intention here is not to mimic the process of invasion when a species is just introduced to a region, but to study the process of recovery if it is reduced to low density on average throughout the region, which is appropriate for the study of species coexistence, especially in the presence of a component of pure spatial environmental variation, which means that invasions in different spatial locations may follow very different courses.

In conducting the invasibility analysis, I shall add the superscript  $-i$  to the competition parameter to indicate that the residents are assumed to have reached their stationary distribution in the absence of species  $i$ , the invader. In these terms, we seek to determine the sign and magnitude of

$$\begin{aligned} \tilde{\lambda}_i &= \bar{\lambda}_i + \text{Cov}(\lambda_i, v_i) \\ &= E[G_i(E_i, C_i^{-i})] + \text{Cov}(G_i(E_i, C_i^{-i}), v_i). \end{aligned} \quad (16)$$

## SPATIAL COEXISTENCE MECHANISMS

Three general classes of coexistence mechanisms arise from variation in space. Two of these, *the storage effect* and *relative nonlinearity of competition*, arise from the behavior of the simple average  $\bar{\lambda}_i$  and are direct analogues of mechanisms applying for temporal variation, which arise from the temporal average,  $\bar{r}_i = \ln \bar{\lambda}_i$ ,

of  $\ln \lambda_i(t)$ . The final class of mechanisms, which as yet has no known temporal counterpart, arises from  $\text{Cov}(\lambda_i, v_i)$ .

### The Spatial Storage Effect

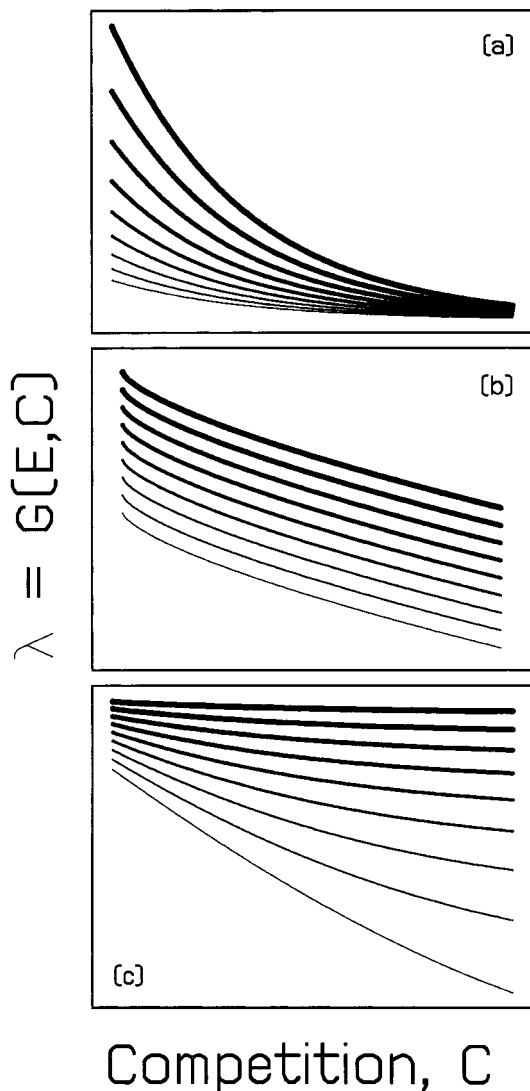
The storage effect arises from an interaction between  $E_j$  and  $C_j$  in their joint determination of  $\lambda_j$  (Chesson, 1988, 1994; Chesson and Huntly, 1997). An interaction means in particular that the value of  $E_j$  alters the effect that  $C_j$  has on  $\lambda_j$ . This is illustrated in Fig. 1. In panel (a) of the figure, increasing the value of  $E_j$  steepens the slope of the relationship between  $\lambda_j$  and  $C_j$ , an effect which is measured by the cross partial derivative

$$\gamma = \frac{\partial^2 G_j}{\partial E_j \partial C_j}. \quad (17)$$

In the case of Fig. 1a, this cross partial derivative is negative, indicating that the negative slope of the relationship between  $\lambda_j$  and  $C_j$  is made more negative by increases in  $E_j$ . This situation is referred to as *subadditive*, because the change in  $\lambda_j$  that results from a joint change in  $E_j$  and  $C_j$  is less than the sum of the changes that each factor causes when varied separately. In spatially-implicit models, subadditivity and the quantity  $\gamma$  should be defined in terms of  $H$  rather than  $G$ ; indeed, for spatially-implicit models  $H$  should be substituted for  $G$  throughout the discussion below.

Subadditivity may be regarded as having a buffering effect on population growth because simultaneously poor conditions, viz. a low value of  $E_j$  and a high value of  $C_j$ , are not as bad as predicted by the sum of their separate effects. Contrasting situations are additive growth rates, corresponding to a zero value of  $\gamma$  (Fig. 1b), and super-additive growth rates with positive  $\gamma$  (Fig. 1c). With additive growth rates,  $E_j$  and  $C_j$  contribute separately to produce  $\lambda_j$  and so the joint effect of  $E_j$  and  $C_j$  is simply the sum of their separate effects. With superadditive growth rates, there is again an interaction between  $E_j$  and  $C_j$  but in this case a low  $E_j$  and a high  $C_j$  is worse than predicted by the sum of their separate effects.

The annual plant model given by Eq. (2) above is subadditive as are most spatial models that can be put in this framework. There is a very simple reason. The finite rate of increase  $\lambda_j$  cannot be less than 0, and it would normally be expected that  $\lambda_j$  would approach 0 as competition becomes severe, regardless of the environmental conditions. Thus, plots of  $G_j(E_j, C_j)$  against  $C_j$  for different  $E_j$  should all converge on zero. Thus, at least for large  $C_j$ , these plots should look like Fig. 1a, subadditivity. This situation does not apply when considering



**FIG. 1.** The finite rate of increase,  $\lambda$ , plotted as a function of the competition parameter  $C$  for increasing values of the environmentally-dependent parameter,  $E$ . Thicker curves are higher values of  $E$ . (a) Subadditivity; (b) additivity; (c) superadditivity.

purely temporal variation for then one is concerned with averaging  $r_j (= \ln \lambda_j)$  which is not bounded below by any definite value. In the temporal case, models with additive growth rates may be formulated realistically, but superadditivity is more difficult to obtain (Chesson and Huntly, 1988; Chesson, 1994).

The biological explanation for the difference between these two situations is that in the spatial case, the buffering of population growth that is associated with subadditive growth rates automatically occurs from the subdivision of the population in space over the varying conditions of  $E_j$  and  $C_j$  because poor performance in some spatial locations is ameliorated by better performance elsewhere. Such



effects do not occur so readily with temporal variation from the simple fact that population growth is multiplicative over time, and so poor performance at one time lowers the starting point from which population growth occurs the next time. Specific life-history traits are needed to counteract such negative effects arising from the multiplicative nature of population growth (Chesson and Huntly, 1988).

Subadditive growth rates not only buffer population growth, they may also lead to species coexistence when combined with two other realistic features of nature. The first of these is *species-specific responses to the environment*: different species have different patterns of variation in environmental responses ( $E_j$ ) in space. The second feature is *covariance between environment and competition*: the competition parameter  $C_j$  increases as a function of the environmentally-dependent parameter,  $E_j$ . Covariance between environment and competition constrains the pattern of joint variation in  $E_j$  and  $C_j$  on which  $\lambda_j$  depends and therefore affects the outcome of the interaction between  $E_j$  and  $C_j$ .

To see how this promotes coexistence, consider the following symmetric example:

*Symmetric example.* Assume

1. There is a common  $G_j = G$  for the different species;
2. There is a common  $C_j = C$ , and the conditional distribution of  $C^{-i}(t)$ , given  $(E_1(t), E_2(t), \dots, E_n(t))$ , depends symmetrically on the resident environmentally-dependent parameters,  $E_r(t)$ ,  $r \neq i$ , and does not vary with the invader environmentally-dependent parameter;
3. Environmental variation is pure spatio-temporal, and the distribution of  $(E_1, E_2, \dots, E_n)$  is symmetrical.

In the special case of the annual plant model, assumption 1 means that  $s_j$  and  $Y_j$  have the same values for all species, assumption 2 means that  $\alpha_j$  is the same for all species, and dispersal does not differ between species. A symmetrical distribution as specified in 3 means that  $(E_{\pi(1)}, E_{\pi(2)}, \dots, E_{\pi(n)})$  has the same distribution as  $(E_1, E_2, \dots, E_n)$  for any permutation  $\pi(1), \pi(2), \dots, \pi(n)$  of  $1, 2, \dots, n$ . In particular, all species have the same distribution for their environmentally-dependent parameters, and all pairs of species have the same correlation between their environmentally-dependent parameters.

Now we add to these assumptions the three ingredients of the storage effect as they apply in this specific example:

4. *species-specific responses to the environment*, which means here that  $E_j - E_l$  has positive variance for any pair of species  $j$  and  $l$ ;

5. *Covariance between environment and competition*: the conditional distribution of  $C^{-i}(t)$ , given  $(E_1(t), E_2(t), \dots, E_n(t))$  is an increasing function of the resident environmentally-dependent parameters,  $E_r(t)$ ,  $r \neq i$ , i.e.,  $P(C^{-i}(t) > c | E_1(t), E_2(t), \dots, E_n(t))$  increases in any  $E_r(t)$  for all constants  $c$ ;

6. *Subadditivity*, which is discussed at length above.

Assumption 5, deserves amplification. The idea is simply that competition should increase as a function of the environment. However, competition is also a function of species densities, which complicates the issue. With an explicit representation of competition in the form

$$C_x(t) = f(E_{1x}(t), E_{2x}(t), \dots, E_{nx}(t), N_{1x}(t), N_{2x}(t), \dots, N_{nx}(t)),$$

where  $f$  is some function increasing in each of the  $E_{jx}(t)$ , then the assumption that the environmental variation is pure spatio-temporal is sufficient for assumption 5 for then the  $N_j(t)$  are statistically independent of the  $E_j(t)$  and so do not interfere with the relationship between  $C(t)$  and  $E_r(t)$ . Those spatially-implicit models in which the  $N_j(t)$  do not vary in space also have this property regardless of whether environmental variation is pure spatio-temporal. In other situations (see examples below), it is often the case that the conditional distribution of local resident densities increases with their respective environmentally-dependent parameters, and as  $f$  would naturally increase as a function of local densities, condition 5 would again be satisfied.

With these assumptions, two equivalent but different derivations for the temporal case given in (Chesson, 1988, 1990) can be extended to show that

$$E[G(E_i, C^{-i})] > E[G(E_r, C^{-i})], \quad (18)$$

i.e., the average value of  $\lambda$  over space for invaders is greater than that for residents ( $\bar{\lambda}_i > \bar{\lambda}_r$ ). Thus, in the case of zero covariance between  $\lambda$  and relative density  $v$ , or if  $G$  is replaced by  $H$ , this is identical to the statement

$$\tilde{\lambda}_i > 1, \quad (19)$$

which is the same for all species as invaders and therefore means that all species coexist according to the invasibility criterion. The derivation for the temporal case in (Chesson, 1990) shows in particular that the difference between  $\tilde{\lambda}$

and 1 increases with the magnitude of subadditivity (as measured by  $\gamma$ ), increases with the variance of  $E_j - E_i$ , and increases with the slope of  $C$  as a function of  $E_j$ .

Thus, it increases with the magnitude of each of three ingredients of the storage effect. In this symmetric case with  $\text{Cov}(\lambda, v) = 0$  or in symmetric spatially-implicit models, the storage effect is the sole and complete mechanism of coexistence. The symmetric case is not realistic in nature, however. It remains of interest because in general  $\tilde{\lambda}_i$  can be expected to vary continuously as a function of deviations from symmetry. Therefore,  $\tilde{\lambda}_i$  will remain above 1 for some range of deviation from symmetry. Of greatest importance are situations where different species have different spatial average fitnesses, which might be reflected, for example, by different average values of the  $E_j$ . Without variation in the environment, these cases lead to domination by a single species, but with sufficient variation and the ingredients above for the storage effect, coexistence is possible in spite of the average fitness disadvantages that some species may have. The quantitative approximations below show how this works.

In spatially explicit models with limited dispersal, inequality (18) still holds under the symmetric assumptions above, and so the storage effect can be considered to contribute to coexistence even though it may be opposed or reinforced by the behavior of  $\text{Cov}(\lambda, v)$ . This issue is clarified by the quantitative results below, which allow simultaneous consideration of multiple mechanisms.

### Spatial Relative Nonlinearity of Competition

Organisms living in the same environment and responding to the same competitive factors may differ by having different nonlinear responses to these competitive factors. For example, expressing the competition parameter in terms of a vector of common competitive factors  $\mathbf{F}$ ,

$$C_j = f_j(\mathbf{F}), \quad (20)$$

$\lambda_j$  takes the form

$$\lambda_j = G_j(E_j, f_j(\mathbf{F})). \quad (21)$$

Species coexistence may be affected when the  $\lambda_j$  are different nonlinear functions of  $\mathbf{F}$  for different species and  $\mathbf{F}$  varies in space. Effects on coexistence are most easily seen in the case of just a single competitive factor,  $F$ . Assuming

that  $\lambda_j$  is monotonic in  $F$  for each  $j$ , then for any two species  $u$  and  $v$ , the common dependence on  $F$  means that the  $\lambda$ s can be expressed in terms of each other and the vector of environmentally-dependent parameters,  $\mathbf{E} = (E_1, E_2, \dots, E_n)$ , by means of some function which may be designated  $h_{uv}$ :

$$\lambda_u = h_{uv}(\mathbf{E}, \lambda_v). \quad (22)$$

The critical issue is the shape of  $\lambda_u$  as a function of  $\lambda_v$ . For example, in Fig. 2, with  $\lambda_u$  a convex function of  $F$  and  $\lambda_v$  a concave function of  $F$ ,  $\lambda_u$  is a convex function of  $\lambda_v$  ( $\partial^2 h_{uv}(\mathbf{E}, \lambda_v) / \partial \lambda_v^2 > 0$ ) and therefore curves upward as  $\lambda_v$  increases. When  $\lambda_u$  is a convex function of  $\lambda_v$ ,  $\lambda_v$  is necessarily a concave function of  $\lambda_u$  assuming that they are both decreasing or both increasing functions of  $F$ . Relative nonlinearity is any deviation from linear relationships between the  $\lambda$ s through their common dependence on  $\mathbf{F}$ , but the strictly convex and concave relationships depicted in Fig. 2 may be called uniform nonlinearities.

Jensen's inequality applies to show that when an invader  $\lambda$  is a convex function of a resident  $\lambda$ ,

$$\bar{\lambda}_i > E[h_{ir}(\mathbf{E}, \bar{\lambda}_r)], \quad (23)$$

which means that spatial variation in  $F$  boosts  $\bar{\lambda}_i$  above the value predicted by the relationship (22) between  $\lambda_i$  and  $\lambda_r$ . With the roles of the species reversed (i.e., the

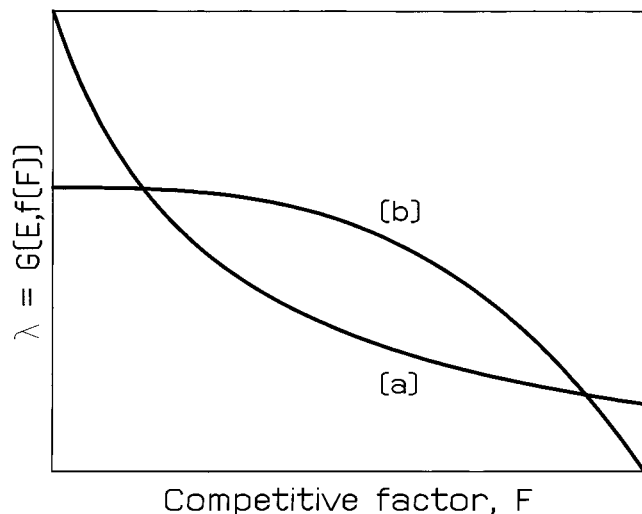


FIG. 2. The finite rate of increase,  $\lambda$ , plotted against a common competitive factor,  $F$ , for two different species in the same community. (a) Convex relative growth rate, (b) concave relative growth rate.

previous resident as the invader), the invader  $\lambda$  is a concave function of the resident  $\lambda$ ,

$$\bar{\lambda}_i < E[h_{ii}(\mathbf{E}, \bar{\lambda}_i)], \quad (24)$$

and  $\bar{\lambda}_i$  is diminished by spatial variation in  $F$ . Thus, variation in a common competitive factor in the presence of a uniform relative nonlinearity pushes one species'  $\bar{\lambda}_i$  down and pushes the other species'  $\bar{\lambda}_i$  up. This asymmetrical effect naturally follows from the asymmetries between species inherent in relative nonlinearities.

A single competitive factor in a spatially- and temporally-uniform environment, i.e., with no variation in  $\mathbf{E}$  or  $F$  in space, would predict dominance by one species because an  $F^*$  rule would apply in analogy with the  $R^*$  and  $P^*$  rules respectively for resource and apparent competition (Holt, Grover, *et al.*, 1994). To see this, note that the equation  $1 = G_j(E_j, f_j(F^*))$  defines species  $j$ 's  $F^*$  value, which is the value of  $F$  at which species  $j$  would not change in population size. Assuming that  $\lambda$  is monotonically decreasing in  $F$ , that species differ in their  $F^*$  values, and that the multispecies system does come to a point equilibrium, homogeneously in space and time, then only the species with highest  $F^*$  value would be present at equilibrium (Holt, Grover, *et al.*, 1994). Applying this result to a system consisting of just two species we see that the average invader growth rate,  $\bar{\lambda}_i = h_{ii}(\mathbf{E}, 1)$ , can only be greater than 1 for one of them, the dominant.

In the presence of spatial variation in  $F$ , the asymmetrical effects of relative nonlinearity on these two species expressed by inequalities (23) and (24) promote coexistence by increasing the  $\bar{\lambda}_i$  of a relatively convex subordinate species as long as the  $\bar{\lambda}_i$  of the dominant is not too greatly decreased. The approximate quantitative results below show how these effects may be achieved. In general, for relative nonlinearity to act as a coexistence mechanism by itself, more variance in  $F$  must be associated with the relatively concave dominant as a resident than with the subordinate as a resident so that the subordinate  $\bar{\lambda}_i$  may rise above 1 without the dominant  $\bar{\lambda}_i$  falling below 1. Relative nonlinearity works here by diminishing fitness differences between species. It does this when the otherwise more fit species is the more concave.

As with the storage effect, changes in  $\bar{\lambda}_i$  due to spatial variation only demonstrate coexistence promoting effects if they are not opposed by changes in  $\text{Cov}(\lambda, v)$  or if  $G$  is replaced by  $H$  in the above discussion, in which case the results apply directly to  $\bar{\lambda}_i$ . In any case, the limited ability for relative nonlinearity to promote coexistence when acting alone means that it is best viewed as modifying other mechanisms such as the storage effect or covariance

between the finite rate of increase and the relative density. It can do this by decreasing the degree of dominance of a superior competitor with a relatively concave growth rate making it easier for other mechanisms to raise all values of  $\bar{\lambda}_i$  above 1. On the other hand if the superior species is relatively convex, competitive exclusion will be promoted by relative nonlinearity.

Relative nonlinearity occurs under different circumstances in space compared with time. For example, the annual plant model described above is not relatively nonlinear as a spatial model because the  $\lambda$ s of different species are linear functions of the same nonlinear function of the competitive factor. However, relative nonlinearity applies in time when species differ in  $s_j$  or  $Y_j$  (Chesson, 1994). In contrast, the insect model given by Eq. (12) always shows relative nonlinearity if the competition parameter is common to all species ( $C_j \equiv C$ ) whenever the  $r_j$  differ between species. However, the corresponding temporal model never shows relative nonlinearity (Chesson, 1994, Sect. 5.1).

### **Covariance between Relative Density and Rate of Increase**

The quantity  $\text{Cov}(\lambda_j, v_j)$  would seem to be affected by many factors including the nature of dispersal and the nature of environmental variation, but as yet there is no general understanding of its properties. However, in the presence of limited dispersal and pure spatial variation it may reasonably be expected to be positive because local populations should then be larger in locations with larger finite rates of increase. This covariance may be larger for invaders than for residents when there are species-specific responses to the environment because residents are more limited by competition and therefore have smaller variance in both  $\lambda_j$  and  $v_j$  which should mean smaller covariance between them. This reasoning suggests that coexistence should be promoted by limited dispersal and pure spatial variation due to  $\text{Cov}(\lambda_j, v_j)$ . To see that this proposition is indeed correct in at least some circumstances, consider the symmetric example discussed above under the subheading *The Spatial Storage Effect*, making assumptions 1–3 with the modification that variation is restricted to *pure spatial* variation.

To specify limited dispersal, assume that each time period,  $t$  to  $t + 1$ , some particular fraction,  $q = 1 - p$ , is dispersed from each locality to join a common pool from which they are uniformly dispersed to all localities. This is a model of *widespread dispersal with local retention* as may be expected in communities of coral reef fishes.

The dynamics at each locality are then given by the equation

$$N_{jx}(t+1) = p\lambda_{jx}(t) N_{jx}(t) + q\bar{N}_j(t+1). \quad (25)$$

It is shown in Appendix II that  $\tilde{\lambda}_i > 1$  if and only if

$$Ef(G(E_i, C_i^{-i})) > Ef(G(E_r, C_r^{-i})), \quad (26)$$

where  $f$  is the function defined by the equation  $f(G) = qG/(1-pG)$ . Thus, the conditions for coexistence that were encountered in the discussion of the storage effect above now apply to  $f(G)$  rather than  $G$ . It follows that if  $f(G)$  is subadditive and there is positive covariance between environment and competition, then condition (26) for coexistence is satisfied. With  $p$  between zero and one,  $f$  is an increasing convex function. It follows that  $f(G)$  is subadditive when  $G$  is additive or subadditive and it is also possible for  $f(G)$  to be subadditive in some cases where  $G$  is superadditive (Appendix II).

At least in the two species case, if  $C$  increases directly as a function of the  $E_j$  or is instead constant as a function of the  $E_j$ , in the functional form  $C_x(t) = f(E_{1x}(t), E_{2x}(t), \dots, E_{nx}(t), N_{1x}(t), N_{2x}(t), \dots, N_{nx}(t))$ , it is nevertheless true that  $C^{-i}$  has positive covariance with the  $E_r$  (Appendix II). It is also possible for  $C^{-i}$  to have positive covariance with the  $E_r$  when  $C$  decreases as a function of the  $E_j$ , with relative densities held fixed. Thus, coexistence occurs provided only that the functions  $G$  are not too superadditive and  $C$  does not decrease too strongly as a function of the  $E_j$ . These results represent substantial broadening of the range of the opportunities for coexistence compared with cases with pure spatio-temporal variation and no variation in relative density. Variation in relative density has two effects. One is to increase covariance between environment and competition and thus contribute to the storage effect by allowing positive covariance between environment and competition even when  $C$  decreases as a function of the  $E_j$ . The second is a positive effect resulting from the covariance between the local finite rate of increase and relative density. This covariance is simply the difference  $\tilde{\lambda} - \bar{\lambda}_j$ , and the comparison of these differences for residents and invaders in this symmetric situation can be regarded as its contribution to species coexistence. It is tempting to regard  $Ef(G) - EG$  as  $\text{Cov}(\lambda, v)$  but this is only true when  $\tilde{\lambda}$  is equal to 1 and therefore only correct for the resident species. However, it is apparent from Appendix II that  $Ef(G) - EG$  may be regarded as a 0th order approximation to  $\text{Cov}(\lambda, v)$  in other cases.

The presence of  $\text{Cov}(\lambda, v)$  leads to effects directly analogous to subadditivity in this particular example.

Could it be that an effect comparable to relative nonlinearity of competition might also occur in some circumstances? A little calculus shows that relative nonlinearity may potentially occur in the case of pure spatial variation considered here when the species differ in the amount of local retention during dispersal, for this means that the functions  $f$  that modify the effect of  $G$  are convex to different degrees for different species.

## QUANTITATIVE RESULTS

The three mechanisms discussed above, the storage effect, relative nonlinearity, and covariance between the growth rate and relative density, can be expressed as additive components of  $\tilde{\lambda}_i$  using a quadratic approximation. Within the accuracy of the quadratic approximation, these three mechanisms dependent on spatial variation, together with mechanisms of coexistence that do not rely on spatial variation (“variation-independent” coexistence mechanisms), seem to exhaust the possibilities for coexistence within the general model. This quadratic approximation technique is developed in detail in (Chesson, 1994) for temporal variation, which is relied on heavily. The technique begins by nonlinear transformation of the environmentally-dependent and competition parameters to a standard form, which expresses them in units of  $\lambda_j$ , i.e., in units that mean the same thing in any particular case of the general model.

### Parameter Standardization

In order to define the standard parameters, a pair of values of  $E_j^*$  and  $C_j^*$  of  $E_j$  and  $C_j$  are chosen satisfying the relationship

$$G_j(E_j^*, C_j^*) = 1, \quad (27)$$

which means no population growth—an equilibrium situation. Species persisting in the system necessarily have their  $\lambda$  values varying around 1. Hence, the existence of parameter values giving the actual value 1 is not a demanding requirement. The particular values  $E_j^*$  and  $C_j^*$  will be referred to as equilibrium values. Unlike  $E_j$  and  $C_j$ , these values do not vary in space. In general, there will be a continuum of choices for the pair of equilibrium values, which leads to some arbitrariness in the analysis, but the rules below constrain  $E_j^*$  to be near the mean of  $E_j$  and make that arbitrariness of small order.

The standard parameters are now defined as

$$\mathcal{E}_j = G_j(E_j, C_j^*) - 1 \quad (28)$$

and

$$\mathcal{C}_j = 1 - G_j(E_j^*, C_j). \quad (29)$$

Provided  $G_j$  is monotonic in each of its arguments, these new parameters contain the same information as the original parameters but are expressed in units of the finite rate of increase  $\lambda_j$ . Like the  $E_j$  and  $C_j$ , the  $\mathcal{E}_j$  and  $\mathcal{C}_j$  vary in space and possibly time also, but this dependence is suppressed in the notation for simplicity. Again, they are best thought of as random variables that take specific values when space and time are specified.

### Quadratic Approximation

In simple models, the formula for  $\lambda_j$  in terms of the standard parameters is very often quadratic in form. Indeed, it is quadratic in all of the examples given here. Naturally, it is also approximately quadratic when the variation in  $\mathcal{E}_j$  and  $\mathcal{C}_j$  is small. Under certain assumptions discussed in Appendix III, small variation in  $\mathcal{C}_j$  follows from small variation in  $\mathcal{E}_j$ . The assumption of small environmental fluctuations is expressed formally as

$$\mathcal{E}_j = O(\sigma) \quad (30)$$

which means here that  $\mathcal{E}_j$  varies within a finite interval containing 0 (a constraint on the choice of  $E_j^*$ ), of order  $\sigma$  (a constraint on the magnitude of variation), where  $\sigma$  is a small parameter. From the assumptions in Appendix III, this means

$$\mathcal{C}_j = O(\sigma). \quad (31)$$

A further constraint on the choice of  $E_j^*$  is the requirement

$$E[\mathcal{E}_j] = O(\sigma^2). \quad (32)$$

Under the appendix assumptions, this implies also that

$$E[\mathcal{C}_j] = O(\sigma^2). \quad (33)$$

As we shall see below, these assumptions and their immediate consequences mean that the magnitudes of the four mechanisms in the expression below are each  $O(\sigma^2)$ , facilitating their comparison.

From (30) and (31), the model can be written in the following general quadratic form

$$\lambda_j - 1 \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j, \quad (34)$$

where the symbol “ $\approx$ ” means equal to  $o(\sigma^2)$ , and  $\gamma_j$  is the cross-partial derivative

$$\gamma_j = \left. \frac{\partial^2 \lambda_j}{\partial \mathcal{E}_j \partial \mathcal{C}_j} \right|_{\mathcal{E}_j = \mathcal{C}_j = 0}. \quad (35)$$

Note that as  $\lambda_j$  is a function of  $\mathcal{E}_j$  and  $\mathcal{C}_j$ , it, like them, is a random variable taking particular values when space and time are specified. The simplicity of expression (34) is a consequence of parameter standardization. It is an exact equation whenever  $\lambda_j$  takes the form

$$\lambda_j = G_j(E_j, C) = d + A(E_j) + B(C_j) + hA(E_j)B(C_j), \quad (36)$$

where constants  $d$  and  $h$ , and functions  $A$  and  $B$ , may depend on the species  $j$ .

To determine the invader rate of increase,  $\tilde{\lambda}_i$ , we can use the fact that the species do belong to the same guild and therefore have certain features in common that can be used to relate the rates of increase of different species to one another. The idea of membership in the same guild might be expressed mathematically in terms of functional relationships between the competition parameters of different species. Here we assume that for each invader species  $i$ , and each set of residents, there is a function  $f$  expressing the competition parameter for the invader in terms of the competition parameters of the residents:

$$\mathcal{C}_i^{-i} = f((\mathcal{C}_r^{-i})_{r \neq i}). \quad (37)$$

Note that when the residents are at equilibrium, i.e.,  $C_r^{-i} = C_r^*$ ,  $r \neq i$ , then  $\mathcal{C}_r^{-i} = 0$ ,  $r \neq i$ . Thus, using Eq. (37) the invader competition parameter when the residents are at their equilibrial values is

$$\mathcal{C}_i^{-i*} = f(\mathbf{0}). \quad (38)$$

The regional finite rate of increase,  $\tilde{\lambda}_r$ , of a resident is necessarily equal to 1. Using this fact, we obtain the following seemingly trivial equation,

$$\tilde{\lambda}_i - 1 = \tilde{\lambda}_i - 1 - \sum_{r \neq i}^n q_{ir}(\tilde{\lambda}_r - 1), \quad (39)$$

where the  $q_{ir}$  are positive constants to be determined. To calculate the  $\tilde{\lambda}_j$ , recall from Eq. (7) that  $\tilde{\lambda}_j$  can be expressed as the sum of the simple average of  $\lambda_j$  over space and the spatial covariance of  $\lambda_j$  and relative density. Thus, combining Eqs. (7) and (39) and approximation (34) leads to the approximation

$$\tilde{\lambda}_i - 1 \approx \Delta E - \Delta C + \Delta I + \Delta \kappa, \quad (40)$$

where (with expectation,  $E$ , meaning spatial average and Cov meaning spatial covariance)

$$\Delta E = E[\mathcal{E}_i] - \sum_{r \neq i}^n q_{ir} E[\mathcal{E}_r], \quad (41)$$

$$\Delta C = E[\mathcal{C}_i^{-i}] - \sum_{r \neq i}^n q_{ir} E[\mathcal{C}_r^{-i}], \quad (42)$$

$$\Delta I = \gamma_i E[\mathcal{E}_i \mathcal{C}_i^{-i}] - \sum_{r \neq i}^n q_{ir} \gamma_r E[\mathcal{E}_r \mathcal{C}_r^{-i}], \quad (43)$$

and

$$\Delta \kappa = \text{Cov}(\lambda_i, v_i) - \sum_{r \neq i}^n q_{ir} \text{Cov}(\lambda_r, v_r). \quad (44)$$

The choice of  $q_{ir}$  that makes the decomposition (40) the sharpest biological comparison makes use of the relationship (37) between the invader and the resident competition parameters to define  $q_{ir}$  as

$$q_{ir} = \left. \frac{\partial \mathcal{C}_i^{-i}}{\partial \mathcal{C}_r^{-i}} \right|_{\mathcal{C}_r^{-i}=0, r \neq i}. \quad (45)$$

With this definition, linear relationships between the species in their dependence on common competitive factors are factored out of  $\Delta C$  (Chesson, 1994). Moreover, Eq. (40) rearranges further to

$$\tilde{\lambda}_i \approx \tilde{\lambda}'_i - \Delta N + \Delta I + \Delta \kappa, \quad (46)$$

where

$$\tilde{\lambda}'_i - 1 = \Delta E - \mathcal{C}_i^{-i*} \quad (47)$$

and

$$\Delta N = \Delta C - \mathcal{C}_i^{-i*}. \quad (48)$$

In (46) the different components of  $\tilde{\lambda}_i$  refer to distinct coexistence mechanisms, as is now explained.

*Interpretation of  $\tilde{\lambda}'_i$ .* Simply put, the quantity  $\tilde{\lambda}'_i$  is the finite rate of increase that the invader would experience in the absence of spatial variation; it measures the effects of variation-independent coexistence mechanisms. It is most easily understood by expressing competition in terms of competitive factors,

$$\mathcal{C}_j = \phi_j(\mathbf{F}) = 1 - G_j(E_j^*, \phi'_j(\mathbf{F})), \quad (49)$$

where, as this equation indicates,  $\phi_j$  may also depend on the equilibrated values of the environmentally-dependent parameters. If  $\mathbf{F}^{-i*}$  is a value of  $\mathbf{F}$  consistent with  $\mathcal{C}_r^{-i} = 0$ ,  $r \neq i$ , then

$$\mathcal{C}_i^{-i*} = \phi_i(\mathbf{F}^{-i*}), \quad (50)$$

which is the value of competition that the invader experiences as a consequence of the resource equilibrium that the residents create. Note that with the assumption above that  $\mathcal{C}_i^{-i}$  is a function of  $\{\mathcal{C}_r^{-i}, r \neq i\}$ , the value of expression (50) is unique although there is no necessity for  $\mathbf{F}^{-i*}$  to be unique.

A negative value of  $\mathcal{C}_i^{-i*}$  means that invasion of species  $i$  is favored by the resident equilibrium: resident equilibrated competition is less competition than needed to keep species  $i$  from the system. One particular example with a single competitive factor is Tilman's  $R^*$  rule (Tilman, 1982) applying to the case where species in a community are limited by a single resource ( $\mathbf{F} = R$ , the resource density). A negative value of  $\mathcal{C}_i^{-i*}$  in that situation means that the  $R^*$  value for species  $i$  is lower than that of resident species. Corresponding remarks apply for the  $P^*$  rule of Holt, Grover, *et al.* (1994) for apparent competition and to the  $F^*$  rule that we use here to embrace both competition and apparent competition. With just a single competitive factor,  $\mathcal{C}_i^{-i*}$  can only be negative for one species, reflecting the fact that only one species can persist at equilibrium under those circumstances. However, with multiple competitive factors, and different species more strongly limited by different competitive factors, it is possible for  $\mathcal{C}_i^{-i*}$  to be negative for all species, potentially allowing equilibrium coexistence.

The contribution of the  $\mathcal{C}_i^{-i*}$  term to coexistence must be added to the other terms in the equation, most importantly to  $\Delta E$  from which it is not truly separate. If this  $\Delta E$  were zero, then  $\tilde{\lambda}'_i$  would just be  $1 - \mathcal{C}_i^{-i*}$ . However,  $\Delta E$  takes account of the possibility that the means of the environmental responses,  $E\mathcal{E}_j$ , may not be zero; in other words the variation in  $\mathcal{E}_j$  may not be centered at zero either because  $E[E_j] \neq E_j^*$  or because  $\mathcal{E}_j$  is a nonlinear function of  $E_j$ . From the development in (Chesson, 1994)

it can be seen that, to  $o(\sigma^2)$ ,  $\mathcal{C}_i^{-i*} - \Delta E$  can be interpreted as the value of  $\mathcal{C}_i^{-i*}$  that would apply if the  $E_j^*$  were adjusted to make the  $E\mathcal{E}_j$  equal to 0, which would mean  $\Delta E = 0$ . As the  $E_j^*$  are arbitrary one might ask, why not choose them so that the  $E\mathcal{E}_j$  are zero? The answer is that this is not always the most natural thing to do. For example, in the case of a single competitive factor, which is of considerable interest in the study of varying environments, it seems most natural to choose the same equilibrium value of the competitive factor for all species so that fluctuations in  $F$  about this common equilibrium value can be considered. The value of the  $E_j^*$  for each species is then determined by the equation  $G_j(E_j^*, \phi'_j(F^*)) = 1$ . If the  $\mathcal{E}_j$  did not vary spatially and each took the value 0, then in general the community would be neutrally stable: over time  $F$  could be expected to approach the common  $F^*$  value everywhere in space, but average densities of the species would not be fixed as there would be an  $n - 1$  dimensional set of values of  $(\bar{N}_1, \bar{N}_2, \dots, \bar{N}_n)$ , each point of which would be a neutrally-stable equilibrium. Such neutral equilibria have limited generality. Having  $E\mathcal{E}_j$  different from zero destroys this neutral equilibrium and in most cases with a single competitive factor leads to competitive exclusion in a constant environment, as discussed above. For example, with a two-species system, the  $\Delta E$  values of the two species would be of opposite sign and the species with positive  $\Delta E$  would exclude the other.

An alternative way of specifying nonneutrality would be to have different  $F^*$  values for different species, while setting  $E\mathcal{E}_j = 0$ . These  $F^*$  values could not differ from one another by more than  $O(\sigma^2)$  under the assumptions of Appendix III for the quadratic approximation to be applicable and for  $\tilde{\lambda}'_i$  to be no larger in magnitude than  $O(\sigma^2)$ . Although a valid approach, specifying different  $F^*$  values for different species produces complications in the development of the  $\Delta N$  term, which is presented below. However, one important interpretational complication arises when the  $E\mathcal{E}_j$  are not zero. The common  $F^*$  is not a species characteristic and is not the same  $F^*$  that specifies a winner in competition according to the  $F^*$  rule. To apply the  $F^*$  rule for competitive exclusion in a constant environment, one must calculate a species-specific  $F^*$  as the value of  $F$  for which  $\lambda_j = 1$  given the actual value of  $\mathcal{E}_j$  that applies to species  $j$ . If the species have the same functions  $G_j$  and  $\phi'_j$  then these species-specific  $F^*$  values are ranked in order of the  $\mathcal{E}_j$  and the winner in competition in a constant environment is the species with the largest value of  $\mathcal{E}_j$ .

*Interpretation of  $\Delta N$ .* The quantity  $\Delta N$ , which measures spatial relative nonlinearity of competition, is best understood in terms of competitive factors. As shown in (Chesson,

1994) all linear terms in competitive factors disappear from  $\Delta N$  by virtue of the definition of the  $q_{ir}$ . Left over are quadratic and higher terms, of which only the quadratic terms are of sufficient magnitude to be of concern here. To understand these, we define

$$\Phi_j^{(2)} = \left( \frac{\partial^2 \mathcal{C}_j}{\partial F_l \partial F_m} \right)^*, \quad (51)$$

where the parentheses mean the matrix with row and columns respectively  $l$  and  $m$  over the indices 1, 2, ...,  $p$  (the number of competitive factors) and the  $*$  means evaluated at  $\mathbf{F}^*$ . Defining

$$\Psi = \frac{1}{2} \left( \Phi_i^{(2)} - \sum_{r \neq i} q_{ir} \Phi_r^{(2)} \right), \quad (52)$$

it follows that

$$\Delta N = \text{trace}\{\Psi V(\mathbf{F})\}, \quad (53)$$

where  $V(\mathbf{F})$  is the matrix of variances and covariances among the elements of  $\mathbf{F}$ . Naturally, in the case of a single competitive factor, this expression is simply the product of two numbers:  $\Psi V(F)$ . As shown in Chesson (1994) for the temporal case, this single competitive factor case admits coexistence of at most two species by relative nonlinearity alone. The values of  $\Psi$  for the two species are necessarily of opposite sign, as are the values of  $\Delta E$ . For coexistence, that species with the relatively more concave finite rate of increase as a function of  $F$  (the one with positive  $\Psi$ ) must be the one with the advantage in  $\Delta E$ , i.e., must be the one with a positive  $\Delta E$ . There must also be higher variance in  $F$  when this species is a resident than when the other species is a resident. The quantitative details are given in Chesson (1994, Sect. 5.2).

*Interpretation of  $\Delta I$ .* The term  $\Delta I$ , the storage effect, has a major influence on the ability of species to coexist in a spatially variable environment. Because  $E[\mathcal{E}_j]$  and  $E[\mathcal{C}_j^{-i}]$  are both  $O(\sigma^2)$ ,  $\Delta I$  can be put in the more useful form

$$\Delta I \approx \gamma_i \chi_{ii}^{-i} - \sum_{r \neq i} q_{ir} \gamma_r \chi_{rr}^{-i}, \quad (54)$$

where

$$\chi_{ij}^{-i} = E(\mathcal{E}_i - E\mathcal{E}_i) \cdot (\mathcal{C}_{ij}^{-i} - E\mathcal{C}_{ij}^{-i}), \quad (55)$$

“covariance between environment and competition,” and differs from  $E\mathcal{E}_i\mathcal{C}_j^{-i}$  by  $O(\sigma^4)$ . A further rearrangement of (54) leads to a still more meaningful expression

$$\Delta I = -\mathbf{q}_i(\mathbf{1} - \Xi_i \mathbf{P}_i) \Gamma \boldsymbol{\chi}, \quad (56)$$

where  $\boldsymbol{\chi}$  is the vector of resident covariances between environment and competition,  $\Gamma$  is the diagonal matrix of resident  $\gamma$  values,  $\mathbf{P}_i$  is the diagonal matrix with  $r$ th diagonal element to the ratio of the correlation coefficients,  $\text{corr}(\mathcal{E}_i, \mathcal{C}_r^{-i})/\text{corr}(\mathcal{E}_r, \mathcal{C}_r^{-i})$ ,  $r \neq i$ ,  $\Xi_i$  is a diagonal matrix with  $r$ th diagonal element equal to  $(\gamma_i \sqrt{V(\mathcal{E}_i)})/(\gamma_r \sqrt{V(\mathcal{E}_r)})$ ,  $\mathbf{1}$  is the  $(n-1) \times (n-1)$  identity matrix, and  $\mathbf{q}_i$  is the row vector of  $q_{ir}$  values. The derivation follows simply by approximating  $\mathcal{C}_i^{-i}$  as a linear function of the  $\mathcal{C}_r^{-i}$  (see Chesson, 1994). Expression (56) is most easily understood by reference to the following two-species case.

With a system consisting of just two species ( $n=2$ ), pure spatio-temporal environmental variation, a cell-based spatial structure, and local competition a function of the local environment (Eq. 4),  $\mathbf{P}_i$  reduces to the scalar  $\rho = \text{corr}(\mathcal{E}_i, \mathcal{E}_r)$ , and so expression (56) reduces to the scalar equation

$$\Delta I = -q_{ir}(1 - \Xi_i \rho) \gamma_r \chi_{rr}^{-i}. \quad (57)$$

The last part of this formula,  $\gamma_r \chi_{rr}^{-i}$ , represents the interaction between environment and competition for the resident species. The correlation coefficient  $\rho$  measures species-specific responses to the environment with  $\rho = -1$  being most specific and  $\rho = 1$  being not specific at all. The quantity  $\Xi_i$  measures symmetry between species in their joint responses to environmental conditions and competition. In this formula, the resident covariance between environment and competition,  $\chi_{rr}^{-i}$ , is the only quantity that might represent a difficult calculation, but it can commonly be approximated up to  $o(\sigma^2)$  using linear approximation techniques, as discussed for the temporal case (Chesson, 1989), and as follows for symmetric multi-species cases.

There are many ways that species may be related to each other in multispecies settings, but of particular interest is the case where species are limited by a common competitive factor, precluding stable coexistence in spatially and temporally homogeneous settings. This being the case, we can assume that

$$\mathcal{C}_j = \beta_j(C - C^*) + O(\sigma^2) \quad (59)$$

for the common competitive factor  $C$ , which is assumed expressible as a function of the local densities and environmentally-dependent parameters, i.e., in the form

(4), which requires cell-based population structure. The  $O(\sigma^2)$  term in (59) allows the consideration of distinct competition parameters for different species provided that distinctiveness is only  $O(\sigma^2)$ . Such distinctions are large enough to affect  $\tilde{\lambda}'_i$ , and possibly  $\Delta N$ , but cause at most  $o(\sigma^2)$  effects in  $\Delta I$ . Note that as each of  $\tilde{\lambda}'_i$ ,  $\Delta N$ ,  $\Delta I$ , and  $\Delta \kappa$  is  $O(\sigma^2)$ , assumption (59) is not a greatly restrictive requirement. A more specific assumption is that each  $V(E_j) = \sigma^2$ , and  $\text{Cov}(E_j, E_i) = \rho\sigma^2$  for  $i \neq j$ , and environmental variation is pure spatio-temporal. The equal variance assumption is less restrictive than at face value, for the environmentally-dependent parameters can be transformed to make this assumption more nearly satisfied in a given setting. The calculations below are then applied to those transformed parameters. The covariance assumption is more specific. It implies that the environmental responses of different species are equally related to one another. Together with the assumption of common competition it means that each species is similarly affected by all other species. In other words, species interactions are diffuse (Chesson, 2000).

Define

$$A_r = \left. \frac{\partial C^{-i}}{\partial \mathcal{E}_r} \right|_{\mathcal{E}_i=0, r \neq i}, \quad a_r = EA_r, \quad \text{and} \quad \alpha_r = \left. \frac{\partial \mathcal{E}_r}{\partial E_r} \right|_{E_r=E_r^*}. \quad (60)$$

Also define the following general notation for averages over products of parameters of resident species

$$\overline{ab \dots} = \frac{1}{n-1} \sum_{r \neq i} a_r b_r \dots \quad (61)$$

The calculations for the temporal case (Chesson, 1994) apply identically here to show that

$$\Delta I \approx -\beta_i \sigma^2 [(1-\rho) \overline{\alpha^2 a \gamma} + \rho \overline{\alpha a} (n-1) (\overline{\alpha \gamma} - \alpha_i \gamma_i)]. \quad (62)$$

In this formula, the  $a_r$ , and hence all the average terms containing them, are commonly on the order of  $1/(n-1)$  (see the examples below), which is understandable because the more resident species there are, the less each is likely to contribute to the total competition experienced. Of the terms inside  $[\ ]$ ,  $(\overline{\alpha \gamma} - \alpha_i \gamma_i)$  measures asymmetries between species in the interaction between environment and competition; this term averages to zero over species. Note therefore that the average over species of  $\Delta I/\beta_i$  equals  $\sigma^2(1-\rho) \overline{\alpha^2 a \gamma}$ , which may be thought of as the average strength of the storage effect for this guild because  $\beta_i$



simply represents the rate of response to common competitive factors and in many cases (see the examples below) is a scaling factor in all components of  $\tilde{\lambda}_i - 1$  and therefore cancels out of any comparison between component mechanisms. The term  $\sigma^2(1 - \rho)$  can be thought of as the species-specific component of the environmental response because  $\sigma^2\rho$  is the fraction of variance in  $\overline{E_j}$  that a species has in common with other species. If  $\alpha^2 a \gamma$  is proportional to  $1/(n - 1)$ , as commonly seems the case (see the examples below), the average strength of the storage effect is proportional to  $\sigma^2(1 - \rho)/(n - 1)$ , which therefore increases with the species-specific component of variance and decreases with the number of competitors that a species has. This decline in strength of the coexistence mechanism with the number of competitor species is a commonly observed feature of coexistence mechanisms in the presence of diffuse competition (Chesson, 2000), which is assumed in these calculations. It is not specifically a property of the storage effect.

*Interpretation of  $\Delta\kappa$ .* Insight on the effects of covariance between relative density and the rate of increase, which is measured by  $\Delta\kappa$ , is available on the assumption that  $v_{jx} = 1 + O(\sigma)$ . As shown in Appendix III, this requirement holds in particular for the case of pool dispersal with local retention presented in the *covariance between relative density and rate of increase* section above. This assumption means that  $(v_j - 1) \mathcal{E}_j \mathcal{C}_j = O(\sigma^3)$  and therefore that

$$\text{Cov}(\lambda_j, v_j) \approx \text{Cov}(\mathcal{E}_j, v_j) - \text{Cov}(\mathcal{C}_j, v_j). \quad (63)$$

With pure spatio-temporal variation, the first term on the RHS is zero, and the covariance between  $\lambda_j$  and  $v_j$  is just a covariance between local density and competition. This is the important effect arising in the spatial Lotka–Volterra competition model of Bolker and Pacala (1999) where there is no environmental variation and Eq. (63) is exact as a consequence of the quadratic form of the model. Because residents cause competition, in many cases  $\text{Cov}(\mathcal{C}_j, v_j)$  is likely to be positive for residents and lesser in magnitude for invaders. Thus, in instances of pure spatio-temporal environmental variation, the term  $\Delta\kappa$  is likely to be positive, promoting coexistence. However, there are no general results demonstrating this effect at the present time.

In the case of pure spatial variation, the component  $\text{Cov}(\mathcal{E}_j, v_j)$  of  $\text{Cov}(\lambda_j, v_j)$  does not vanish and potentially has major effects. Assuming pool dispersal with local

retention, it is shown in Appendix III for both residents and invaders that

$$v_{jx} = 1 + (p/q)(\lambda_{jx} - 1) + O(\sigma^2) \quad (64)$$

and hence that

$$\text{Cov}(\lambda_j, v_j) \approx (p/q) V(\lambda_j), \quad (65)$$

which implies that invaders gain an advantage in terms of  $\Delta\kappa$  if they have higher spatial variance in their finite rates of increase than residents. This variance can be expanded in terms of variance in the environmentally-dependent and competition parameters and the covariance between them using approximation (40) above, but it is most instructive in the symmetric case where  $G$  is the same for each species and there is a common competitive factor, as explicitly assumed in the section above on *covariance between the rate of increase and relative density*. All this symmetry means that  $q_{ir} = 1/(n - 1)$ , and then  $\Delta\kappa$  reduces to

$$\frac{p}{q} \left[ \frac{1}{n-1} \sum_{r \neq i} \chi_{rr}^{-i} - \chi_{ii}^{-i} \right], \quad (66)$$



which takes a form identical to the storage effect in such symmetric situations. In fact it is equivalent to  $\Delta I$  with  $\gamma = -p/q$ . Thus, in this symmetric situation,  $\Delta\kappa$  can be regarded as simply replacing  $\gamma$  with  $\gamma - p/q$ . As  $\gamma$  will be negative in the common subadditive coexistence-promoting scenario, the effect of  $\Delta\kappa$  will commonly be equivalent to an enhanced storage effect, consistent with the earlier findings above.

## EXAMPLES

Three examples illustrate the concepts and techniques developed here.

### **Model of Insects Laying Eggs in Ephemeral Patches of Food**

This model, which is described above in the section on the general model, is most easily analyzed with a symmetric competition structure with intraspecific coefficients,  $\alpha_{jj}$ , the same for each species  $j$  (equal to  $\alpha$ ), and interspecific coefficients,  $\alpha_{jl}$ ,  $j \neq l$ , all equal to  $\beta$ . So that

the effects of differences between interspecific and intraspecific competition are of comparable magnitude to the effects of a variable environment, I shall assume that  $\alpha - \beta = O(\sigma^2)$ . Natural choices for the equilibril values are  $E_i^* = 1$  and  $C_i^* = 1$ . With these definitions, we find that

$$\mathcal{E}_j = E_j - 1 \quad \text{and} \quad \mathcal{C}_j = 1 - e^{r_j(1 - C_j)}. \quad (67)$$

This model is spatially implicit, and so it is possible to work with  $H_j$  rather than  $G_j$ ;  $H_j(E_j, C_j) - 1$  can be expressed as the exact quadratic form

$$\lambda_j v_j - 1 = \mathcal{E}_j - \mathcal{C}_j - \mathcal{E}_j \mathcal{C}_j \quad (68)$$

from which it is immediately apparent that  $\gamma_j = -1$ . Although this formula is exact, we will nevertheless make use of small variance approximations to estimate the expected values of its components, viz.  $\tilde{\lambda}'_i$ ,  $\Delta N$ , and  $\Delta I$ . Because these are based on  $H_j$  rather than  $G_j$ , the term  $\Delta \kappa$  does not appear. For these calculations, rather than use  $E_j$  as the environmentally-dependent parameter, it is better to transform to the log scale and use  $\varepsilon_j = \ln E_j$ . On this scale, the symmetry assumptions  $\sigma^2 = V(\varepsilon_j)$  and  $\rho = \text{corr}(\varepsilon_j, \varepsilon_l)$ , for any  $j$  and  $l$ , are more reasonable. In addition, define  $\mu_j = E[\varepsilon_j] = O(\sigma^2)$ . Using the symmetric competition structure assumed above, the competition parameter can be expressed simply in terms of two competitive factors,

$$C_j = F + F_j, \quad (69)$$

where

$$F = \beta \sum_{l=1}^n E_l N_l \quad \text{and} \quad F_j = (\alpha - \beta) E_j N_j. \quad (70)$$

As  $\alpha - \beta = O(\sigma^2)$  this means  $C_j = F + O(\sigma^2)$ , a fact that allows the calculations of relative nonlinearity and the storage effect to proceed as if there were only one competitive factor. This is not so, however, for  $\tilde{\lambda}'_i$ , where the full expression for  $C_j$  is important.

Table 1 gives the values of various parameters based on the assumptions of this model. To calculate  $\tilde{\lambda}'_i$ , note that as the invader does not experience intraspecific competition,

$$C_i^{-i} = F. \quad (71)$$

TABLE 1

Parameters of the Insect Aggregation Model

$\alpha_j$	1
$\beta_j$	$r_j$
$\gamma_j$	-1
$q_{is}$	$\frac{r_i/r_s}{n-1 + (\alpha-\beta)/\beta} = \frac{r_i/r_s}{n-1} + O(\sigma^2)$
$F^*$	$\frac{\beta(n-1)}{\beta(n-1) + \alpha - \beta}$
$\Psi$	$-\frac{r_i}{2}(r_i - \bar{r})$

Substituting the equilibril value of  $F^*$  from Table 1, we see that

$$\begin{aligned} \mathcal{C}_i^{-i*} &= 1 - \exp \left\{ r_i \left( 1 - \frac{\beta(n-1)}{\beta(n-1) + \alpha - \beta} \right) \right\} \\ &\approx -\frac{r_i(1 - \beta/\alpha)}{n-1}, \end{aligned} \quad (72)$$

which means that

$$\tilde{\lambda}'_i \approx \Delta E + \frac{r_i(1 - \beta/\alpha)}{n-1}. \quad (73)$$

The formula for  $\Delta E$  can be written in terms of the  $\mu$ s and  $\sigma^2$  as follows

$$\Delta E \approx r_i \left( \frac{\mu_i + \frac{1}{2}\sigma^2}{r_i} - \frac{1}{n-1} \sum_{s \neq i} \frac{\mu_s + \frac{1}{2}\sigma^2}{r_s} \right), \quad (74)$$

which in the case of equal  $r$ s, just reduces to the difference between  $\mu_i$  and the average of the  $\mu$ s of  $i$ 's competitors.

To calculate  $\Delta I$ , we can make use of the symmetric environment theory for one competitive factor above, noting that Eq. (59) is satisfied here and so the symmetric theory applies. The fact that the  $\alpha_j$  are all 1 and the  $\gamma_j$  are all -1 makes this especially simple. The only quantity that is at all difficult to calculate is  $\bar{a} = -\alpha^2 a \gamma$ , which is shown in Appendix IV to be  $1/(n-1) + O(\sigma^2)$ . It follows that

$$\Delta I \approx \frac{r_i \sigma^2 (1 - \rho)}{n-1}. \quad (75)$$

To calculate  $\Delta N$ , we can consider  $F$  to be the only competitive factor, and then taking  $\Psi$  from Table 1, we have

$$\Delta N \approx -\frac{r_i}{2}(r_i - \bar{r}) V(F) \quad (76)$$

which leaves us with the thorny issue of the value of  $V(F)$ . A little algebra shows this to reduce to

$$V(F) \approx \beta^2 \sigma^2 \left( (1 - \rho) \sum_{s \neq i} \bar{N}_s^2 + \rho \left[ \sum_{s \neq i} \bar{N}_s \right]^2 \right). \quad (77)$$

The sum of the resident densities at their equilibrium is  $1/\beta + O(\sigma^2)$  (Appendix IV), but it is not so easy to determine the sum of the squares unless the residents have identical parameters, in which case they have equal densities and the sum of squares is therefore  $1/\beta^2(n-1) + O(\sigma^2)$ , which means that in this special case, which is the only case for a single resident ( $n=2$ ),

$$\Delta N \approx -\frac{r_i}{2}(r_i - \bar{r}) \sigma^2 \left( \frac{1 - \rho}{n - 1} + \rho \right). \quad (78)$$

We see that  $\Delta N$  boosts the invasion rate of species that has a high value of  $r_i$  relative to its competitors. A species with a lower  $r_i$  suffers a disadvantage. Unlike the storage effect, relative nonlinearity gives the invasion rates of all species no uniform boost. Its effect therefore must be considered in terms of how it trades off against other terms. For example, examining  $\Delta E$  we see that for positive  $\mu_s$ , species with relatively lower  $\mu_s$  should be disadvantaged. But to interpret that scenario, we have to decide what the  $\mu_s$  mean. If there is no mortality during dispersal, i.e., the  $r_j$  already take into account losses that would occur during dispersal, then  $E[E_{jx}] = 1$ , which implies that  $\mu_j + \frac{1}{2}\sigma^2 = o(\sigma^2)$ , preventing appreciable variation in the  $\mu_s$  between species and rendering the  $\Delta E$  term above negligible. However, in other cases,  $\mu_j$  might reasonably be assumed to reflect survivorship during dispersal. Then  $\mu_j + \frac{1}{2}\sigma^2$  must be negative, and the formula for  $\Delta E$  implies that high survival is essential to compensate for small  $r_i$ , which may also compensate for the disadvantage arising from  $\Delta N$ .

The full expression for  $\tilde{\lambda}_i - 1$  is the combination of Eqs. (73), (75), and (76). For the special case of equal values of the  $r_j$ ,  $\tilde{\lambda}_i - 1$  takes on the particularly simple form

$$\tilde{\lambda}_i - 1 \approx \mu_i - \bar{\mu} + r \left( \frac{1 - \beta/\alpha}{n - 1} + \sigma^2 \frac{1 - \rho}{n - 1} \right). \quad (79)$$

The case of equal  $r_j$  naturally eliminates any effect of relative nonlinearity from this expression, which is the

price of simplicity. This expression, however, contains the features most important to multispecies coexistence, for, as we have seen, relative nonlinearity gives no uniform boost to growth from low density. The two mechanisms that remain are resource partitioning, whose magnitude is measured by  $(1 - \beta/\alpha)/(n - 1)$ , and the storage effect, represented by  $\sigma^2(1 - \rho)/(n - 1)$ . These two mechanisms take on very similar forms because they both assume diffuse competition; i.e., each species competes similarly with every other species.

Resource partitioning is a variation-independent mechanism and could represent differential dependence of the insect larvae on the different food substances or qualities within a patch. The variation-dependent mechanism, the storage effect, may be looked upon as resource partitioning on a larger spatial scale with differences in the  $E_{jx}$  between species representing species differences in oviposition preferences at the level of the patch. Much of the literature on species coexistence in this and related models refers to ‘‘aggregation’’ as the mechanism of coexistence (Atkinson and Shorrocks, 1981; Ives, 1988), but Ives (1988) emphasizes that aggregation must be greater within species than between species and that this may come about by differential responses of searching females to environmental conditions. Interpreted in this way, aggregation as a mechanism of coexistence is a special case of the spatial storage effect.

### The Lottery Model

The lottery model is for perennial sedentary iteroparous organisms with larvae dispersing widely in space (Chesson, 1985). It has particular application to coral reef fish communities where the arrival of larvae ready to settle on a reef varies greatly in time and space and is often discussed under the heading of *recruitment variation*. The spatial lottery model is specified by the equation

$$N_{jx}(t + 1) = (1 - \delta_j) N_{jx}(t) + E_{jx}(t) \bar{N}_j(t) / C'_{jx}(t), \quad (80)$$

where  $N_{jx}$  is the number of adults of species  $j$  at location  $x$ ,  $\delta_j$  is the adult death rate ( $(1 - \delta_j) N_{jx}(t)$  is the number of adults surviving from time  $t$  to time  $t + 1$ ), and  $E_{jx}(t) \bar{N}_j(t)$  is the number of juveniles arriving at site  $x$  during the interval  $t$  to  $t + 1$ . These juveniles represent the pooled reproduction and larval survival from all sites, which are then redistributed into sites depending on spatio-temporally-varying site characteristics, captured by the environmentally-dependent parameter  $E_{jx}(t)$ . These

juveniles compete with juveniles of all species for space vacated by adult death according to the formula

$$C'_{jx} = \sum_{l=1}^n E_{lx} \bar{N}_l(t) \bigg/ \sum_{l=1}^n \delta_l N_{lx}(t). \quad (81)$$

Comins and Noble (1985) define a similar model with the  $E_j$  representing spatio-temporally-varying competitive ability, with dispersal being widespread with local retention.

Assuming that the environment is pure spatio-temporally variable, we can take a conditional expectation in (80) to obtain

$$E[N_j(t+1) | E_1, \dots, E_n] = H_j(E_j, C) \bar{N}_j(t), \quad (82)$$

where

$$H_j(E_j, C) = 1 - \delta_j + E_j/C \quad (83)$$

and the common competition parameter is

$$C = \sum_{l=1}^n E_l \bar{N}_l(t) \bigg/ \sum_{l=1}^n \delta_l \bar{N}_l(t).$$

The difference between  $C'_j$  and  $C$  is simply that  $C'_j$  depends on the actual amount of space,  $\sum_l \delta_l N_{lx}$ , available for juveniles at a particular site,  $x$ , while  $C$  depends on the average amount of space competed for over all sites,  $\sum_l \delta_l \bar{N}_l$ .

As  $C$  is a common competitive factor, it is natural here to choose a common equilibrium value  $C^*$  for  $C_j$ . The equilibrium relationship (34) therefore means that  $E_j^* = \delta_j C^*$ .

The standard parameters become

$$\mathcal{E}_j = \delta_j (E_j/E_j^* - 1) \quad (84)$$

and

$$\mathcal{C}_j = \delta_j (1 - C^*/C) \quad (85)$$

and the quadratic approximation is exact here because Eq. (83) is in the form (36) with  $\gamma_j = -1/\delta_j$ . As the  $\mathcal{C}_j$  are linearly related between species, there is no relative non-linearity ( $\Delta N = 0$ ). The  $q_{ir}$  are easily seen to be equal to  $\delta_i/[\delta_r(n-1)]$ . Again assuming a symmetric variance structure for the  $E_j$  on a log scale, and defining  $\mu_j = E[\ln E_j] - \ln \delta_j$ , it follows from the results in the quantitative section that

$$\tilde{\lambda}_i - 1 \approx \delta_i (\mu_i - \bar{\mu}) + \delta_i \frac{\sigma^2(1-\rho)}{n-1}, \quad (86)$$

where the first term on the RHS is  $\tilde{\lambda}'_i$  and the second term is  $\Delta I$ . Note that  $C^*$  does not appear in this expression. Although an arbitrary choice, it is unimportant in the final result.

These results provide an interesting comparison with the temporal form of the lottery model (Chesson, 1994), where complex relative nonlinearity terms intrude whenever the  $\delta$ s vary with the species and, where the storage effect disappears as  $\delta_i$  approaches 1, the nonoverlapping generation case. They show in particular that spatio-temporal recruitment variation has the potential to be an important mechanism of coexistence for coral reef fishes and also for other organisms where migration of dispersive forms into patches is spatio-temporally variable and differential between species.

### The Annual Plant Model

The annual plant model given above also takes an exact quadratic form. Note that, as defined,  $C_j$  is independent of  $j$  and is once again a common competitive factor and that a common value  $C^*$  of  $C_j^*$  will be chosen. In the absence of variation, there would only be one winner in competition in this system. Analogous to Tilman's  $R^*$  rule for determining the winner in competition, there is a natural  $C^*$  rule here for determining that winner. Let  $\bar{C}_j^*$  be the value that would keep species  $j$  at equilibrium when the environment is fixed at  $E[E_j]$ . Then without variation in space the winner in competition would be the species with the largest value of  $\bar{C}_j^*$ . To see what happens when there is spatial variation in the environment, assume that seeds are widely dispersed so that the local neighborhood density can be approximated by the regional density,  $\bar{N}_j$ , and assume locally varying germination fractions,  $E_j$ , with symmetric variance structure on a log scale. Then, as is shown in Appendix V,

$$\tilde{\lambda}_i - 1 = \frac{\theta_i}{C^*} \left\{ (\bar{C}_i^* - \bar{C}^*) + \frac{C^* - 1}{n-1} \sigma^2(1-\rho) \right\}, \quad (87)$$

where  $\theta_i = 1 - s_i(1 - E[E_i])$  (the mean fraction of seeds that are lost from the seed bank by germination or death in one unit of time),  $\bar{C}^*$  is the resident average of the  $\bar{C}_j^*$ , and  $C^*$  is the common equilibrium value of the  $C_j$ . Here  $C^*$  is probably most appropriately defined as the average over all species of  $\bar{C}_j^*$ , which differs a little from  $\bar{C}^*$ , and the average only over the residents.

This formula exhibits the interesting fact that the stronger competition is on average, as determined by  $C^*$ , the stronger storage effect up to a finite supremum approached when  $C^*$  is much larger than 1. At that point only proportional differences in the competition tolerated

by different species are important, consistent with the claims of (Chesson and Huntly, 1997) that coexistence does not depend on the magnitude of competition. In contrast to the temporal version of this model (Chesson, 1994), there is no relative nonlinearity, and again the storage effect does not vanish in the spatial case when generations are nonoverlapping, i.e., when  $s_i = 1$ .

## DISCUSSION

This work has a different approach than commonly pursued in theoretical modeling studies in community ecology. Rather than take one model that is presumed representative of a class of models and study it in detail, with the hope of drawing general conclusions, the approach here is to study a class of models with the expectation of elucidating general principles that demonstrably apply to all models in the class. The outcomes are principles that may at first appear rather abstract and mathematical in form, but when investigated further can be seen to be the development of biological concepts that can be understood in terms of the features of specific systems. Second, as a by-product of the general analysis, this work provides methods by which specific models can be analyzed.

This work has been successful in extending to the spatial domain concepts and principles previously demonstrated for models in a temporally varying environment. It has shown that the three major classes of coexistence mechanisms previously identified for models of temporal variation, viz. variation-independent mechanisms and the two variation-dependent mechanisms (relative nonlinearity of competition and the storage effect), have natural analogues in the spatial domain. However, these two variation-dependent mechanisms arise under different circumstances in the spatial context. Unlike the temporal storage effect, the spatial storage effect does not rely on life-history stages insensitive to environment and competition. Instead, dispersion of the population in space provides the requisite buffering. Indeed, given species-specific responses to spatially-varying environmental factors, the spatial storage effect seems to be inevitable under realistic scenarios and seems best regarded as a formalization of the concepts of spatial and spatio-temporal niches. In contrast, spatial relative nonlinearity seems to arise under more restricted conditions than temporal relative nonlinearity, at least in simple models, but requires further study to assess its importance.

This work has also suggested that species coexistence in the presence of spatial variation involves phenomena

with no direct temporal analogues. These new phenomena arise from covariance between local population growth and local population density. The formula for growth of an invader, which is used to quantify coexistence, contains an additional term due to this covariance that is not present in the temporal case. The behavior of this term has not been studied in general but the special cases investigated here suggest that it may be best regarded as modifying the storage effect and relative nonlinearity, rather than as entirely new. However, the limited evidence presented here suggests that it potentially has a very powerful role promoting species coexistence in the presence of spatial variation. This phenomenon was explored recently in a spatial version of the lottery model by Muko and Iwasa (2000). Recent findings of Bolker and Pacala (1999) on species coexistence relying on differing dispersal distances in a spatially explicit model appear to be a special case of this phenomenon.

The most serious shortcoming of this work is the absence of a full definition of the circumstances under which the invasion criterion can be defined and implemented. The rate of recovery of a population from low density seems a very natural way of quantifying the strength of species persistence in a system, but has received insufficient study in spatial models. It most clearly applies in spatially implicit models where it is related to persistence in the sense of permanence (Hutson, Moran, *et al.*, 1983; Hutson and Vickers, 1983; Hutson and Law, 1985; Law and Morton, 1996). As used here, the invasion criterion requires a stable point equilibrium for the regional-scale densities of residents and corresponding stationary behavior of the patterns of spatio-temporal fluctuations. The majority of spatial models of competition that do not specifically include pure temporal environmental variation have this property, although some models of predator-prey interactions lead to long-term cycles and spatial homogeneity. An understanding of coexistence as a result of temporal fluctuations, however, is given in previous work (Chesson, 1994), which this article extends to space. Missing therefore from current knowledge is a general approach capable of incorporating both spatial variation and temporal variation that persists at the level of the total regional population. There is at least one particular example, the lottery model (Chesson, 1985), in which a full range of possibilities for variation in space and time is considered and solved, but the general case has not been addressed and is beyond the scope of this article.

Within the limitations discussed above, however, the approach used here does provide a very general understanding of the opportunities for species coexistence in a spatially-varying environment. Moreover, the quadratic

approximation technique implemented in the specific examples is a powerful method for uncovering the behavior of simple models in elementary terms. This technique is only implemented here for spatially-implicit models, and it is bound to be much more difficult to apply in spatially-explicit models with local dispersal. However, the quadratic representation of local population growth given here is exact in many simple cases even with spatially-explicit models; therefore, the decomposition of the invader growth rate into four terms representing different mechanisms is exact also. Factors affecting these terms, such as non-additivity and relative nonlinearity, are simple to obtain analytically even if other features, such as variances in competitive factors and covariance between environment and competition, are more difficult to estimate and may require simulation or other forms of approximation such as moment closure approximations (Bolker and Pacala, 1997). Thus, the techniques presented here provide important information on the nature and properties of the mechanisms occurring in a model even when they do not lead to full quantification of the mechanism.

## APPENDIX I

It is often helpful to adopt the perspective of formal probability theory and add to each of  $E_{jx}(t)$ ,  $C_{jx}(t)$ , and  $N_{jx}(t)$  a fourth argument,  $\omega$ , which belongs to a sample space  $\Omega$  with associated  $\sigma$ -field and probability measure. Then  $E_{jx}(t)$ ,  $C_{jx}(t)$ , and  $N_{jx}(t)$  would be random variables themselves, not realizations of random variables  $E_j$ ,  $C_j$ , and  $N_j$ . For example, in simulations of the system,  $E_{jx}(t)$ ,  $C_{jx}(t)$ , and  $N_{jx}(t)$  would take different values in different simulations, with  $E_{jx}(t, \omega)$ ,  $C_{jx}(t, \omega)$ , and  $N_{jx}(t, \omega)$  being realized values and  $\omega$  being equivalent to the random number seed. This perspective is most helpful in discussion of the concepts of pure spatial variation and pure spatio-temporal variation. Pure spatio-temporal environmental variation can then be defined as the situation where the vector random variables ( $E_{1x}(t)$ , ...,  $E_{nx}(t)$ ) are independently and identically distributed over all pairs of times and locations  $(t, x)$ . For pure spatial variation ( $E_{1x}(t)$ , ...,  $E_{nx}(t)$ ) is independently and identically distributed over locations  $x$ , but is constant over time.

Under this perspective, the expected value  $E[G_j(E_{jx}(t), C_{jx}(t))]$ , as formally defined in probability theory, would in general depend on  $x$  and therefore would not be equivalent to the spatial average implied by the expression  $E[G_j(E_j, C_j)]$  (Eq. 8). However, for many spatial geometries used in modeling, and for many suitable initial conditions, it is possible to assume without loss of

generality that the vector of stochastic processes ( $E_{jx}(t)$ ,  $C_{jx}(t)$ ,  $N_{jx}(t)$ ,  $j = 1, \dots, n$ ,  $t \geq 0$ ) has the same distribution for every  $x$ . For this to be true, it just has to be possible to randomize the values of  $E_{jx}$ , and any initial conditions, relative to the location in space. For example, consider space to be intertidal habitat around an island, which is topologically equivalent to a circle. A location  $x$  is a point on the circle, and it will have certain fixed environmental characteristics due, for example, to whether it is on the north or south side, facing the prevailing currents, or in their lee. It will also have temporally varying characteristics due, for example, to temporal variation of currents. The stochastic process  $\{E_{jx}(t), t \geq 0\}$  is assumed to summarize these characteristics. Regardless of the spatially fixed nature of some factors contributing to  $\{E_{jx}(t), t \geq 0\}$ , the  $\{E_{jx}(t), t \geq 0\}$  can be made formally identically distributed for different  $x$  by random choice of the origin for the measurement of  $x$ . Such randomization has no effect on the nature of the model, but it does render expected values such as  $E[G_j(E_{jx}, C_{jx})]$  independent of  $x$ . With effectively infinite space and an ergodic theorem implying degenerate convergence of spatial averages, expectations such as  $E[G_j(E_{jx}(t), C_{jx}(t))]$  are then equal to their corresponding spatial averages. If the critical variables ( $E_{jx}(t)$ ,  $C_{jx}(t)$ ,  $N_{jx}(t)$ ,  $j = 1, \dots, n$ ) cannot be set up so that they have the same distribution for every  $x$ , then the expected values of the text (e.g.,  $E[G_j(E_j, C_j)]$ ) have to be defined explicitly as spatial averages. In the limit of large space, these spatial averages are equivalent to the spatial averages of the expectation for each spatial location (e.g.,  $E[G_j(E_{jx}(t), C_{jx}(t))]$ ), which would naturally be the most convenient way of calculating them mathematically.

## APPENDIX II

Equation (25) for the model with pure spatial variation and widespread dispersal implies the following iteration for relative local density:

$$v_{jx}(t+1) = p(\lambda_{jx}(t)/\tilde{\lambda}_j(t)) v_{jx}(t) + q. \quad (88)$$

Assuming that residents come to an equilibrium at each locality, resident values of  $\lambda_x$  are constant over time. For residents, Eq. (88) implies the following equation for resident relative densities:

$$v_{rx} = \frac{q}{1 - p\lambda_{rx}}. \quad (89)$$

The invader's  $\lambda_x$  are also constant over time as they depend only on the temporally-constant environment and temporally-constant resident densities. Thus, invader relative densities are given by the equation

$$v_{ix} = \frac{q}{1 - p\lambda_{ix}/\tilde{\lambda}_i}. \quad (90)$$

From the fact that the  $\tilde{\lambda}_j$  values are the spatial averages of  $v_{jx}\lambda_{jx} = v_{jx}G(E_{jx}, C_{jx})$  we see that

$$E \left[ \frac{qG(E_r, C_r^{-i})}{1 - pG(E_r, C_r^{-i})} \right] = \tilde{\lambda}_r = 1 \quad (91)$$

and for invaders

$$E \left[ \frac{qG(E_i, C_i^{-i})}{1 - pG(E_i, C_i^{-i})/\tilde{\lambda}_i} \right] = \tilde{\lambda}_i. \quad (92)$$

Equation (92) rearranges to

$$E \left[ \frac{qG(E_i, C_i^{-i})}{\tilde{\lambda}_i - pG(E_i, C_i^{-i})} \right] = 1. \quad (93)$$

As the LHS of Eq. (93) is a decreasing function of  $\tilde{\lambda}_i$  it follows that  $\tilde{\lambda}_i$  is greater than 1 if and only if the following inequality is satisfied

$$E \left[ \frac{qG(E_i, C_i^{-i})}{1 - pG(E_i, C_i^{-i})} \right] > E \left[ \frac{qG(E_r, C_r^{-i})}{1 - pG(E_r, C_r^{-i})} \right], \quad (94)$$

in other words if and only if

$$Ef(G(E_i, C_i^{-i})) > Ef(G(E_r, C_r^{-i})),$$

where  $f$  is defined by the equation  $f(G) = qG/(1 - pG)$ , as stated in the text.

To see when  $f(G(E, C))$  is subadditive, the cross partial derivative works out to be

$$\begin{aligned} \frac{\partial^2 f(G(E, C))}{\partial E \partial C} &= f''(G(E, C)) \frac{\partial G}{\partial E} \cdot \frac{\partial G}{\partial C} \\ &+ f'(G(E, C)) \frac{\partial^2 G(E, C)}{\partial E \partial C}. \end{aligned} \quad (96)$$

The first term on the RHS is negative, as  $G$  decreases in  $C$  and increases in  $E$ . The second term is zero for additive  $G$  and negative for subadditive  $G$ . Thus, the whole expression is negative ( $f(G(E, C))$  is subadditive) whenever  $G$  is subadditive, additive, or merely weakly superadditive.

To see when covariance between environment and competition occurs in this model, assume that  $C_{rx}^{-i} = f(E_{rx}, N_{rx}) = f(E_{rx}, \bar{N}_r v_{rx})$ , for some function  $f$ , and let  $f_1$  and  $f_2$  refer to partial derivatives with respect to the first and second arguments of  $f$  (similarly for  $G$ ); then

$$\frac{dC_{rx}^{-i}}{dE_{rx}} = f_1 + \bar{N}_r \frac{dv_{rx}}{dE_{rx}} f_2. \quad (97)$$

But Eq. (89) implies that

$$\frac{dv_{rx}}{dE_{rx}} = pq \left( G_1 + G_2 \frac{dC_{rx}^{-i}}{dE_{rx}} \right) / (1 - pG)^2. \quad (98)$$

Substituting into (97) and rearranging gives

$$\begin{aligned} \frac{dC_{rx}^{-i}}{dE_{rx}} &= (f_1 + pq\bar{N}_r f_2 G_1 / (1 - pG)^2) / \\ &(1 - pqG_2 \bar{N}_2 f_2 / (1 - pG)^2). \end{aligned} \quad (99)$$

As both numerator and denominator are positive whenever  $f_1 \geq 0$ , we see that as  $E_{rx}$  varies in space,  $C_{rx}^{-i}$  varies as an increasing function of  $E_{rx}$ , which implies positive covariance.

## APPENDIX III

I shall prove order relations  $\mathcal{C}_j = O(\sigma)$ , and  $E[\mathcal{C}_j] = O(\sigma^2)$  just for cell-based models, with local population sizes being continuous variables. First of all note that for a random variable, such as  $\mathcal{C}_j$ , the statement  $\mathcal{C}_j = O(\sigma)$  will be taken to mean that  $|\mathcal{C}_j| < k\sigma$  for some nonrandom quantity  $k$  that does not vary with  $t$ ,  $x$ ,  $\sigma$ , or the  $\omega$  of Appendix I. Note also that the conclusion  $\mathcal{C}_j = O(\sigma)$  will generally be false for integer population sizes and realistic demographic stochasticity, and so there is no point trying to cover that case.

To begin with, we shall assume that there is a common competition parameter for different species and that it can be written as a function of the local environmentally-dependent parameters,  $\mathbf{E}_x(t) = (E_{1x}(t), \dots, E_{nx}(t))$ , and local densities  $\mathbf{N}_x(t) = (N_{1x}(t), \dots, N_{nx}(t))$ :

$$C_x(t) = f(\mathbf{E}_x(t), \mathbf{N}_x(t)). \quad (100)$$

Assume also that the appropriate equilibril values have been subtracted so that the environmentally-dependent and competition parameters vary about zero. Assuming

that the functions  $G_j$  are smooth, the assumption that  $\mathcal{E}_j = O(\sigma)$  means also that  $E_{jx}(t) = O(\sigma)$ .

Define  $\lambda_x(t) \cdot \mathbf{N}_x(t) = (\lambda_{1x}(t) N_{1x}(t), \dots, \lambda_{nx}(t) N_{nx}(t))$ , and

$$C'_x(t+1) = f(\mathbf{E}_x(t+1), \lambda_x(t) \cdot \mathbf{N}_x(t)). \quad (101)$$

Note that  $C'_x(t+1)$  is the competition parameter that would apply at time  $t+1$  if there were no dispersal from or to the patch. Using regulatory conditions (given below) on the functions  $G_j$  and  $f$ , Chesson (1994, Appendix II) shows that there are constants  $k > 0$  and  $\rho < 1$  such that, whenever  $|C_x(t)|$  is sufficiently small,

$$|C'_x(t+1)| < \rho |C_x(t)| + k\sigma. \quad (102)$$

This result implies that

$$\sup_x |C'_x(t+1)| \leq \rho \sup_x |C_x(t)| + k\sigma. \quad (103)$$

We add here the assumption

$$|C_x(t+1)| \leq \sup_x |C'_x(t+1)| + k'\sigma \quad (104)$$

which is an assumption about the nature of competition and dispersal to be discussed below. With assumption (104), inequality (103) becomes

$$\sup_x |C_x(t+1)| \leq \rho \sup_x |C_x(t)| + (k+k')\sigma. \quad (105)$$

This means that

$$|C_x(t)| \leq (k+k')\sigma/(1-\rho) \quad (106)$$

for all  $t$  whenever  $|C_x(0)|$  is sufficiently small, i.e., whenever  $|C_x(0)| \leq (k+k')\sigma/(1-\rho)$  for  $\sigma$  sufficiently small. This proves the required result  $\mathcal{E}_j = O(\sigma)$  whenever there is a common competitive factor and the appropriate regularity conditions hold.

These regularity conditions are stated as follows:

Let  $\varepsilon$  be a positive number and let the vectors  $\mathbf{E}$ ,  $\mathbf{E}'$ ,  $\mathbf{N}$ ,  $\mathbf{N}'$ , and scalar  $C$  satisfy the conditions,  $|\mathbf{E}| < \varepsilon$ ,  $|\mathbf{E}'| < \varepsilon$ ,  $|f(\mathbf{E}'', \mathbf{N})| < \varepsilon$  for some  $\mathbf{E}''$  with  $|\mathbf{E}''| < \varepsilon$ ,  $\mathbf{N}' = \mathbf{N} \cdot \mathbf{G}(\mathbf{E}, C)$ , and  $|C| < \varepsilon$ , where  $\mathbf{G}(\mathbf{E}, C) = (G_1(E_1, C), \dots, G_n(E_n, C))$ .

With these constraints holding, define

$$\rho = \sup \left| 1 + \frac{\partial f(\mathbf{E}, \mathbf{N} \cdot \mathbf{G}(\mathbf{0}, C))}{\partial C} \right|, \quad (107)$$

$$k_1 = \sup |\nabla f(\mathbf{E}'', \mathbf{N}')|_{\mathbf{E}'' = \mathbf{E}'}, \quad (108)$$

where  $\nabla$  is the operator  $(\partial/\partial E_1'', \dots, \partial/\partial E_n'')$ , and

$$k_2 = \sup |\nabla f(\mathbf{E}'', \mathbf{N} \cdot \mathbf{G}(\mathbf{E}, C))|_{\mathbf{E}'' = \mathbf{E}}. \quad (109)$$

The regularity conditions are then that for  $\varepsilon$  sufficiently small, these quantities are all finite and  $\rho < 1$ . Then,  $k$  is defined as  $2k_1 + k_2$ . That  $k_1$  and  $k_2$  should be finite is essentially a smoothness condition on the functions. Competition naturally has negative feedback to itself, and the condition on  $\rho$  ensures that this negative feedback is stabilizing.

A final condition was introduced here that has no counterpart in the temporal models and that is  $|C_x(t+1)| \leq \sup_x |C'_x(t+1)| + k'\sigma$ . This means that any increase in local density due to dispersal cannot increase competition any more than  $O(\sigma)$  above the maximum competition applicable if there were no dispersal. This is not a greatly restrictive assumption under realistic dispersal and competition scenarios.

All of the above is simply for the case of a common competitive factor. Following Chesson (1994) this result extends to the case where the competition parameters can be expressed in the form

$$C_{jx}(t) = C_x(t) + h_{jx}(t) \quad (110)$$

with  $|h_{jx}(t)| < k_j \sigma^2$  for constants  $k_j$ .

To obtain the result  $E[\mathcal{E}_j] = O(\sigma^2)$ , we first consider a resident ( $j=r$ ), and we assume that dispersal and local dynamics are such that  $v_{rx} - 1 = O(\sigma)$ . Given the quadratic approximation, we have

$$0 = E[(\lambda_r - 1)v_r] \approx E\mathcal{E}_r v_r - E\mathcal{C}_r v_r + \gamma E\mathcal{E}_r \mathcal{C}_r v_r. \quad (111)$$

Now  $\mathcal{E}_r v_r = O(\sigma^2) = \mathcal{E}_r \mathcal{C}_r v_r$ , and so their expected values are  $O(\sigma^2)$  also. Therefore, Eq. (111) implies  $E\mathcal{C}_r v_r = O(\sigma^2)$ . Given  $v_{rx} - 1 = O(\sigma)$ , this means  $E\mathcal{C}_r = O(\sigma^2)$  too. Equation (110) coupled with smoothness of the functions  $G_j$  now implies that  $E\mathcal{C}_i = O(\sigma^2)$ , which then covers all the needed cases.

Note that in the case of pure spatial variation and widespread dispersal with retention, formula (89) of Appendix II justifies the requirement  $v_{rx} - 1 = O(\sigma)$ : formula (89) implies that

$$v_{rx} = 1 + (p/q)(\lambda_{rx} - 1) + O((\lambda_{rx} - 1)^2), \quad (112)$$

and the results in this appendix show that  $(\lambda_{rx} - 1) = O(\sigma)$ , from which the statement  $v_{rx} - 1 = O(\sigma)$  follows. The results here also imply that  $(\lambda_{ix} - 1) = O(\sigma)$ , which implies  $\lambda_i - 1 = O(\sigma)$ . Substituting this in Eq. (90) we see that  $v_{ix} - 1 = O(\sigma)$ . Combining this with the fact that



$E[\lambda_i] = O(\sigma^2)$ , from the results above, leads to  $\tilde{\lambda}_i - 1 = O(\sigma^2)$ . Substituting this back in Eq. (90), we can see that  $v_{ix} = 1 + (p/q)(\lambda_{ix} - 1) + O(\sigma^2)$ , which proves Eq. (64) of the text for  $j = i$  as well as  $j = r$ .

## APPENDIX IV

For the model of insects laying eggs in ephemeral patches of food, we need to calculate  $\bar{a}$ . Now

$$C^{-i} = \beta \sum_s E_s N_s, \quad (113)$$

which means  $A_s = \beta N_s$ , and so

$$\bar{a} = \frac{\beta}{n-1} \sum_{s \neq i} \bar{N}_s. \quad (114)$$

Because  $E_j = 1 + O(\sigma)$  and  $E[E_j] = 1 + O(\sigma^2)$ , we can substitute 1 for the  $E_j$  in the resident growth equation  $EH_s(E_s, C_s^{-i}) = 1$  to give the approximation

$$\exp \left\{ r_s \left( 1 - \beta \sum_{r \neq i} \bar{N}_r + (\alpha - \beta) \bar{N}_s \right) \right\} = 1 + O(\sigma^2), \quad (115)$$

which implies

$$\beta \sum_{r \neq i} \bar{N}_r + (\alpha - \beta) \bar{N}_s = 1 + O(\sigma^2). \quad (116)$$

Summing over residents,  $s$ , reveals the result

$$\sum_{s \neq i} \bar{N}_s = \frac{n-1}{(n-1)\beta + (\alpha - \beta)} + O(\sigma^2) \quad (117)$$

which then implies

$$\begin{aligned} \bar{a} &= \frac{\beta}{(n-1)\beta + (\alpha - \beta)} + O(\sigma^2) \\ &= \frac{1}{n-1} + O(\sigma^2), \end{aligned} \quad (118)$$

as stated in the text. This means also that  $\sum_{s \neq i} \bar{N}_s = (1/\beta) + O(\sigma^2)$ . Although this formula for the resident densities may not appear to be the closest approximation, it is on the same order of accuracy as approximation (117) and gives a more understandable result.

## APPENDIX V

In the annual plant model, for simplicity assume that the different species all have the same value  $\alpha$  of  $\alpha_j$ , the competitive effect of a seedling of species  $j$ . Here, we shall use the symbol  $\alpha_j$  for the quantity  $\partial \mathcal{E}_j / \partial \varepsilon_j$  evaluated under equilibril conditions, where  $\varepsilon_j = \ln E_j$  and  $E_j$  is the germination fraction. The small effects approximations will all be done on the log scale, and therefore  $\varepsilon_j$  will be substituted for  $E_j$  in the relevant formulae. We choose a common equilibril value  $C^*$  for the competition parameters. The  $E_j^*$  are determined by  $C^*$  and the  $s_j$ . The basic parameters derived from these are given in Table 2. Calculating  $\Delta I$  by making use of the symmetry assumptions, note that  $\alpha_j \gamma_j = -1$  and therefore  $\overline{\alpha \gamma} - \alpha_i \gamma_i = 0$ . Also,  $\overline{\alpha^2 a \gamma} = -\overline{\alpha a}$ , with

$$\sum_{r \neq i} \alpha_r a_r = \sum_{r \neq i} \alpha \bar{N}_r E_r^* = C^* - 1 + O(\sigma^2), \quad (119)$$

and hence  $\overline{\alpha^2 a \gamma} = -(C^* - 1)/(n-1)$ . It follows that

$$\Delta I = \beta_i \frac{C^* - 1}{n-1} \sigma^2 (1 - \rho). \quad (120)$$

There is no relative nonlinearity and, with a common competitive factor and a consensus choice  $C^*$  for equilibril competition,  $\mathcal{C}_i^{-i*} = 0$ . It remains to calculate  $\Delta E$ .

The formula for  $q_{ir}$  from the table means

$$\Delta E = \beta_i \left( \frac{E \mathcal{E}_i}{\beta_i} - \frac{1}{n-1} \sum_{r \neq i} \frac{E \mathcal{E}_r}{\beta_r} \right), \quad (121)$$

but  $\beta_j = (1 - s_j [1 - E_j^*])/C^* = (1 - s_j [1 - E[E_j]])/C^* + O(\sigma^2)$ , and as  $E \mathcal{E}_j = O(\sigma^2)$ , it follows  $E \mathcal{E}_j / \beta_j = C^* E \mathcal{E}_j / \theta_j + o(\sigma^2)$ , where  $\theta_j = (1 - s_j [1 - E[E_j]])$ . However,  $C^* E \mathcal{E}_j / \theta_j + C^* = \bar{C}_j^*$ , the equilibrium value of competition for species  $j$  with the germination fraction constant at  $E[E_j]$ . It follows that  $\Delta E$  can be written as

$$\Delta E = \beta_i (\bar{C}_i^* - \bar{C}^*). \quad (122)$$

TABLE 2

Parameters of the Annual Plant Model

$\alpha_j$	$1 - s_j$
$\beta_j$	$(1 - s_j [1 - E_j^*])/C^*$
$\gamma_j$	$-1/(1 - s_j)$
$q_{ir}$	$\beta_i / \beta_r (n-1)$

Combining the formulas for  $\Delta E$  and  $\Delta I$  and noting that  $\theta_j/C^*$  can be substituted for  $\beta_j$  without changing the order of accuracy of the results, we obtain Eq. (87).

## ACKNOWLEDGEMENTS

I am grateful to Tony Ives, Claudia Neuhauser, and Steve Pacala for comments on drafts of this manuscript. This work was supported in part by NSF Grant DEB 9981926.

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