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## Geometry, Heterogeneity and Competition in Variable Environments [and Discussion]

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# Geometry, heterogeneity and competition in variable environments

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## SUMMARY

The effects of environmental fluctuations on coexistence of competing species can be understood by a new geometric analysis. This analysis shows how a species at low density gains an average growth rate advantage when the environment fluctuates and all species have growth rates of the particular geometric form called subadditive. This low density advantage opposes competitive exclusion. Additive growth rates confer no such low density advantage, while superadditive growth rates promote competitive exclusion.

Growth-rate geometry can be understood in terms of heterogeneity within populations. Total population growth is divided into different components, such as may be contributed by different life-history stages, phenotypes, or subpopulations in different microhabitats. The relevant aspects of such within-population heterogeneity can be displayed as a scatter plot of sensitivities of different components of population growth to environmental and competitive factors, and can be measured quantitatively as a covariance. A three-factor model aids the conceptual division of population growth into suitable components.

## INTRODUCTION

Do environmental fluctuations explain the high diversity of some animal and plant communities (Abrams 1984; Armstrong & McGehee 1976; Chesson & Huntly 1989; Comins & Noble 1985; Connell 1978; Grubb 1977; Sale 1977; Shmida & Ellner 1985; Woodin & Yorke 1975)? Hutchinson (1961) suggested that environmental fluctuations could favour different species at different times, and that this would permit coexistence of many species. Similar ideas form part of Grubb's (1977, 1986) conception of the regeneration niche. These ideas are now supported by mathematical models, with some provisos, as can be seen below.

It has also been suggested that environmental events affecting all species similarly may promote coexistence when they occur in the form of disturbance, causing pulses of mortality (Connell 1978). This idea is best developed for models of successional systems in patchy environments (Hastings 1980).

Models argue against the common conception that environmental variability promotes diversity by keeping species' densities at levels where there is little competition (Chesson & Huntly, in preparation). Diversity maintenance usually involves different species being favoured at different times by environmental or competitive conditions (Chesson & Huntly 1989). Thus while the initial effects of disturbance may be similar mortality for all species, diversity maintenance involves differential responses to the ensuing sequence of competitive conditions.

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It is also important to keep in mind that environmental variability need not have the same effect in different systems. Models show a strong dependence on the biological details of the component species, including life-history properties, physiology and behaviour (Chesson 1988). Depending on these details, environmental variability may promote diversity, promote competitive exclusion, or have no effect at all on diversity.

At least for the case of temporal environmental variability, there is a general understanding of the sorts of situations leading to these different effects of environmental variability (Chesson & Huntly 1989). It is the purpose of this article to explore this in two specific ways. First we consider a geometric approach to stochastic competition that shows how geometric properties of population growth rates can oppose competitive exclusion in some circumstances, but promote it in others. We will then explore the origin of the important geometric relations in the biology of a population. Heterogeneity within a single species population is of special importance to the geometry of a species' population growth rate and therefore of special importance in the outcome of interactions with other species.

## A GENERAL COMPETITION MODEL

Environmental effects in competition models are usually represented through some population parameter that is sensitive to fluctuating environmental factors. The choice of an environmentally dependent parameter depends on the actual ecological community that one is trying to represent, but in general, it is

something like a density-independent birth rate, mortality rate, seed germination rate, or resource uptake rate. A population can be expected to have several environmentally dependent parameters (Chesson & Warner 1981), but for simplicity it is here assumed that each species has just one key environmentally dependent parameter, denoted by the symbol  $E_i(t)$ , where  $i$  is the species and  $t$  is time. Often time,  $t$ , will be suppressed for notational simplicity.

A second important ingredient in stochastic competition models is the competition parameter. This is taken as a single number  $C_i(t)$  representing for the time period  $t$  to  $t+1$ , the effect of competition both with and between species on the growth rate of the given species  $i$ . This competition parameter is presumed to depend on the densities of the species in the system and also on their environmentally dependent parameters. Thus, it can be represented as

$$C_i(t) = c_i(E_1, X_1, E_2, X_2, \dots, E_n, X_n), \quad (1)$$

where  $X_1, X_2, \dots, X_n$  are the population densities of the  $n$  competing species in the system, and  $c_i$  is some function.

Environmentally dependent parameters can be expected to affect the amount of competition occurring through their effects on the abundances of competing forms. For example, if the environmentally dependent parameter is a germination rate, it will affect the abundance of seedlings, which potentially strongly affects the intensity of competition as these seedlings grow. This indirect effect of  $E_i$  through its effect on competition depends on the density of the species, and vanishes when the species' density is 0.

With these definitions, population dynamics in discrete time can be represented as:

$$X_i(t+1) = G_i(E_i, C_i) X_i(t), \quad (2)$$

where the function  $G_i$  combines  $E_i$  and  $C_i$  to give the finite rate of increase of species  $i$  from time  $t$  to time  $t+1$ . A particular example of a model within this general class of models is shown in Table 1.

To analyse the model, we express population growth on the log scale, writing

$$\ln X_i(t+1) - \ln X_i(t) = g_i(E_i, C_i), \quad (3)$$

where  $g_i$  is simply  $\ln G_i$ . Changes in  $\ln$  population size over any period of time can be found as the sum of  $g_i$

Table 1. *Seed-bank model*

$X_i(t+1) = [(1 - E_i(t)) s_i + E_i(t) Y_i / C_i(t)] X_i(t)$ .
$X_i(t)$ : size of seed bank of species $i$ at the beginning of year $t$ before germination.
$E_i(t)$ : germination fraction of species $i$ in year $t$ .
$s_i$ : yearly survival rate for ungerminated seeds.
$Y_i$ : seed yield per germinated seed in the absence of competition.
$C_i(t)$ : Reduction in seed yield due to competition. A function of the number of seeds germinating, e.g. $C_i(t) = 1 + \sum_{j=1}^n \alpha_{ij} E_j(t) X_j(t)$ , for constants $\alpha_{ij}$ .
$G_i(E_i, C_i)$ : $[(1 - E_i(t)) s_i + E_i(t) Y_i / C_i(t)]$ , the finite rate of increase for species $i$ .

over that period. It follows that the observed trend in population growth over any period of time is the simple arithmetic average of  $g_i$  for the period. Thus, to predict future trends in population growth, we average  $g_i(E_i, C_i)$  over the theoretical probability distribution of  $E_i$  and  $C_i$ .

According to the standard invasibility analysis (Turelli 1981; Chesson & Ellner 1989), a species will persist in the presence of its competitors if its population recovers after fluctuations to low density. Such recovery is determined by the mean low density growth rate, which is defined as the average value,  $\Delta_i$ , of  $g_i(E_i, C_i)$ , with  $X_i(t)$  set equal to 0. This is expressed mathematically as

$$\Delta_i = E[g_i(E_i, \hat{C}_i)], \quad (4)$$

where the  $E$  outside the square brackets is the mathematical symbol for averaging the quantity inside over its theoretical probability distribution. The notation  $\hat{C}_i$  means  $C_i$  evaluated with  $X_i$  set equal to 0.

If  $\Delta_i$  is positive, we know that species  $i$  will tend to increase from low density, and thus avoid competitive exclusion. If it is negative, species  $i$  will tend to decrease from low density and may become extinct.

For two-species communities, under certain conditions, Chesson & Ellner (1989) showed that positive values for the  $\Delta$ s of both species imply coexistence in the sense that both species show steady fluctuations, and always recover from excursions to lower densities (figure 1). Negative values for both species mean that they have positive probability of converging to extinction and that one of them must eventually do so, a situation that can be described as random competitive exclusion.

Finally, if the  $\Delta$ s of the two species are of opposite sign, the species with the negative  $\Delta$  is driven extinct by the other species. No such rigorous analysis has been completed for the  $n$  species situation, but Turelli (1980) and Ellner (1985) have found the invasibility approach to be generally supported by computer simulations.

Invasibility analysis requires knowledge of the probability distribution of  $\hat{C}_i$ . To get this, one assumes

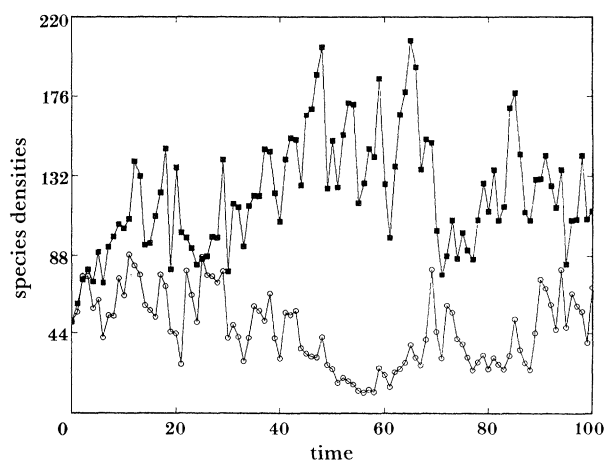


Figure 1. Competition between two species satisfying the seed-bank model of table 1. The species with open circles is competitive subordinate with  $Y$  value 80% of that of the other species. The  $E_i$  have independent rectangular distributions,  $s_1 = s_2 = 0.9$ , and  $\alpha_{ij} = 1$  for all  $i, j$ .

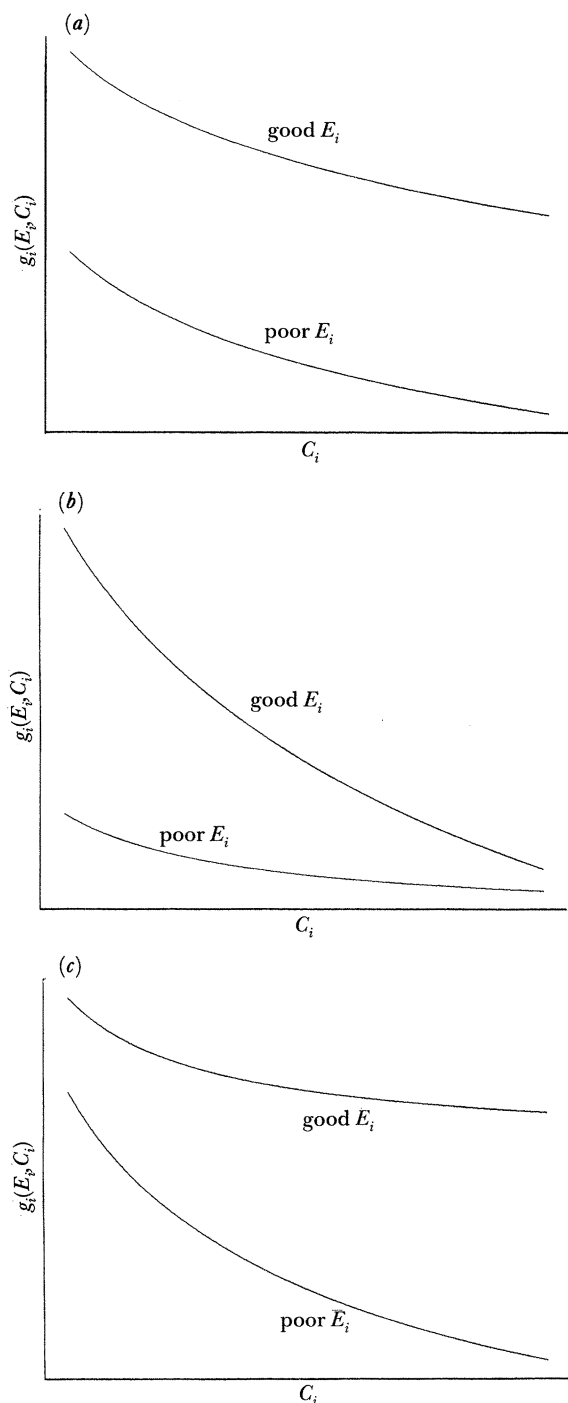


Figure 2. Change in log population size ('growth rate'), as a function of  $C_i$  for different values of the environmentally dependent parameter. (a) additive; (b) subadditive; (c) superadditive.

that the other species in the system have settled down to the sort of fluctuations that they achieve in the long-run after the removal of species  $i$ . This means in particular that the probability distribution of any species  $j$ , say, has no further changes over time, i.e. is described by a stationary probability distribution (Turelli 1981).

Stationary distributions are difficult to calculate in general, which means that we must resort to various tricks to get enough information about them. One such trick is recognizing that if species  $j$  is at its stationary distribution, then  $E[\ln X_j(t+1)]$  and  $E[\ln X_j(t)]$  are the

same because the probability distribution of  $X_j$  used to calculate these averages is the same at both times  $t$  and  $t+1$ . It follows that the difference between them is 0, i.e.

$$E[g_j(E_j, \hat{C}_j)] = 0. \quad (5)$$

By using these ideas it is possible to show that the shapes of the functions  $g_i$  are critical in determining the effect of environmental fluctuations on coexistence. Figure 2 shows the three possible shapes that growth rates can have. These different general types of growth rates are called additive, subadditive or superadditive, depending on whether the plot of  $g_i(E_i, C_i)$  against  $C_i$  for different values of  $E_i$  gives parallel curves, converging curves or diverging curves. These shapes are generally associated with diversity neutral, diversity promoting and diversity demoting effects of environmental fluctuations (Chesson 1988), respectively. How these different effects come about is best understood by the geometric approach presented here.

### COEXISTENCE AND THE GEOMETRY OF POPULATION GROWTH RATES

To introduce this geometric approach, I make a number of simplifying assumptions. I assume that the species differ only in their responses to environmental factors. Thus I shall assume that the  $g_i$ s are all the same, and so we can drop the subscript. Similarly, I assume that the  $C_i$  are all the same. Thus all species are affected by the same, possibly composite, competitive factor.

With these assumptions we can set about calculating  $\Delta_i$  for any species, arbitrarily designated as  $i$ , within this  $n$  species system. We use the technique of conditional expectations, which allows us to evaluate  $\Delta_i$  in stages. We compare the growth rate of species  $i$  at low density with the growth rate of some other species  $j$ , assuming that  $j$  and all other species are at their stationary distribution. Thus species  $j$  has a mean growth rate equal to 0 in accordance with equation (5).

The environmentally dependent parameters of species  $i$  and  $j$ ,  $(E_i, E_j)$ , have some bivariate probability distribution. Let  $(\epsilon_+, \epsilon_-)$  be one point chosen from this distribution with  $\epsilon_+ > \epsilon_-$ . We consider the effects of  $(E_i, E_j)$  fluctuating between the two values  $(\epsilon_+, \epsilon_-)$  and  $(\epsilon_-, \epsilon_+)$ . This is equivalent to conditioning on the event that  $(E_i, E_j)$  takes one or the other of these two values. We also condition on the environmentally dependent parameters of all other species, and all species population densities. Thus, we consider all these things as fixed for the time being. The only uncertainty left is whether  $(E_i, E_j)$  takes the value  $(\epsilon_+, \epsilon_-)$  or  $(\epsilon_-, \epsilon_+)$ . These restrictions let us focus on the most important aspects of population dynamics geometrically (figure 3).

Under the imposed conditions,  $\hat{C}$  can only vary with  $E_j$  as  $\hat{C}$  does not depend on  $E_i$  when  $X_i = 0$ , and everything else is being conditioned on (is fixed for now). Thus  $\hat{C}$  can take just the values

$$\epsilon_- = c(E_1, X_1, E_2, X_2, \dots, \epsilon_-, X_j, \dots, E_n, X_n), \quad (6)$$

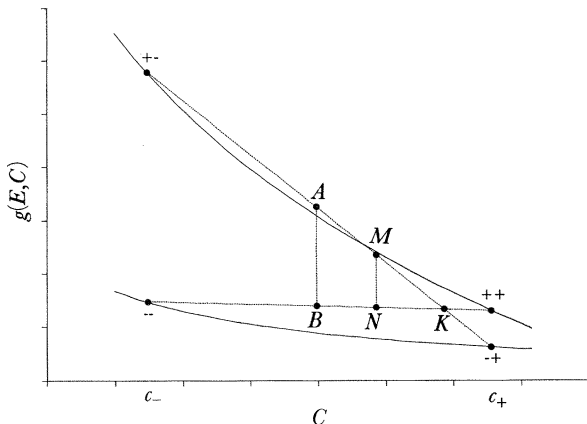


Figure 3. The growth rates  $g(E_i, \hat{C})$  (top curve) and  $g(\epsilon_-, \hat{C})$  (bottom curve), as functions of  $\hat{C}$  for the subadditive case.

and

$$c_+ = c(E_1, X_1, E_2, X_2, \dots, \epsilon_+, X_j, \dots, E_n, X_n). \quad (7)$$

It follows that  $g(E_i, \hat{C})$  fluctuates between the two values  $g(\epsilon_+, c_-)$  and  $g(\epsilon_-, c_+)$ , while  $g(E_j, \hat{C})$  fluctuates between the values  $g(\epsilon_-, c_-)$  and  $g(\epsilon_+, c_+)$ . Labelling these values of  $g$  as  $g_{+-}$ ,  $g_{--}$ , etc. these fluctuations can be located on the figure 3 as fluctuations between the point  $+-$  and  $-+$  for species  $i$ , and  $--$  and  $++$  for species  $j$ . These points have the respective coordinates  $(c_-, g_{+-})$ ,  $(c_+, g_{--})$ ,  $(c_-, g_{--})$ ,  $(c_+, g_{++})$ .

Their probabilities will generally not be equal. If  $p$  is the probability that  $(E_i, E_j)$  takes the value  $(\epsilon_+, \epsilon_-)$ , then the points  $+-$  and  $--$ , have probability  $p$  and the points  $++$  and  $-+$  have probability  $q = 1 - p$ .

The first stage in calculating  $\Delta_i$  is averaging  $g_i$  for the restricted conditions of figure 3. This average is found at the point  $M = (\bar{c}, \bar{g}_i) = (pc_- + qc_+, pg_{+-} + qg_{--})$ , which lies on the line joining  $+-$  and  $-+$ , dividing it in the ratio  $q:p$ . Depicted here is a situation where  $q > p$ . If  $q$  were equal to  $p$ ,  $M$  would lie at the point  $A$  dividing the line segment  $+-$  to  $-+$  in equal portions. The corresponding point  $(\bar{c}, \bar{g}_j)$  for species  $j$  lies at the point  $N$ , shown here below  $M$ .

Figure 3 shows that  $M$  lies above  $N$ , so that  $\bar{g}_i > \bar{g}_j$ , whenever these points are to the left of the point  $K$ . In this situation species  $i$  has a higher average growth rate than species  $j$  for fluctuations between the two chosen environmental states. Thus species  $i$  has an advantage in average growth rate. This advantage comes from the fact that its growth rate fluctuates between  $+-$  and  $-+$  while species  $j$  has fluctuations between  $--$  and  $++$ , which in turn comes from the fact that species  $i$  is at low density (an invader) while species  $j$  is a resident.

This low-density advantage means that species  $i$  can experience a sizeable disadvantage in frequency of favourable environmental states ( $p \ll q$ ), and yet still have a higher average growth rate than other species. For example, in the specific geometry of the figure,  $K$  divides the lines  $--++$  and  $+- -+$  roughly in the ratio 6:1, which means that species  $i$  would have to have a greater than 6:1 disadvantage to species  $j$  in frequency of favourable conditions, before it had a lower average growth rate.

Under what conditions does this low-density advantage mean that a species will be able to coexist with its competitors? The low density average growth rate,  $\Delta_i$ , is the average value of  $\bar{g}_i$  when all the variables that were fixed to construct figure 3, are now varied over their distribution of possible values. Because species  $j$  is assumed at its stationary distribution, the average of  $\bar{g}_j$  is 0. It follows that

$$\Delta_i = E[\bar{g}_i - \bar{g}_j], \quad (8)$$

which is the average of the difference between points  $M$  and  $N$  in figure 3, when the environmentally dependent parameters and species densities vary over their joint probability distribution of possible values. Thus if species  $i$  is never at such a disadvantage to its competitors that  $M$  and  $N$  lie to the right of  $K$ , then species  $i$  must persist in the system. If this is true for each species considered individually in the low-density state, then all species coexist together in spite of potentially significant average disadvantages that some species may have.

The situation just considered, however, is not very realistic. It is more likely, when there are inequalities between species, that the points  $M$  and  $N$  will lie to the right of the point  $K$  for some values of  $\epsilon_+$ ,  $\epsilon_-$ , for some population densities and some values of the environmentally dependent parameters of other species, which are held fixed to construct figure 3. The final average value,  $\Delta_i$ , of  $\bar{g}_i - \bar{g}_j$  is then an average of situations in which  $MN$  is to the left of  $K$  and situations where it is to the right of  $K$ . The geometry of the figure biases the outcome such that positive values of  $\bar{g}_i - \bar{g}_j$  will tend to predominate, leading to a positive result for  $\Delta_i$  unless species  $i$  is too greatly inferior to other species. The situation is far from straightforward, however, as is best understood through some specific examples.

Consider a two-species model of strong competition for space, such as the lottery model (Chesson & Warner 1981). If reproduction is always sufficient to fill the available space in spite of fluctuations in the environmentally dependent parameters, then the population density of the resident species  $j$  does not fluctuate with time. The line  $--++$  is horizontal and  $\bar{g}_j = 0$ . If the environment does only fluctuate between two states, figure 3 tells the complete story, for then  $\Delta_i = \bar{g}_i$ . If the inferior species is not so inferior that  $NM$  is at or to the right of  $K$ , the species coexist.

How do we proceed to the more useful situation where the environmentally dependent parameters take on a continuum of values? This is surprisingly simple for the lottery model if the birth rates are the environmentally dependent parameters and the logs of these are normally distributed, possibly correlated between species, with equal variances but different means. For low adult death rates, and any given set of model parameters, it can be shown that  $MN$  is always to the left of  $K$  or always to the right. This is also true if one makes the assumption that the mean differences between species and the variances are small, but that the adult death rates have any value. In other cases, it can be expected that some chosen values of  $(\epsilon_+, \epsilon_-)$  will

have  $MN$  to the left of  $K$  while for others it will be to the right, leading to some positive values of  $\bar{g}_i$  and some negative values. The final sign of  $\Delta_i$  in such situations necessarily involves averaging the  $\bar{g}_i$  values over the distribution of  $(\epsilon_+, \epsilon_-)$ .

As a further illustration, consider symmetric competition between species, as discussed by Chesson (1988). This means in particular that the competition function depends on all species in the same way, and the probability distributions of environmentally dependent parameters are the same for all species. Until now, we have not made the usual 'white noise' assumption that the environment process is independent over time. Indeed, the forgoing results apply for any colour of the noise process. However, it is now important to make the white noise assumption that the environment process takes values in the next time period that do not depend on values it has taken in previous time periods. This assumption means that conditioning on population densities, whatever they may be, does not upset the symmetric relation between the environmentally dependent parameters of the invading species  $i$  and the chosen test species resident  $j$ . (The analysis can be done with any of the  $n-1$  resident species without affecting the results.)

In this setting, the symmetry of the relations among the species means that  $p = \frac{1}{2}$ ,  $MN$  coincides with  $AB$  and divides the lines  $+- - +$  and  $- - + +$  exactly in half. In the subadditive situation of figure 3,  $K$  lies right of  $AB$ , unless  $\epsilon_+ = \epsilon_-$ , in which case the figure collapses to a single point. Thus whenever  $\epsilon_+$  differs from  $\epsilon_-$ ,  $\bar{g}_i - \bar{g}_j$  is positive. It follows that if the species can have different values for their environmentally dependent parameters, i.e. show some differences in their responses to the environment,  $\Delta_i$  is positive for all species. Thus these  $n$  species coexist.

Symmetry is not realistic, but the power of the symmetric example is that very few assumptions are needed along with symmetry to prove coexistence. Thus, setting symmetry aside, it is very general indeed. Moreover, the final result, coexistence of all  $n$  species, can be expected to be robust to small departures from symmetry, because the  $\Delta_i$  will usually change continuously with continuous deformation of the model. Thus small departures from symmetry are unlikely to make any of the  $\Delta_i$  negative or zero, and so coexistence is likely to be preserved. Sufficient departures from symmetry, however, will lead to competitive exclusion of some species.

Our analysis suggests that the stronger the convergence of the growth curves in figure 3, the more asymmetry can be tolerated before exclusion occurs, and this expectation is supported by approximate formulae for the  $\Delta_i$  (Chesson 1989). The reason for this is that  $K$  will then be a long way to the right of  $AB$ , and so quite small  $p$ -values, i.e. large disadvantages to species  $i$ , can be tolerated before  $\bar{g}_i - \bar{g}_j$  becomes negative.

In some cases the growth rates do not merely converge, but cross. This is the case with the seed bank model of table 1, depicted in figure 4. Then it is possible for fluctuations to occur between environmental states that always lead to a greater growth rate

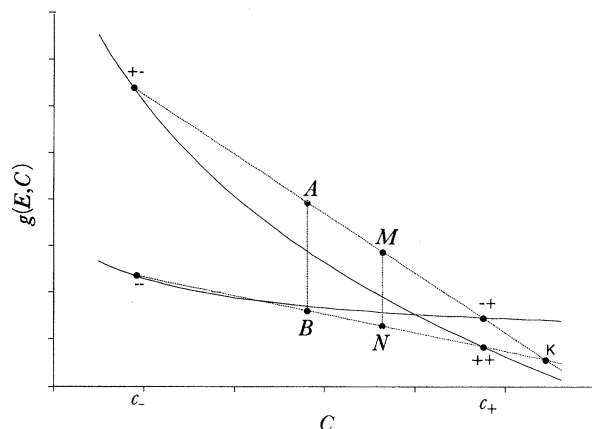


Figure 4. Intersecting subadditive growth rates of the seed-bank model.

for a species at low density, and  $\bar{g}_i - \bar{g}_j$  is positive even when  $p = 0$  (figure 4).

### COMPETITIVE EXCLUSION

Figure 2 shows three possibilities for the growth rate  $g_i(E_i, C_i)$ . In addition to the subadditive case (figure 2*b*) discussed above, the growth rate could be additive (figure 2*a*) or superadditive (figure 2*c*). The geometry of the additive case means the sign of  $\bar{g}_i - \bar{g}_j$  is simply the sign of  $p - q$ . Thus additivity confers no advantage on a species at low density that might offset other disadvantages, and we cannot expect environmental fluctuations to promote coexistence or competitive exclusion.

The superadditive case is easily seen to confer a disadvantage on a species at low density. This can offset advantages that a species may have, allowing dominance by other species, or promoting a situation where all species have negative low-density growth rates. The latter situation leads to random competitive exclusion (Chesson & Ellner 1989).

### GENERATION OF NON-ADDITIVITY BY WITHIN POPULATION HETEROGENEITY

The simplest sorts of population models tend to be additive (Chesson 1988). Additivity comes about when the action of competition does not affect the action of the environment and vice versa, given their values. This means that the finite rate of increase,  $G(E, C)$ , takes the general form

$$G(E, C) = A(E)/B(C), \quad (9)$$

where now I have dropped the species subscript for simplicity of notation. Note that this assumption is quite independent of the idea above that the actual value of  $C$  depends on the value of  $E$ . Taking logs of this gives

$$g(E, C) = \ln A(E) - \ln B(C), \quad (10)$$

which is the additive form giving the parallel growth rates of figure 2*a*. Departures from the additive

situation can be measured by the quantity  $\gamma$ , defined by

$$\gamma = \frac{\partial^2 g}{\partial E \partial C}, \quad (11)$$

which is zero in the additive case.

The independence of action of  $E$  and  $C$  expressed in (9) can also be thought of as meaning that competitive and environmental factors operate uniformly across all individuals in the population. Thus the fact that an individual has been affected a certain way by the environment does not alter the effect that competition will have. The seed-bank model of table 1 gives an obvious departure from this situation. The effect of environment is to bring on seed germination or not. If an individual does not germinate, it is assumed to experience no competition. On the other hand, an individual that germinates is exposed to competition from other individuals as they grow. It follows that the environmental factor and the competitive factor are far from independent in action. If the environment increases the germination fraction, it necessarily increases the fraction of the population that is exposed to competition.

Dependence of action comes about because the population is subdivided into groups of individuals that are doing different things at the same time, and these different groups are affected differently by environmental and competitive factors. Thus we can represent the growth rate of the entire population, subdivided into different contributions to population growth, as follows:

$$G(E, C) = \sum_{l=1}^k G_l(E, C), \quad (12)$$

where  $G_l(E, C)$  simply represents a contribution to the growth rate from the  $l$ th of  $k$  possible sources. In the seed bank model, for example, we have  $G_1(E, C) = (1-E)s$ , and  $G_2(E, C) = EY/C$ .

It is important to note that the components of the growth rate in equation (12) could each be additive; that is within components, the action of environment and competition could be independent, but the overall effect when they are combined is interactive, not independent (Chesson & Huntly 1988). To see how this comes about, we define sensitivity to environment, competition, and their interaction for each of the components of population growth as follows:

$$\alpha_l = \frac{\partial g_l}{\partial E}, \quad \beta_l = -\frac{\partial g_l}{\partial C}, \quad \gamma_l = \frac{\partial^2 g_l}{\partial E \partial C}, \quad (13)$$

where  $g_l = \ln G_l$ .

We can now express the deviation of the total population growth rate,  $g(E, C)$ , from additivity by the formula

$$\gamma = \bar{\gamma} - \sum_{l=1}^k (\alpha_l - \bar{\alpha})(\beta_l - \bar{\beta}) G_l / \sum_{l=1}^k G_l \quad (14)$$

where  $G_l$  is just a shorthand for  $G_l(E, C)$ , and  $\bar{\alpha}$ ,  $\bar{\beta}$ ,  $\bar{\gamma}$ , are the weighted averages

$$\bar{\alpha} = \sum_{l=1}^k \alpha_l G_l / \sum_{l=1}^k G_l, \quad (15)$$

etc.

Equation (14) gives the measure of nonadditivity,  $\gamma$ , as an average of the nonadditivity that may occur in each component by itself minus the weighted covariance between  $\alpha_l$  and  $\beta_l$ . The weights in these calculations,  $G_l$ , are each component's contribution to population growth.

This representation of non-additivity,  $\gamma$ , is most useful when the  $\gamma_l$  are zero, meaning that the components have been chosen such that within a component, environment and competition act uniformly across all individuals. If the  $\gamma_l$  are not zero this may mean that the components are themselves heterogeneous with respect to the operation of environment and competition, and can be further subdivided. In some cases, however, non-additivity arises within a component as a behavioural or physiological response that is not easily reducible (Chesson 1988).

In the case when the  $\gamma_l$  are zero, the population-level nonadditivity is simply minus the weighted covariance of the  $\alpha_l$  and the  $\beta_l$ , which can best be understood by means of a scatter plot of the  $\alpha_l$  and  $\beta_l$ . For example, the seed bank model of table 1 is shown as the two-point scatter plot, figure 5. Point A is for the seeds that remain in the soil. The fraction of seeds in this component is  $1-E$ , where  $E$ , the germination fraction, is the environmentally dependent parameter. The number of seeds in this component is therefore negatively sensitive to  $E$ . Dormant seeds do not compete, and so the sensitivity of this component to competition is zero. Thus the point A has a negative value of  $\alpha_l$  and a zero value of  $\beta_l$ .

The point B in the figure corresponds to seeds that germinated, and therefore grow and compete with each other and plants of other species. This component is increased by germination, and experiences competition; thus it represents positive values for both  $\alpha_l$  and  $\beta_l$ . The covariance measures common linear variation among the two variables  $\alpha_l$  and  $\beta_l$ , which is perhaps best understood by appreciating that it equals the correlation between them times the product of their standard deviations. Thus it involves how closely they lie on a straight line, the sign of the line's slope, as well as the amount of variation shown by each variable.

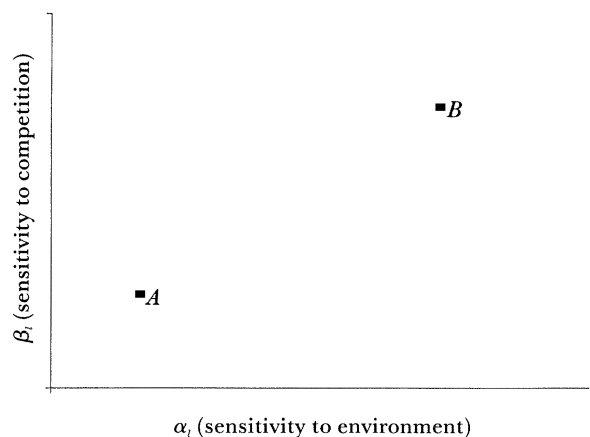


Figure 5. Two-point scatter plot for a population with two distinct components to its growth rate showing positive covariance of sensitivities to environmental and competitive factors.

The relation between the covariance and non-additivity can be seen intuitively, also. As the environmentally dependent parameter is increased, components with higher sensitivity to the environment contribute relatively more to population growth compared with other components. Positive covariance of sensitivity means that these same components are those with higher sensitivity to competition, and so the population as a whole has more average sensitivity to competition. Thus, the change from low slope to a more negative slope shown in figure 2*b*, which means that  $\gamma$  is negative.

The seed bank example is perhaps a further worthwhile illustration. As  $E$  increases, more of the seeds germinate, and are exposed to competition. Thus, average population sensitivity to competition increases. One can also view this from the perspective that as  $E$  increases, more of the population is at point  $B$  in figure 5 (where there is high sensitivity to competition) and less at point  $A$  (where there is low sensitivity to competition).

One can use scatter plots like this to assess nonadditivity whenever a population can be divided into components with differing sensitivities to environment and competition. A few more examples will serve to illustrate. In many organisms the juvenile phase is especially sensitive to environmental and competitive factors, compared with the adult organism. Thus point  $B$  in figure 6 could represent these juveniles and point  $A$  the adult phase. Thus, again there is positive covariance of sensitivities, and a negative value of  $\gamma$ . Previously this situation has been discussed under the heading of the storage effect (Warner & Chesson 1985), which now can be seen as a special case of the more general concept, subadditivity.

Another example involves subpopulations in different habitats. Spatial variation in the quality of living conditions occurs for all organisms, as has been documented extensively in plants (Harper 1977; Gross 1984; Silvertown 1987). Are there places, however, that are less sensitive to environmental factors than elsewhere, and also less sensitive to competition? It may well be that in plant populations, areas that are relatively and permanently harsh may qualify. Such

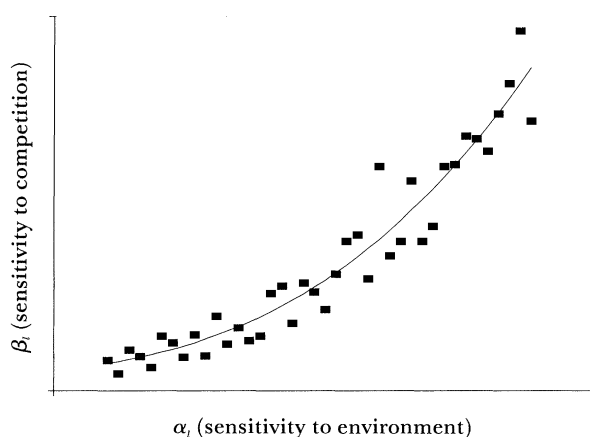


Figure 6. Scatter plot for a population whose growth rate has many components, showing positive covariance of sensitivities. The line represents an ideal  $l$  factor causing a strict relation between  $\alpha_i$  and  $\beta_i$ .

harshness may limit individual growth making it unresponsive to other factors, including temporally fluctuating environmental factors and fluctuating competition.

An alternative example involves cases where recruitment into especially favourable spots is limited, thus keeping densities low. For example, considering species that compete for moisture, small naturally moist areas may never achieve densities high enough for much competition if they are so small that most dispersal is away from them (DeAngelis *et al.* 1979). Lowered sensitivity to the environment must go along with this lowered sensitivity to competition if  $\gamma$  is to be negative. In the situation just envisaged, lowered stress might make individuals less sensitive to the environment. Clearly, this need not always be so, as removal of moisture limitation might make individuals more responsive to other factors. If that occurred, the covariance of sensitivities would be negative, and the measure of non-additivity,  $\gamma$ , would be positive giving the superadditive situation of figure 2*c*.

In addition to spatial variation, variation with life-history stage or population growth process, one could also consider phenotypic variation. This is of particular interest in relation to the seed bank model, because the same individual plant may produce different phenotypes of seeds with the potential for different germination properties and different competitive abilities (Cavers & Steel 1984; McGinley *et al.* 1987; Fenner 1985; Venable & Brown 1988; Silvertown 1989). Covariation in these traits might well be another source of non-additivity.

### THE THREE FACTOR SCHEME

There seems to be an endless variety of ways in which populations could be heterogeneous and through which non-additivities could occur. The purpose of this section is to provide some general way of viewing the possibilities to aid the investigation of the relevant sorts of heterogeneity. In general, it can be expected that there will be a host of factors contributing to individual survival, growth and reproduction, and ultimately population growth. Some factors are consumed, and as a result of consumption become less available. More generally, some factors create a negative feedback loop for the affected species in the community (Andrewartha 1970). We associate such factors with competition, and we refer to them as  $C$  factors.

Other factors may not lead to any kind of feedback for the relevant biological populations. I divide these into two sorts,  $E$  factors and  $l$  factors. The  $E$  factors are those that vary over time. The  $l$  factors are those that do not vary over time, but instead vary within a single species population (one member of a community of similar species). For simplicity, we shall think of a population as having just one of each of the three sorts of factors. These of course could be composite factors, but thinking of them as single factors will help sharpen intuition. These three factors,  $C$ ,  $E$ , and  $l$ , lead to competitive parameters, environmentally dependent parameters, and population subdivision respectively, as discussed in the models above.



The importance of the factor  $l$  is its effects on the other two factors. For plant species it is known that some factors (essential or interactively essential resources) have strong effects on the sensitivities of the organisms to other factors (Tilman 1988). An example is perhaps shade as a factor in the dynamics of species in the understory of forests (Dahlem & Boerner 1985). Shade is an  $l$  factor if we assume that understory species are shaded by trees but do not shade each other, and that tree canopy density varies.

Plant growth is sensitive to temperature (Larcher 1983), but light limitation through shade restricts a plant's ability to respond to warmer weather. Perhaps more importantly, shade moderates temperatures. Thus shade should affect the sensitivity of plant growth to variation in the weather, which can be the  $E$  factor, and would be measured in some standardized way such as plant temperature in full sunlight.

Shade, through light limitation is also likely to affect competition for resources such as nutrients (Tilman 1988), which might be the  $C$  factor. Thus we see that shade, the  $l$  factor, leads to joint positive variation in sensitivity to the  $E$  and  $C$  factors. A scatter plot such as in figure 6 would be obtained. The different points in the figure represent different places on the forest floor. Ideally, if  $E$ ,  $C$ , and  $l$  were all truly single factors, and there were no other factors present, these points would all lie on the single curve through the points. In reality, however, other factors varying from place to place are likely to make it a scatter. The positive covariance of sensitivities shown here means that growth rates for the population encompassing the points in the scatter plot, would be subadditive. Thus according to the community theory presented here, we should expect that a scatter plot like that in figure 6 should help maintain species diversity in a fluctuating environment.

The factor  $l$  might in some cases be qualitatively different from the other factors. In the seed bank model, for instance, the factor  $l$  simply distinguishes between the class of individuals growing above ground and those remaining as seeds. Thus it is simply a label for two somewhat incomparable components. In the case of seed phenotypes, the factor  $l$  might be seed size, and there is evidence that seed size affects response to both environmental and competitive conditions (McGinley *et al.* 1987; Fenner 1985; Venable & Brown 1988; Silvertown 1989).

While this theory involving  $E$ ,  $C$  and  $l$  factors may have elements in common with Tilman's (1982) theory of plant competition, it nevertheless has important differences. For example, in this theory coexistence can occur if all species are limited by the same competitive factor. In other words  $C$  can be identical for different species. In contrast Tilman's theory requires  $C$  to be different for different species. In this regard, it is important to note that the  $l$  factor here is not a competitive factor and can affect all species similarly. The environmental factor,  $E$ , however, must distinguish between species at least quantitatively. For example, different species might have different abilities to benefit from higher temperatures.

## CONCLUSION

The likely broad occurrence of non-additivity in nature implies that temporal environmental fluctuations quite generally modify the outcomes of competitive interactions between species. However, the actual effect of environmental fluctuations depends on whether non-additivity is in the subadditive or super-additive direction. How much environmental fluctuations modify the outcomes of competition depends on the strength of non-additivity as measured here by a covariance of within-population heterogeneity.

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### Discussion

P. J. GRUBB (*Botany School, University of Cambridge, U.K.*). Would Professor Chesson please show how his analyses may be used to determine the limiting similarity between species?

P. CHESSON. This paper explores just one of many different ways that species may differ from one another. Within this restricted context it shows how dissimilarity of responses to environmental factors gives an advantage to a species at low density, opposing competitive exclusion. This effect depends on growth rates being subadditive (figure 2*b*), and its strength depends on the magnitude of subadditivity, or the rate of convergence of growth-rate curves for different environmental conditions. How increased dissimilarity increases the low-density advantage can be seen from figure 3. More dissimilarity means that the points labeled + – and – – will be further separated from + + and – +. It is easiest to imagine these points as shifted to more extreme positions on the depicted growth rate curves, but in fact these curves also change making the contrast in slope greater. However this is viewed, the important outcome is the same: more dissimilarity increases the contrast between the distances – – to + – and – + to + +, with the effect that the low density advantage given by the distance MN is increased.

This geometric approach helps in understanding how a limit to similarity arises in populations in a fluctuating environment. Quantitative measurement of the limit to similarity is best pursued by approximate formulae for the mean low density growth rate that I have presented elsewhere (Chesson 1989). These allow classical niche dissimilarity involving resource use to be considered in concert with dissimilarity arising through differences of responses to fluctuating environmental factors.