

# Multispecies Competition in Variable Environments

PETER CHESSON

*Ecosystem Dynamics Group, Research School of Biological Sciences,  
Institute of Advanced Studies, Australian National University,  
Canberra, ACT 0200, Australia*

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A general model of competition between several species in a variable environment is presented and analyzed using a general method that unifies treatment of different specific models. This method yields broad conclusions that are independent of the details of a model. It is used here to show that mechanisms of coexistence and competitive exclusion are largely restricted to three broad categories. One of these categories includes classical mechanisms that do not depend on fluctuations over time. Another category includes mechanisms which may be referred to collectively as the storage effect. These mechanisms involve species-specific responses to environmental fluctuations, a relationship between fluctuations in competition and fluctuations in the environment, and an interaction between environment and competition. The final category depends on fluctuating competition and nonlinear responses to competition that differ between species. These general results are illustrated with analyses of several specific models, including a Lotka–Volterra model, a model of nonlinear resource consumption, and models of recruitment fluctuations for iteroparous organisms and for annual plants. © 1994 Academic Press, Inc.

## 1. INTRODUCTION

Fluctuations over time are one of the most striking features of natural ecosystems. Fluctuations occur in the densities and relative densities of organisms and in the environments in which they live. In this article, I ask: How do fluctuations over time affect the outcomes of interactions between species? More generally, I ask: How is community structure affected by fluctuations? There has long been a belief that fluctuations must have a major influence on the structure of communities (e.g., Hutchinson, 1961; Connell, 1978), but until recently there was no satisfactory theory addressing this question. Models providing a theoretical framework now exist. Commonly, these models assume that fluctuations in population densities originate with environmental fluctuations. Hence the resulting theory might be called *variable environment theory*.

There are two main sorts of variable environment theory. First is theory based on simultaneous fluctuations in space and time of equal magnitude

(spatio-temporal models). Most models of disturbance are in this class (Slatkin, 1974; Caswell, 1978; Hastings, 1980; Hanski, 1983). More recently, models have been developed in which local immigration rates or competitive conditions fluctuate in time for unspecified reasons (Comins and Noble, 1985; Chesson, 1985; Ives, 1988).

Second is theory emphasizing fluctuations over time alone (e.g., Abrams, 1984; Chesson and Huntly, 1988). For this class of theory, which is the focus of this article, it has been possible to show that a few general principles permit understanding of a variety of different particular systems (Chesson, 1988, 1989). In essence, there is a unified theory of temporal fluctuations. This unified theory deals mostly with models having stochastic environmental fluctuations, but some models with deterministic fluctuations also have been fitted into this framework (Chesson and Huntly, 1989; Ebenhoh, 1992; Loreau, 1992). Moreover, this unified theory can be extended to cover a class of spatio-temporal models (Chesson and Ives, unpublished manuscript).

The unified theory has continuity with classical community ecology based on a point equilibrium. In particular, the idea that species must be sufficiently ecologically distinct to coexist is preserved in the unified theory (Chesson, 1991). The unified theory, however, considers a much broader range of ways in which species can be ecologically distinct than was ever considered in the classical point-equilibrium approach to community ecology.

This success in finding general principles governing community dynamics suggests that further gains can be made. In this article, I develop a general model of a multispecies system of competitors in a temporally varying environment, and I use it to develop a general quantitative criterion for the persistence of a species in the presence of its competitors. This criterion provides a quantitative understanding of mechanisms of coexistence and competitive exclusion ("coexistence-affecting mechanisms") in a fluctuating environment.

This quantitative criterion extends the two-species results of Chesson (1989) to the multispecies case. Its main limitation is that it depends on a quadratic approximation of the model. Nevertheless, it provides a broadly applicable beginning to the quantitative understanding of some very general phenomena (Chesson, 1990). It points to a method of understanding the operation of mechanisms on different timescales, and demonstrates a way of assessing the relative contributions of various mechanisms to species coexistence.

These general findings are illustrated with analyses of several specific models, including a Lotka-Volterra model, a model of nonlinear resource consumption, and models of recruitment fluctuations for iteroparous organisms and annual plants.

## 2. OVERVIEW OF MODELS AND MECHANISMS

To study coexistence-affecting mechanisms, we must first formulate population growth mathematically and decide what we mean by coexistence. Let  $X_i(t)$  be the population density of some species  $i$  at time  $t$ , and express its population density at time  $t + 1$  as

$$X_i(t + 1) = \lambda_i(t) X_i(t), \quad (1)$$

where  $\lambda_i(t)$  is the *finite rate of increase* of species  $i$ , for the time interval  $t$  to  $t + 1$ . (For the convenience of readers, a list of general notation is given in Appendix I.) On the log scale, Eq. (1) becomes

$$Z_i(t + 1) - Z_i(t) = r_i(t), \quad (2)$$

where  $Z_i(t) = \ln X_i(t)$ , and  $r_i(t) = \ln \lambda_i(t)$ . Note that  $r_i(t)$  is the rate of change of log population size. We refer to it simply as the *growth rate*.

The log scale is important because averages of  $r_i(t)$  over time determine long-term population growth and form the basis of the standard invasibility approach to species coexistence (Turelli, 1981; Chesson and Ellner, 1989; Ellner, 1989). Invasibility analysis identifies one particular average of  $r_i(t)$ , denoted by  $\bar{r}_i$ , as especially significant. The average  $\bar{r}_i$  is the mean low-density growth rate, which is the average of  $r_i(t)$  for the case where species  $i$  has been introduced to the system at very low (effectively zero) density while other species have been present for an essentially indefinite period of time. We refer to it as the long-term low-density growth rate because the invasibility approach to coexistence identifies it as the growth rate that applies in the long term at low density.

A positive value of  $\bar{r}_i$  means that species  $i$  can invade the system if introduced at low density, but more importantly, the value of  $\bar{r}_i$  measures the rate at which the species recovers from fluctuations to low density. A negative value of  $\bar{r}_i$  means that the species cannot invade the system. A negative value means also that when species  $i$  is present and can attain low densities, e.g., as a result of an accumulation of chance fluctuations, it is likely to go extinct. For a fuller discussion of these issues see Chesson (1990).

In the two-species variable environment theory (Chesson, 1988, 1989), which is generalized here, the growth rate  $r_i(t)$  is expressed as a function of environment and competition. Therefore, the long-term growth rate  $\bar{r}_i$  can be expressed in terms of a mean environmental effect,  $\Delta E$ , a mean competition effect,  $\Delta C$ , and a mean of their interaction,  $\Delta I$ , as follows:

$$\bar{r}_i = \Delta E - \Delta C + \Delta I \quad (3)$$

(cf. two-factor experimental models, Sokal and Rohlf, 1981, p. 329). However, each of these mean effects is not an absolute effect but a comparison of an effect on species  $i$  with an effect on species  $i$ 's competitor (Chesson, 1989), hence the notation  $\Delta$ .

The term  $\Delta E$  compares average effects of the environment. The term  $\Delta C$  consists of two parts. The first part is a difference between interspecific competition and intraspecific competition that does not depend on environmental fluctuations. Together with  $\Delta E$ , this difference would completely determine the value of  $\bar{r}_i$  under constant environmental conditions, and hence whether the two species could coexist in the absence of fluctuations over time. The first part of  $\Delta C$  therefore can be thought of as incorporating coexistence-affecting mechanisms operating on timescales shorter than the unit of time considered in the model.

The second part of  $\Delta C$  depends on fluctuations in competition from one unit of time to the next. It depends also on different nonlinear responses to competition by the two species (Chesson and Huntly, 1989). Different nonlinear responses to competition occur, for example, if species compete for the same resource but have curves of different shapes describing the dependence of their growth rates on that resource (Fig. 1). Armstrong and McGehee show how such *relative nonlinearity* can result from species having different functional responses to a common prey (the resource). We shall see here that relative nonlinearity can result from as simple a difference between species as a difference between their longevities in some particular stage of the life cycle—see Subsection 5.4, below.

Relative nonlinearity, coupled with fluctuations in competition, leads to a decrease in  $\Delta C$  if species  $i$  has the more convex response to competition

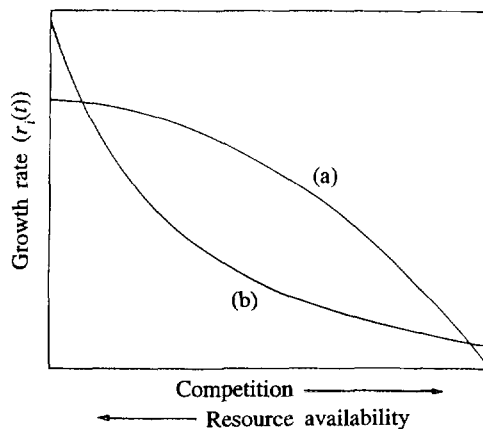


FIG. 1. Population growth rates of two species showing relatively nonlinear responses to competition or a common limiting factor.

(curve [b] in Fig. 1); otherwise there is an increase in  $\Delta C$ . The reason is simple: extreme values of competition (high or low) associated with high variance put the growth rate for species  $i$  above that of its competitor. Intermediate values of competition associated with low variance reverse this situation. Levins (1979) and Armstrong and McGehee (1980) pointed out that a decrease in  $\Delta C$  generated by fluctuating competition and relatively nonlinear responses to competition can permit an otherwise inferior species to coexist with its competitor. As we shall see here, depending on the circumstances, these factors can also be a mechanism of competitive exclusion. We shall refer to this coexistence-affecting mechanism as *relative nonlinearity*.

The interaction term,  $\Delta I$ , in the two-species theory depends on three ingredients (Chesson, 1989; Chesson and Rosenzweig, 1991), which can be measured quantitatively and combined to give the actual value of  $\Delta I$ . The first ingredient is *species-specific responses to the environment*. For example, if temperature fluctuates and the species have different temperature optima for growth, then some increases in temperature will be good for some species but bad for others. Thus, responses to a fluctuating environment will be asynchronous between species, and the correlations between species responses to the environment will be less than 1. The  $\Delta I$  term can be nonzero if responses to the environment are positively correlated between species, but  $\Delta I$  increases in magnitude as such correlations decrease.

The second ingredient is *covariance between environment and competition*, which measures how much fluctuations in competition covary with fluctuations in the environment. For example, an improvement in environmental conditions for a species may increase its density or the density of one of its life-history stages, and increase the demand on resources. Evaluation of this covariance is discussed below. The important point for the present is that a nonzero value for  $\Delta I$  requires a nonzero covariance.

The third ingredient is the way the growth rate of a species responds jointly to environmental and competitive conditions. This is illustrated in Fig. 2. In the *additive* case (a), the response of the growth rate to competition does not depend on environmental conditions—the environmental state alters the vertical position of the growth-rate curve without affecting its slope. In the *subadditive* case (b), there is a stronger response to competition when environmental conditions are good, while in the *superadditive* case (c) the stronger response to competition occurs when environmental conditions are bad. Only the subadditive and superadditive cases (collectively *nonadditive* cases) lead to nonzero values for  $\Delta I$ .

Chesson (1988, 1990) and Chesson and Huntly (1988) discuss a variety of ways in which nonadditivity arises in nature. Nonadditivity results commonly whenever a population can be subdivided into different classes of individuals with different responses to environment and competition.

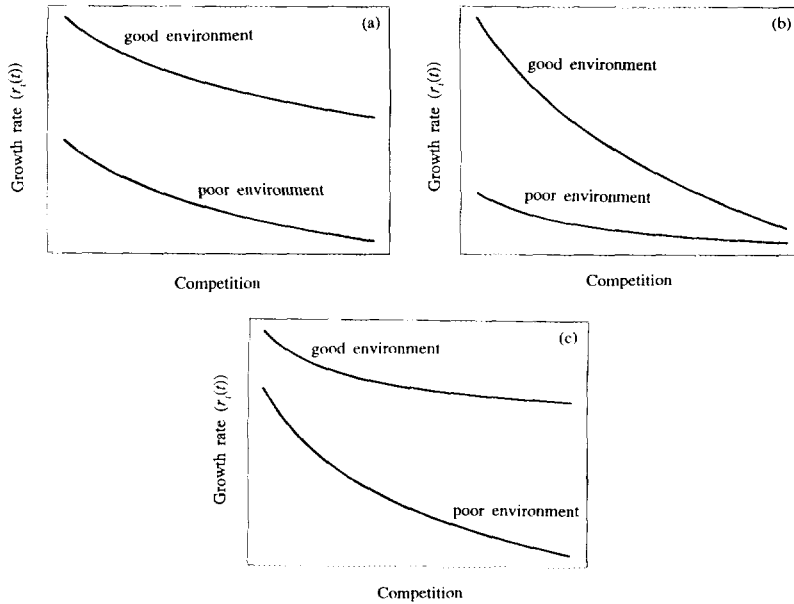


FIG. 2. Population growth rates illustrating interactions between environment and competition. The two curves in each panel are for the same species under different environmental conditions. (a) No interaction: additivity. (b) Negative interaction: subadditivity. (c) Positive interaction: superadditivity.

Subadditivity occurs when classes of individuals that are more sensitive to environment than the average for the population are also more sensitive to competition than average. For example, juveniles in a population often are much more sensitive to both environment and competition than are adults in a population of long-lived iteroparous (multiply reproducing) organisms. In general, the different classes of individuals in a population need not be defined by life history, as in this example, but instead might be defined by phenotypes or even the micro-environments over which a population is spread. There are so many ways in which nonadditivity can arise that it seems doubtful that any real populations could be additive, although approximate additivity might be common.

Nonadditivity combines quantitatively with the other two ingredients, species-specific responses to the environment and covariance between environment and competition to give  $\Delta I$ . For example, Chesson and Huntly (1989) explain how subadditivity means that a species can have periods of exceptionally strong growth when competition is relatively low and environmental conditions are relatively good. In the same population, the reverse situation of poor environmental and competitive conditions does not lead to exceptionally poor growth rates.

Covariance between environment and competition determines the pattern of fluctuations in environmental and competitive conditions affecting the growth rate. Species-specific responses to the environment mean that this covariance, or pattern of environmental and competitive fluctuations, depends on the density of the species. Chesson and Huntly (1989) explain how the dependence of this pattern on density, coupled with subadditivity, can lead to more periods of relatively high growth rate as the density of a species decreases. While there may also be more periods of low growth rate, these low growth rates are of lesser magnitude and cannot cancel the benefits of the periods when the growth rate is relatively high. As a consequence there is an increase in the average growth rate, which is measured by  $\Delta I$ , and which promotes coexistence. Negative values of  $\Delta I$ , promoting competitive exclusion, can also arise, for example from superadditive growth rates, or different patterns of covariance between environment and competition (see, e.g., Chesson, 1988, 1990).

The coexistence-affecting mechanism measured by  $\Delta I$  can be referred to as the *storage effect*. Previously (e.g., Chesson and Rosenzweig, 1991), the term storage effect has been used to refer to just a subset of mechanisms contributing to  $\Delta I$ . The model of Subsection 5.5 below provides a good example. In that model, favorable periods of growth can markedly increase the amount of seed stored in the soil seed bank. Unfavorable periods, however, can only slowly reduce the seed bank. Coexistence depends critically on the storage of the benefits of favorable periods in this seed bank. More generally, mechanisms leading a positive  $\Delta I$  value involve storage of the benefits of favorable periods in the population, whether this storage can be traced to a seed bank of something else. The term storage is a metaphor for the potential for periods of strong positive growth that cannot be canceled by negative growth at other times. We can think of a negative value of  $\Delta I$  as measuring a negative storage effect where positive growth cannot be of sufficient magnitude to cancel strong negative growth.

In summary, general models of two-species competition in fluctuating environments have yielded three general coexistence-affecting mechanisms that we can call *fluctuating-independent mechanisms*, *relative nonlinearity*, and *the storage effect*. In the rest of this manuscript, our task is to achieve a similar understanding in quantitative terms of general mechanisms of coexistence in multispecies models. This is based on a general model to which a general method of quadratic approximation is applied.

### 3. THE GENERAL MODEL

To develop the multispecies theory we must express the growth rate,  $r_j(t)$ , for each species  $j$  in a community of  $n$  competing species in terms of

environmental and competitive effects. (We use the symbol  $j$  for an arbitrary member of the community, reserving the symbol  $i$  for an "invader"—a species at effectively zero density.)

To incorporate environmental effects in a population model, one does not deal with the environment directly, but in essence with a bioassay of the environment, an *environmentally dependent parameter* (Chesson, 1988). An environmentally dependent parameter is a population parameter such as a birth rate, survival rate, or seed germination rate that depends on the environment, but not on the population densities of any of the species in the community. An environmentally dependent parameter could depend on other species provided these other species are not affected by the densities of the  $n$  species that make up the community under consideration. The key point is that an environmentally dependent parameter should not be affected by the densities of any of the  $n$  species in the community.

The notation  $E_j(t)$  means the environmentally dependent parameter of species  $j$  for the period  $t$  to  $t + 1$ , and the notation  $\mathbf{E}(t)$  means the vector,  $(E_1(t), \dots, E_n(t))$ , of all species' environmentally dependent parameters.

Competition is incorporated through a competition parameter,  $C_j(t)$ , which is a measure of the total amount of competition experienced by species  $j$ . More general density-dependent effects such as *apparent competition* (*sensu* Holt, 1977) could also be measured by this competition parameter.

We generally assume that the amount of competition is affected by the environmentally dependent parameter of a species. For example, if  $E_j(t)$  is a species' germination fraction, and competition occurs between seedlings as they grow, the value of  $E_j(t)$  will affect the number of competing seedlings and determine the intensity of competition. We assume that the effect of  $E_j(t)$  on competition depends on the value of  $X_j(t)$ , and that  $E_j(t)$  has no causative effect on  $C_j(t)$  if  $X_j(t) = 0$ . This does not, however, prevent  $E_j(t)$  from being correlated with  $C_j(t)$ , which is likely when  $E_j(t)$  is correlated with environmentally dependent parameters of other species or with other factors on which  $C_j(t)$  depends.

The parameters  $E_j(t)$  and  $C_j(t)$  are combined to yield the growth rate according to some function  $g_j$ :

$$r_j(t) = g_j(E_j(t), C_j(t)). \quad (4)$$

This expression incorporates the idea that the environment will have a direct effect on population growth through the first argument of  $g_j$  and an indirect effect through the dependence of the second argument, the competition parameter, on environmentally dependent parameters.

Naturally,  $g_j$  decreases in the second argument,  $C_j(t)$ : competition is detrimental to population growth. Although not strictly necessary, we



generally assume that  $g_j$  increases in the first argument,  $E_j(t)$ . While we would not expect population growth to depend monotonically on an environmental variable such as temperature, it is quite likely to depend monotonically on an environmentally dependent parameter such as a survival rate or birth rate, which we think of as a bioassay of the favorability of the environment for a species. By appropriate definition of  $E_j(t)$ , e.g., as a survival rate rather than a mortality rate, it is usually possible to have  $g_j$  an increasing function of  $E_j(t)$ .

### 3.1. Assumptions and Standardization

As given above, the model is very general indeed. Before we can draw conclusions we must introduce a few restrictions, which we list as numbered assumptions below. Alternative forms of assumptions, that apply only when specifically indicated, are marked with a prime (').

First, we need some assumptions concerning the functions  $g_j$ . In general we expect the value of  $g_j(E_j(t), C_j(t))$  to fluctuate about 0, as positive values correspond to population increase and negative values correspond to population decrease. It is not unreasonable to expect therefore that

- (a1) There exist values  $E_j^*$  and  $C_j^*$  of  $E_j(t)$  and  $C_j(t)$  such that

$$g_j(E_j^*, C_j^*) = 0. \quad (5)$$

The pair of values  $E_j^*$  and  $C_j^*$  will generally not be unique, but choosing one of the pair will fix the other. The values  $E_j^*$  and  $C_j^*$  serve as a point about which we can approximate the function  $g_j$ . We therefore choose  $E_j^*$  somewhere in the middle of the range of fluctuations of  $E_j(t)$ . Other assumptions below then assure that  $C_j^*$  is within the range of fluctuations of  $C_j(t)$ .

Because the values  $E_j^*$  and  $C_j^*$  specify a situation of no population growth, they can be thought of as defining an equilibrium for each species individually. It is important to note, however, that we make no assumption that these individual equilibria are stable, although it is not an unreasonable expectation for each of the species living in a single-species setting. Most importantly, we do not assume that all species can come to equilibrium simultaneously in the multispecies setting, nor do we assume that any such equilibrium would be stable.

We use the values  $E_j^*$  and  $C_j^*$  to define parameter transformations that unify the treatment of different models. One difficulty in obtaining unity is that the parameters  $E_j(t)$  and  $C_j(t)$  can refer to different things in different models. For example, in one model  $E_j(t)$  might be the fraction of seeds that break dormancy, but in another it might be the rate of nutrient uptake (Abrams, 1984). These quantities are not only very different, but are measured in different units, making any kind of unified treatment difficult.

To overcome these problems we introduce new parameters,  $\mathcal{E}_j(t)$  and  $\mathcal{C}_j(t)$ , which we shall call *standard parameters*, as transformations of the original parameters:

$$\mathcal{E}_j = g_j(E_j, C_j^*) \quad (6)$$

and

$$\mathcal{C}_j = -g_j(E_j^*, C_j). \quad (7)$$

Provided  $g_j$  is monotonic in each of its arguments, the standard parameters contain the same information as the original parameters but are expressed in units of growth rate. In all models they express the effect of environment and competition directly in terms of the growth rate, and thus have the same meaning in different models. These standard parameters take on both positive and negative values. Indeed, in most circumstances they fluctuate about 0. To calculate their variances and covariances we need the linear approximations

$$\mathcal{E}_j = \alpha_j(E_j - E_j^*) + O((E_j - E_j^*)^2) \quad (8)$$

and

$$\mathcal{C}_j = \beta_j(C_j - C_j^*) + O((C_j - C_j^*)^2), \quad (9)$$

where  $\alpha_j$  and  $\beta_j$  are respectively  $\partial\mathcal{E}_j/\partial E_j$  and  $\partial\mathcal{C}_j/\partial C_j$  evaluated for equilibrium values of the environmentally dependent and competition parameters, and we use the standard order notation (Appendix II).

Some assumptions about environmental fluctuations are needed. For unambiguous meaning to the notion of long-term averages, we have to assume that the environment, as measured by the vector  $\mathbf{E}(t)$  of environmentally dependent parameters, has some long-term repeatability. The mildest form of this assumption, which encompasses all the usual sorts of "environmental noise" (Nisbet and Gurney, 1982), is the following:

(a2) The sequence of vectors  $\mathbf{E}(t)$ ,  $t = 0, 1, 2, \dots$ , forms an ergodic stationary stochastic process (see Karlin and Taylor, 1975).

For some of the examples we will need to assume that environmental fluctuations are independent from one time to the next, and in that case we specialize assumption (a2) to the usual white noise assumption,

(a2') The environment process  $\mathbf{E}(t)$ ,  $t = 0, 1, 2, \dots$ , takes on independent values at every point in time, and the distribution of  $\mathbf{E}(t)$  is the same for every  $t$ .

Readers unfamiliar with ergodic stationary processes can simply assume (a2') without affecting the correctness of the results given here. Note that

while (a2') means that the environment at one point in time is uncorrelated with the environment at other points in time, in no case do we assume environmentally dependent parameters of different species to be uncorrelated.

In order to approximate the function  $g_j$  appropriately, it is necessary to restrict the range of fluctuations of  $E_j(t)$ , but at this point it is more useful to shift attention to  $\mathcal{E}_j(t)$ . We introduce the symbol  $\sigma$  as "a small parameter" indicating the magnitude of variation in the environment. We write

$$(a3) \quad \mathcal{E}_j(t) = O(\sigma).$$

We say that  $\mathcal{E}_j$  fluctuates in a finite range of order  $\sigma$ , and we can assume that the standard deviations of the  $\mathcal{E}_j$  are proportional to  $\sigma$ .

We assume that  $\sigma$  is small enough to enable quadratic approximation of the function  $g_j$ . This requirement is not necessarily restrictive because for the two-species lottery model, it is known that quadratic approximation is adequate for variation that is in fact quite large (Chesson, 1989; Hatfield and Chesson, 1989). However, at present there is no general theory on the adequacy of such approximations for large environmental fluctuations.

It is important also to consider the meaning of large in the context of environmental fluctuations. The idea that environmental fluctuations in nature are large is not an absolute judgment but a claim that environmental fluctuations are large relative to other factors. We have several ways of incorporating this idea in the model. First, we make the range of environmental fluctuations large relative to their mean effects. Thus, we have

$$(a4) \quad E\mathcal{E}_j(t) = O(\sigma^2),$$

where "E" means expectation or theoretical mean value, and we have suppressed  $t$  for notational convenience.

It follows from (a3) and (a4) that

$$V(\mathcal{E}_j(t)) = O(\sigma^2), \quad (10)$$

where the symbol  $V$  means variance.

Restricting the range of environmental fluctuations has the effect of restricting the range of fluctuations in competition under some general circumstances. This conclusion is discussed in detail in Appendix II, where order  $\sigma^2$  restrictions are imposed on the competitive differences between different species. These restrictions mean that competitive differences between species are of similar magnitude to the means and variances of environmental fluctuations, allowing the relative effects of competitive differences and environmental fluctuations to be assessed in a situation where they can all be expected to contribute to long-term population

dynamics. It is then shown in Appendix II that the following proposition is justified:

$$(a5) \quad \mathcal{C}_j(t) = O(\sigma), \text{ and } E\mathcal{C}_j(t) = O(\sigma^2).$$

Note that this proposition implies that  $V(\mathcal{C}_j(t)) = E(\mathcal{C}_j(t))^2 = O(\sigma^2)$ .

To understand the effects of competition on coexistence, it is necessary to be able to relate interspecific and intraspecific competition. A species at zero density (or a density low enough to make negligible contributions to the competition) experiences only interspecific competition. It therefore seems not unreasonable to suppose that the competition parameter of an invading species can be represented as a function of the competition parameters of other species. Indeed, this is commonly the case in competition models. We can formally state this assumption by introducing the notation  $\mathcal{C}_j^{-i}$  for standard competition parameter of some arbitrary species  $j$  in the community, with species  $i$  as an invader, i.e., a species whose density is set at zero. Then we state that

(a6) There is some function  $f$  jointly of the  $\mathcal{C}_r^{-i}$ , for  $r \neq i$ , such that

$$\mathcal{C}_i^{-i} = f(\mathcal{C}_1^{-i}, \dots, \mathcal{C}_n^{-i}), \quad (11)$$

with  $f(0, \dots, 0) = O(\sigma^2)$ .

Note that the condition  $f(0, \dots, 0) = O(\sigma^2)$  means that when the resident species experience equilibrium competition, the invading species experiences competition of order  $\sigma^2$ . This is consistent with the imposition of order  $\sigma^2$  competitive differences between species imposed in Appendix II to obtain proposition (a5).

In general, it is helpful to think of the  $\mathcal{C}_j$  as functions of species densities and their environmentally dependent parameters,

$$(a7) \quad \mathcal{C}_j(t) = c_j(E_1(t), X_1(t), \dots, E_n(t), X_n(t)), \quad (12)$$

where  $c_j$  is some function. Many of the examples given in Sect. 5, below, have competition parameters in this form, and this form is used in the derivation of (a5), above. However, the development below permits much more general dynamics for competition including situations where separate dynamical equations are necessary for resources. In general, the development here depends much more on the relationships between competition parameters of different species and their dependence on the environment than it does on the details of the dynamics of the competition parameters.

#### 4. ANALYSIS OF THE GENERAL MODEL

To simplify notation, we shall suppress time,  $t$ , in our notation, unless it is needed for clarity or emphasis.

The restrictions  $\mathcal{E}_j = O(\sigma)$  and  $\mathcal{C}_j = O(\sigma)$  (a3 and a5 above) allow quadratic approximation of the growth rate  $r_j$  in  $\mathcal{E}_j$  and  $\mathcal{C}_j$ , with an error equal to  $o(\sigma^2)$ . The definitions, (6) and (7), of the standard parameters lead to an especially simple form for this quadratic approximation. First, note that zero values of  $\mathcal{E}_j$  and  $\mathcal{C}_j$  correspond to the equilibrium values  $E_j^*$  and  $C_j^*$  of the original parameters  $E_j$  and  $C_j$ . Second, note that  $r_j = \mathcal{E}_j$ , when  $\mathcal{C}_j = 0$ , and  $r_j = -\mathcal{C}_j$ , when  $\mathcal{E}_j = 0$ . Defining the symbol “ $\approx$ ” to mean an approximation error equal to  $o(\sigma^2)$ , it follows that the full quadratic approximation of  $r_j$  in terms of  $\mathcal{E}_j$  and  $\mathcal{C}_j$  is

$$r_j \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j, \tag{13}$$

where

$$\gamma_j = \frac{\partial^2 r_j}{\partial \mathcal{E}_j \partial \mathcal{C}_j}. \tag{14}$$

The parameter  $\gamma_j$  measures nonadditivity. It defines the change in slope of the growth rate as a function of competition as the environmentally dependent parameter is varied, as discussed in Section 2, and illustrated in Fig. 2. For  $\gamma_j = 0$ , the additive case (Fig. 2a), there is no interaction. For  $\gamma_j < 0$ , the interaction is subadditive (Fig. 2b) and for  $\gamma_j > 0$ , the interaction is superadditive (Fig. 2c).

Given this approximation to  $r_j$ , how do we determine the long-term low-density growth rate,  $\bar{r}_i$ , of a species? As discussed above, according to the invasibility criterion, the sign of the long-term low-density growth rate determines whether a species can persist in the presence of its competitors, and in case it is positive (persistence), the magnitude measures the strength of that persistence.

The standard procedure for invasibility analysis (Turelli 1981) is to set the given species (the invader) at zero density and calculate  $\bar{r}_i$  as the theoretical mean growth rate,  $E r_i$ , under the assumption that the state variables for the system consisting of the remaining  $n - 1$  species (“the residents”) have converged on a unique stationary distribution and form an ergodic stationary process. Note that these state variables are the species densities, their environmentally dependent parameters, and other variables such as resource densities, depending on the details for a specific version of the general model. We shall use the term *resident distribution* to refer to the stationary distribution that these state variables achieve.

To make the calculations easier to follow, we reserve the use of the subscript  $i$  for the invading species, and use subscripts  $r$  and  $s$  to refer “resident” species. The subscripts  $j$  and  $k$  refer to arbitrary species. The superscript  $-i$  is attached to a variable to indicate that it is calculated under the assumption that species  $i$  is an invader, the other  $n - 1$  species

are residents, and the resident stationary distribution has been achieved. The  $-i$  superscript on a vector means additionally that the component corresponding to species  $i$  has been deleted.

In this notation, we can now express the long-term low-density growth rate of an invader as

$$\bar{r}_i \approx E\mathcal{E}_i - E\mathcal{C}_i^{-i} + \gamma_i E\mathcal{E}_i\mathcal{C}_i^{-i}. \quad (15)$$

The quantity  $E\mathcal{E}_i\mathcal{C}_i^{-i}$  is approximately equal to  $C(\mathcal{E}_i, \mathcal{C}_i^{-i})$ . It is a covariance between environment and competition for which we use the notation

$$\chi_{jk}^{-i} = E[(\mathcal{E}_j - E\mathcal{E}_j)(\mathcal{C}_k^{-i} - E\mathcal{C}_k^{-i})]. \quad (16)$$

Because  $E\mathcal{E}_j$  and  $E\mathcal{C}_k^{-i}$  are both  $O(\sigma^2)$ , we have

$$\chi_{jk}^{-i} \approx E\mathcal{E}_j\mathcal{C}_k^{-i} \quad (17)$$

and therefore

$$\bar{r}_i \approx E\mathcal{E}_i - E\mathcal{C}_i^{-i} + \gamma_i \chi_{ii}^{-i}. \quad (18)$$

Expression (18) represents the growth rate in terms of mean environmental effects, mean competition effects, and the mean of their interaction. However, it is not by itself very useful. Much more is to be gained by comparing each of the terms in the equation with the corresponding terms for resident species. This comparison is made as follows.

We note first that a resident species  $r$  must have a zero value for  $E r_r = E[\ln X_r(t+1) - \ln X_r(t)]$ , because at the resident stationary distribution,  $E \ln X_r(t+1) = E \ln X_r(t)$ . Any linear combination,  $\sum_r q_{ir} E r_r$ , for constants,  $q_{ir}$ , will also be zero, but the components of the linear combination will not be; thus we can write

$$\bar{r}_i = \Delta E - \Delta C + \Delta I, \quad (19)$$

where

$$\Delta E = E\mathcal{E}_i - \sum_r q_{ir} E\mathcal{E}_r, \quad (20)$$

$$\Delta C = E\mathcal{C}_i^{-i} - \sum_r q_{ir} E\mathcal{C}_r^{-i}, \quad (21)$$

and

$$\Delta I = \gamma_i E\mathcal{E}_i\mathcal{C}_i^{-i} - \sum_r q_{ir} \gamma_r E\mathcal{E}_r\mathcal{C}_r^{-i} \quad (22)$$

$$\approx \gamma_i \chi_{ii}^{-i} - \sum_r q_{ir} \gamma_r \chi_{rr}^{-i}. \quad (23)$$

The significance of partitioning the mean low density growth rate,  $\bar{r}_i$ , into the components  $\Delta E$ ,  $\Delta C$  and  $\Delta I$  stems from the fact that with a suitable choice of the  $q_{ir}$ , these components measure the contributions of different coexistence-affecting mechanisms. The choice made here is

$$q_{ir} = \frac{\partial \mathcal{C}_i^{-i}}{\partial \mathcal{C}_r^{-i}}, \tag{24}$$

evaluated for  $\mathcal{C}_i^{-i} = 0$ ,  $r \neq i$ . With this definition of the  $q_{ir}$ , resident species are weighted to reflect the relationship between competition experienced by the residents and that experienced by invaders, under assumption (a6). This choice is justified by the results that it gives. It leads to a clear partitioning of mechanisms of coexistence, as shown in Subsection 4.2, below.

Each component of the mean low-density growth rate,  $\bar{r}_i$ , can now be examined in a meaningful way. By exploring these three components we can come to a general understanding of quantitative contributions of the three general mechanisms of coexistence discussed above, namely, *fluctuation-independent mechanisms*, *relative nonlinearity*, and *the storage effect*. Note, however, that  $\Delta C$  consists of the combined effects of the first two mechanisms, and that  $\Delta E$  summarises not a mechanism but differences between species in the average effects of the environment. We now examine in detail each of the terms  $\Delta E$ ,  $\Delta C$ , and  $\Delta I$  contributing to  $\bar{r}_i$ .

#### 4.1. The storage effect, $\Delta I$

Section 2, above, explained that the coexistence-affecting mechanism called the storage effect consists of three ingredients. How are these ingredients measured quantitatively, and how do they combine to yield  $\Delta I$ ?

The first ingredient, species-specific responses to the environment, can be measured by a diagonal matrix  $\mathbf{P}_i$  whose  $r$ th diagonal element is given by

$$(\mathbf{P}_i)_r = \frac{\chi_{ir}^{-i} / \sqrt{V(\mathcal{E}_i)}}{\chi_{rr}^{-i} / \sqrt{V(\mathcal{E}_r)}} = \frac{\text{corr}(\mathcal{E}_i, \mathcal{C}_r^{-i})}{\text{corr}(\mathcal{E}_r, \mathcal{C}_r^{-i})}, \tag{25}$$

where ‘‘corr’’ means correlation. If species  $i$  and species  $r$  have perfectly correlated responses to the environment, i.e.,  $\mathcal{E}_i$  is an increasing linear function of  $\mathcal{E}_r$ , then  $(\mathbf{P}_i)_r = 1$ . In other cases, species  $i$  and  $r$  have specific responses to the environment, the relevant aspects of which appear in the comparison of the correlations of  $\mathcal{E}_i$  and  $\mathcal{E}_r$  with  $\mathcal{C}_r^{-i}$ .

Usually,  $\mathcal{E}_i$  will be less correlated with  $\mathcal{C}_r^{-i}$  than is  $\mathcal{E}_r$  because  $\mathcal{C}_r^{-i}$  is a function of  $\mathcal{E}_r$ , but not of  $\mathcal{E}_i$ . Low or negative values of  $(\mathbf{P}_i)_r$  reflect high specificity, as they indicate that  $\mathcal{E}_i$  and  $\mathcal{E}_r$  have distinctly different patterns of fluctuation in response to common environmental fluctuations. This is clearest in the case of just a single resident species with a white noise environment (assumption (a2’)), for then it can be seen from Chesson

(1989) that  $(\mathbf{P}_i)_r$  is just the ordinary Pearson correlation between  $\mathcal{E}_i$  and  $\mathcal{E}_r$ , which is an unambiguous measure of the relative patterns of responses of the two species to environmental fluctuations. The multispecies case is more complex. In particular, the ratio of correlation coefficients,  $(\mathbf{P}_i)_r$ , is not always a correlation coefficient and it is possible for  $(\mathbf{P}_i)_r$  to exceed 1 if  $\mathcal{E}_r$  contributes little variation to competition compared with the environmentally dependent parameters of other resident species, and  $\mathcal{E}_i$  is more strongly correlated with these than is  $\mathcal{E}_r$ .

The second ingredient of the storage effect, covariance between environment and competition, is quantified by the vector  $\chi = (\chi_{11}^{-i}, \dots, \chi_{nn}^{-i})'$  of covariances between environmentally dependent and competition parameters of resident species. The difference between resident and invader covariances is important, but this difference results from species-specific responses to the environment and is summarised in the matrix  $\mathbf{P}_i$ .

The third ingredient of the storage effect, nonadditivity, is measured by the diagonal matrix  $\Gamma = \text{diag}(\gamma_1, \dots, \gamma_n)$  of  $\gamma$  values of resident species.

To combine these ingredients and to take account of average asymmetries between species, especially between residents and invaders, we need the row vector  $\mathbf{q}_i = (q_{i1}, \dots, q_{in})$ , of  $q_{ir}$  values, and the diagonal matrix  $\Xi_i$  with  $r$ th diagonal element

$$(\Xi_i)_r = \frac{\gamma_i \sqrt{V(\mathcal{E}_i)}}{\gamma_r \sqrt{V(\mathcal{E}_r)}}. \quad (26)$$

Now, the definition of  $q_{ir}$  (Eq. (24)) entails

$$\mathcal{C}_i^{-i} = \mathbf{q}_i \mathcal{C}^{-i} + O(\sigma^2), \quad (27)$$

where  $\mathcal{C}^{-i}$  is the column vector  $(\mathcal{C}_1^{-i}, \dots, \mathcal{C}_n^{-i})'$  of resident standard competition parameters with the resident stationary distribution. It follows that

$$\chi_{ii}^{-i} \approx \mathbf{q}_i (\chi_{i1}^{-i}, \dots, \chi_{in}^{-i})' \quad (28)$$

and

$$\gamma_i \chi_{ii}^{-i} \approx \mathbf{q}_i \Xi_i \mathbf{P}_i \Gamma \chi.$$

We can now rewrite the storage effect as

$$\Delta I \approx -\mathbf{q}_i (\mathbf{1} - \Xi_i \mathbf{P}_i) \Gamma \chi, \quad (29)$$

where  $\mathbf{1}$  is the  $n-1$  dimensional identity matrix.

To understand expression (29), note that  $\Gamma \chi$  is simply the product of nonadditivity and covariance for each of the individual resident species. This product affects coexistence to the extent that the value for an invader



differs from these. The diagonal elements of the matrix  $\mathbf{1} - \mathbf{\Xi}_i \mathbf{P}_i$  determine such resident–invader differences. Most importantly, this matrix incorporates species-specific responses to the environment which determine how the covariance between environment and competition compares between the residents and invader. The vector  $\mathbf{q}_i$  then combines individual resident–invader comparisons.

We shall see examples below where the term  $\Delta I$  has the same sign for all species in a community. Therefore, it can simultaneously add or subtract from all species growth rates. When it is positive, it promotes coexistence by making it more likely that all species recover from perturbations to low density. Conversely, negative values of  $\Delta I$  promote competitive exclusion.

#### 4.2. The $\Delta E$ and $\Delta C$ Terms

The mean environmental term ( $\Delta E$ ) and mean competition term ( $\Delta C$ ) of the mean low-density growth rate are best understood in relation to each other. To understand these terms, we first consider linear and additive cases where environmental variation does not have a role.

4.2.1. *Linear Additive Models.* Populations that have a very simple structure are often modeled in the following additive way (Chesson, 1988):

$$g_j(E_j, C_j) = E_j - C_j. \quad (30)$$

Specific examples are given in Section 5, below. Although a seemingly more general additive model is

$$g_j(E_j, C_j) = A_j(E_j) - B_j(C_j),$$

for arbitrary functions  $A_j$  and  $B_j$ , the form (30) can always be obtained by redefinition of the parameters. Additive models are characterized by parallel curves for plots of the growth rate against competition for different values of the environmentally-dependent parameter (Fig. 2a). The interaction coefficient,  $\gamma$ , is 0.

The standard parameters of the model (30) are simply changes of origin of the original parameters:  $\mathcal{E}_j = E_j - E_j^*$ ,  $\mathcal{C}_j = C_j - C_j^*$ . Thus, the standard form of the growth rate is just the same as (30):

$$g_j(E_j, C_j) = \mathcal{E}_j - \mathcal{C}_j. \quad (31)$$

The competition parameters of a model are *linear* if they can be expressed linearly in terms of common quantities,  $F_l$ , which we shall call limiting factors (Levin, 1970), as follows:

$$C_j = \sum_{l=1}^P \phi_{jl} F_l \quad (32)$$

for constants  $\phi_{ji}$ . The  $F_l$  may, for example, represent measures of resource shortage. However, Levin (1970) pointed out that such limiting factors can include predation and therefore we can regard "competition" in our model as covering apparent competition (Holt, 1977). The Lotka–Volterra model discussed in the Section 5, below, provides a familiar example of an additive model with linear dependence on limiting factors. In the invasibility analysis, the actual set of limiting factors in question may depend on which species is the invader; for example, this is the case in the Lotka–Volterra model of Section 5, where  $F_l$  is a function of the density of species  $l$ .

The linear structure (32) leads to explicit formulae for the coefficient  $q_{ir}$  relating competition experienced by an invader to that experienced by residents. Let  $\Phi$  be the matrix with  $jl$ th element  $\phi_{jl}$ . Define  $\phi_i$  to be the  $i$ th row of  $\Phi$ , let  $\Phi^{-i}$  be  $\Phi$  with  $i$ th row deleted, and let the superscript "–" mean generalized inverse (Rao, 1973). (See Appendix III for examples and useful information on generalized inverses.) Assumption (a6) that the invader's competition parameter can be expressed in terms of the competition parameters of the residents is satisfied whenever  $\phi_i$  is linearly dependent on the rows of  $\Phi^{-i}$ . Defining  $C^{-i}$  to be the vector of resident competition parameters,  $C_r^{-i}$ , and  $\mathbf{q}_i$  to be the vector of  $q_{ir}$  values, we have

$$C_i^{-i} = \mathbf{q}_i C^{-i}, \quad (33)$$

where  $\mathbf{q}_i$  is given here by the special formula

$$\mathbf{q}_i = \phi_i(\Phi^{-i}). \quad (34)$$

Now  $\Delta C$  is by definition

$$\Delta C = E[\mathcal{C}_i^{-i} - \mathbf{q}_i \mathcal{C}^{-i}],$$

where  $\mathcal{C}^{-i}$  is the vector of standard competition parameters. For the additive model (30),  $\mathcal{C}_j = C_j - C_j^*$ , and so

$$\mathcal{C}_i^{-i} - \mathbf{q}_i \mathcal{C}^{-i} = [C_i^{-i} - \mathbf{q}_i C^{-i}] - [C_i^* - \mathbf{q}_i C^{*-i}],$$

where  $C^{*-i}$  is the vector of resident equilibril competition parameters. Relation (33) means that the first term in brackets on the RHS is zero, and so

$$\mathcal{C}_i^{-i} - \mathbf{q}_i \mathcal{C}^{-i} = \mathbf{q}_i C^{*-i} - C_i^*. \quad (35)$$

The RHS of this equation is the value of the competition parameter of species  $i$ , when the parameters of its competitors are at their equilibril values, less the equilibril value of the competition parameter of species  $i$ . Thus, with species  $i$  as an invader and the residents at equilibrium, it is the

difference between the amount of competition that species  $i$  receives and its equilibrium value. We shall use the notation  $\mathcal{C}_i^{-i*}$  for this amount of competition, as the relation  $\mathcal{C}_j = C_j - C_j^*$  means that the RHS of (35) is simply the standard unit value of competition that species  $i$  receives as an invader with the residents at equilibrium.

As  $\Delta C$  is just the expected value of (34), and this is a constant,  $\Delta C$  is simply

$$\Delta C = \mathbf{q}_i \mathbf{C}^{*-i} - C_i^* = \mathcal{C}_i^{-i*}. \quad (36)$$

Thus, for additive linear models,  $\Delta C$  is just the difference between the amount of competition that the invading species  $i$  receives from the residents at equilibrium, and species  $i$ 's equilibrium value of competition.

For this additive model, the  $\Delta E$  value also takes a simple form. In general, the  $\Delta E$  value consists of a comparison of the mean value of the standard environmentally dependent parameter,  $\mathcal{E}_i$ , of the invading species with that of its competitors,  $\Delta E = E\mathcal{E}_i - \mathbf{q}_i E\mathcal{E}^{-i}$ , where  $\mathcal{E}^{-i}$  is the vector of resident standard environmentally dependent parameters. But in the additive model (30),  $\mathcal{E}_j = E_j - E_j^*$ , and so  $E\mathcal{E}_j$  represents the deviation of the average environmental condition from that needed to maintain the species at equilibrium. Thus,  $\Delta E$  is positive if the mean of species  $i$ 's environmentally dependent parameter exceeds equilibrium to a greater extent than do mean environmentally dependent parameters of resident species, as measured with the standard of comparison  $\mathbf{q}_i$ .

For additive models, the mean low-density growth rate is just  $\Delta E - \Delta C$ , and for this linear case, it specialises further to

$$\bar{r}_i = \Delta E - \mathcal{C}_i^{-i*}. \quad (37)$$

Thus, overall population increase from low density is determined by deviations from equilibrium due to the environmental state, and deviations from equilibrium due to a difference between the equilibrium amount of competition for species  $i$  and the competition that species  $i$  actually receives with the residents at equilibrium.

There are two important points to be made. First, in this linear additive model, fluctuations have no role in coexistence, as the long-term growth rate (37) just depends on means of the environmentally dependent parameters and the equilibrium values of the environmentally dependent and competition parameters.

Second, some care is needed in the interpretation of the partitioning of  $\bar{r}_i$  into  $\Delta E$  and  $\Delta C$ , as this partitioning is not necessarily unique. Different choices for  $E_j^*$  and  $C_j^*$  can lead to different values for  $\Delta E$  and  $\Delta C$ . In general, the only constraint on  $E_j^*$  and  $C_j^*$  is the relationship  $g_j(E_j^*, C_j^*) = 0$ , which allows  $(E_j^*, C_j^*)$  to vary on a one-dimensional continuum. For example, in the linear additive model, this constraint reduces

to  $C_i^* = E_i^*$ . If we choose  $E_i^* = E[E_i]$ , then we find that  $\Delta E = 0$ , and  $\bar{r}_i = -\mathcal{C}_i^{-i*}$ , so that the long-term growth rate is interpreted in terms of deviations from equilibrium competition. On the other hand, if it is possible to choose  $C_i^* = \mathbf{q}_i C^{-i}$ , then  $\Delta C = 0$ , and  $\bar{r}_i = \Delta E$ , so that the long-term growth rate is interpreted in terms of environmental deviations from equilibrium. When such different choices are possible, we should be aware that they can lead to different interpretations.

This interpretational ambiguity results from the fact that changing an environmental state commonly alters a competitive equilibrium. The competitive equilibrium and environmental equilibrium spoken of here are not really separate things, which means that separate interpretation of  $\Delta E$  and  $\Delta C$  is not advised without an independent rationale for the choice of the equilibrial values of the environmentally dependent and competition parameters. However, in Section 5, below, we shall see that natural choices often arise which limit such ambiguity, and Subsection 4.3 demonstrates an alternative partitioning of  $\bar{r}_i$  in which this ambiguity is absent.

In these linear additive models, the calculation of  $\Delta E$  and  $\Delta C$  is a straightforward exercise. However, such ease is associated with the fact that fluctuations play no role. Hence, the mechanisms measured by  $\Delta E$  and  $\Delta C$  in this subsection are classical mechanisms that can operate on a short timescale. To go beyond such classical mechanisms, we must study models that are nonadditive or nonlinear.

4.2.2. *Nonlinear and Nonadditive Situations.* In the general case of the model, the standard competition parameter takes the form

$$\mathcal{C}_i = -g_j(E_j^*, C_j). \quad (38)$$

The relationship between  $\mathcal{C}_i$  and a vector of limiting factors  $\mathbf{F}$  may be nonlinear because  $C_j$  depends nonlinearly on  $\mathbf{F}$  or because  $\mathcal{C}_i$  is a nonlinear function of  $C_j$ . We begin our discussion with the case where the additive form (30) continues to hold, but  $C_j$  depends nonlinearly on  $\mathbf{F}$ ,

$$C_j = \phi_j(\mathbf{F}), \quad (39)$$

where  $\phi_j$  is some nonlinear function.

To understand the effect of nonlinearity, we expand the functions  $\phi_j$  to quadratic terms of  $\mathbf{F}$ , omitting  $o(\sigma^2)$  terms. To do this we assume that  $\mathbf{F}$  can be expressed as a smooth function of  $C^{-i}$  for then fluctuations in  $\mathbf{F}$ , like fluctuations in  $C^{-i}$ , would have an amplitude equal to  $O(\sigma)$  (Appendix II). Such a situation is possible in general by redefinition of the limiting factors, if necessary. For example, under assumption (a6), the invader's competition parameter can be expressed as a smooth function of the resident's competition parameters. Hence the resident's competition parameters qualify as limiting factors with the desired properties.

We specify an  $\mathbf{F}^*$  value in terms of the equilibril values of the competi-  
tion parameters of the residents by the relationship

$$C_r^* = \phi_r(\mathbf{F}^*), \tag{40}$$

for resident species  $r$ , which may constrain the possible values of the  $C_r^*$ .  
See Appendix III for the situation when this is not possible.

The matrix  $\Phi = (\phi_{jl})$  is defined by the equation

$$(\phi_{jl}) = \left( \frac{\partial C_j}{\partial F_l} \right)^*, \tag{41}$$

where the superscript  $*$  means evaluated at  $\mathbf{F}^*$ . The vector  $\mathbf{q}_i$  is defined in  
terms of  $\Phi$  as before (Eq. (34)). With nonlinear dependences, however, we  
must expand  $C_j$  to quadratic terms in  $\mathbf{F}$ . Thus, we define

$$\Phi_j^{(2)} = \left( \frac{\partial^2 \phi_j(F)}{\partial F_l \partial F_m} \right)^*, \tag{42}$$

where the parentheses mean the matrix over rows  $l=1$  to  $p$  and columns  
 $m=1$  to  $p$ .

With these definitions, the comparison between invader and resident  
competition becomes

$$\mathcal{C}_i^{-i} - \mathbf{q}_i \mathcal{C}^{-i} \approx \phi_i(\mathbf{F}^*) - C_i^* + (\mathbf{F} - \mathbf{F}^*)' \Psi (\mathbf{F} - \mathbf{F}^*), \tag{43}$$

where

$$\Psi = \frac{1}{2} \left( \Phi_i^{(2)} - \sum_{r \neq i} q_{ir} \Phi_r^{(2)} \right). \tag{44}$$

Like the linear additive model, linear terms in competition do not appear  
in this comparison, but unlike the linear additive model, there is a  
quadratic term in addition to the constant term. The constant term has the  
same interpretation as before: It is the difference between the amount of  
competition that species  $i$  receives from residents at equilibrium and species  
 $i$ 's equilibril value of competition.

As  $\mathcal{C}_i^{-i*} = \phi_i(\mathbf{F}^*) - C_i^*$ , we can write

$$\Delta C \approx \mathcal{C}_i^{-i*} + E[(\mathbf{F} - \mathbf{F}^*)' \Psi (\mathbf{F} - \mathbf{F}^*)]. \tag{45}$$

But because  $E\mathbf{F} - \mathbf{F}^* = O(\sigma^2)$ , (Appendix II)  $\Delta C$  can also be written

$$\Delta C \approx \mathcal{C}_i^{-i*} + E[(\mathbf{F} - E\mathbf{F})' \Psi (\mathbf{F} - E\mathbf{F})]. \tag{46}$$

These expressions show that the  $\Delta C$  term reflects variation in  
competition in addition to equilibrium aspects. This is so whether we view

variation about the mean (46) or about equilibrium values (45). Indeed, we can see that expression (46) is a function of the variances and covariances among the  $F_j$  by applying the result commonly recognized in multivariate statistics (Rao, 1973) that  $\text{trace}\{E[(\mathbf{F} - E\mathbf{F})' \Psi(\mathbf{F} - E\mathbf{F})]\} = \text{trace}\{E[\Psi(\mathbf{F} - E\mathbf{F})(\mathbf{F} - E\mathbf{F})']\} = \text{trace}\{\Psi V(\mathbf{F})\}$ , where  $V(\mathbf{F})$  is the matrix of variances and covariances among the  $F_j$ . Expression (46) can thus be rewritten as

$$\Delta C = \mathcal{C}_i^{-i*} + \text{trace}\{\Psi V(\mathbf{F})\}. \quad (47)$$

It is not difficult to generalize these results to nonadditive models. Expression (39) is simply replaced by

$$C_j = \phi'_j(\mathbf{F}), \quad (48)$$

for some function  $\phi'_j(\mathbf{F})$ , and the function  $\phi_j$  is then defined as

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

and  $\mathcal{C}_i^{-i*} = \phi_i(\mathbf{F}^*)$ . With these modifications, the formulae associated with  $\Delta C$  remain the same as in the additive nonlinear case. As remarked above, the resident competition parameters qualify as limiting factors. This means it is always possible to express the general model, as defined in Section 3, above, in terms of limiting factors. Formula (47) therefore applies to the general model without restrictions.

#### 4.3. Mechanistic Partitioning of the Growth Rate

The representation of  $\bar{r}_i$  in terms of  $\Delta E$ ,  $\Delta C$ , and  $\Delta I$  follows naturally from the quadratic approximation of  $g_i$ . However, it is apparent from the above analysis that the separate  $\Delta E$  and  $\Delta C$  terms are not entirely satisfactory. First, there is a degree of arbitrariness in the  $\Delta E$  and  $\Delta C$  terms depending on the choice of the equilibrium environmentally dependent and competition parameters, such that only  $\Delta E - \Delta C$  is unique, not their separate values. Second,  $\Delta C$  combines fluctuation-dependent and fluctuation-independent coexistence-affecting mechanisms, which are more usefully considered separately. These problems can be solved by splitting the  $\Delta C$  term into its two component parts and combining one of these with  $\Delta E$ .

We define

$$\bar{r}'_i = \Delta E - \mathcal{C}_i^{-i*} \quad (50)$$

and

$$\begin{aligned} \Delta N &= \Delta C - \mathcal{C}_i^{-i*} \\ &\approx E[(\mathbf{F} - E\mathbf{F})' \Psi(\mathbf{F} - E\mathbf{F})] \\ &= \text{trace}\{\Psi V(\mathbf{F})\}, \end{aligned} \quad (51)$$

which give the alternative representation of the long-term low-density growth rate as

$$\bar{r}_i \approx \bar{r}'_i - \Delta N + \Delta I. \tag{52}$$

Here,  $\bar{r}'_i$  represents fluctuation-independent coexisting-affecting mechanisms or, alternatively, mechanisms operating on a shorter timescale than the unit of time considered explicitly in the model. The term  $\Delta N$  measures the contribution of relative nonlinearity and  $\Delta I$  continues to express the storage effect. Thus, the representation (52) of  $\bar{r}_i$  segregates the contributions of the three general coexistence-affecting mechanisms that this work identifies. Hence, it shall be referred to as the *mechanistic representation* of the long-term low-density growth rate.

### 5. EXAMPLES

#### 5.1. A Lotka–Volterra Model

The Lotka–Volterra model has figured much in discussions of the effects of variable environments (see, e.g., Turelli, 1981). However, the common linear and additive formulation of the model in a variable environment makes its behavior rather special. To understand this special behavior, we first express it in the discrete time form

$$r_j(t) = b_j \left( 1 - \sum_{k=1}^n \alpha_{jk} X_k \right) + E_j, \tag{53}$$

which we can rewrite in our framework as

$$r_j(t) = b_j - C_j + E_j \tag{54}$$

with

$$C_j = b_j \sum_{k=1}^n \alpha_{jk} X_k. \tag{55}$$

This formulation deviates slightly from (30) but nevertheless it is a linear additive model to which the results of Subsection 4.2.1 apply. As such, the results obtained here are exact for any level of environmental variability.

Zero is a natural choice for the  $E_j^*$  when viewing environmental variation as a perturbation of an otherwise deterministic system. With this choice for  $E_j^*$ ,  $C_j^* = b_j$ . The species densities,  $X_i$ , can be the limiting factors,  $F_i$ , remembering that for the invasion analysis  $X_i$  is not a limiting factor because it is fixed at 0.

The coefficients  $\phi_{ji}$  (Eq. (32)) take the values  $b_j\alpha_{ji}$ . Let  $\mathbf{A}^{-i}$  be the matrix of competition coefficients ( $\alpha_{ji}$ ) after deletion of the row and column for species  $i$ , and let  $\mathbf{B}$  be the matrix with diagonal elements  $b_1, \dots, b_n$ , with  $i$ th element missing. Then the matrix  $\Phi^{-i}$  equals  $\mathbf{B}\mathbf{A}^{-i}$ . If, further,  $\mathbf{A}^{-i}$  is of full rank, then  $\Phi^{-i}$  is invertible with inverse  $(\mathbf{A}^{-i})^{-1}\mathbf{B}^{-1}$ . It follows from Eq. (34) that

$$\mathbf{q}_i = b_i(\alpha_{i1}, \dots, \alpha_{in})(\mathbf{A}^{-i})^{-1}\mathbf{B}^{-1}, \quad (56)$$

and so

$$\begin{aligned} \mathbf{q}_i\mathbf{C}^{*-i} - C_i^* &= b_i(\alpha_{i1}, \dots, \alpha_{in})(\mathbf{A}^{-i})^{-1}(1, \dots, 1)' - b_i \\ &= b_i \sum_{r \neq i} \alpha_{ir}X_r^* - b_i, \end{aligned} \quad (57)$$

where the  $X_r^*$  are solutions of the equations  $\sum_{r \neq i} \alpha_{sr}X_r^* = 1$  for  $s \neq i$ . Note that this means the  $X_r^*$  ( $= F_r^*$ ) are the deterministic equilibrium values for the residents. Because this is a linear additive model, expression (57) gives the full value of  $\Delta C$ .

If environmental fluctuations are mean zero perturbations of the growth rate, i.e.,  $E[E_j] = 0$ , then  $E\mathcal{E}_j = 0$  also, and  $\Delta E = 0$ . As  $\Delta I = 0$ , in this additive model,  $\bar{r}_i$  just reduces to  $-\Delta C$ , i.e.,

$$\bar{r}_i = b_i \left( 1 - \sum_{r \neq i} \alpha_{ir}X_r^* \right), \quad (58)$$

which is the value of the growth rate that we would obtain using the standard deterministic invasibility analysis (MacArthur and Levins, 1967). Note that in expression (58),  $\bar{r}_i = \bar{r}'_i$ , the fluctuation-independent component, reiterating Turelli's (1981) conclusion that environmental variability has no effect on coexistence in this discrete-time Lotka-Volterra model.

The case considered so far with  $E_j^* = E[E_j] = 0$  is for unbiased perturbations of the growth rate. However, in the context of disturbance (e.g., Huston, 1979), we might want environmental variation to have a negative average effect on the growth rate, so that  $E[E_j] < 0$ . Then  $\Delta E$  is given by the formula

$$\Delta E = E[E_j] - \mathbf{q}_i E[\mathbf{E}^{-i}], \quad (59)$$

where  $\mathbf{E}^{-i}$  is the vector of resident environmentally dependent parameters. It follows that  $\bar{r}_i$  takes the form

$$\bar{r}_i = E[E_j] + b_i \left( 1 - \sum_{r \neq i} \alpha_{ir}(X_r^* + \Delta X_r^*) \right), \quad (60)$$



where the  $\Delta X_r^*$  values are solutions of the equation  $\sum_{r \neq i} \alpha_{sr} \Delta X_r^* = E[E_s]/b_s$ . Note that the  $X_i^* + \Delta X_i^*$  are the equilibrium densities for the deterministic case of a fixed nonzero environmental perturbation corresponding to  $E[E_j] = E_j^* \neq 0$ . Thus, Eq. (60) represents effects on the long-term low-density growth rate that are the same whether the environment fluctuates or remains fixed at its mean—it comes down again to just the deterministic invasion criterion.

While Eq. (53) or similarly behaved expressions have been popular models of Lotka–Volterra competition in a variable environment, the Lotka–Volterra model of de Mottoni and Schiaffino (1981) is outside our framework because the competition parameter of the invader cannot be expressed as a function of the resident. I.e., assumption (a6) is violated. In their Lotka–Volterra model it is possible for the variance of environmental fluctuations to affect coexistence, in contrast to (53), where only the mean of the environmentally dependent parameter is important.

5.2. *An Additive Model with Relative Nonlinearity*

Additive models with a common limiting factor frequently arise in the literature, for example, as models of several predator species competing for a common prey (Armstrong and McGehee, 1980) or phytoplankton competing for a limiting nutrient (Grover, 1990). In such models, the growth rate takes the form

$$r_j(t) = E_j(t) - \phi_j(F(t)). \tag{61}$$

In the predator–prey context,  $F(t)$  is the density of the prey species and  $-\phi_j$  is proportional to the functional response of the  $j$ th predator species to the common prey. As Armstrong and McGehee (1980) point out, the functional responses, or more generally the rates of resource consumption, are often nonlinearly related between species. In the predator–prey case, this can come about simply by the different predators having different handling times for the same prey species.

In this model it is most natural to define the  $E_j^*$  and  $C_j^*$  in terms of a choice of a common  $F^*$  value:  $E_j^* = C_j^* = \phi_j(F^*)$ . The fact that all species have equilibrium competition at the same value of  $F$  means that  $\mathcal{C}_i^{-i} = 0$ , and therefore  $\Delta C = \Delta N$ . To calculate  $\Delta N$  we note that  $\Psi$  reduces to the scalar expression

$$\Psi = \frac{1}{2} \left( \phi_i^{(2)} - \sum_{r \neq i} q_{ir} \phi_r^{(2)} \right). \tag{62}$$

With a single competitive factor, the  $q_{ir}$  are not uniquely defined, but a natural choice is  $q_{ir} = (\phi_i^{(1)}/\phi_r^{(1)})/(n-1)$ , where  $\phi_j^{(1)} = d\phi_j/dF$  at  $F = F^*$ . Defining  $\tau_j = \phi_j^{(2)}/2\phi_j^{(1)}$ ,  $\mu_j = E\mathcal{E}_j/\phi_j^{(1)}$ , we find that

$$\Delta C = \Delta N = \phi_i^{(1)}(\tau_i - \bar{\tau}) V(F^{-i}), \tag{63}$$

where  $\bar{\tau}$  is the average of the  $\tau$  values for the resident species and the superscript  $-i$  has been added to  $F$  to emphasize that the variance is calculated at the resident distribution. As  $\Delta I$  is necessarily 0, the analysis is completed by the observation

$$\Delta E = \phi_i^{(1)}(\mu_i - \bar{\mu}), \quad (64)$$

and therefore

$$\bar{r}_i = \phi_i^{(1)}(\mu_i - \bar{\mu}) - \phi_i^{(1)}(\tau_i - \bar{\tau}) V(F^{-i}). \quad (65)$$

For this particular example, it is possible to calculate the variance of the limiting factor whenever there are at least two resident species using the fact that the average growth rate of resident populations must be 0. We find that

$$Eg_r(E_r, C_r)/\phi_r^{(1)} - Eg_s(E_s, C_s)/\phi_s^{(1)} = (\mu_r - \mu_s) - (\tau_r - \tau_s) V(F^{-i}). \quad (66)$$

As this must be 0,

$$V(F^{-i}) = (\mu_r - \mu_s)/(\tau_r - \tau_s). \quad (67)$$

A little algebra now shows that when (67) is substituted in (65) it is impossible for more than two species to have positive  $\bar{r}_i$  values, i.e., in this additive model with a single nonlinear limiting factor, at most two species can coexist.

Applying formula (65) to the case of a two-species interaction, we can deduce some relationships for two coexisting species,  $j$  and  $k$ , say. Let  $\tau_j > \tau_k$  (they cannot be equal for coexistence); then coexistence also implies that  $\mu_j > \mu_k$ . Indeed, a necessary and sufficient condition for both species to have positive long-term low-density growth rates is

$$V(F^{-j}) < (\mu_j - \mu_k)/(\tau_j - \tau_k) < V(F^{-k}). \quad (68)$$

This condition shows that the variance of the limiting factor in each of the two single-species systems must bracket the variance that would apply under coexistence. In addition, the species with the greater positive nonlinearity (larger value of  $\tau$ ) must cause greater variance in the limiting factor and must have a higher value of the mean of its environmentally dependent parameter, scaled by  $\phi^{(1)}$ , (i.e., higher  $\mu$ ).

Competitive nonlinearity thus provides a mechanism of coexistence of two species. This mechanism relies on species differing in the degree of nonlinear dependence on a common competitive factor, and also differing with respect to how much variance they generate in the dynamics of the limiting factor. The clearest example of this mechanism in the literature is given by

Armstrong and McGehee (1980). In their example, however, the fluctuations are purely deterministic in origin. Ellner (1987) provides an example involving competition between annual plants with a seed bank that is non-additive but has zero covariance between environment and competition. Thus, in Ellner's example, the nonadditive terms do not contribute to coexistence. Differences between species in the survival rates of dormant seeds give different nonlinear responses to competition that promote coexistence in some circumstances, but promote competitive exclusion in other circumstances.

The quantity  $\Psi$  in the analysis of relative nonlinearity is not easy to grasp in general but in this situation of coexistence between two species on a single limiting factor, it is not so difficult. The  $\tau_j$  are simply rates of change of slope per unit slope times one-half—a kind of curvature if you like—for the graph of  $r_j$  against the limiting factor. The difference  $\tau_i - \tau_r$  is just the difference in these. Referring to Fig. 1, one in effect adjusts the vertical scales for the two species to give them slope 1 at the chosen value of  $F^*$  ( $\equiv C^*$ , there) and then takes the difference in rates of change of slope on the resulting diagram. The quantity  $\Psi$  is similar. For it, one adjusts only the resident's slope, but makes this slope equal to that of the invader before taking the difference between rates of change of slope for the two species.

As we have shown here, relative nonlinearity, when acting alone, can only explain coexistence of two species. However, it may well be able to explain a larger number of species when acting in concert with other mechanisms by providing the needed additional amount to make the  $\bar{r}_i$  values positive. It is also possible that this mechanism might negate the effects of other mechanisms in some circumstances by subtracting enough from some  $\bar{r}_i$  values to make them negative. As we see from expression (65), competitive nonlinearity will add to the  $\bar{r}$ 's of some species and subtract from those of others. It will only promote coexistence when it increases low  $\bar{r}$ 's while not decreasing high  $\bar{r}$ 's too much.

Nonlinearities more complicated than quadratic could alter this conclusion that only two species can coexist by this mechanism when there is just a single limiting factor. It seems likely that coexistence of arbitrarily many species would be possible from higher order nonlinearities together with higher order moments. The analysis here suggests, however, that coexistence of more than two species will at best be weak because the values of  $\bar{r}_i$  will be quite small, except in highly nonlinear situations with large fluctuations in the competitive factor.

Further opportunities for coexistence by relative nonlinearity could come with more limiting factors. With  $p$  limiting factors, there are  $p(p+1)/2$  independent components of the critical quantities  $\Phi_j^{(2)}$  and  $V(F^{-j})$ , for each species  $j$ . While such cases are yet to be explored, they would seem to promise the potential for many species to coexist.

### 5.3. Symmetric Nonadditive Models

The examples above have illustrated the terms  $\bar{r}'_i$  and  $\Delta N$ . We now turn our attention to  $\Delta I$ . Unlike  $\Delta N$ , the quantity  $\Delta I$  has the potential to permit coexistence of many species affected by a single limiting factor. Moreover, Section 2 explains that nonadditivity should be the rule in nature. To gain a better understanding of the  $\Delta I$  term, we study the special case of a single limiting factor so that there is a single measure of competition that is good for all species:

$$C_j(t) = C(t) = F(t). \quad (69)$$

The model takes the form

$$r_j(t) = g_j(E_j, C).$$

The special case of competition for a common resource, which may be a composite resource, is important as it provides the most difficult case for coexistence by classical mechanisms. It has also been argued that the situation where the number of species greatly exceeds the number of distinct resources commonly arises for terrestrial plant species (Silvertown and Law, 1987), and space holding marine organisms (Sale, 1977). This means that we should expect to be able to quantify resource availability by a single measure that is suitable for all species.

To simplify further calculations, we make some assumptions about environmental variation. We choose a symmetric variance structure. We assume that each  $E_j$  has the same variance  $\sigma^2$ , that there is a common correlation  $\rho$  between the environmentally dependent parameters of different species, and that environmental fluctuations over time are independent (assumption (a2')).

Although the  $C_j$  are all the same, the  $\mathcal{C}_j$  differ between species, unless the  $g_j$  are equal. However, this difference is simple, provided we choose a common equilibrial value of competition:  $C_j^* = C^*$ . Then by relation (9)

$$\mathcal{C}_j = \beta_j(C - C^*) + O(\sigma^2). \quad (70)$$

Thus,

$$\chi_{jk}^{-i} \approx \beta_k E \mathcal{C}_j(C^{-i} - C^*), \quad (71)$$

where the superscript  $-i$  on  $C$  means the resident stationary distribution applies to  $C$ . If  $C^{-i}$  is twice continuously differentiable in the standard environmentally dependent parameters, we can write

$$C^{-i}(t) - C^* \approx \sum_{r \neq i} A_r(t) \mathcal{E}_r(t) + b(t), \quad (72)$$

where  $A_r(t)$  and the variable  $b(t)$  are independent of  $\mathcal{E}(t)$  because of assumption (a2')—independence of the environment over time. Moreover, (a5) implies that  $b(t) = O(\sigma)$ .

We define  $a_r = EA_r$  and  $\bar{a}$  to be the simple average of the  $a_r$ . Equation (8), relating the standard environmentally dependent parameters to the original environmentally dependent parameters, means that

$$E\mathcal{E}_r(C^{-i} - C^*) \approx \sum_{s \neq i} E\alpha_r(E_r - E_r^*) \alpha_s(E_s - E_s^*) A_s \approx \alpha_r \sigma^2 [\rho(n-1) \bar{a} + (1-\rho) \alpha_r a_r], \tag{73}$$

where we use the general bar notation for averages of combinations of parameters of resident species:

$$\overline{abc \dots pq} = \frac{1}{n-1} \sum_{r \neq i} a_r b_r c_r \dots p_r q_r.$$

A similar calculation yields

$$E\mathcal{E}_i(C^{-i} - C^*) \approx \alpha_i \sigma^2 \rho(n-1) \bar{a}. \tag{74}$$

These expressions imply that the  $r$ th diagonal element of  $\mathbf{P}_i$  is

$$\frac{\rho \bar{a} (n-1)}{\rho(n-1) \bar{a} + (1-\rho) \alpha_r a_r}. \tag{75}$$

Recall that this quantity incorporates species-specificity of response to the environment. Lower values of  $\rho$  mean greater species-specificity and lower values of  $\mathbf{P}_i$ .

Note also that (73) and (74) imply that the covariances (elements of  $\chi$ ) are given by the formula

$$\chi_{rr}^{-i} \approx \alpha_r \beta_r \sigma^2 [(n-1) \bar{a} \rho + (1-\rho) \alpha_r a_r]. \tag{76}$$

To complete the calculation of the storage effect,  $\Delta I$ , we must calculate the vector  $\mathbf{q}_i$  defining the relative responses to competition of the different species. In the case of a common competition parameter, the  $q_{ir}$  are not unique. However, it seems reasonable to treat the resident species in an equivalent manner, and then we can write

$$\mathcal{E}_i^{-i} = \beta_i \frac{1}{n-1} \sum_{r \neq i} \beta_r^{-1} \mathcal{E}_r^{-i} + O(\sigma^2), \tag{77}$$

which leads to the expression

$$q_{ir} = \left( \frac{1}{n-1} \right) \frac{\beta_i}{\beta_r}. \tag{78}$$

The matrix  $\Xi_i$  has  $r$ th diagonal element  $\alpha_i \gamma_i / \alpha_r \gamma_r$ , and we can now calculate  $\Delta I$  as

$$\Delta I = -\beta_i \sigma^2 [(1 - \rho) \overline{\alpha^2 a \gamma} + \rho \bar{\alpha} \bar{a} (n - 1) (\bar{\alpha} \bar{\gamma} - \alpha_i \gamma_i)]. \quad (79)$$

We shall see applications below where the functions  $g_j$  are all the same, in which case it follows that the  $\alpha_j$ ,  $\beta_j$ , and  $\gamma_j$  do not vary with the species,  $j$ . Expression (79) then reduces to

$$\Delta I = \beta \bar{a} (-\gamma) (1 - \rho) \alpha^2 \sigma^2. \quad (80)$$

In this case, there is no relative nonlinearity in competition. Indeed, the standard competition parameters are the same for different species. Thus,  $\Delta C = \Delta N = 0$ , and we see that

$$\bar{r}_i = \Delta E + \Delta I = \Delta E + \beta \bar{a} (-\gamma) (1 - \rho) \alpha^2 \sigma^2, \quad (81)$$

where here  $\Delta E$  is just the expected value of the standard environmentally dependent parameter (or  $\alpha$  times the original environmentally dependent parameter) of species  $i$  less the average value of this expectation for resident species.

With this assumption of common growth rate functions  $g_j$ , the three ingredients of the storage effect,  $\Delta I$ , are manifested in a simpler form than in the general expression (29). Nonadditivity is still measured by  $\gamma$ , but we can think of  $1 - \rho$  as quantifying species specificity of response to the environment because the total variance of  $E_j$  consists of a proportion  $\rho$  that it has in common with other species and a proportion  $(1 - \rho)$  that is independent of other series. Covariance between environment and competition is reflected by two components,  $\bar{a}$  and  $\alpha^2 \sigma^2$ . The quantity  $\bar{a}$  is the average responsiveness of competition to changes in the environmentally dependent parameters, and  $\alpha^2 \sigma^2$  is the variance of these environmentally dependent parameters. While the product  $\bar{a} \alpha^2 \sigma^2$  is not the covariance between environment and competition as defined earlier, is nevertheless a different quantification of the same idea. Likewise,  $(1 - \rho)$  and  $\mathbf{P}_i$  are not the same but they quantify the same concept.

Note that the  $\Delta I$  term in expression (81) is the same for all species. Thus, it adds or subtracts the same amount from the long-term low-density growth rate of all species in the system. We shall see several examples below where  $\Delta I$  is positive, which has the effect of raising the  $\bar{r}_i$  of every species and promoting coexistence. Many species can coexist by this mechanism because there is no constraint preventing  $\Delta I$  from exceeding  $-\Delta E$  for all species and giving all species positive values of  $\bar{r}_i$ . This outcome is clear in the more specific examples that follow.

Negative values of  $\Delta I$  can occur, especially in cases of superadditivity (Chesson, 1988). In such cases, this resulting "negative storage effect" lowers the  $\bar{r}_i$  values. Crudely, we may think of this as promoting competitive exclusion. However, in the present situation with common functions  $g_j$ , there is no diversity-maintaining mechanism, and only one species would persist in the system without the  $\Delta I$  term. Lowering the  $\bar{r}_i$  values may have the effect of increasing the rate at which competitive exclusion occurs. More interestingly, the situation can arise where every species has a negative value of  $\bar{r}_i$ . In this case the order in which extinctions occur and the identity of the surviving species are subject to chance (Chesson and Ellner, 1989).

5.4. *The Lottery Model*

What form does  $\Delta I$  take for particular systems and how might it compare with the other terms of the  $\bar{r}_i$  in such systems? In iteroparous populations, reproduction and juvenile survival are often more sensitive to environmental and competitive factors than is adult survival and this commonly leads to subadditivity (Chesson, 1984, 1988). The lottery model of competition for space (Chesson and Warner, 1981) gives a simple illustration of such situations. The dynamical equations are

$$X_j(t + 1) = (1 - \delta_j) X_j(t) + \left[ \sum_{k=1}^n \delta_k X_k \right] \left[ \frac{B_j(t) X_j(t)}{\sum_{k=1}^n B_k(t) X_k(t)} \right], \quad (82)$$

where  $X_j$  is the number of adult organisms in the system,  $\delta_j$  is the death rate of adults, and  $B_j(t)$  is a parameter combining the birth rate and juvenile survival rate up to stage where the organisms begin to compete for the space that they hold as adults. The quantity  $B_j(t)$  can also incorporate a factor reflecting a species' relative competitive ability (Chesson and Warner, 1981).

The quantity  $B_j(t)$  is an environmentally dependent parameter, but to analyze the model it is simpler if it is transformed to the log scale to reflect the fact that ratios of  $B_j(t)$  values are more important than absolute values. Thus, we define

$$E_j = \ln B_j. \quad (83)$$

The quantity

$$\left[ \sum_{k=1}^n \delta_k X_k(t) \right] \quad (84)$$

represents the amount of space available for settlement of juveniles as a result of death of adults. Competition for space can then be assessed by

comparing the available space with the demand on space (the number of juveniles competing for the available space):

$$\sum_{k=1}^n B_k(t) X_k(t). \tag{85}$$

Again, it is simplest to express this on a log scale, and so we define the competition parameter as

$$C = \ln \left\{ \frac{\sum_{k=1}^n B_k(t) X_k(t)}{\sum_{k=1}^n \delta_k X_k(t)} \right\}, \tag{86}$$

which is independent of the species.

In our framework, the growth rate can be expressed as

$$g_j(E_j, C) = \ln \{ (1 - \delta_j) + e^{E_j - C} \}. \tag{87}$$

The standard environmentally dependent and competition parameters are

$$\mathcal{E}_j = \ln \{ (1 - \delta_j) + e^{E_j - C^*} \}$$

and

$$\mathcal{C}_j = -\ln \{ (1 - \delta_j) + e^{E_j^* - C} \}.$$

Table I gives the important quantities for the model analysis.

Defining  $E_j^\wedge = E_j - E_j^*$  and noting that by Taylor expansion  $\mathcal{E}_j = \delta_j E_j^\wedge + \frac{1}{2} \delta_j (1 - \delta_j) (E_j^\wedge)^2$ , we see that

$$\begin{aligned} \Delta E &= E \mathcal{E}_i - \frac{\delta_i}{n-1} \sum_{r \neq i} E \mathcal{E}_r / \delta_r \\ &\approx \delta_i (E[E_i^\wedge] - E[\bar{E}^\wedge]) - \frac{1}{2} \delta_i (\delta_i - \delta) \sigma^2, \end{aligned} \tag{88}$$

which in this case is equal to  $\bar{r}'_i$ , as the common choice of  $C^*$  means  $\mathcal{C}_i^{-i^*} = 0$ . In addition, we have  $\Delta C = \Delta N$ , which can be written simply as

$$\Delta C = \Delta N = \frac{1}{2} V(C^{-i}) \delta_i (\delta_i - \delta). \tag{89}$$

TABLE I  
Parameters of the Lottery Model

$\alpha_j$	$\delta_j$
$\beta_j$	$\delta_j$
$\Phi_j^{(2)}$	$-\delta_j(1 - \delta_j)$
$\gamma$	$1 - \delta_i^{-1}$
$q_{ir}$	$\delta_i / [\delta_r(n - 1)]$
$\Psi$	$\frac{1}{2} \delta_i (\delta_i - \delta)$



This nonlinearity term involves species differences in adult death rates, reflecting the fact that different adult death rates lead to relatively non-linear responses of species' growth rates to competition.

To calculate the storage effect, we assume that the environment satisfies the same assumptions as the general symmetric model of Subsection 5.3. The lottery model is then a special case of that model. Applying expression (79) and Appendix IV we conclude that

$$\Delta I = \sigma^2 \delta_i [(1 - \rho)(1 - \bar{\delta})/(n - 1) + \rho(\delta_i - \bar{\delta})], \tag{90}$$

where  $\bar{\delta}$  is a weighted mean of the resident  $\delta$ 's with weight given to  $\delta$ , equal to the expected fraction of the total pool of competing juveniles coming from species  $r$  (Appendix IV).

To develop an understanding of these results, we first consider the special case where the adult death rates,  $\delta_j$ , do not differ between species. Then we have  $\Delta C = \Delta N = 0$  and  $\Delta E = \bar{r}'_i \approx \delta(E[E_i] - E[\bar{E}])$ . Noting that an adult death rate of  $\delta$  means an expected longevity of  $1/\delta$ , we can express the long-term low-density growth rate in per generation units as

$$\bar{r}'_i/\delta \approx E[E_i] - E[\bar{E}] + \sigma^2(1 - \rho)(1 - \delta)/(n - 1). \tag{91}$$

Note that for fixed values of the other quantities, the magnitude of the storage effect declines as the number of resident species increases, making it increasingly difficult for new species to invade the system.

Expression (91) can be rearranged to give a condition for all species to coexist. First, we recall that  $E[\bar{E}]$  is the average of  $n - 1$  values of  $E[E_r]$  for resident species. Defining  $E[\bar{E}^n]$  as the average of the  $E[E_i]$ s for all species (including the invader  $i$ ), and noting that  $E[E_i] - E[\bar{E}] = n(E[E_i] - E[\bar{E}^n])/(n - 1)$ , we obtain the coexistence criterion

$$\sigma^2(1 - \rho) > n \max_j (E[\bar{E}^n] - E[E_j])/(1 - \delta), \tag{92}$$

which agrees exactly with a formula derived by Hatfield (1986) using a diffusion approximation.

Note that the left hand side of the coexistence condition (92) is the variance of the species-specific response to the environment. The term  $\max_j (E[\bar{E}^n] - E[E_j])$  can be regarded as the maximum average disadvantage conferred on any species by the environment. This term shows that coexistence is easy if species are very similar in average properties. As expected intuitively, coexistence becomes more difficult as the number of species  $n$ , is increased, and easier as the value of  $\delta$  is decreased. Note, however, that  $\delta$  has little effect on this coexistence condition once it has become small—the criterion quickly approaches a finite limit as  $\delta$  approaches 0.

In the case where the  $\delta_j$  differ between species, the expression for  $\bar{r}_i$  requires a knowledge of fluctuations in population density in order to calculate  $V(C^{-i})$  and hence a nonzero value for  $\Delta N$  (Eq. (89)). For this we need the resident stationary distribution. For the two-species case (Chesson, 1989), this is trivial, as there is just a single resident, which occupies all space and is unaffected by environmental fluctuations—they are cancelled exactly by fluctuations in competition. For the three-species case, we can make use of the two-species resident distribution determined by Hatfield and Chesson (1989). Appendix V shows that for the case  $E[E_r] = E^*$ ,

$$V(C^{-i}) \approx \sigma^2 \left( \rho + \frac{(1-\rho)(1-\bar{\delta})}{2(1-\bar{\delta})^2 + \bar{\delta}(1-\bar{\delta})} \right). \quad (93)$$

It follows that for the case where  $E[E_j] = E^*$ ,

$$\bar{r}_i = \frac{1}{2} \sigma^2 (1-\rho) \delta_i \left( (1-\delta_i) + (\bar{\delta} - \bar{\delta}) - \frac{(\delta_i - \bar{\delta})(1-\bar{\delta})}{2(1-\bar{\delta})^2 + \bar{\delta}(1-\bar{\delta})} \right). \quad (94)$$

Expression (94) differs very little from (91), when specialized to the case  $E[E_j] = E^*$ . The similarity occurs because in the three-species lottery model, the nonzero  $\Delta C$  ( $\Delta N$ ) term arising when the  $\delta$ 's are unequal is largely canceled by additional terms in  $\Delta I$  and  $\Delta E$ . Indeed, if the  $\delta$ 's are small (the situation when these nonadditivities and nonlinearities assume the most importance in the lottery model) there is negligible error using (91), with  $\delta$  interpreted as  $\delta_i$ , in place of (94).

### 5.5. Seedbank Model

Annual plants with a seed bank provide another example where sub-additivity results from differing sensitivities of different life-history stages to environment and competition. While such annual plant communities have been discussed qualitatively in within this general framework several times (Chesson, 1988), this is the first quantitative analysis. The equations defining population growth are

$$X_j(t+1) = s_j(1 - E'_j(t)) X_j(t) + E'_j(t) [Y_j/C'(t)] X_j(t), \quad (95)$$

where  $X_j(t)$  is the density of seeds of species  $j$  in the soil seed bank at time  $t$ ,  $E'_j(t)$  is the fraction of these seeds germinating in the period  $t$  to  $t+1$ ,  $Y_j$  is the field of seeds from each germinating seed with competition,  $C'(t)$ , at the value 1, and  $s_j$  is the survival rate of seeds that do not germinate during  $t$  to  $t+1$  (assumed constant).

Note that the first term of the sum in (95) is number of seeds that do not germinate but survive from time  $t$  to time  $t+1$ . The second term is production of new seeds from plants that do germinate. All species are assumed to be affected in the same way by competition.

TABLE II  
Parameters of the Seedbank Model

$\alpha_j$	$1 - s_j = \delta_j$
$\beta_j$	$1 - s_j(1 - e^{E_j})$
$\Phi_j^{(2)}$	$-\beta_j(1 - \beta_j)$
$\gamma_j$	$1 - \delta_i^{-1}$
$q_{ir}$	$\beta_i / [\beta_i(n - 1)]$
$\Psi$	$\frac{1}{2}\beta_i(\beta_i - \beta)$

Equation (95) is not a full description of dynamics, as we have not specified  $C'$ . A model for competition is

$$C' = \sum_{j=1}^n c_j E_j' X_j, \tag{96}$$

where the  $c_j$  are constants. In essence, the model assumes that the reduction in seed yield due to competition is proportional to a linear combination of the numbers of seeds germinating for each species. This model has been discussed elsewhere in the literature (Levin *et al.*, 1984), and enjoys considerable empirical support.

The log scale once again proves beneficial and so we define

$$E_j(t) = \ln E_j'(t) \quad \text{and} \quad C(t) = \ln C'(t). \tag{97}$$

Thus

$$G_j(E_j, C) = s_j(1 - e^{E_j}) + Y_j e^{E_j - C} \tag{98}$$

and

$$g_j(E_j, C) = \ln[s_j(1 - e^{E_j}) + Y_j e^{E_j - C}]. \tag{99}$$

The form of  $g$  is now very similar to that in the lottery model, and it should not be surprising that the results take a similar form. The important quantities for analyzing the model are in Table II. Making the environmental assumptions of Subsection 5.3, the results of that subsection and Appendix IV now yield the components of  $\bar{r}_i$ —Table III. Note that  $\bar{\delta}$  is again a weighted average of resident  $\delta$  values with weights being expected proportionate contributions to competition (Appendix IV).

TABLE III  
Results of the Seedbank Model

$\Delta E(\bar{r}_i)$	$E\delta_i - \sum_{r \neq i} q_{ir} E\delta_r$
$\Delta C(\Delta N)$	$\frac{1}{2}V(C^{-1})\beta_i(\beta_i - \beta)$
$\Delta I$	$\sigma^2\beta_i[(1 - \rho)(1 - \bar{\delta})/(n - 1) + \rho(\delta_i - \bar{\delta})]$

As in the lottery model, the  $\Delta C$  term contains the unknown  $V(C^{-i})$ , but again this term vanishes when all the  $\beta_j$  are the same. Equal seed mortality rates  $\delta_j$ , and equal yields  $Y_j$  together give equal  $\beta_j$ 's. However, this outcome can occur in other circumstances too. The formula for  $\beta_j$  (Table II) shows that species with larger values of  $s$  must also have larger values of  $E^*$  if the  $\beta_j$ 's are the same for all species. To understand this, note that relation (5), defining equilibril values, implies that the  $E_j^*$  values must obey the formula

$$Y_j \exp(-C^*) = 1 + \delta_j (\exp(-E_j^*) - 1), \quad (100)$$

which means that  $Y_j$  must decrease if both  $s_j$  and  $E_j^*$  increase for fixed  $C^*$ . It follows that invariance of the  $\beta_j$  implies a tradeoff between  $Y_j$  and  $\delta_j$  with increased yields corresponding to higher seed mortality, which is not an unreasonable qualitative form for such a tradeoff in nature.

With a zero  $\Delta C$  term (following from equality of the  $\beta_j$ 's), we obtain (Appendix IV)

$$\bar{r}_i = \Delta E + \sigma^2 \beta_i \left( (1 - \rho) \frac{1 - \bar{\delta}}{n - 1} + \rho (\delta_i - \bar{\delta}) \right). \quad (101)$$

In this model, a zero  $\Delta C$  term does not require species to have the same growth-rate function  $g$ . Differences between  $g$ 's show up in the  $\Delta I$  term as  $\rho(\delta_i - \bar{\delta})$ , which adjusts the average growth of the invading species  $i$  due to its deviation from the average seed mortality rate. The sign of the  $\Delta I$  term may differ between species if the  $\delta_j$  vary too greatly, and  $\rho$  is not small. However, the main messages of the lottery model are retained: Large variance in the species-specific component of response to the environment can permit coexistence of many species, and the benefit of this variance to the  $\bar{r}_i$  decreases in inverse proportion to the number of resident species.

### 5.6. Simultaneous Recruitment Variation and Resource Partitioning

The general theory discussed here represents the mean low-density growth rate  $\bar{r}_i$  in terms of several mechanisms that do not depend on the fluctuations and mechanisms that do. In this subsection these two sorts of mechanisms are combined in one specific model. As in Subsection 5.4, we envisage an interoparous population with environmental fluctuations leading to variation in recruitment to an adult population. We use the same growth rate equation with the same meanings, except that we modify the competition term to represent differences between intraspecific and interspecific competition among juveniles. The formula for the growth rate in terms of environment and competition is

$$g_j(E_j, C_j) = \ln \{ (1 - \delta) + e^{E_j - C_j} \}, \quad (102)$$

where it is assumed for simplicity that the adult death rates are the same for all species.

The competition parameter takes the form

$$C_j = \sum_{k=1}^n \alpha_{jk} e^{E_k} X_k, \tag{103}$$

where  $\exp\{E_j\}$  represents the juvenile production rate, and we can define the “limiting factors” in this case as the numbers of juveniles of the different species,  $F_l = \exp\{E_l\} X_l$ , and in the terminology of Section 4, above, we have

$$C_j = \Phi'_j(\mathbf{F}) = \sum_{l=1}^n \alpha_{jl} F_l. \tag{104}$$

For the invasion analysis, however,  $F_i$  is omitted as a competitive factor because it is fixed at zero.

To simplify analysis, we assume that all intraspecific coefficients are the same,  $\alpha_{jj} = \alpha$ , and all interspecific coefficients are the same,  $\alpha_{jk} = \beta$ , for  $j \neq k$ . In order to satisfy the assumptions of  $O(\sigma^2)$  differences between competitive effects experienced by different species, we specify  $\alpha - \beta = O(\sigma^2)$ . We make the same environmental assumptions as in the two previous models.

Although the competition parameters are here unique to a species, we specify a common equilibrial value,  $C_j^* = C^*$ , which fits with the symmetry assumptions of the model. This means that the  $E_j^*$  have a common value  $E^* = C^* + \ln \delta$ . The vector  $\mathbf{q}_i$  is calculated in Appendix III as

$$\mathbf{q}_i \approx \{1 - (\alpha - \beta)/[\alpha(n - 1)]\} \mathbf{p}_{n-1}, \tag{105}$$

where  $\mathbf{p}_{n-1}$  is the  $n - 1$  dimensional row vector  $(1, \dots, 1)/(n - 1)$ , which averages the elements of column vector that it multiplies. Note that that  $\mathbf{q}_i$  differs from  $\mathbf{p}_{n-1}$  only by  $O(\sigma^2)$ . Given that  $E\mathcal{E}_j = O(\sigma^2)$  (assumption a4), and noting by Taylor expansion that  $E\mathcal{E}_j \approx \delta(E[E_j] - E^*) + \frac{1}{2}\delta(1 - \delta)\sigma^2$ , we see that

$$\Delta E \approx \delta(E[E_i] - E[\bar{E}]). \tag{106}$$

To calculate  $\mathcal{E}_i^{-i*} = -g_i(E_i^*, \phi'_i(\mathbf{F}^*))$ , we note that  $\phi'_i$  is linear, and therefore the methods of Subsection 4.2.1 above apply to give

$$\phi'_i(\mathbf{F}^*) = \mathbf{q}_i \mathbf{C}^{*-i} \approx \{1 - (\alpha - \beta)/[\alpha(n - 1)]\} C^*. \tag{107}$$

Expanding  $-g_i(E_i^*, \phi'_i(\mathbf{F}^*))$  in  $\phi'_i(\mathbf{F}^*)$  about  $C^*$  yields

$$\mathcal{E}_i^{-i*} = \delta(\beta/\alpha - 1) C^*/(n - 1). \tag{108}$$

Combined, (106) and (108) give

$$\bar{r}_i = \delta \{ E[E_i] - E[\bar{E}] + C^*(1 - \beta/\alpha)/(n-1) \}. \quad (109)$$

The relative nonlinearity term  $\Delta N$  is  $o(\sigma^2)$ , because  $V(\mathbf{F}) = O(\sigma^2)$  and  $\Psi = O(\sigma^2)$  ( $\alpha - \beta = O(\sigma^2)$ ). Thus, it remains to calculate  $\Delta I$ . This, however, turns out to be a straightforward application of the results of Subsection 5.3 above because  $\mathcal{C}_r^{-i} = \mathcal{C}_i^{-i} + O(\sigma^2)$ , and so all the calculations of covariances can proceed as if there were just a single limiting factor. Similarly, the  $O(\sigma^2)$  difference between  $\mathbf{q}_i$  and  $\mathbf{p}_{n-1}$  has only an  $o(\sigma^2)$  effect on  $\Delta I$  and can be ignored. Appendix IV shows that  $\bar{a} = C^*/\delta(n-1)$  and so we see from formula (79) that

$$\Delta I = \delta(1 - \delta)(1 - \rho) \sigma^2 C^*/(n-1). \quad (110)$$

Combining all terms of the growth rate, we now obtain

$$\bar{r}_i/\delta \approx E[E_i] - E[\bar{E}] + \frac{(1 - \beta/\alpha) C^*}{n-1} + \frac{(1 - \delta)(1 - \rho) \sigma^2 C^*}{n-1}. \quad (111)$$

This result appears to depend on the arbitrary parameter  $C^*$ , but it does not really, as  $C^* = E^* + \ln \delta^{-1}$  and  $E[E_i] = E^* + O(\sigma^2)$ , and so  $E[\bar{E}] + \ln \delta^{-1}$  can be substituted for  $C^*$  above without affecting the accuracy of the approximation. When this is done, the expressions (109)–(111) all become independent of the choice of the equilibrial parameters.

These results lead to essentially the same form of interaction term as in the lottery and seedbank models. The symmetry assumptions applied here ensure that this is the case. However, of particular note is that  $-\mathcal{C}_i^{-i*}$  has a similar form and similar effect to  $\Delta I$ . In essence, the fluctuation-independent or short-timescale mechanisms have the same effect as the fluctuation-dependent mechanisms when both are viewed on a long timescale. The correlation between the environmentally dependent parameters of different species corresponds to the ratio of competition coefficients  $\beta/\alpha$ . The correlation  $\rho$  determines how much different species tend to have periods of high juvenile production simultaneously, when these juveniles will be thrown into competition with each other. The ratio  $\beta/\alpha$  measures the similarity of competition between versus within species for any fixed environmental conditions. Thus, these two quantities summarise similar things but for different timescales.

Unlike  $\rho$ , however,  $\beta/\alpha$  can be greater than 1, but can never be less than 0. If  $\beta/\alpha$ , interspecific competition between juveniles is greater than intraspecific competition between juveniles, lowering the values of  $\bar{r}_i$ , and opposing the coexistence promoting effect of  $\Delta I$ . In the present model,  $\Delta I$

can only be nonnegative. However, if the model were superadditive, for example if environmental fluctuations had their greatest impact on adult survival, and competition covaried positively with this, then the  $\Delta I$  term would be negative as a consequence of a positive value of  $\gamma$ . These results serve to illustrate the deep connections that exist between competitive processes on different scales, which are often obscured by the scale on which we view them.

## 6. DISCUSSION

This last decade has been marked by a vigorous debate on the sorts of generalizations that are possible concerning the dynamics and structure of ecological communities (Kareiva, 1989; Roughgarden, 1989). The present work provides evidence that certain kinds of broad generalizations are indeed possible in community ecology. This evidence is derived here from a general model that is capable of representing a broad range of different sorts of communities. In spite of these broad possibilities, it was nevertheless shown that there is a limited range of mechanisms capable of affecting species coexistence. These mechanisms are represented quantitatively in the three natural terms,  $\bar{r}'_i$ ,  $\Delta N$ , and  $\Delta I$ , whose structure can be examined in detail for quite general situations. Other mechanisms of coexistence and competitive exclusion either do not exist within this model or are more subtle than can be revealed by the quadratic parts of the model.

The specific examples served further to illustrate unity. They showed that the  $\Delta I$  term takes a very similar form in different models though they may have different functional forms for competition or may involve different life histories. Moreover, the recruitment variation example of Subsection 5.6 illustrated similarity between mechanisms on different scales. When the effects of fluctuation-independent mechanisms and the storage effect are both viewed on a long timescales, their operation can appear very much the same. Thus, it appears that not only are there a restricted number of mechanisms of coexistence, but these mechanisms have connections at fundamental levels which can be revealed when viewed appropriately.

Of the two fluctuation-dependent mechanisms considered here, the storage effect seems by far the more important because when acting alone it is capable of permitting coexistence of an arbitrary number of species. On the other hand, relative nonlinearity of competition requires complex scenarios before it can lead to coexistence of more than two species.

The several examples illustrating the storage effect in Section 5 imply that the strength of the storage effect changes in inverse proportion to the number of species in the system provided correlations between the responses of pairs of species to environmental factors are of similar magnitude for

all pairs of species. The recruitment variation example of Subsection 5.6 shows that the corresponding assumptions applied to classical resource partitioning lead to a similar inverse proportionality of the strength of the coexistence-affecting mechanism as the number of species decreases. Such dependence of the strength of mechanism on the number of species potentially provides a basis for predicting the species richness of a system.

This article emphasises the long-term low-density growth rate as the means of assessing the strength of a mechanism. Moreover, this long-term growth rate allows comparisons of the quantitative contributions of different mechanisms to coexistence in the most likely situations in nature where several mechanisms may act together (Connell, 1978).

The technique of partitioning the long-term low-density growth rate to reveal the contributions of different mechanisms shows in particular how mechanisms operating on different timescales can be considered simultaneously. The  $\bar{r}_i$  term of this can be viewed as summarizing all those mechanisms of coexistence and competitive exclusion occurring on shorter timescales than the time unit in the model. In principle, the  $\bar{r}_i$  term could itself be expanded into three terms showing mechanisms associated with fluctuations on some timescale and other mechanisms associated with yet shorter timescales. Thus, the model forms a conceptual framework for dealing with multiple timescales situations, and can contribute to the development of hierarchy theory (Allen and Starr, 1982; O'Neill *et al.*, 1986).

The results presented here, however, are not without their limitations. Most troublesome is the small effects approximation. We would like to have some assurance that the results are applicable to realistic levels of environmental fluctuation. The accuracy of the quantitative formulae is of most concern, as it is clear that the existence of these mechanisms is independent of the range of fluctuations (Chesson, 1990). We can expect that in some particular models the approximation will hold up broadly, but in other particular models serious errors will occur for all but very small levels of environmental fluctuation. This is analogous to the corresponding problems in the stability analysis of deterministic models. Guidelines on how to distinguish these cases are yet to be developed.

A number of other limitations have been addressed satisfactorily in special forms of the general model or are the subject of other publications. These are the restriction to just one environmentally dependent parameter per species (Chesson and Warner, 1981), the assumption of independence of environmental fluctuations over time (Chesson and Warner, 1981; Chesson, 1990), and the requirement that the invader's competition parameter can be expressed as a function of residents' competition parameters (Chesson and Rosenzweig, manuscript). Moreover, there is an analogous development of the theory to the case of spatial variation (Comins and Noble, 1985; Chesson and Ives, manuscript).



APPENDIX I: GENERAL NOTATION

$C_j$	Competition parameter of species $j$
$C_j^*$	Equilibril value of $C_j$
$\mathcal{C}_j$	$-g_j(E_j^*, C_j)$ : standard competition parameter
$\mathcal{C}_j^{-i}$	$\mathcal{C}_j$ with species $i$ as an invader
$\mathcal{C}^{-i}$	$(\mathcal{C}_1^{-i}, \dots, \mathcal{C}_n^{-i})'$ , with $i$ th place missing
$E_j$	Environmentally dependent parameter of species $j$
$E_j^*$	Equilibril value of the environmentally dependent parameter
$\mathbf{E}$	$(E_1, \dots, E_n)'$
$\mathcal{E}_i$	$g_i(E_i, C_i^*)$ : standard environmentally dependent parameter
$\mathcal{E}^{-i}$	$(\mathcal{E}_1, \dots, \mathcal{E}_n)'$ with $i$ th component deleted
$i$	Label for invading species
$j, k$	Labels for arbitrary species
$r, s$	Labels for resident species
$r_j(t)$	Growth rate: $\ln X_j(t+1) - \ln X_j(t) = \ln \lambda_j(t)$
$\bar{r}_j$	Long-term low-density growth rate
$G_j(E_j(t), C_j(t))$	General form of $\lambda_j(t)$
$g_j(E_j(t), C_j(t))$	General form of $r_j(t)$
$\mathbf{P}_i$	Diagonal matrix with $r$ th diagonal element $(\chi_{ir}^{-i}/\chi_{rr}^{-i})/\sqrt{V(\mathcal{E}_i)/V(\mathcal{E}_r)}$
$q_{ir}$	$\partial \mathcal{C}_i^{-i}/\partial \mathcal{C}_r^{-i}$
$\mathbf{q}_i$	$(q_{i1}, \dots, q_{in})$
$X_j(t)$	Population size of species $j$
$Z_j(t)$	$\ln X_j(t)$
$\Delta C$	Mean competition effect
$\Delta E$	Mean environmental effect
$\Delta I$	Storage effect
$\Delta N$	Effect of relative nonlinearity
$\alpha_j$	$d\mathcal{E}_j/dE_j$ at $E_j = E_j^*$
$\beta_j$	$d\mathcal{C}_j/dC_j$ at $C_j = C_j^*$
$\gamma_j$	$\partial^2 g_j/(\partial \mathcal{E}_j \partial \mathcal{C}_j)$ at $(\mathcal{E}_j, \mathcal{C}_j) = (0, 0)$ : nonadditivity
$\mathbf{\Gamma}$	$\text{diag}(\gamma_1, \dots, \gamma_n)$ with $i$ th diagonal element deleted
$\lambda_j$	$X_j(t+1)/X_j(t)$ : finite rate of increase of species $j$
$\Xi_i$	Diagonal matrix with $r$ th diagonal element $(\gamma_i \sqrt{V(\mathcal{E}_i)})/(\gamma_r \sqrt{V(\mathcal{E}_r)})$
$\sigma$	Small parameter proportional to $\sqrt{\mathcal{E}_j}$
$\chi_{jk}^{-i}$	$C(\mathcal{E}_j, \mathcal{C}_k^{-i})$ : Covariance between environment and competition
$\chi$	$(\chi_{11}^{-i}, \dots, \chi_{nn}^{-i})'$ with $i$ th component deleted
$\mathbf{1}$	$n-1 \times n-1$ identity matrix
$\approx$	Approximately equal to with an $o(\sigma^2)$ error

## APPENDIX II

The approximations in the text use the standard order notation  $y = O(\sigma)$  and  $y = o(\sigma)$ , meaning respectively  $|y| < K\sigma$  for some constant  $K$  and  $y/\sigma \rightarrow 0$  as  $\sigma \rightarrow 0$ .

The small effects approximation of the text requires that fluctuations in the competition parameters be restricted to finite ranges of order  $\sigma$  about their equilibril values. We seek conditions under which values initially satisfying this constraint, will satisfy it for all time. Consider just the case where the competition parameters can be expressed as functions of environmentally dependent parameters and species densities alone (assumption (a7')). To begin with, we assume that the different species have a common competition parameter  $C(t)$ . We then go on to consider the general case. We find conditions under which  $C(t) - C^* = O(\sigma)$ . Under the reasonable assumption that  $\mathcal{C}_j$  is a smooth function of  $C(t)$ ,  $\mathcal{C}_j = O(\sigma)$ .

For simplicity of notation assume that  $C(t)$  has been adjusted so that  $C^* = 0$ . We write

$$C(t) = c(\mathcal{E}(t), \mathbf{Z}(t)), \quad (\text{A1})$$

where  $\mathbf{Z}(t)$  is the vector of log population densities, and  $\mathcal{E}(t)$  is the vector of standard environmentally dependent parameters. Note that

$$\mathbf{Z}(t+1) = \mathbf{Z}(t) + \mathbf{g}(\mathcal{E}(t), C(t)), \quad (\text{A2})$$

where  $\mathbf{g}$  is the vector of growth rates in terms of the standard environmental parameter vector and the common competition parameter.

$C(t+1)$  can now be expanded as follows:

$$\begin{aligned} C(t+1) &= c(\mathcal{E}(t+1), \mathbf{Z}(t+1)) \\ &= c[\mathcal{E}(t+1), \mathbf{Z}(t) + \mathbf{g}(\mathcal{E}(t), C(t))] \\ &= P(t) + Q(t) + R(t) + C(t), \end{aligned} \quad (\text{A3})$$

where

$$P(t) = c[\mathcal{E}(t), \mathbf{Z}(t) + \mathbf{g}(\mathbf{0}, C(t))] - c[\mathcal{E}(t), \mathbf{Z}(t)] \quad (\text{A4})$$

$$Q(t) = c[\mathcal{E}(t+1), \mathbf{Z}(t+1)] - c[\mathcal{E}(t), \mathbf{Z}(t+1)] \quad (\text{A5})$$

$$R(t) = c[\mathcal{E}(t), \mathbf{Z}(t) + \mathbf{g}(\mathcal{E}(t), C(t))] - c[\mathcal{E}(t), \mathbf{Z}(t) + \mathbf{g}(\mathbf{0}, C(t))]. \quad (\text{A6})$$

Each of these differences represents a comparison of a change in one value of an argument of a function. With sufficient regularity (e.g., locally Lipschitz of order 1), we can expect to bound these differences by linear functions as follows:

$$|P(t) + C(t)| < \rho C(t) \tag{A7}$$

$$|Q(t)| < k_1 |\mathcal{E}(t+1) - \mathcal{E}(t)| \leq 2k_1 \sigma \tag{A8}$$

$$|R(t)| < k_2 |\mathcal{E}(t)| \leq k_2 \sigma. \tag{A9}$$

Under these circumstances we find that

$$|C(t+1)| < \rho |C(t)| + (2k_1 + k_2)\sigma. \tag{A10}$$

If  $\rho < 1$ , we can define

$$K = (2k_1 + k_2)/(1 - \rho), \tag{A11}$$

and then

$$|C(t)| < K\sigma \tag{A12}$$

for all  $t$  whenever  $|C(0)| < K\sigma$ .

The mean value theorem for differentiable functions provides formulae for these critical constants,  $\rho$ ,  $k_1$ , and  $k_2$ . We choose some positive number  $\varepsilon$ , and assume that  $\mathbf{z}$ ,  $\mathbf{z}'$ ,  $\mathcal{E}$ , and  $\mathcal{E}'$ , and  $C$  satisfy the conditions  $|\mathcal{E}| < \varepsilon$ ,  $|\mathcal{E}'| < \varepsilon$ ,  $|c(\mathcal{E}_0, \mathbf{z})| < \varepsilon$  for some  $\mathcal{E}_0$  with  $|\mathcal{E}_0| < \varepsilon$ ,  $\mathbf{z}' = \mathbf{z} + \mathbf{g}(\mathcal{E}, C)$ , and  $|C| < \varepsilon$ . Under these conditions we define

$$\rho = \sup \left| 1 + \frac{\partial c[\mathcal{E}, \mathbf{z} + \mathbf{g}(0, C)]}{\partial C} \right|. \tag{A13}$$

Second

$$k_1 = \sup |\nabla c(\mathcal{E}', \mathbf{z}')|, \tag{A14}$$

where  $\nabla$  is the operator vector  $(\partial/\partial \mathcal{E}_1, \dots, \partial/\partial \mathcal{E}_n)$ . Finally,

$$k_2 = \sup |\nabla c(\mathcal{E}_1, \mathbf{z} + \mathbf{g}(\mathcal{E}, C))|,$$

where  $\mathcal{E}_1$  is set equal to  $\mathcal{E}$  after the taking of derivatives. A  $K$  such that (A12) holds, for  $\sigma$  sufficiently small, exists if there is a positive  $\varepsilon$  such that  $k_1$  and  $k_2$  are finite and  $\rho$  is less than 1. Sufficiently small  $\sigma$  is such that  $K\sigma$  and  $\sigma$  are both  $< \varepsilon$ .

The conditions that  $k_1$  and  $k_2$  be finite are essentially regularity conditions on the functions defining the model. The condition that  $\rho$  be less than 1 means that the feedback from  $C$  to itself, which is necessarily negative, does not approach zero while  $|C| < \varepsilon$  and  $|\mathcal{E}| < \varepsilon$ , and that this feedback is not too strong.

It is not difficult to show that these conditions are satisfied for the seed bank model in the text. However, in the lottery model, the feedback from

$C$  to itself approaches 0 as equilibrium is approached. Therefore the above methods do not work. The lottery model is unusual in this respect. However, it is not difficult to show directly that

$$\min_j \{E_j - E_j^*\} \leq C \leq \max_j \{E_j - E_j^*\}$$

and therefore that  $C$  is bounded by  $\sigma$  in the lottery model.

To demonstrate that  $\mathcal{C}_j = O(\sigma)$  more generally, we assume that it is possible to transform the competition parameters so that there are a function  $C(t)$ , functions  $h_j(t)$ , and constants  $\kappa_j$  such that

$$C_j(t) = C(t) + h_j(t)$$

with  $|h_j(t)| < \kappa_j \sigma^2$  for  $C(t)$  and  $\mathcal{E} = O(\sigma)$ . A minor modification of the above derivation then demonstrates that competition parameters are bounded in a finite range of order  $\sigma$  in this more general case. The model of recruitment variation, Subsection 5.6, can be shown to satisfy these conditions provided  $C^* < 2/\delta$ .

We need to show also that the expected value of the competition parameter is  $O(\sigma^2)$ . Note that the small-effects approximation for resident species implies that

$$E\mathcal{E}_r - E\mathcal{C}_r + \gamma_r E\mathcal{E}_r \mathcal{C}_r = o(\sigma^2). \quad (\text{A15})$$

All terms on the left except possibly  $E\mathcal{C}_r$  are  $O(\sigma^2)$ . It follows that  $E\mathcal{C}_r$  must be  $O(\sigma^2)$  also. This result extends to invaders by the assumption that competitive differences between species are at most  $O(\sigma^2)$ .

We must show also  $E\mathbf{F} - \mathbf{F}^* = O(\sigma^2)$  in the competitive factor model, but this is immediate from the assumption that there is a smooth bijective relationship between  $\mathcal{C}^{-i}$  and  $\mathbf{F}$ , which will normally be so when the dimension of  $\mathbf{F}$  is not more than  $n-1$  when there are  $n-1$  residents species.

### APPENDIX III

The idea of a generalized inverse is used in the text in the context of explicit representation of the solutions of equations. Rao (1973, p. 24) defines a generalized inverse  $\mathbf{A}^-$  of a  $n \times m$  matrix  $\mathbf{A}$  by the property

$$\mathbf{A}\mathbf{A}^-\mathbf{A} = \mathbf{A}. \quad (\text{A16})$$

If the system of linear equations  $\mathbf{A}\mathbf{x} = \mathbf{b}$  has a solution, then  $\mathbf{A}^-\mathbf{b}$  is a solution of these equations. Unless  $\mathbf{A}$  itself is invertible, however,  $\mathbf{A}^-$  is not

unique. I give two elementary examples of generalized inverses of relevance to the text.

Consider the linear additive models of Subsection 4.2.1. If there is just a single limiting factor  $F$ , then we have  $C_j = \phi_j F$  and  $\Phi^{-i} = (\phi_1, \dots, \phi_n)'$ , with the  $i$ th element deleted. A generalized inverse of this matrix is given by the formula  $(\Phi^{-i})^- = (1/\phi_1, \dots, 1/\phi_n)/(n-1)$ , as can easily be checked against the defining relation (A16). By formula (34), we then obtain  $\mathbf{q}_i = \phi_i(1/\phi_1, \dots, 1/\phi_n)/(n-1)$ , a formula for  $\mathbf{q}_i$  that arises commonly in the text. Because the generalized inverse is not unique (e.g., in this example, an alternative formula is  $(\Phi^{-i})^- = [1/\phi_1, 0, \dots, 0]$ ), some care is needed in the interpretation of the results of these analyses to be ensure that they do not depend importantly on the arbitrariness of the choice of  $(\Phi^{-i})^-$ .

In cases where  $\Phi^{-i}$  is a square matrix of full rank, the generalized inverse is the same as the inverse and is unique. For example, if we define  $\mathbf{U}$  to be an  $n-1$  by  $n-1$  matrix of 1's, Eq. (104) leads to the matrix  $\Phi'^{-i} = (\alpha - \beta)\mathbf{1} + \beta\mathbf{U}$  relating the resident competition parameters to the limiting factors in the model of Subsection 5.6. This matrix is square with full rank provided  $\alpha \neq \beta$ , and the unique inverse is easily seen to be  $\mathbf{1}/(\alpha - \beta) - \beta\mathbf{U}/(\alpha - \beta)[\alpha - \beta + (n-1)]$ . This result can be used to calculate  $\mathbf{q}_i$  by the formula (34), ignoring the distinction between  $\mathcal{C}_j$  and  $C_j$ , because  $(\partial\mathcal{C}_j/C_j)^* = \delta$  for every species. As  $\phi'_i = \beta(1, \dots, 1) = \beta(n-1)\mathbf{p}_{n-1}$ , by definition of  $\mathbf{p}_{n-1}$ , we obtain  $\mathbf{q}_i = (n-1)\beta\mathbf{p}_{n-1}/[(n-1)\beta + \alpha - \beta] \approx \{1 - (\alpha - \beta)/[\alpha(n-1)]\}\mathbf{p}_{n-1}$ , as stated in the text.

In linear additive models, the vector  $\mathbf{q}_i$  leads to a  $\Delta C$  value equal to the difference between competition experienced by an invader from equilibrial resident competition and the invader's equilibrial competition. Nonlinear and nonadditive models are more complex, but have a similar equilibrial term  $\mathcal{C}_i^{-i*} = \phi_i(\mathbf{F}^*) - C_i^*$ , provided we make the assumption that the equilibrial values for residents satisfy the equation  $C_r^* = \phi_r(\mathbf{F}^*)$ . If we do not make this assumption,  $\mathcal{C}_i^{-i*}$  is replaced in formulas (45)–(47) by

$$[\phi_i(\mathbf{F}^*) - C_i^*] - \mathbf{q}_i[\phi^{-i}(\mathbf{F}^*) - \mathbf{C}^{-i*}], \tag{A17}$$

where  $\phi^{-i}$  is the vector of functions  $\phi$  for residents, and  $\mathbf{C}^{-i*}$  is the vector of resident equilibrial competition parameters. Equation (17) represents an invader-resident comparison of deviations between competition parameters at equilibrial  $F$  values, and equilibrial values of these competition parameters. Formula (A17) applies in linear cases also, showing that expression (36) can be split into these same two components whenever the equilibrial competition parameters are not chosen to be consistent with equilibrial limiting factors.

## APPENDIX IV

An important component of the covariance between environment and competition is the quantity  $\bar{a}_r = EA_r$ , where

$$A_r = \frac{\partial C^{-i}}{\partial \mathcal{E}_r}, \quad (\text{A18})$$

evaluated at  $\mathcal{E} = \mathbf{0}$ . In the lottery model, we find that

$$\begin{aligned} A_r &= e^{E_r^*} X_r \left( \delta_r \sum e^{E_s^*} X_s \right)^{-1} \\ &= X_r / \left( \sum \delta_s X_s \right) \end{aligned} \quad (\text{A19})$$

as the equilibrational equation (5) implies that  $E_r^* = C^* + \ln \delta_r$ . It follows that

$$\bar{\delta a} = \frac{1}{n-1}. \quad (\text{A20})$$

In addition

$$\frac{\bar{\delta a}}{(1-\delta)\delta a} = \frac{1-\tilde{\delta}}{n-1}, \quad (\text{A21})$$

where

$$\tilde{\delta} = \sum_r \delta_r E Y_r, \quad (\text{A22})$$

with  $Y_r = \delta_r X_r / \sum_s \delta_s X_s$ . Note that this is a weighted average of the  $\delta_r$  with weight of  $\delta_r$  equal to the expected value of the fraction of newly available space opened up by species  $r$ . Because  $E[E_r] = E_r^* + O(\sigma^2)$  and  $E_r^* = C^* + \ln \delta_r$ , we have the approximation

$$\tilde{\delta} = E \frac{\sum \delta_r e^{E_r} X_r}{\sum e^{E_r} X_r} + O(\sigma^2), \quad (\text{A23})$$

which expresses  $\tilde{\delta}$  as a weighted average with weights equal to the expected proportionate contributions of each species to the total pool of competing juveniles.

With two resident species,  $r$  and  $s$ , the probability density of  $X_r$  is

$$c[\delta_r x + \delta_s(1-x)]^2 x^{y_r-1} (1-x)^{y_s-1} \quad (\text{A24})$$

(Hatfield and Chesson, 1989), where  $c$  is a constant, and in the special case  $E[E_j] = E_j^*$ ,  $v_j = \delta_j^{-1} - 1$ . This probability density can be used to calculate the special case. Using this to evaluate (A22), we find that

$$\tilde{\delta} = \frac{\delta_r(1 - \delta_r)(2 - \delta_s) + \delta_s(1 - \delta_s)(2 - \delta_r)}{(1 - \delta_r)(2 - \delta_s) + (1 - \delta_s)(2 - \delta_r)}. \tag{A25}$$

For small  $\delta$  values,  $\tilde{\delta}$  is well approximated by  $\delta$ .

The seedbank model has a very similar functional form for the competition parameter. The essential difference is that the supply of resources being competed for is a constant in the seedbank model but depends on the densities of the species in the lottery model. However, as the resource supply does not depend on the environment, and is an additive term in the formula for the competition parameter, it does not affect the  $A_r$ . For the seedbank model we find that

$$A_r = c_r e^{E_r^*} X_r \left( \delta_r \sum c_s e^{E_s^*} X_s \right)^{-1}. \tag{A26}$$

Thus

$$\overline{\delta a} = \frac{1}{n - 1} \tag{A27}$$

and

$$\overline{(1 - \delta) \delta a} = \frac{1 - \tilde{\delta}}{n - 1}, \tag{A28}$$

where

$$\begin{aligned} \tilde{\delta} &= \sum_r \delta_r E \left[ c_r e^{E_r^*} X_r \left( \sum_s c_s e^{E_s^*} X_s \right)^{-1} \right] \\ &= \sum_r \delta_r E \left[ c_r e^{E_r} X_r \left( \sum_s c_s e^{E_s} X_s \right)^{-1} \right] + O(\sigma^2), \end{aligned} \tag{A29}$$

or in essence a weighted average of the  $\delta_r$  with weights equal to expected proportionate contributions to competition from each of the resident species.

The recruitment variation model of Subsection 5.6 has

$$C_i^{-i} = \beta \sum_{r \neq i} e^{E_r} X_r, \tag{A30}$$

which to  $O(\sigma^2)$  is a common limiting factor for the species in this system.

Thus, we calculate the  $A_r$  and  $\bar{a}$  for this quantity. Very simply  $A_r = \delta^{-1} \beta \exp\{E_r^*\} X_r$ , and therefore

$$\bar{a} = \frac{1}{\delta(n-1)} E\beta \sum_{r \neq i} \exp(E_r^*) X_r. \quad (\text{A31})$$

But this is within  $O(\sigma^2)$  of  $EC_i^{-1}/\delta(n-1)$ , and since  $EC_i^{-1} = C^* + O(\sigma^2)$ , this means that

$$\bar{a} = C^*/\delta(n-1) + O(\sigma^2),$$

which is sufficient to establish  $AI$  to  $o(\sigma^2)$ .

## APPENDIX V

To calculate the variance of competition in the lottery model, we note that  $E_j^* = \ln \delta_r + C^*$ , and so with symmetric covariance structure the  $E_r$  can be written in the form

$$E_r = U + V_r + \ln \delta_r + C^*, \quad (\text{A32})$$

where  $U$  has zero mean and variance  $\rho\sigma^2$  and is uncorrelated with  $V_r$  of variance  $(1-\rho)\sigma^2$  and mean  $O(\sigma^2)$ . The  $V_r$  are uncorrelated with each other. With  $Y_r$  defined as in Appendix IV, we find

$$C - C^* = U + \sum_r V_r Y_r + O(\sigma^2). \quad (\text{A33})$$

It follows that

$$V(C) \approx \sigma^2 \left( \rho + (1-\rho) \sum_r EY_r^2 \right). \quad (\text{A34})$$

We can evaluate this for the case of two resident species with  $E_j = E_j^*$ , using the density (A24). We find in that case that

$$EY_r^2 + EY_s^2 = \frac{2 - (\delta_r + \delta_s)}{[2 - (\delta_r + \delta_s)]^2 + \delta_r(1 - \delta_r) + \delta_s(1 - \delta_s)}, \quad (\text{A35})$$

from which the variance formula (93) in the text follows.

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