

# Temporal Hierarchies of Variation and the Maintenance of Diversity

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**Abstract** A general model shows how the long-term growth rate of a population can be partitioned into components representing various mechanisms of maintenance of species diversity. One component summarises the effects of fluctuation-independent mechanisms, which include classical resource partitioning and frequency-dependent herbivory. Two other components represent fluctuation-dependent mechanisms, the storage effect and relative nonlinearity of competition.

The general model shows how a community will track an equilibrium set by fluctuation-independent mechanisms and the environmental state when community dynamics are faster than the rate of environmental change. Fluctuation-dependent mechanisms can be important for diversity maintenance with or without such tracking, but on long timescales their effects are indistinguishable from those of fluctuation-independent mechanisms.

These considerations lead to a hierarchical view of mechanisms of diversity maintenance where the effects of different timescales are partitioned or merged depending on the timescale of observation. These issues are illustrated with model examples involving various combinations of resource partitioning, fluctuations in recruitment rates, variation in the timing of germination, and seasonality. The very long timescales associated with climate change contain many complexities but nevertheless many ideas applicable to shorter timescales may be useful in a modified form.

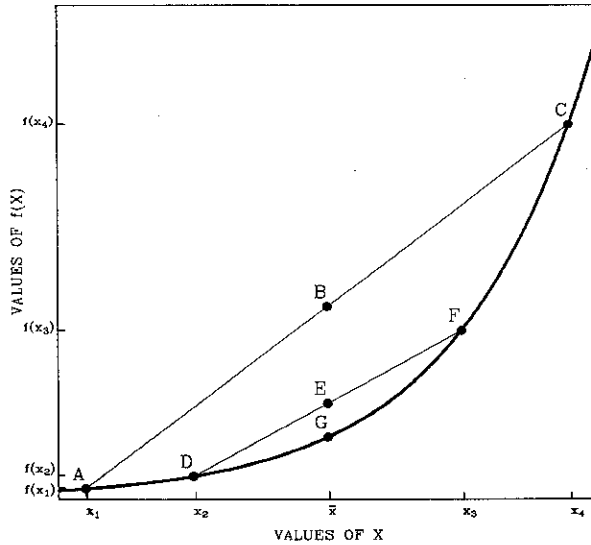
**Key words:** diversity maintenance, competition, storage effect, temporal hierarchy.

Ecologists have long believed that variation matters a great deal in the maintenance of diversity, and that an important aspect of variation is the scale on which it occurs. However, a conceptual framework permitting an understanding of variation and scale has been emerging only recently. Hierarchy theory (Allen and Starr, 1982; O'Neill et al., 1986; O'Neill, 1989) has given some ways of thinking about temporal scale of variation, and models of community dynamics have provided an understanding of temporal variation as a mechanism of diversity maintenance (Abrams, 1984; Chesson, 1989, 1994; Ebenhoeh, 1991; Loreau, 1992).

An important issue is the extent to which a community at a particular place and time is explicable by conditions observable at that place and time (Davis, 1986). The traditional equilibrium approach to communities seeks conditions for a stable equilibrium in terms of current conditions. Implicit in this approach is faith that current conditions can explain communities. How can such an approach be reconciled with temporal environmental variation? There is no contradiction if communities follow or "track" an equilibrium determined by environmental conditions. Then a community as cur-

rently observed is determined by current conditions. Tracking an equilibrium, however, requires a community to approach equilibrium at a faster rate than the rate of change in the equilibrium (Roughgarden, 1975, 1979).

Irrespective of tracking on any scale, a major influence on community dynamics arises from the manner in which variation propagates up a hierarchy of temporal scales (Chesson, 1991). This effect comes from the phenomenon of nonlinear averaging—see Fig. 1. When nonlinear averaging occurs, variation on one scale appears as a systematic effect on another scale, and has the potential for qualitative as well as quantitative effects on community dynamics. The predictions of models of environmental variation (e.g. Chesson and Huntly, 1989), including models of disturbance (e.g. Hastings, 1980) depend on such nonlinear averaging. For example, Chesson and Huntly (1989) show how nonlinear averaging can convert instability on a short timescale to stability on a long timescale. In their model, the community is unstable for any fixed environmental conditions and would lose species over time. However, environmental fluctuations mean that the rank order of dominance in the community changes with time. Nonlinear averaging can convert this fluctuating rank order of dominance into a stable coexistence.



**Fig. 1.** Illustration of nonlinear averaging: The variable  $X$  on the horizontal axis fluctuates between the values  $x_1$  and  $x_4$ , with equal frequency, or the values  $x_2$  and  $x_3$ , with equal frequency. In both cases the average value of  $X$  is  $\bar{x}$ . The function  $f$ , whose graph is given by the thick line, represents some property of a biological system dependent on the fluctuating variable  $X$ . Because the graph of  $f$  is nonlinear (not a straight line) the average value of  $f(X)$  is not given by the point  $G$  (with vertical coordinate  $f(\bar{x})$ ) but by the point  $B$  or the point  $E$ , the mid point of the straight line joining the points  $A$  and  $C$  or the points  $D$  and  $F$ , because the vertical coordinates of these points  $B$  and  $E$  are respectively the averages of  $f(X)$ ,  $1/2[f(x_1) + f(x_4)]$  and  $1/2[f(x_2) + f(x_3)]$ . Note that the difference between  $f(\bar{x})$  and the average of  $f(X)$  increases with the variance of the fluctuations.

### Environmental Tacking and Nonlinear Averaging

A general model of Chesson (1989, 1994) provides an approach to temporal hierarchies in communities of competing species. A particular example serves to illustrate the important concepts. Consider a community of  $n$  iteroparous perennial organisms with fluctuating recruitment rates. Let a unit of time be a year and express the population density of species  $i$  at time  $t+1$  ( $X_i(t+1)$ ) in terms of population density at time  $t$ , environment, and competition according to the formula

$$X_i(t+1) = s_i X_i(t) + E_i(t) X_i(t) / C_i(t), \quad (1)$$

where  $s_i$  is the survival rate of mature (adult) individuals of species  $i$ ,  $E_i(t)$  is the rate of recruitment to the adult population in the absence of competition, and  $C_i(t)$  represents the multiple by which such recruitment is reduced by competition between immature individuals. If population density is measured in terms of biomass per

unit area instead of numbers of individuals, this model also applies to organisms that increase in size as adults, and as a consequence increase their fecundity. In such cases,  $s_i$  is not the mortality rate but the rate of attrition of adult biomass, thus summarising mortality and growth (Warner and Chesson, 1985).

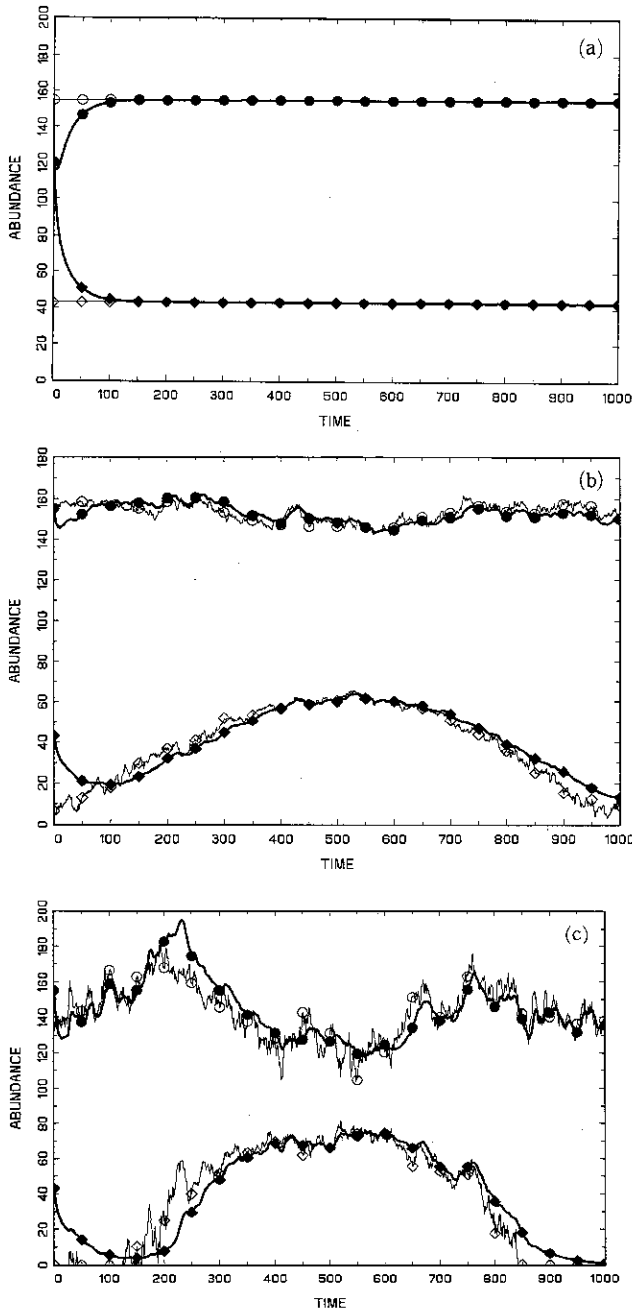
We use the Ricker form of the competition parameter,  $C_i(t)$ , popular in discrete time models (e.g. Turelli, 1981). This competition parameter is here specialised for competition between immature individuals, whose numbers are assumed proportional to  $E_j(t)X_j(t)$  for species  $j$ :

$$C_i(t) = \exp \left\{ \sum_{j=1}^n \alpha_{ij} E_j(t) X_j(t) \right\}. \quad (2)$$

In this formula,  $\alpha_{ij}$  is the coefficient of competition for the impact of immatures of species  $j$  on survival of immatures of species  $i$ . The combined model consisting of equations (1) and (2) will be referred to as the "Ricker recruitment model." As is well known, resource partitioning at the immature stage can lead to coexistence. Resource partition is manifested in these equations by intraspecific competition coefficients,  $\alpha_{ij}$ , that exceed the corresponding interspecific competition coefficients,  $\alpha_{ji}$ . In the absence of environmental variation, such a system can come to an equilibrium as depicted in Fig. 2a. (Parameters of all simulations are given in Appendix I.) What will the effect of environmental variation be on such an equilibrium?

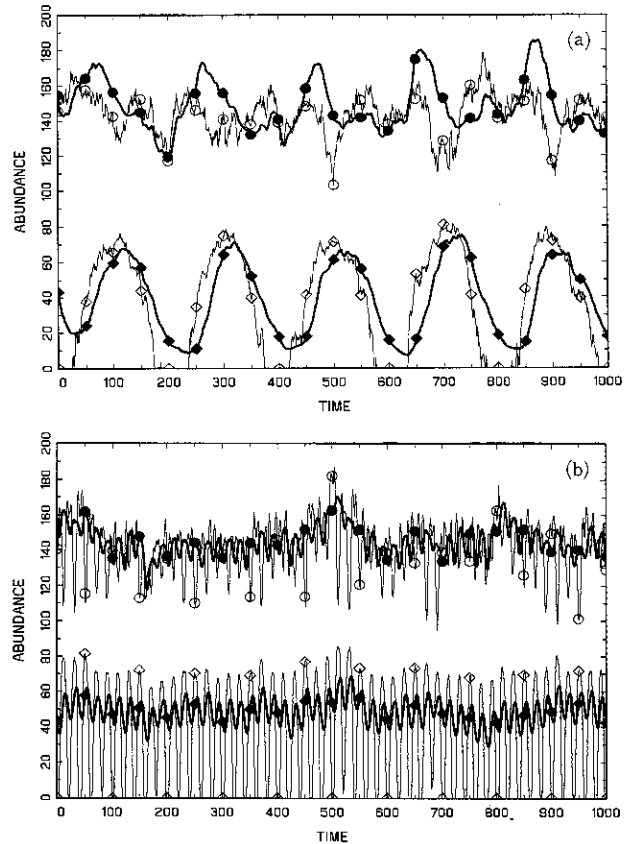
The environmental conditions at any particular time can be regarded as setting an equilibrium, an environmentally-dependent equilibrium, that changes over time as the environment varies. Such a changing equilibrium is depicted in Fig. 2b. The figure shows the effects of environmental variation on two scales, a short timescale of year to year variation, and a longer timescale, representing long-term variation in climate. The actual population densities closely track the major variation in this environmentally-dependent equilibrium, but the short-term variation is not tracked—it tends to be averaged over.

The tendency of a community to track environmental variation depends on a number of factors. First is the magnitude of the variation itself. Fig. 2c shows a higher magnitude of variation than Fig. 2b and we see that the equilibrium is tracked less well. In particular, one of the two species sometimes has an environmentally-dependent equilibrium of zero. This species fails to converge on the extinction state, and lags behind the environmentally-dependent equilibrium when recovering from low densities. Second, frequency of environmental change of a given magnitude has a major influence on tracking as is illustrated in by comparing Figs. 2c, 3a, b. Tracking becomes progressively worse until in Fig. 3b, there is very little tracking at all. Third, tracking tendency is influenced by life-history characteristics. The more abundant species in these figures has twice the adult



**Fig. 2.** Output of the Ricker recruitment model with two species and resource partitioning. The thick lines are the population abundances and the thin lines are the environmentally dependent equilibria. (a) No environmental fluctuations. (b) Slow low amplitude environmental fluctuation. (c) Higher amplitude environmental fluctuation.

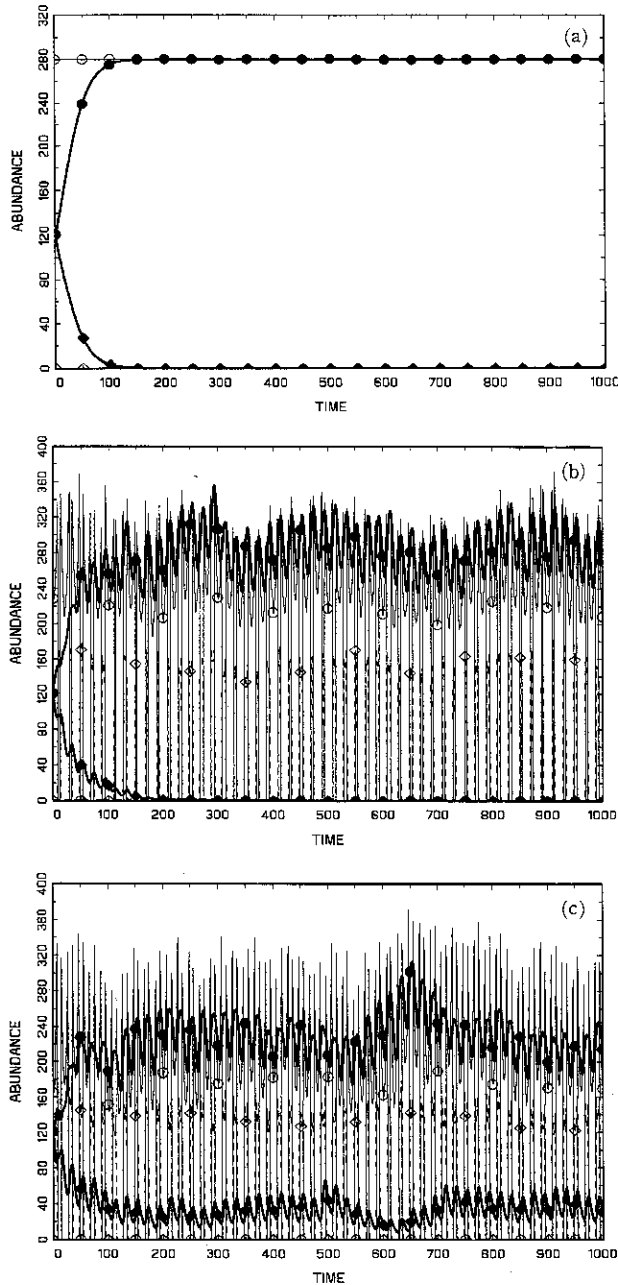
longevity of the other species, and it shows much less tendency to track the equilibrium. The findings are in general agreement with the detailed studies by Roughgarden (1975, 1979) of discrete-time logistic



**Fig. 3.** Output of the Ricker recruitment model as for Fig. 2 but with higher frequencies of environmental fluctuation.

and Lotka-Volterra models. However, timelags due to the discreteness of Roughgarden's models decreased tracking tendency. Adult longevity considered here is another form of timelag that also reduces tracking tendency.

In the case of very little tracking, as in Fig. 3b, it is tempting to assert that the population is simply at some average environmental state. But several things are immediately clear. First, the population densities of both species are quite considerably above the average equilibrium value. Moreover as can be seen by comparison with Fig. 2a, in which environmental conditions are constant at an average value, the population densities in the presence of fluctuations deviate from the equilibrium densities for average environmental conditions. Rather than wash out, the fluctuations in the system have a much more subtle effect. To gain a better understanding of this effect, we can remove resource partitioning so that the species are no longer able to coexist in a constant environment (Fig. 4a). Putting environmental variation back in the model (Fig. 4b), we see a slowing of the rate at which extinction is approached. Increasing the magnitude of environmental variation (Fig. 4c), we see that environmental variation



**Fig. 4.** Output of the Ricker recruitment model as for Fig. 2 but with no resource partitioning. (a) No environmental fluctuations. (b) and (c) Environmental fluctuations respectively of moderate and larger magnitude.

can actually lead to long-term stable coexistence. Note that as there is no resource partitioning in Figs. 4b and 4c, the environmentally-dependent equilibria always specify one of the two species as extinct.

Such contributions of environmental fluctuations to coexistence are due to the nonlinear nature of averaging in this system. These contributions to coexistence

are present, though less obvious, even when the system tends to track the environmentally-dependent equilibrium. To understand these issues we need to take a quantitative approach.

**Quantifying the Long-term Effects of Fluctuations on Community Dynamics**

Rate of decline to extinction and rate of recovery from low density are useful currency for the study of coexistence. To quantify them, we use the long-term low-density growth rate, which is defined by averaging  $r_i(t) = \ln X_i(t+1) - \ln X_i(t)$  over time for a population starting at low density. At low density, the growth rate of the population is insensitive to changes in the actual density of the species itself, and just depends on the densities of other species. Then the average of  $r_i(t)$  over time,  $\bar{r}_i$ , corresponds to the slope of the straight line connecting the initial and final values of  $\ln X_i(t)$  involved in the average (Fig. 5). If these initial and final times are respectively 0 and  $T$ , then

$$\ln X_i(T) - \ln X_i(0) = T\bar{r}_i \tag{3}$$

and so  $\bar{r}_i$  defines the actual change in population size over the defined period. There is no important loss of information by averaging.

This long-term low-density growth rate,  $\bar{r}_i$ , has been determined approximately for the Ricker recruitment model under the assumption that the adult survival rates  $s_i$  are the same for all species and that the environment fluctuates independently from one time to the next (Chesson, 1994). The expression for  $\bar{r}_i$  splits into two components,

$$\bar{r}_i = \bar{r}'_i + \Delta J \tag{4}$$

The first component,  $\bar{r}'_i$ , is contributed by classical resource partitioning, and takes the form

$$\bar{r}'_i = \delta \left\{ \mu_i - \bar{\mu} + \frac{(1 - \beta/\alpha)C^*}{n - 1} \right\} \tag{5}$$

where,  $\delta = 1 - s$  is the adult mortality rate,  $\mu_i$  is the average of  $\ln E_i$  over time,  $\bar{\mu}$  is average of the  $\mu_j$  for the competitors of species  $i$ ,  $\beta$  is the interspecific competition coefficient, which is assumed to be of similar magnitude to  $\alpha$ , the intraspecific competition coefficient, and  $C^*$  is the average level of competition in this system.

The second component,  $\Delta J$ , depends on environmental fluctuations. It takes the form

$$\Delta J = \frac{\delta s(1 - \rho)\sigma^2 C^*}{n - 1} \tag{6}$$

where  $\sigma^2$  is the variance of  $\ln E_i(t)$ , the natural log of the

rate of recruitment to the adult population in the absence of competition, and  $\rho$  is the correlation between  $\ln E_i(t)$  values for different species—it measures how much species differ from one another in their responses to environmental conditions.

The quantity  $\bar{r}_i$  is an average, and yet as we see in the formula for  $\Delta I$ , it depends on environmental fluctuations. Indeed,  $\Delta I$  is proportional to  $\sigma^2$ , the variance of the environmentally-dependent parameter. How can this occur? Figure 1 illustrates how averages can be affected by variance when the average is nonlinear. The average  $B$  is higher than  $E$  in Fig. 1 because of a greater variance contribution to  $B$ . Nonlinearity is critical in the effect of variance on the average. Figure 1, illustrates just one-dimensional nonlinear averaging, but more complex forms of nonlinear averaging occur with more dimensions. Figure 6b illustrates a two-dimensional nonlinearity, called *subadditivity* (Chesson and Huntly, 1989; Chesson, 1994), arising in the Ricker recruitment model. The figure plots the growth rate as a function competition for high and low values of the environmentally-dependent parameter, corresponding respectively to favourable and unfavourable environmental conditions. Subadditivity is recognised in the figure by convergence of the growth rates with increasing competition. In contrast Fig. 6a illustrates the additive case where the curves are parallel. The subadditivity shown in Fig. 6b depends on adults surviving for more than one breeding season, in other words, having a nonzero value of  $s$ .

A detailed discussion of nonlinear averaging in sub-additive and more generally nonadditive models is given elsewhere (Chesson, 1990); however, the most

important thing to note is that subadditivity leads to the potential for strong population growth if environmental conditions happen to be good while competition is low (point A in Fig. 6b). In contrast, when competition is strong and environmental conditions are bad the value of the growth rate is not much different from the situation of good environmental conditions together with strong competition (point C in Fig. 6b compared with point D). In the additive situation depicted in Fig. 6a this is not the case, as the points A and C are symmetrically located. Thus, points A and C are equally extreme, and the gains made by occurrence of A are cancelled by occurrence of C as the growth rate is averaged over time to give the long-term trend. The different outcome in the subadditive case (Fig. 6b) compared with the additive case (Fig. 6a) is an important form of two-dimensional nonlinear averaging that can act as a diversity maintaining mechanism.

To act as a diversity maintenance mechanism, however, subadditivity must be combined with two other factors. First, eqn (2) shows that competition depends directly on response to the environment. In particular, if a species is at high density, an improvement in the environment simply leads to more competition through the production of more competing immatures. In other words, there is covariance between environment and competition. In terms of Fig. 6, this covariance between environment and competition means that fluctuations between the points B and D are more likely to occur than fluctuations between the points A and C.

Second, it is important that covariance between environment and competition does not apply in the same way to a species at low density. A species at low densi-

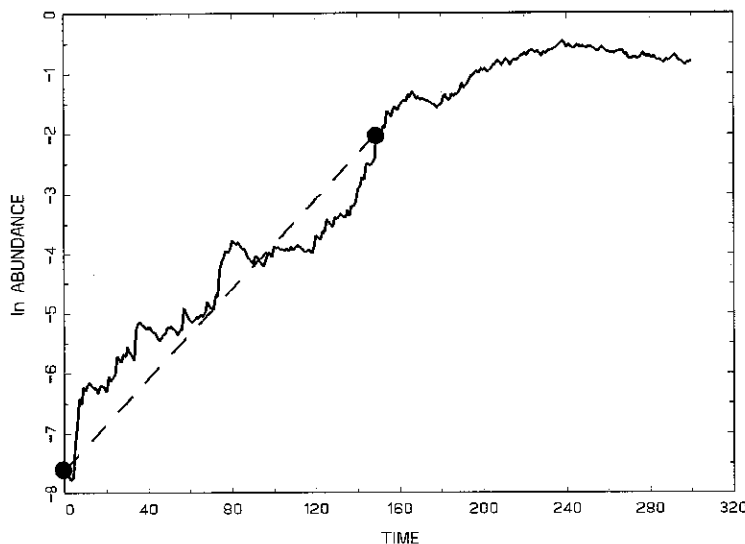


Fig. 5. Graph of the natural log of population abundance for a population starting at low density. Population growth is density-independent for a time as indicated by approximately straight line growth. The dashed line summarises the result of this initial growth.

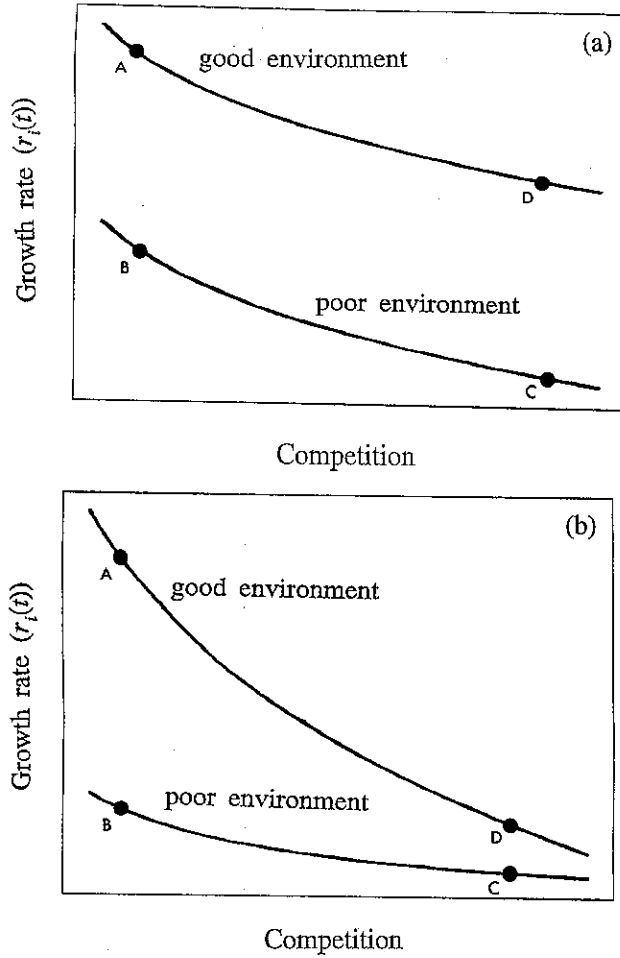


Fig. 6. The population growth rate (change in  $\ln$  abundance over time) as a function of competition, plotted for two different environmental situations. (a) Additive growth rates. (b) Subadditive growth rates.

ty contributes little to competition. Therefore, there is little direct effect on competition as a consequence of such a species being favoured by environmental conditions. Competition comes from other species, and whether a species at low density will experience high competition simultaneously with good environmental conditions depends on how closely correlated its response to the environment is with that of other species. A value of  $\rho < 1$  means less coupling of environment and competition for a species at low density compared with a species at high density, and consequently a more favourable pattern of fluctuations in environmental and competition, i.e. a larger fraction of fluctuations between A and C on Fig. 6b than between B and D. As a consequence a positive value of  $\Delta/$  can result (Chesson, 1990).

The occurrence of this positive value of  $\Delta/$  is called the storage effect (Chesson, 1994). We have seen that

there are three ingredients to this storage effect, sub-additivity, covariance between environment and competition and a value of  $\rho < 1$ , which results from species-specific responses to the environment. The name storage effect comes from the idea that the gains made from the occurrence of A in Fig. 6b are in effect stored by build up of the population in a way that cannot be cancelled immediately by the occurrence of poorer conditions.

The storage effect is an important form of nonlinear averaging that can be a powerful promoter of coexistence, and we have argued elsewhere that its three essential ingredients are likely to be common in nature (Chesson and Huntly, 1989). However, another form of nonlinear averaging can affect species coexistence. Figure 7 depicts the growth rates of two species as nonlinear functions of competition. These growth rates are *relatively nonlinear* as they curve in different directions. Curving in the same direction but by different amounts is also a form of relative nonlinearity. Comparison of Fig. 7 with Fig. 1 shows that fluctuations in competition will increase the average growth rate of species b, but decrease that of species a. Such relative changes in average growth rates can promote or demote coexistence depending on the circumstances, and so are part of a coexistence-affecting mechanism called relative nonlinearity (Chesson, 1994).

These coexistence-affecting mechanisms, the storage effect and relative nonlinearity, have been studied for models of the general form

$$r_i(t) = g_i(E_i(t), C_i(t)), \quad (7)$$

of which the the Ricker recruitment model is a special

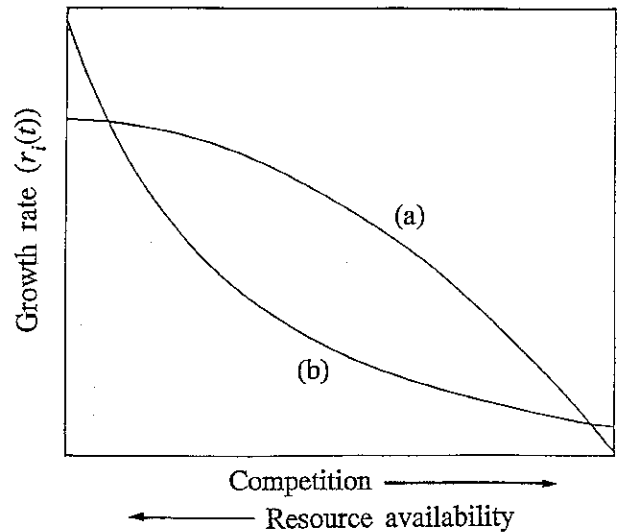


Fig. 7. Population growth rates of two species (a) and (b) as functions of competition showing relatively nonlinear responses—different sorts or magnitudes of nonlinearity.

case with

$$g_i(E_i(t), C_i(t)) = \ln\{s_i + E_i(t)/C_i(t)\}. \quad (8)$$

In the general case (7), however,  $g_i(E_i(t), C_i(t))$  can be essentially any function that decreases in the variable  $C_i(t)$ . The critical point is that  $E_i(t)$  is a population parameter, called an environmentally-dependent parameter, independent of population density but dependent on environmental factors. The variable  $C_i(t)$ , the competition parameter, is a measure of the reduction in population growth due to competition. The function  $g_i$  then combines these two parameters of population growth into overall growth of the population.

This model leads to the general conclusion that the long-term low-density growth rate of a species can be represented in the form

$$\bar{r}_i = \bar{r}_i' - \Delta N + \Delta I, \quad (9)$$

where  $\bar{r}_i'$  summarises fluctuation-independent or classical coexistence-affecting mechanisms (e.g. resource partitioning, frequency-dependent herbivory),  $\Delta I$  is the storage effect, and  $\Delta N$  is relative nonlinearity.

The formula (9) explicitly recognises three timescales. First is the unit of time, which sets the maximum resolution of fluctuations in the model. Second are lengths of time less than a unit, on which classical fluctuation-independent mechanisms, such as resource partitioning, may operate. Third is "long-term", which is the length of time over which the growth rate  $r_i(t)$  is averaged to produce the long-term growth rate. This timescale is commonly infinite in theoretical models but this is not essential; it can in fact represent a particular finite amount of time as depicted in Fig. 5. As emphasised in eqn (3), the long-term growth rate  $\bar{r}_i$  is an accurate summary of actual population growth from low density for any period  $T$  units in length ( $t$  to  $t+T$ , say) provided  $\bar{r}_i$  is calculated for the actual period of time in question.

In formula (9), the mechanisms  $\Delta N$  and  $\Delta I$  depend on there being fluctuations from one unit of time to the next, and so these mechanisms have been referred to as fluctuation-dependent mechanisms. While we have referred to the mechanisms represented in  $\bar{r}_i'$  as fluctuation-independent mechanisms, there is nothing in the equations to say that they are independent of fluctuations within one unit of time, a timescale on which the model gives only a summary outcome. The Ricker recruitment model gives very similar results for both fluctuation-dependent and fluctuation-independent mechanisms when viewed on a long timescale (compare eqns 5 and 6, disregarding  $\mu_j - \bar{\mu}$ ) suggesting that the distinction between fluctuation-dependent and fluctuation-independent mechanisms depends very much on the timescale. We shall explore this further by considering models in which more timescales can be considered explicitly.

## Fluctuations on Several Scales

Consider a community in which recruitment occurs continuously throughout a year and maturation of new individuals takes place on a short timescale such as a month. An example is the understorey herbaceous community of moist eucalypt forests of eastern Australia, if we regard a ramet as individual (pers. obs.). The equation for population growth can still be eqn (1) with the interpretation that a unit of time is a calendar month. Instead of the Ricker expression (2) for competition we shall use the lottery form

$$C = \ln \left\{ \frac{\sum_{k=1}^n E_k(t) X_k(t)}{\sum_{k=1}^n \delta_k X_k(t)} \right\} \quad (10)$$

which is the same for all species in the system and therefore precludes the possibility of a classical equilibrium coexistence. This model of competition has been discussed at length in the literature as a model of random allocation of space (e.g. Chesson and Warner, 1981). Contrary to popular perception, random allocation of space per se does not enable coexistence of competitors. Rather the storage effect, a concept which is independent of lottery competition, as we have seen here, is responsible for coexistence in the model.

Simulations of the lottery model for two species in a strictly seasonal environment, with species differences in seasonal patterns of growth, is given in Fig. 8a. Figure 8b shows the same thing but with random patterns of growth from month to month in contrast to the sinusoidal patterns considered in Fig. 8a. The variable plotted is the relative abundance of species 1 defined as species 1's proportion of the total amount of space occupied by the two species. Because the total amount of space occupied by the species in this model is constant, a relative abundance between 0 and 1 means that the species coexist. Note that a nice coexistence occurs, and there is little to difference between random (or aseasonal) and regular seasonal variation. Most interesting is the fact that in both cases the population trajectories are well approximated by the sort of smooth approach to an equilibrium abundance normally associated with classical coexistence mechanisms and illustrated in Fig. 2a.

To see what is happening in these simulations, we first convert the model into a standard form by transforming the environmentally-dependent and competition parameters so that they are measured in units of the growth rate (Chesson, 1994). We then approximate the model by a quadratic equation. The lottery model becomes

$$g_i(E_i, C_i) = E_i - C_i + \gamma_i E_i C_i \quad (11)$$

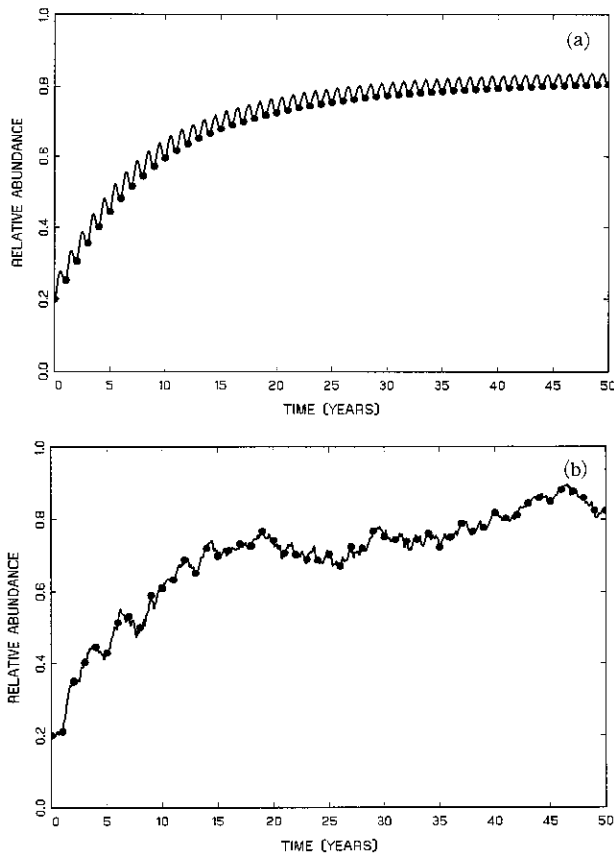


Fig. 8. Output of the lottery model for a population recruiting monthly. (a) Regular seasonal environmental variation. (b) Random or aseasonal variation within a year.

where  $\gamma_i$  is a quantitative measure of nonadditivity, here equal to  $-s/\delta$  (Chesson, 1994), with a negative value meaning the model is subadditive. (All models in the form (7) above produce this approximation (11), the differences between models being expressed in the value of  $\gamma$  and the details of  $C_i$  and  $E_i$ .) With a model in this form we can then evaluate the average of the growth rate over a period of one year (Appendix II) to obtain

$$\bar{r}_i^Y = \bar{E}_i^Y - \bar{C}_i^Y + I_i^Y(\mathbf{X}, \mathbf{E}) + \gamma \bar{E}_i^Y \cdot \bar{C}_i^Y, \quad (12)$$

where a bar over variable with a superscript  $Y$  means that the variable has been averaged over a period of the length of a year. The function  $I_i^Y(\mathbf{X}, \mathbf{E})$  summarises the effects of fluctuations within a year. It depends on the vector  $\mathbf{X}$  of population densities at the beginning of the year and the variation in the environment for that year symbolised by  $\mathbf{E}$ . This function summarises the outcome of the storage effect within a year. But what is this function like? For the lottery model in the situation depicted in Fig. 8 where population densities do not

change a great deal over a period of a year, we find (Appendix II) that

$$I_i^Y(\mathbf{X}, \mathbf{E}) = -(s/\delta) \sum_{j=1}^n X_j \sigma_{ij}^Y. \quad (13)$$

The coefficient  $\sigma_{ij}^Y$  is the covariance between  $E_i$  and  $E_j$ , calculated for a specific year in question. This is a linear function of densities—in essence Lotka-Volterra competition—similar to the specification for immatures in eqn (2) above. The covariances  $\sigma_{ij}^Y$  are analogous to the competition coefficients in eqn (2) summarizing the effects of resource partitioning. However, these covariances are functions of variation. They are not prescribed in the formulation of the model, and there is no resource partitioning in the model. Rather this Lotka-Volterra result is an emergent property of fluctuations over time due to nonlinear averaging. In other words, the Lotka-Volterra result could not be predicted from the behaviour of the model at any given time. It is only evident when times are combined to yield longer-term dynamics.

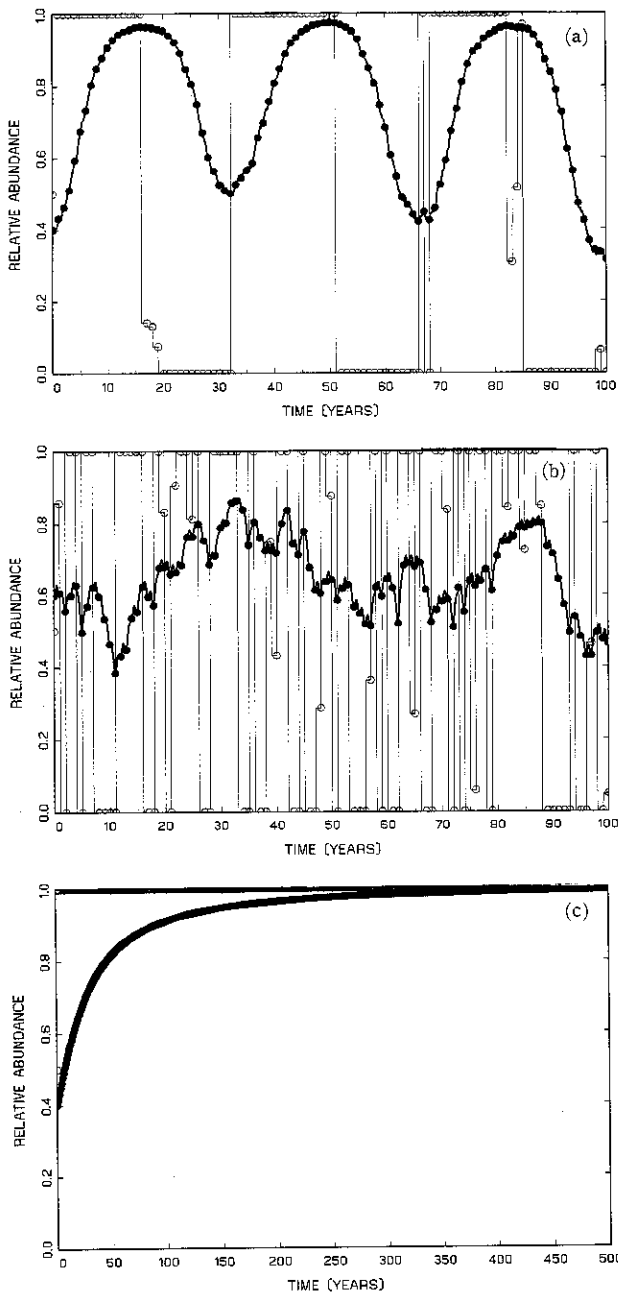
To see that this linear function (13) of the densities is capable of explaining the dynamics seen in Fig. 8, we form the difference between the growth rate of species  $i$  and the average of the growth rates of its competitors, and then we obtain a growth rate of relative abundance as follows,

$$\begin{aligned} \bar{r}_i^Y - \bar{r}^Y = \bar{E}_i^Y - \bar{E}^Y + (s/\delta) \sum_{j=1}^n X_j (\bar{\sigma}_{ij}^Y - \sigma_{ij}^Y) \\ + \gamma (\bar{E}_i^Y - \bar{E}^Y) \bar{C}_i^Y, \end{aligned} \quad (14)$$

where the bar over a variable with a dot subscript signifies the average over other species (not species  $i$ ).

Under the assumptions of the simulations of Fig. 8, there is respectively no environmental variation and negligible environmental variation from year to year in the strictly seasonal and aseasonal versions of the model. This means that the first term in eqn (14) can be regarded as a constant while the last term is approximately zero. Therefore, all the important action is in the middle term of eqn (14), which defines a stable equilibrium for the system on the yearly timescale. Thus, on a timescale appreciably longer than the timescale of fluctuations, we see that a fluctuation-dependent mechanism can produce dynamics indistinguishable from the dynamics of classical deterministic models of resource partitioning, even though such classical mechanisms are not included in the model. In fact the stable equilibrium in Fig. 8 results from the storage effect, with subadditivity contributing the nonzero multiplier  $s/\delta$ , covariance between environment and competition being responsible for existence of the sum of densities multiplied by environmental covariances, and species-specific responses to the environment giving the differences between  $\sigma_{ij}^Y$  and  $\bar{\sigma}_{ij}^Y$  that are necessary for this term to create a stable





**Fig. 9.** Output of the lottery model as for Fig. 8. The thick line is relative abundance of species 1, and the thin line is the equilibrium determined by variation within a year. (a) Aseasonal variation within a year and slow environmental change from year to year. (b) Regular seasonal variation with random environmental variation from year to year. (c) As for (b) but with no year to year variation. Note the change in scale of the time axis to show exclusion (c). Competitive exclusion illustrated by (c) arises whenever variation on either scale is omitted from the simulations in (a) or (b).

equilibrium. This equilibrium is an emergent property of the system on the yearly timescale; it is not prescribed by the equations on the monthly timescale.

Now consider the two levels of variation, within-year variation and variation from year to year. Figure 9a shows random variation within a year and regular long-term variation from year to year. In contrast, Fig. 9b shows regular seasonal variation with random fluctuations from year to year. The first thing to note is that with regular long-term variation there is a tendency toward tracking of the equilibrium set by the within-year variation. In the case of random between-year variation, an appreciable tendency to track is only evident when there is a run of similar years; otherwise there is very little tracking. However, whether there is tracking or not, variation on both timescales contributes to coexistence. To demonstrate that this is so, these particular simulations have been constructed with the property that elimination of variation on either of the timescales leads to competitive exclusion (Fig. 9c).

A quantitative understanding of the two levels of variation can be gained by averaging eqn (12) over a longer timescale (Appendix II). Although the general equation is complex we can nevertheless gain an appreciation of the essentials by considering again the case where population densities themselves do not change greatly during the averaging period, (e.g. Fig. 9b). For the Lottery model we then obtain the formula

$$\bar{r}_1^D - \bar{r}_1^D = \bar{E}_1^D - \bar{E}_1^D + (s/\delta) \sum_{j=1}^n X_j \{ (\bar{\sigma}_j^D - \sigma_j^D)^D + (\bar{\sigma}_j^D - \sigma_j^D) \} + \gamma (\bar{E}_1^D - \bar{E}_1^D) \bar{C}^D \quad (15)$$

where the bar with a *D* superscript stands for averaging the variable over two timescales. The covariances  $\sigma_{ij}^D$  are the covariances of  $E_i^D$  and  $E_j^D$ , over the *D* timescale. We now have variation on two timescales, with the potential for species differences on both the yearly scale and the longer scale denoted here simply as *D*, creating an equilibrium on that scale. Essentially we see the accumulation of effects on several scales even though the nonlinearity in question arises on the shortest of these scales.

### Qualitatively Different Timescales

The example above incorporated no fundamental differences in biological processes occurring on the different timescales of environmental variation. Often there will be, however. The cycle of seasons within a year provides important variation that may maintain diversity (Stewart and Levin, 1973; Armstrong and McGehee, 1976; Brown, 1989a, b; Loreau, 1989). For example, consider communities of winter annual plants of the

Chihuahuan Desert of southwestern U.S.A. These plants show variation in the fraction of seeds germinating in any year. With survival in the seed bank, this can lead to species coexistence by the storage effect (Ellner, 1985; Chesson, 1994). However, within any given year there are differences between species in the timing of germination. While these differences interact with yearly variation in weather patterns to produce between-year variation in germination (Huntly and Chesson, manuscript), within-year differences in germination patterns may also have important effects. In addition, it is important to consider growth in size of the individuals in any given year, in addition to changes in numbers of individuals growing. For example, some species may differ in their times of cessation of growth, or simply their rates of growth at different times of year in relation to such factors as temperature and solar radiation.

These environmental effects can be summarised as a "species activity measure,"  $E_i(t)$ , which incorporates both the fraction of the seed bank of species  $i$  that has emerged, and the rate of growth in relation to time of year, temperature and solar radiation. Water availability will also affect plant growth, but water availability may be affected by competition and so it cannot be incorporated in  $E_i(t)$ . Instead, water availability contributes to  $C_i(t)$ . For species  $i$ , let  $B_i(t)$  be the total biomass  $i$ , and  $R_i(t)$  be the per unit rate of increase in biomass ( $R_i(t) = [dB_i(t)/dt]/B_i(t) = d[\ln B_i(t)]/dt$ ), then the growth of biomass of species  $i$  during a year can be represented as

$$R_i(t) = E_i(t)f_i(W(t)), \quad (16)$$

where  $W(t)$  is the water potential of the soil, and  $f_i$  is a function relating soil water potential to growth of individuals in the population.

Eqn (16) expresses the relative growth of biomass in the population in a similar form to eqn (11). Indeed, when we interpret the absolute value of water potential  $|W(t)|$  as a competition parameter (i.e. consumption of water increases  $|W(t)|$ ), a plot of  $R_i(t)$  against  $|W(t)|$  for different values of  $E_i(t)$  yields the subadditive growth rates illustrated in Fig. 6b. Covariance between environment and competition occurs because soil moisture is depleted by a species in relation to its activity  $E_i(t)$  and its biomass  $B_i(t)$ . Species differences in germination and growth over time mean that the temporal patterns of variation in the environmentally-dependent parameters,  $E_i(t)$ , will be species-specific. Thus, growth of biomass within a season in this system has all the ingredients necessary for the storage effect to operate. If seed production is proportional to final biomass at the end of the year, these processes within a year are suitably linked to population growth, and we conclude that the storage effect operating on species patterns of activity within a year is capable of contributing to diversity maintenance.

What are the special features of timescales much longer than a year? Trees can be very long-lived and with climate change may sometimes be found in areas where they seem quite maladapted because they are no longer able to reproduce sexually. However, some species persist by vegetative means for long periods of time after climate change has removed the potential for sexual reproduction (Neilson and Wullstein, 1983; Allen and Hoekstra, 1990). Such ability of a genet to resist death can make growth rates very strongly subadditive in models and should contribute importantly to the maintenance of species diversity.

Climate change often leads to major changes in species distributions (Davis, 1986, 1989; Huntley and Webb, 1989). However, a species may persist in a region in refugia. And from these refugia it can expand again to reoccupy the larger region when favourable conditions return. In this way refugia may represent subadditivity that is seen only when large temporal and spatial scales are considered. Indeed, spatial patchiness similar to this is known to cause subadditivity in models of year to year variation (Chesson, 1990). Moving to a larger spatial scale such as the North American continent, the fact that a species will often have the potential of migrating to a different area with a suitable physical and biological environment is undoubtedly a major factor maintaining diversity of North America as a whole.

It has been emphasised (Davis, 1989; Huntley and Webb, 1989) that species change their distributions in response to climate change at rates that depend on the species' life-history characteristics, similar to the effects of life-history parameters on tracking in the models discussed here. Differences in life-history characteristics mean that the associates of a species on this larger timescale will be in constant flux. Indeed, the picture on such large spatial and temporal scales is of constant spatio-temporal variation in species composition and in the associates of any species. We have no models that adequately address such timescales, which will also be complicated by major evolutionary processes. However, the indications from models for much shorter timescales are that such spatio-temporal flux should be a major factor in the maintenance of biological diversity both within communities and within species (genetic diversity; Chesson, 1985; Gillespie, 1991).

## Conclusion

Communities may track an equilibrium specified on a short timescale, thereby reducing the necessity to understand longer term variation to understand communities. Tracking, however, will nearly always be imperfect and some variation will be averaged rather than

tracked. Such averaging will invariably be nonlinear and as a consequence, will have the potential to contribute to diversity maintenance. Nonlinearities leading to nonlinear averaging can arise in a variety of ways on a variety of timescales. Nonlinear averaging can in effect create a new equilibrium on a longer timescale. Indeed, dynamics on different timescales, when viewed appropriately, need not appear very different from each other even though the fundamental biological processes involved may be very different.

A variety of timescales can contribute to the maintenance of species diversity, and, as we have seen, different timescales can act in concert. A full understanding of diversity maintenance would seem to demand consideration of this possibility, posing a challenge to ecologists to develop methods of studying contributions from multiple mechanisms and on multiple scales. The method of partitioning long-term growth rates given here is intended as a theoretical tool to this end.

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**APPENDIX I: Parameters of the simulations**

In all simulations of the Ricker recruitment model we set  $\alpha_{ij} = \alpha$ , and  $\alpha_{ij} = \beta = 0.01$ . The adult survival rates  $s_i$  are respectively 0.95 and 0.9. The natural logs of the environmentally-dependent parameters ( $\ln E_i(t)$ ) are equal to the sum of a normal autoregressive process, and a sine function. The normal autoregressive process has autocorrelation  $0.95^t$  and variance  $\sigma^2$ , and is independent between species. The sine function is one half cycle out of phase between species, has amplitude  $a$  and period  $p$  in years. The means of the  $\ln E_i(t)$  are 0.1 and 0.2 for species 1 and 2. The values of the varied parameters are as follows:

Figure	$\alpha$	$\sigma^2$	$a$	$p$
2a	0.015	0	0	—
2b	0.015	0.01	0.2	1000
2c	0.015	0.1	0.4	1000
3a	0.015	0.1	0.4	200
3b	0.015	0.1	0.4	20
4a	0.01	0	0	—
4b	0.01	0.1	0.4	20
4c	0.01	0.1	0.7	20

The runs of the lottery model all assume that the adult death rates are 0.05 per month. The dynamics of the two species depend also on the ratio of the environmentally-dependent parameters  $E_1/E_2$ , which is equal to the ratio of the recruitment rates of the two species. The natural log of this ratio has a mean of  $\mu$ . This  $\ln$  recruitment rate ratio varies with a sinusoidal component having period  $p_1$  months, and variance  $\sigma_1^2$ , and a random normal component with time between changes  $p_2$  months and variance  $\sigma_2^2$ . The values of these parameters in the simulations are as follows:

Figure	$p_1$	$\sigma_1^2$	$p_2$	$\sigma_2^2$	$\mu$
8a	12	1	—	0	0.3
8b	—	0	1	1	0.3
9a	400	0.2	1	0.2	0.1
9b	12	0.2	12	0.2	0.1
9c	12	0.2	—	0	0.1

**APPENDIX II: Averaged dynamical equations**

Chesson (1994) shows how a nonlinear parameter transformation allows models of the form (7) in the text to be reexpressed in the form

$$g_i(E_i, C_i) = E_i - C_i + \gamma_i E_i C_i, \quad (\text{A1})$$

under the assumption that the variances of the environmentally-dependent parameters are small. (How small depends on the model in question, but in the lottery model it is known [Hatfield and Chesson, 1989] that even rather large variances permit this approximation.) Averaging expression (A1) over some interval of time, arbitrarily designated here as a year, we immediately obtain

$$\bar{r}_i = \bar{E}_i - \bar{C}_i + \gamma_i \bar{E}_i \bar{C}_i, \quad (\text{A2})$$

where

$$\begin{aligned} \gamma_i(\mathbf{X}, \mathbf{E}) &= \gamma C^Y(E_i, C_i) \\ &= \frac{\gamma}{T} \cdot \sum_{s=t}^{T+t-1} (E_i(s) - \bar{E}_i)(C_i(s) - \bar{C}_i), \end{aligned} \quad (\text{A3})$$

in other words,  $\gamma$  times the within-year covariance between the environmentally-dependent and competition parameters.

For the lottery model, Chesson (1994) shows that  $\gamma = -s/\delta$ . It is also easily seen from Chesson (1994) that with equal adult death rates, the transformed competition parameter is adequately approximated by

$$C_i = \sum_{j=1}^n X_j E_j \quad (\text{A4})$$

from which eqn (13) in the text follows under the assumption that the species densities do not vary greatly within a year. An indication of the error involved in this assumption can be gained by substituting the species densities at the end of the year in this expression instead of the values at the beginning of the year.

In general there is no difficulty averaging expression (A2) over a longer period of time arbitrarily indicated by the symbol  $D$ —for simplicity think of it as a decade. We then obtain

$$\bar{r}_i = \bar{E}_i^D - \bar{C}_i^D + \gamma_i \bar{E}_i^D \bar{C}_i^D, \quad (\text{A5})$$

where the main feature of significance is the iterative formula

$$\bar{r}_i(\mathbf{X}, \mathbf{E}) = \bar{r}_i^D(\mathbf{X}, \mathbf{E}) + \gamma_i C^D(\bar{E}_i^D, \bar{C}_i^D). \quad (\text{A6})$$

Assuming again only small variation in the species abundances over the periods of these averages, formula (15) for the lottery model follows.