

6. Quantifying and Testing Species Coexistence Mechanisms

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6.1. Introduction

The species diversity of natural communities has long been an inspiration (Margalef 1963), and a challenge to ecologists (Hutchinson 1959; Hubbell 2001). Both the consequences of diversity (Elton 1958; Margalef 1963; Tilman, Lehman and Bristow 1998; Chesson, Pacala and Newhauser 2001), and its causes (Hutchinson 1959; Tilman 1994; Chesson 2000b; Hubbell 2001), are problems of long standing. The causes of diversity can be considered on many scales of space and time, but on any scale the observed diversity is the net outcome of the establishment of species and their loss or retention. Integral to both establishment and retention on any scale are species coexistence mechanisms (Chesson and Case 1986), which likely also have roles in speciation (Chesson and Huntly 1997). On the largest scales of both space and time, speciation and global extinctions are the clear issues, but even those considerations involve interactions between species, which form the traditional focus of coexistence mechanisms and community ecology more generally.

Hutchinson (1959) directed the attention of species coexistence studies within trophic levels, to species with similar niches, likely interacting competitively with one another. Essentially, these species form *guilds*, subsets of communities that for the purpose of study we hope form coherent community modules. We should expect, however, that species with similar niches interact not just by competing for resources, but by sharing predators too. They are thus subject to apparent competition, potentially as able as competition to limit community membership (Holt, Grover and Tilman 1994). Although the term "competition" here can in general be

extended to apparent competition, for simplicity the discussion is framed mostly in terms of competition.

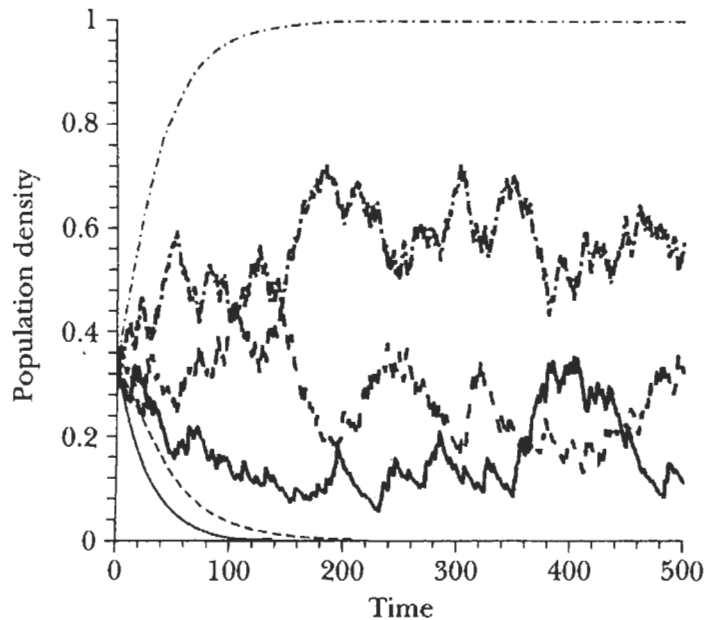
Hypotheses about coexistence of species within guilds are many and varied (Chesson 2000b), but convincing tests of species coexistence hypotheses are few, and confidence in any particular hypothesis is weak in general. Nevertheless, there have been some strong and convincing tests of species coexistence mechanisms, especially for hypotheses involving the roles of relatively specialized natural enemies (see Wills et al. 1997; Packer and Clay 2000; Klironomos 2002). These studies stand out by demonstrating the presence in the study system of dynamical processes at the heart of the functioning of the mechanism under test. Although there have been notable tests of mechanisms in other areas (e.g. those associated with the storage effect, such as Pake and Venable 1995; Cáceres 1997; Kelly and Bowler 2002; Descamps-Julien and González 2005), many tests of mechanisms tend to be weak, being based on predictions or correlations not definitively associated with the mechanism. How can strong tests of species coexistence mechanisms be constructed more generally? Recent results show how species coexistence mechanisms can be quantified. Moreover, the resulting measures of mechanism strength can be expressed in terms of key functional components of the mechanisms. The suggestion here is that strong tests of coexistence mechanisms can be derived by using these measures to quantify functional components of mechanisms from field and laboratory experiments. Such tests should work in the messiness of the natural world where multiple mechanisms and numerous complications are to be expected.

In this chapter, I review theory leading to the functional quantification of species coexistence mechanisms, and suggest how to use this quantification to provide definitive tests of species coexistence mechanisms in the field. On the way, we shall see that by quantifying mechanisms, we learn a lot about species coexistence generally. I begin with a definition of stable coexistence and show how this definition naturally leads to quantification. By quantifying mechanisms, we see also how different mechanisms combine to produce an overall coexistence promoting effect. We thus obtain not only a route to testing mechanisms individually, but also the ability to assess the relative contributions of different mechanisms in a given system.

6.2. Stable coexistence mechanisms, and their quantification

To say that species coexist is to say at a minimum that they continue to be found in the same defined area on some defined timescale. But ecologists usually expect something more than this. I focus here on one kind of coexistence, *stable coexistence*. For that we require not just co-occurrence, but recovery of populations from low density. Thus, species must not undergo the endless drifts or random walks of neutral models (Hubbell 2001); instead, they must show a tendency to recover from low density extremes. This recovery need not be steady growth in density, but can be a long-term trend for recovery compatible with short-term fluctuations (Chesson and Huntly 1989), as illustrated in figure 6.1. However, this recovery must occur without the benefit of immigration from some other area (Chesson 2000b). Coexistence mechanisms have spatial scales associated with them, and a mechanism working within a unit of area on a particular spatial scale does not require inputs from other areas on the same or larger scales for its operation. Migration is not ruled out, but it must not be necessary for recovery if the mechanism is to be called a stable coexistence mechanism working within the area in question.

Coexistence mechanisms that depend on variation in space, either in population densities, or environmental factors (spatial mechanisms, see Chesson 2000a; Bolker, Pacala and Neuhauser 2003) would not be expected to give stable coexistence on a small spatial scale, as defined here in terms of a tendency for recovery without immigration. However, they normally would yield this recovery on a larger spatial scale, that is, on a scale that includes the variation in space on which the mechanism depends. Examples are mechanisms involving spatial niche differences (Shmida and Ellner 1984; Chesson 1985; Comins and Noble 1985; Muko and Iwasa 2003; Snyder and Chesson 2003; Snyder and Chesson 2004), disturbance in spatial forms (Connell 1979; Lavorel and Chesson 1995; Chesson and Huntly 1997), competition-colonization trade-offs (Hastings 1980; Tilman 1994) and related mechanisms (Bolker and Pacala 1999). Nearly all coexistence mechanisms, except neutral and near neutral mechanisms (see Chesson 2000b), have this prop-

FIGURE 6.1: Simulations of the dynamics of three competing species

Note: The thick lines show fluctuating coexistence arising from the storage effect coexistence mechanism—note the tendency for any species to recover whenever it falls substantially below its average density. The thin lines show the same species in absence of temporal fluctuations. Competitive exclusion occurs in this case because the coexistence mechanism is fluctuation dependent.

erty of recovery from low density on some spatial scale, and are therefore stable coexistence mechanisms.

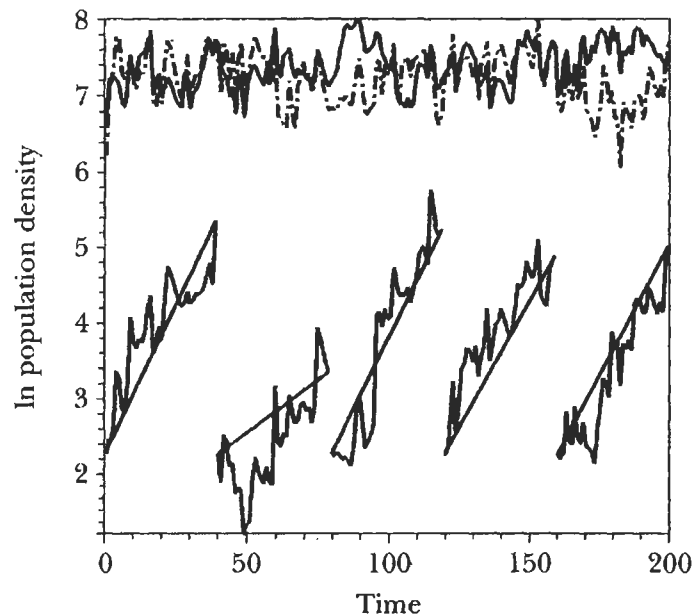
6.2.1. Measuring recovery from low density

The rate of recovery from low density is the key to quantification of stable coexistence mechanisms. We shall first see how this rate of recovery is defined in models, and then use the results of models to quantify coexistence mechanisms in a way that suggests tests of coexistence mechanisms in nature. To define the rate of recovery in models, we start with the per capita growth rate of a population. This per capita growth rate is r_i , defined mathematically in continuous time as: $(dN/dt)/N$. This rate is calculated for a closed community model, so that immigration from outside the system is excluded. The system can, however, include a spatially varying landscape, so that local populations within the system itself can certainly be open (Bolker and Pacala 1999). The recovery rate that we seek is \bar{r}_i , which is the average of r_i over time for a given species i perturbed to low density, with the rest of the species unconstrained, and fluctuating as they normally would in the ab-

sence of species i (Chesson 1994, 2000a) (see figure 6.2). Mathematically, these quantities are measured in the limit as species i converges to low density. Species i is then referred to as an *invader*, because it behaves from such densities as if it has just been introduced to the system. The rest of the species are referred to as *residents*. It is important to keep in mind that these labels are for states prepared experimentally in a model, in the lab or in the field. Thus, invader does not refer here to an invasive species, but simply to a species perturbed to a low density situation, with the rest of the community given time to adjust to the given species' rarity.

The average, \bar{r} , of r_i over time for any species, invader or not, has some very important properties. For example, if calculated for a finite interval of time, 0 to T , say, this average tells us exactly how much population change has occurred over that interval of time because the actual change in \ln population size is equal to the time elapsed times the average growth rate: i.e. $\ln N(T) - \ln N(0) = T \cdot \bar{r}$. This is true as a consequence of the mathematical fact that: $r_i = (dN/dt)/N = d \ln N / dt$,

FIGURE 6.2: Measuring the recovery of one species repeatedly perturbed to low density in the presence of unperturbed competitors



Note: In each of the five recoveries, the straight line connects the first and last values of \ln population density ($\ln N_i(t)$). Because this is a log scale, the slope of this line is equal to the value of \bar{r}_i applicable for that recovery. The theoretical \bar{r}_i used for invasion analysis is equivalent to the average of the \bar{r}_i 's, from infinitely many repetitions of this simulated invasion experiment, but taken in the limit as $N_i(0) \rightarrow 0$.

so that the average of r_i over time must reflect the actual change over that interval in $\ln N$. In the usual invasibility analysis of community models, however, the invasion rate, \bar{r}_i , is calculated for the limit as T goes to infinity with the invader density set at zero so that it cannot actually increase. This \bar{r}_i thus does not give the actual change for any particular finite period of time. Instead, it gives the trend about which the population would be predicted to vary in the initial phase of growth before its density becomes large enough to have much effect on the system itself. Although limited, such predictions about this early phase of growth from low density are good enough for studies of species coexistence (Ellner 1989; Chesson 1994).

In discrete time, which is especially useful for actual experimental systems, but also for many stochastic models, the per capita growth rate r_i is defined in this body of theory as $\ln N_{i+1} - \ln N_i$, i.e. it is defined as $\ln \lambda_i$, where: $\lambda_i = N_{i+1}/N_i$, the finite rate of increase. Of most importance, with this definition, the average of r_i over time has the same properties in discrete as continuous time, and the one theory covers both cases.

The invasibility criterion for coexistence of competing species says that the species coexist if each member of the guild can increase from low density while the other species in the guild are at the densities they would have in the long run without the given species. If there are n species in the guild, we require that \bar{r}_i be positive for each i , where i ranges from 1 to n (Chesson 1994). The actual magnitudes of the recovery rates, \bar{r}_i , indicate how rapidly the species recover from low density, and can be used to define the strength of species coexistence. This idea is similar to the traditional approach in equilibrium models of using the rate of approach to equilibrium, based on eigenvalues, as a stability measure (May 1974). Stability based on \bar{r}_i , however, is more broadly applicable.

6.2.2. Quantifying coexistence

We begin with some examples from Chesson (2000b) to motivate measures of mechanism strength based on the recovery rates, \bar{r}_i . These examples assume diffuse interactions where each species interacts to the same extent with each other species. Thus, although conspecific and heterospecific interactions may differ in

magnitude, all heterospecific interactions are of equal magnitude, as are all conspecific interactions. These rather restrictive assumptions give simple results that are nevertheless instructive more generally. With these assumptions, the recovery rate can typically be put in the following form, at least approximately:

$$\bar{r}_i = b_i \{ k_i - \bar{k} + A \} \quad (6.1)$$

The quantity b_i is a positive rate constant, to be discussed later. Of primary interest are the terms inside the braces, because these tell us about species coexistence. The term $k_i - \bar{k}$ measures how well the invader species i is adapted to its environment on average, compared with the average adaptedness of its competitors. Thus, k_i is a measure of the average fitness of species i , and \bar{k} is the average of this quantity for the other species in the guild (the *residents*). In the absence of the quantity A , this term would imply that only those species with greater than average fitness could in fact recover from low density. Thus, not all species would coexist in this system. Indeed, assuming that k_i is a property of species i alone, this equation means that the species with the largest value of k would exclude all other guild members from the system. However, in the presence of a stable coexistence mechanism, the quantity A will be positive, and can overcome fitness disadvantages. With positive A , any species i with fitness disadvantage (measured as $\bar{k} - k_i$) less than A , will have a positive \bar{r}_i . Thus, although such a species may be inferior to other species on average, it nevertheless coexists with them due to the quantity A . These ideas are illustrated in figure 6.1 where in the absence of the coexistence mechanism, the species with largest k dominates. In this particular example, in the presence of the coexistence mechanism (i.e. positive A) differences in average fitnesses do not lead to competitive exclusion but instead to differences in average abundance.

A positive value of the quantity A means that average inferiority ($k_i < \bar{k}$) is not inferiority under all conditions that the species encounter, and A itself can be thought of as a measure of mechanism strength. Stable coexistence requires that species differ in ecologically significant ways that prevent any species from dominating under all conditions (Chesson 2000b). It is instructive to see how these

requirements appear in the formula for A . Mechanisms that involve species differing in the resources they use, or when and where they use them, often lead to the following approximate formula for A :

$$A = \frac{(1 - \rho)D}{n - 1} \quad (6.2)$$

(Chesson 1994; 2000a; 2000b). Here, ρ is a measure of overlap between species in either the resources they use, or when or where they use them. The constant D is a measure of maximum strength of the mechanism, and n is the number of species. The overlap measure ρ has its maximum value of 1 when species have complete overlap in the resources they use, and when and where they use them. This measure is zero if the species have no overlap in resource use, or overlap completely, but use these common resources independently in time or space. Thus, we see that the quantity A is larger with more resource-use differentiation between species, and requires some resource differentiation to be present at all.

The quantity D in expression (6.2) can be quite complicated (Chesson 2003) but as a particular example, consider the lottery model of resource competition for species in an iteroparous perennial community (Chesson 1994), illustrated in figure 6.1. Here, D is equal to a measure of variance over time in the organisms' responses to the physical environment, multiplied by the adult survival rate (Chesson 1994). This variance depends both on the sensitivity of the organisms to the physical environment, and on the variation over time in the physical environment itself. The quantity $1 - \rho$, multiplied by this variance, partitions out the component of variance common to all species. Thus, it says that common responses across species to the physical environmental have no effect on coexistence. Instead, what is important is the independent or species-specific variance component of the response to the physical environment. Recall also that D is proportional to the adult survival rate in the lottery model. Thus, higher survival is more favorable to coexistence, which is a particular feature of temporal differentiation in resource use that we will come back to below.

There are two ways in which the constant A defines the strength of the mechanism that creates it. First, A is the maximum disadvan-

tage ($\bar{k} - k_i$) that a species can have in average fitness and still persist in the system: the larger the value of A , the wider the tolerance for weaker species. Second, A measures how much the mechanism boosts the recovery rate of each species. The absolute boost for species i is $b_i A$, but often the quantity $1/b_i$ defines a natural scale for the growth of a species so that A in fact measures the boost on this natural scale. For example, in some models, such as the lottery model, $1/b_i$ is the generation time for species i , and so \bar{r}_i/b_i is the recovery rate measured per generation rather than according to the often arbitrary time unit for the formulation of the model. More generally, b_i is the rate at which the growth rate, r_{ii} , of a species changes in response to changes in the magnitude of competition (Chesson 2003). In such cases, A represents the boost in recovery rate in competition units, in essence in units of competition overcome, which are natural units for this context. Thus, measuring coexistence mechanisms in terms of the change in \bar{r}_i/b_i , rather than \bar{r}_i , represents a natural measurement, and I shall simply refer to \bar{r}_i/b_i as \bar{r}_i in *natural units*. Hence, the quantity in braces, expression (6.1), is \bar{r}_i in natural units. Of most importance, A is the common boost in recovery rate for all species in natural units.

Mechanisms that create a positive A , or increase its value, are called stabilizing mechanisms, because they make it possible for coexistence to be stabilized by allowing a range of species with different average fitnesses to increase from low density (Chesson 2000b; Snyder, Borer and Chesson 2005). A larger positive value of A gives more stable coexistence in the sense that recovery rates are faster, and larger average fitness differences are tolerated. In addition, species ought to spend less time at low densities, and should not fall as low, although these latter two outcomes are not guaranteed (Chesson 1982). Some mechanisms, however, might yield negative values of A and be destabilizing. The classic illustration is the Lotka-Volterra competition model with interspecific competition stronger than intraspecific competition (Levin 1974), but the lottery model with variable adult death rates also has negative A , destabilizing coexistence rather than stabilizing it (Chesson and Warner 1981). A sufficiently large negative A overcomes fitness advantages, $k_i - \bar{k}$, so that all species have negative growth rates at low density, and no species can in fact invade a resident community.

Some mechanisms might affect the k 's rather than or in addition to A . They might do this by reducing the fitness advantages that some species have over others. For example, mortality that falls selectively on competitive dominants generally has this effect, and reduces the range of k values. Thus, A can be smaller, and the species can still coexist. Such mechanisms are referred to as equalizing mechanisms, as they tend to equalize average fitnesses, making stable coexistence easier (Chesson 2000b; Snyder, Borer and Chesson 2005). However, a mechanism that has only equalizing properties, i.e. makes the k 's more equal, but does not affect A , cannot enable stable coexistence by itself. A stabilizing mechanism must be present to make A positive. Some mechanisms might affect the k 's in ways that lead to greater fitness inequalities between species. For example, mortality falling more heavily on competitive inferiors would do this. Such mechanisms would have an unequalizing role.

As we shall see below, it is possible for a mechanism to affect both stability and equality, depending on the circumstances. In most circumstances, we can expect that a given mechanism will have unequal effects on the different species because of the many differences between species normally found in natural communities. Thus, although a mechanism may have major stabilizing or destabilizing effects, in a given situation it is also likely to modify fitness inequality either decreasing it or increasing it. Simple formulae like expression (6.2) for A generally ignore most of these species differences, focusing instead only on the minimal set of species differences that define the mechanism. A given mechanism likely benefits the different species to different extents, thus modifying average fitness differences, and leading to equalizing or unequalizing effects of the mechanism in the guild as a whole, as we shall see below in the section on community average measures of mechanisms.

6.3. Partitioning the growth rate into contributions from different mechanisms

Recent developments have shown how the recovery rate can be partitioned into contributions from different mechanisms of coexistence (Chesson 1994; 2000a). This means further that the stabiliz-

ing term A , discussed above, and the average fitness comparisons, $k_i - \bar{k}$, can also be partitioned into contributions from different mechanisms (Chesson 2003). Thus, the relative contributions of different mechanisms to both stability and fitness equality can be compared (Snyder and Chesson 2004; Snyder, Borer and Chesson 2005). Moreover, relative contributions of the same or different mechanisms on different timescales can also be considered (Chesson and Huntly 1993). The results of Chesson (1994) show how this partitioning is done based on two different timescales, a short one and a long one. The assumption is that the observer is interested in mechanisms that require fluctuations in environmental or competitive factors on the longer timescale, and is not focusing on fluctuations on the shorter timescale. By changing these timescales, mechanisms that depend on fluctuations (*fluctuation-dependent mechanisms*), on the various timescales of interest, come into focus. For any given decision on these timescales, the recovery rate partitions as

$$\bar{r}_i = \bar{r}'_i - \Delta N + \Delta I \quad (6.3)$$

The first term, \bar{r}'_i , represents all mechanisms on the shorter temporal scale. These mechanisms include traditional *equilibrium* or *fluctuation-independent mechanisms* (Chesson 1994, 2000b) and spatial mechanisms, as well as fluctuation-dependent mechanisms relying on short-term fluctuations. The mechanisms represented by ΔN and ΔI are fluctuation-dependent mechanisms driven by fluctuations on the longer timescale.

The term ΔI is *the storage effect*, and represents contributions to the recovery rate from temporal partitioning of resources, or temporal partitioning of predation, and depends on responses of the species jointly to their temporally varying physical environment and temporally varying competition or apparent competition. The term ΔN depends on fluctuations in the intensity of competition (or apparent competition) alone, but requires that different species respond to competition in relatively nonlinear ways, as discussed below.

Particular examples of equation (6.3) are worked out in Chesson (1994, 2003). We consider as an illustration just one example, the partitioning of the recovery rate for a model of iteroparous peren-

nial organisms competing as juveniles for the resources needed for recruitment to adulthood. These organisms might represent a guild of coral reef fishes (Warner and Chesson 1985), or a guild of forest trees (Leigh Jr. 1982; Comins and Noble 1985; Warner and Chesson 1985; Hubbell 2001; Kelly and Bowler 2002). It is assumed that recruitment fluctuates over time, with species potentially differing in the periods that are most favorable to them. If it is assumed also that they potentially partition resources at any given time, and interact diffusely as defined above, then equation (6.3) takes the following approximate form:

$$\bar{r}_i \approx d \left\{ k_i - \bar{k} + \frac{(1 - \beta/\alpha)\bar{C}}{n-1} + \frac{(1 - \rho)\sigma^2(1-d)\bar{C}}{n-1} \right\} \quad (6.4)$$

(Chesson 1994). Here, d is the adult death rate of these organisms, which for simplicity is assumed to be the same for all species, \bar{C} is the average intensity of competition, α is the intraspecific competition coefficient, β is the interspecific competition coefficient, σ^2 is a measure of variance of recruitment over time, and ρ is a measure of correlation between species in the timing of recruitment. The adult death rate d equals the constant b_i , which means that the natural units here are per generation units.

The first terms of equation (6.4) can be grouped as \bar{r}'_i of equation (6.3) in natural units, i.e:

$$\bar{r}'_i \approx k_i - \bar{k} + \frac{(1 - \beta/\alpha)\bar{C}}{n-1} \quad (6.5)$$

This expression consists of the mean fitness comparison, $k_i - \bar{k}$, of the previous section, plus the effects of equilibrium resource partitioning. The resource partitioning term, $(1 - \beta/\alpha)\bar{C}/(n-1)$, is positive if the organisms do not completely overlap in the resources that they use for maturation during a recruitment period, because then intraspecific competition, α , exceeds interspecific competition, β , during such periods. The last term, $(1 - \rho)\sigma^2(1-d)\bar{C}/(n-1)$, is the storage effect.

Note that both mechanisms in expression (6.4) take the general form of equation (6.2). This fact indicates consistencies in the way

stable coexistence occurs regardless of whether the mechanism is fluctuation dependent or fluctuation independent. Most critically, species must be differentiated in resource use, as reflected respectively by the quantities $1 - \beta/\alpha$ and $1 - \rho$ for these two mechanisms. Proportionality to \bar{C} indicates that species gain more by being differentiated from each other when the average level of competition is higher. The common decline in competition at the rate $1/(n-1)$, as the number of species n increases, reflects the diffuse nature of competition. Some dissimilarities reflect specific features of the mechanisms. The presence of the term $\sigma^2(1-d)$, in the storage effect term, indicates that the efficacy of temporal partitioning depends both on the amount of temporal variation and on the adult survival rate, $(1-d)$.

As mentioned above, the term \bar{r}'_i can be assumed to include spatial mechanisms also, as these do not involve fluctuations over time in the whole system. Indeed, the difference between α and β above could represent spatial partitioning. More generally, in discrete time, spatial mechanisms are formulated in terms of the spatial recovery rate from low density, $\tilde{\lambda}_i$, with r and λ having the relationship, $r = \ln \lambda$. Thus, in the presence of spatial mechanisms, \bar{r}'_i above would be equated with $\ln \tilde{\lambda}_i$ (Chesson 2000a; Snyder and Chesson 2003). We consider here just the special case where there is no overall temporal variation, although simultaneous variation in time and space may occur (Chesson 2000a). Then, the spatial recovery rate satisfies the equation:

$$\bar{N}_i(t+1) = \tilde{\lambda}_i \bar{N}_i(t) \quad (6.6)$$

where \bar{N}_i is the density of species i averaged over a spatially varying landscape—it is just the landscape-level population density as it would ordinarily be measured (Chesson 2000a; Chesson et al. 2005).

The spatial recovery rate is itself partitioned into contributions from different mechanisms (Chesson 2000a):

$$\tilde{\lambda}_i = \tilde{\lambda}'_i - \Delta N + \Delta I + \Delta \kappa \quad (6.7)$$

Here $\tilde{\lambda}'_i$ corresponds to mechanisms that do not depend on variation in space, at least at the spatial resolution assumed, just as \bar{r}'_i

corresponds to mechanisms that do not depend on variation over time, at the given temporal resolution. The familiar symbols ΔN and ΔI refer to spatial versions of the corresponding temporal mechanisms, and $\Delta \kappa$ is a spatial mechanism without a clear temporal counterpart, called *fitness-density covariance* (Chesson et al. 2005), or *growth-density covariance* (Snyder and Chesson 2003). It involves the fact that species vary in density in space, and this variation may be correlated with local fitness differences. One outcome of this correlation is reinforcement of the spatial niche differentiation that occurs with the spatial storage effect (Chesson 2000a; Snyder and Chesson 2003; Chesson et al. 2005). True spatial mechanisms as represented by ΔN , ΔI and $\Delta \kappa$, depend on variation in space of population densities or environmental factors and are therefore referred to as *variation-dependent mechanisms* (Chesson 2000a).

6.4. Expressing mechanism contributions in terms of functional components

Of most importance for scientific study, the mechanism measures ΔI , ΔN , and $\Delta \kappa$, have general formulae in terms of their functional components. These formulae are then key to general understanding of these mechanisms, and to testing them in the field. A word of caution, however, is in order before we study these formulae. In most cases, the formulae we discuss are not exact, and except in special circumstances can only be considered accurate when the mechanism in question is weak (Chesson 1994, 2000a). Nevertheless, they reveal the features of mechanism functioning that are needed to devise strong tests of coexistence mechanisms in nature. We begin our study with the *storage effect*, the best known and most easily tested of these mechanisms.

6.4.1. The storage effect

The storage effect can be thought of most generally as explaining coexistence in terms of niche differences based on aspects of the physical environment that vary in time or space (Chesson, Pacala and Neuhauser 2001; Chesson et al. 2004). At its most basic, time within a year or within a day can be thought of as an aspect of

the physical environment, and is associated with many physical properties. Stable coexistence from such environmental-niche differences arises from interactive effects of species, environmental, and competitive factors on population growth. To understand this mechanism, we first need to understand the concepts of *environmental response* and *competitive response*. Then, we shall see how these responses interact, and how covariance between them affects the net outcome of this interaction when integrated over time or space, creating a coexistence promoting effect which is expressed quantitatively in terms of these critical components.

Environmental response

By *environment*, we mean the physical environment, or more generally any factor that does not form a feedback loop of any significance with the densities of organisms from the guild under consideration, on the temporal and spatial scales under consideration. The obvious examples are weather, topography, soil properties, currents, and so on. Feedbacks do occur for many physical properties on some temporal or spatial scales, but those feedbacks that are weak, on very large scales, or for which any individual species has negligible effect, can be neglected. Most organisms have direct physiological and behavioral reactions to temperature, for example, but we do not normally think of the densities of individual species as controlling the temperature experienced in their habitat in any strong way, although species interactions mediated by temperature modifications are certainly possible (Ball et al. 2002). Thus, temperature tends to be a good environmental factor. Water is a more complex factor. Although there may be climate and vegetation feedbacks, for our purposes, we can assume that the abundance of any individual plant species has a negligible effect on the timing and amount of rainfall, and so these factors also belong to the *environment* as intended here. However, plants deplete soil moisture through transpiration, and the more dense they are, the greater the effect we expect them to have. Thus, soil moisture does not qualify here as an environmental factor, although the amount and timing of rainfall do.

In some cases, organisms outside the guild in question qualify as environmental factors. For example, in the study of annual plants in arid regions, we may think of perennials as relatively unaffected

by the annuals due to their larger size, longer timescale and slower growth. However, the local abundance of perennials may greatly affect the annual community. For annuals, perennials can in effect be habitat features, creating specific microenvironments, with major effects on annual plant performance. In this way, perennials are spatially varying environmental factors for the guild of annual plants, and are often treated this way in experimental studies (Pake and Venable 1995).

How do organisms respond to their environments? Fundamentally, the responses of interest are contributions of individual organisms to future populations. Thus, survival and reproduction are key. For an annual plant to reproduce, it must first germinate. Germination in annual plants is known to be highly sensitive to physical environmental conditions, notably temperature when rain falls (Baskin, Chesson and Baskin 1993; Baskin and Baskin 2004). Growth within a year appears also to be dependent on the physical characteristics of the year in which the individuals grow (Pake and Venable 1995) as well as on the physical conditions of the spatial location (Pantastico-Caldas and Venable 1993). Temperature alone has major effects on growth and survival of individuals of most organisms. Activity patterns of organisms, which in turn affect survival growth and reproduction, are often cued by physical environmental patterns, such as photoperiod (reviewed in Chesson et al. 2001).

An *environmental response* is a fitness component such as survival, germination, reproduction or individual growth considered as a function of physical environmental conditions. Separate fitness components might be combined to produce one overall response, viz the overall contribution of an individual to the population at the next unit of time (Chesson 1994; 2000a), if working in discrete time, or next instant of time, if working in continuous time (Chesson et al., 2005). In discrete time, this overall response is an individual's value of λ , i.e. its probability of survival to the next unit of time, plus the number of surviving offspring attributable to it, considered as a function of the environment. In continuous time, it is the individual's contribution to r , i.e. $(dN/dt)/N$, as a function of the environment.

In theoretical models of communities, environmental responses are simply parameters of the model that relate to organism per-

formance. They can be vital rates, such as birth rates, death rates, and germination rates, if these do not depend on the densities of guild members (Chesson 1994). Alternatively, environmental responses can be parameters in density-dependent models of vital rates (Descamps-Julien and Gonzalez 2005). These parameters are then made to vary over time or in space according to some probability distribution (Chesson 1994; 2000a), or according to some defined deterministic variation in space or time (Muko and Iwasa 2003; Snyder and Chesson 2003). If the model is developed for a specific application, parameter variation may be determined observationally or experimentally (see Caceres 1997; Descamps-Julien and Gonzalez 2005).

How is an environmental response defined in an experimental setting? Let us suppose that we can measure the response of an individual organism to its current conditions, through survival, reproduction, or perhaps most easily, individual growth. Call this response R_{xt} , where the two subscripts x and t indicate that the response is assumed to depend on the conditions defined by the current physical location, x , and current time, t . These conditions include environmental conditions, as defined above, and the effects of the densities of other organisms. To get a pure environmental response, we need to remove the effects of the densities of these other organisms. The obvious thing to do is to measure the response of an individual organism alone, with other individuals of all guild members removed. This sort of thing is commonly done in neighborhood competition studies in plants (Goldberg et al. 1999). Other plants from the guild in question are removed from a defined radius about the plant, and the growth of the individual as a function of the environmental conditions alone is studied.

The above sort of experimental determination of an environmental response is not so practical with mobile animals. Experiments that vary the densities of the organisms, and model the effects of these densities, might be used to remove density effects from the response of an organism to the conditions where it lives. Similar techniques might be used to remove the effects of density, if any, from plant responses such as germination, in cases where there is a reasonable expectation of density dependence (Inouye 1980).

Competitive responses

Having defined response to the environment, we now need to understand the response to competition (Goldberg 1990). In the present context, we can think of the response to competition as the decrease in performance of an individual organism due to the densities of all guild members. This definition first requires identification of the organism's performance when not faced with competition, i.e. when the densities of all guild members are zero. The environmental response, as defined above, can serve in this capacity. Then the response to competition comes from a comparison between the environmental response and the response to the full conditions that the organism encounters, including both environment and density. For example, return to our hypothetical neighborhood competition experiment, discussed above, with R_{xt} representing the final size of a plant at the end of the growing season. Then we define the environmental response, E_{xt} , to be the value that R_{xt} has with all neighbors of the individual removed. Finally, with R_{xt} representing the full response, including the effects of neighbors, we might define the competitive response to be:

$$C_{xt} = E_{xt} / R_{xt} \quad (6.8)$$

Turning this expression around, we see that:

$$R_{xt} = E_{xt} / C_{xt} \quad (6.9)$$

i.e., we have formulated the response of the organism jointly to environment and competition as the response to the environment divided by the response to competition. Thus, the response to competition is here the proportional amount by which the response to the environment must be reduced to obtain the response of the organism to the full conditions that it experiences.

The formulation (6.8) of the response to competition makes the assumption of proportional effects, which may or may not be appropriate. However, for quantities like final size over a discrete interval of time, this formulation is common and natural. For example, a common model in studies of plant competition is:

$$R_{jxt} = \frac{a_{jxt}}{1 + \sum_{k=1}^n \alpha_{jkxt} N_{kxt}} \quad (6.10)$$

(see Freckleton and Watkinson 1997), where N_{kxt} is some appropriate measure of density or biomass of guild member k in a suitable neighborhood around the point x in space where species j is growing during growing season t . The quantity α_{jkxt} is the coefficient of competition for the effect of species k on species j in location x at time t , and a_{jxt} is a species, location and time specific constant. More complex forms are sometimes justified, but for our purposes are inconsequentially different from equation (6.10). Setting densities to zero in equation (6.10) gives $R_{jxt} = a_{jxt}$. Thus, the environmental response, E_{jxt} , equals a_{jxt} . The competitive response, C_{jxt} , then works out to be:

$$C_{jxt} = 1 + \sum_{k=1}^n \alpha_{jkxt} N_{kxt} \quad (6.11)$$

These definitions lead back to equations (6.8) and (6.9) above. Thus, the standard sorts of models of plant growth justify the definition (6.8) of the response to competition.

Interactions between environment and competition

Responses to environment and competition must now be related back to the per capita growth of the population. Thus, we determine how r_{jxt} or λ_{jxt} depends jointly on E_{jxt} and C_{jxt} . Of most importance, we need to know if there is an *interaction* between the environmental response and the competitive response in their determination of r_{jxt} or λ_{jxt} . The basic kinds of interactions are presented in figure 6.3. The plant example above provides a simple route to understanding the origin of interactions. To get λ_{jxt} , the final size, R_{jxt} , is first converted to seed yield. If yield is proportional to final size, with Y_j being yield per unit mass, then $Y_j R_{jxt}$ is the number of seeds produced. If all seeds either germinate or die in any given year—i.e. there is no between-year seed bank—then:

$$\lambda_{jxt} = Y_j R_{jxt} = Y_j E_{jxt} / C_{jxt} \quad (6.12)$$

To get the per capita growth rate, r_{jxt} , we take the natural log of this equation, and find that:

$$r_{jxt} = Y'_j + E'_{jxt} - C'_{jxt} \quad (6.13)$$

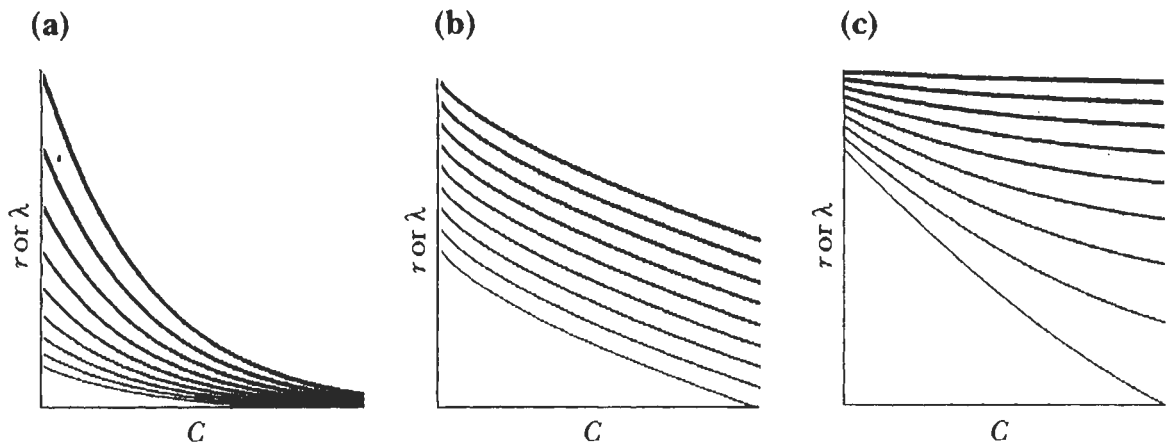
where the primes on the variables just mean the logs of the original variables (e.g. $E'_{jxt} = \ln E_{jxt}$). Of particular note here is the fact that the per capita growth rate, r_{jxt} , depends additively on the environmental and competitive responses: it is a sum of a function of the response to the environment plus a function of the response to competition. Thus, in this model there is no interaction between environment and competition in their determination of r_{jxt} (figure 6.3b). This absence of an interaction precludes the storage effect, acting on temporal variation, from being found in this case, as we shall see below.

Most organisms do not have per capita growth rates that are additive in environmental and competitive responses. Consider, for example, the more common case of an annual plant species with a seed bank. Two more parameters must be introduced: a germination rate, G_j , and a dormant seed survival rate, s_j . Then, the finite rate of increase consists of two components:

$$\lambda_{jxt} = s_j (1 - G_j) + Y_j E_{jxt} G_j / C_{jxt} \quad (6.14)$$

The per capita growth rate, r_{jxt} , is simply the natural log (\ln) of this (table 6.1, model 2), and is not additive in environment and competition. Instead, environment and competition combine interactively to determine r_{jxt} . The easiest way to see this is to note that r_{jxt} can never be smaller than $\ln\{s_j(1 - G_j)\}$, i.e. it can never be smaller than the contribution to the population growth rate of survival of dormant seeds. This component of population growth is independent of seed production, and so it does not matter how unfavorable the environment is for plant growth, or how much competition reduces plant growth, r_{jxt} can simply never become less than the value determined by survival in the seed bank. Most important, when environmental conditions are unfavorable for the plant growth in species j , (i.e. the environmental response, E_{jxt} , is very small), r_{jxt} is very close to this minimum value determined by sur-

FIGURE 6.3: Interactions between environment and competition in their determination of population growth rates (r or λ)



Note: Within each panel, each curve represents a different value of the environmental response, E , with thick lines indicating more favorable environments. (a) Buffered population growth (negative γ indicating a negative interaction): growth rates converge as the competitive response, C , increases. (b) Additive growth rates ($\gamma = 0$): growth rates remain parallel as C increases, indicating the absence of an interaction between E and C . (c) Positive γ (positive interaction), or the opposite of a buffer: growth rates diverge as C increases.

vival of dormant seeds. Moreover, r_{jxt} varies hardly at all as competition is varied. Thus, if the plants have a difficult time growing regardless of competition, it matters little how much competition there is, provided dormant seeds survive. This fact leads to the converging growth rates in panel figure 6.3a.

In contrast to annual plant dynamics with a seed bank, if there is no dormant seed survival, as in the previous model (table 6.1, model 1), then r_{jxt} still depends on competition, regardless of the physical environment. Without survival in the seed bank, poor environmental conditions do not diminish the importance of competition to r_{jxt} . Poor environmental conditions may guarantee that little new seed is produced, but without a seed bank, any seed production, no matter how little, is important, and competition has the same effect on r_{jxt} regardless of the environmental conditions. Without a seed bank, poor environmental conditions and high competition create a doubly bad situation. However, with survival in a seed bank, there is a limit to how bad things can get, and so poor environmental conditions and high competition are little worse than poor environmental conditions alone. The seed bank provides a buffer for population growth and this buffer leads to

interactive effects of environment and competition on the growth of the population, with, as we shall see, important implications for species coexistence.

Table 6.1 gives several other models illustrating how the per capita growth rate, r_{jxt} , can be buffered against jointly unfavorable environmental and competitive effects. In model 3, the germination fraction becomes the environmental response, E_{jxt} , consistent with the common observation of strong environmental dependence of germination in annual plants (Baskin, Chesson and Baskin 1993; Baskin and Baskin 2004). The average final size of a plant is given there as V_j . The buffering effect there is even stronger because not only does a poor environmental response reduce the effect of competition, but it also increases the fraction of seed persisting in the seed bank.

Model 4, of table 6.1 is for perennial organisms, with standard examples being coral reef fishes and forest trees (Chesson 2003). In perennials, reproduction and juvenile survival are processes most strongly varying with environmental factors and competition (Warner and Chesson 1985). Adult survival is relatively insensitive

TABLE 6.1: Models of population growth

Model	λ_{jxt}	r_{jxt}	Type of guild
1	$Y_j E_{jxt} / C_{jxt}$	$Y'_j + E'_{jxt} - C'_{jxt}$	Annuals with no seed bank; E_{jxt} = final plant size.
2	$s_j(1 - G_j) + Y_j E_{jxt} G_j / C_{jxt}$ or $s_j(1 - G_j) + Y_j G_j \exp(E'_{jxt} - C'_{jxt})$	$\ln\{s_j(1 - G_j) + Y_j E_{jxt} G_j / C_{jxt}\}$ or $\ln\{s_j(1 - G_j) + Y_j G_j \exp(E'_{jxt} - C'_{jxt})\}$	Annuals with a seed bank, but a fixed fraction germinating; E_{jxt} = final plant size.
3	$s_j(1 - E_{jxt}) + Y_j E_{jxt} V_j / C_{jxt}$	$\ln\{s_j(1 - E_{jxt}) + Y_j E_{jxt} V_j / C_{jxt}\}$	Annuals; E_{jxt} = fraction germinating
4	$s_j + E_{jxt} / C_{jxt}$ or $s_j + \exp(E'_{jxt} - C'_{jxt})$	$\ln\{s_j + E_{jxt} / C_{jxt}\}$ or $\ln\{s_j + \exp(E'_{jxt} - C'_{jxt})\}$	Perennials with E_{jxt} = recruitment without competition

Note: λ_{jxt} : individual-level finite rate of increase; r_{jxt} : individual-level per capita growth rate; j : species; x : location in space; t : time; Y_j : new seed per unit final biomass; E_{jxt} : environmental response; C_{jxt} : competitive response; s_j : survival rate of dormant seed (models 2 and 3) and adult survival (model 4); G_j : germination fraction; V_j : final plant size. Primes mean natural log, e.g. $E'_{jxt} = \ln E_{jxt}$.

to these factors. Thus, in model 4, adult survival is represented as a constant, and the environmental response, E_{jxt} , represents per capita production of juvenile organisms. The environmental response therefore involves both reproduction and environmentally-dependent early survival. These juveniles then compete for resources for maturation, and so the actual per capita recruitment of new adults of species j is E_{jxt}/C_{jxt} . Here adult survival buffers variation in recruitment to the adult population, and causes environment and competition to interact in their determination of r_{jxt} . In contrast, if adult survival rather than recruitment were to be environmentally dependent, its interaction with competition would be the opposite of a buffer (Chesson and Huntly 1988), as depicted in figure 6.3c.

Interactive contributions of environment and competition to r_{jxt} are relevant to buffering of variation over time. For spatial variation, with dynamics considered in discrete time (see table 6.1), we must consider interactive contributions of environment and competition to λ_{jxt} (Chesson 2000a). Buffering in space is then nearly always automatic because poor performance in one spatial location is buffered by superior performance elsewhere, provided locations are connected by at least some dispersal. Mathematically, this buffering reflects the fact that the relevant quantity for understanding spatial dynamics, the finite rate of increase, λ_{jxt} , is always nonnegative, and therefore bounded below by zero. In contrast, the corresponding quantity for consideration of temporal variation, r_{jxt} , in general is not bounded below at all, and so buffering life-history traits, like the seed bank, are needed to introduce interactive effects of environment and competition. To see that the relevant interactive effects do commonly arise with spatial variation, note that in all of the models of table 6.1, E_{jxt} is divided by C_{jxt} in the formula for λ_{jxt} . It follows that the effect of the environment on λ_{jxt} depends on the amount of competition present, i.e. E_{jxt} and C_{jxt} are interactive in their determination of λ_{jxt} .

Covariance between environment and competition

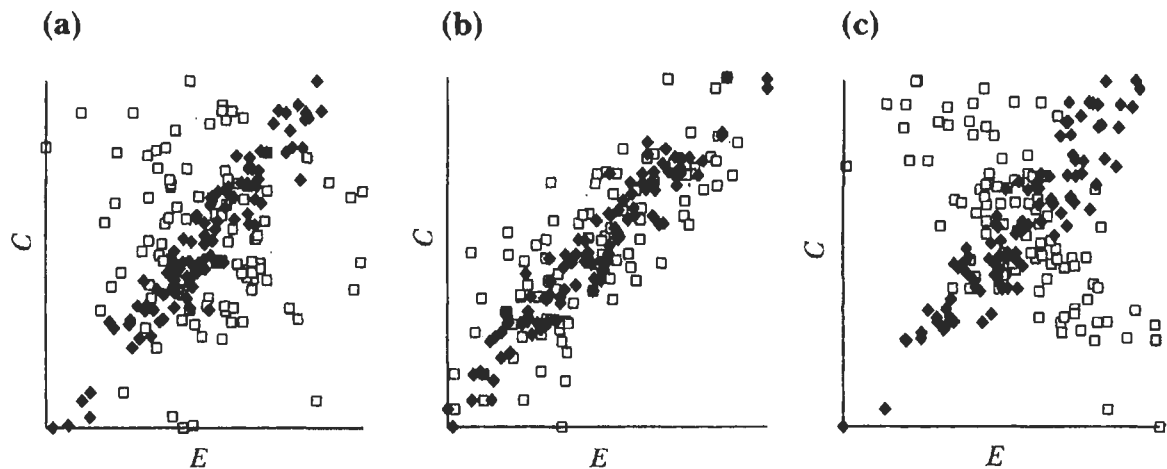
Interactions between environment and competition concern how the quantities E_{jxt} and C_{jxt} combine, after their magnitudes have been determined, to give the values of r_{jxt} and λ_{jxt} . Now we turn attention to the magnitudes of E_{jxt} and C_{jxt} . Of most importance,

there is every reason to expect the value of C_{jxt} to depend on E_{jxt} , i.e. the response to competition should depend on the response to the environment, or at least be correlated with it. This is the concept of *covariance between environment and competition*, which is independent of the concept of the *interaction between environment and competition*, our concern above. The concept of covariance between environment and competition is illustrated by the scatter plots of figure 6.4, and is perhaps most easily understood for the case of annual plants where the environmental response is the germination fraction. We naturally expect higher germination to lead to a higher magnitude of competition. For example, if N_{kxt} is equal to the number of seeds of species k in a competitive neighborhood of the point x , then it is reasonable to have competition linearly related to the densities, $E_{kxt} N_{kxt}$, of growing plants, e.g.:

$$C_{jxt} = 1 + \sum_{k=1}^n \alpha_{jk} E_{kxt} N_{kxt} \quad (6.15)$$

so that higher germination leads to higher competition. Similarly, in the case of perennial organisms competing for the resources

FIGURE 6.4: Scatter plots illustrating covariance between environment and competition



Note: Each point represents the environmental response, E , and competitive response, C , for a particular species at a particular time and location. The closed diamonds in each panel are for a species in a resident state showing strong positive covariance. The open squares are for a species in the invasion state. Correlations between resident and invader E are (a) 0, (b) 0.8, and (c) -0.8 , giving respectively 0, positive and negative covariance between environment and competition for the invader. In all cases invader covariance is less than resident covariance.

necessary for recruitment, higher juvenile production rates (higher E_{kxt} 's), lead to higher numbers of juveniles and hence more competition for the scarce resources needed for juveniles to successfully mature as adults.

In these examples, the link between environment and competition is particularly evident, but occurs in many other cases too. For instance in the plant growth model given by equation (6.10), with E_{kxt} being the final size without competition, α_{jkxt} might plausibly be proportional to E_{kxt} , e.g. it might take the form $\alpha_{jk} E_{kxt}$, because demand for resources should be higher when the environment promotes faster growth (Chesson et al. 2001). Thus, formula (6.15) might reasonably apply in this case too.

These examples all show that the competitive response of species j , C_{jxt} , is not just related to its own environmental response, E_{jxt} , but to the environmental responses of all species, i.e. to E_{kxt} , $k = 1, \dots, n$. Moreover, how much it is related to any of these environmental responses depends on the species' densities. So when a species is very rare, the competition that it experiences depends only weakly on its own environmental response. Instead, it depends directly more on the environmental responses of other species. However, if a rare species, or more correctly for our considerations here, a species i in an *invader state*, has an environmental response that is closely correlated with the environmental response of an abundant species (a species r in a *resident state*), then its environmental and competitive responses will nevertheless be correlated. So even though there is no direct causation between C_{ixt} and E_{ixt} in such cases, there is likely a correlation. This correlation depends on the correlation between E_{ixt} and the E_{rxt} 's of abundant species.

Although ecologists focus on correlations to understand strengths of relationships, here we need to use the related concept of covariance. Covariance comes into play because we need to understand the magnitude of the joint relationship, not just the closeness of it, which the correlation measures. The covariance between C_{jxt} and E_{jxt} is equal to the correlation between each of these variables multiplied by the product of their standard deviations. Thus, it includes the variation in each of these variables separately, and also how closely they are related through their correlation. One

might ask how this is important. This is important because when covariance between environment and competition is positive, favorable values of E_{jxt} are offset by increases in C_{jxt} . Thus, although the physical environment may be favorable, higher competition associated with that favorable physical condition reduces the benefit that an organism would gain from it. When there is little covariance between C_{jxt} and E_{jxt} the benefit of a favorable physical environment is not, on average, offset by higher competition (figure 6.4a page 142). Moreover, it is possible for covariance between environment and competition to be negative, for example, for an invader whose environmental response is negatively correlated with those of residents (figure 6.4c). Then the boost the invader gains from favorable environmental conditions is frequently augmented by reduced competition.

This behavior of covariance between environment and competition is at the heart of the storage effect. At high density, a species tends to have positive covariance between environment and competition (figure 6.4, resident species plots). Thus, the gains it might make through favorable environmental conditions are diminished by increased competition. The reverse is also true: losses that it might experience during unfavorable environmental conditions are offset by reduced competition during those times. However, when a species drops to low density, covariance between environment and competition weakens, or even becomes negative, depending on the correlations between the species' environmental response and those of its higher-density competitors. This means that when a species drops to low density, it experiences a greater variety of conditions for population growth than does a species at high density (figure 6.4, invader plots). These conditions potentially include strongly favorable combinations of environmental and competitive conditions as well strongly unfavorable conditions (Chesson et al. 2004).

The storage effect converts these differences in variation, experienced at high and low density, into a low-density advantage, provided an interaction between environment and competition buffers population growth. A buffer does not occur, however, in all situations. For example, for annuals without a seed bank (model 1 of table 6.1 page 140), affected only by temporal variation, the long-

term growth rate of a species depends just on the average over time of E'_{jxt} and C'_{jxt} separately because r_{jxt} depends just on the difference between E'_{jxt} and C'_{jxt} , i.e. is additive in environment and competition (figure 6.3b page 139). Thus, covariance between environment and competition has no effect in the long run. Fundamentally, in the long run it does not matter whether a species experiences a more variable or less variable growth rate, the long-term outcome is the same when there is no interaction between environment and competition. However, when population growth is buffered (e.g. annuals with a seed bank, or long-lived perennials), unfavorable conditions for growth count less than favorable conditions (Chesson and Huntly 1989; Chesson et al. 2004). Thus, variation leads to a positive bias over what would occur without variation. The mean growth rate therefore is increased, i.e., the recovery rate, r_i^- , from low density is increased, promoting species coexistence.

Note that the situation is different with spatial variation, for then $\tilde{\lambda}_i$ determines the invasion rate, and this is the average of λ_{ixt} over individuals experiencing different conditions in different spatial locations. As remarked above, buffering of spatially varying conditions for population growth arises simply from dispersal, even with annual plants that lack a seed bank. Hence, the spatial storage effect can be expected to be found whenever covariance between environment and competition is present and weakens or changes from positive to negative between resident and invader states. These conditions will normally be met in circumstances where we think of the organisms as having spatial environmental niches (Chesson et al. 2001).

Quantifying the storage effect

Table 6.2 (page 149) gives the quantitative measure, ΔI , of the storage effect in terms of the components above. Covariance between environment and competition for species i , as an invader, is given as χ_i^{-i} , and this is compared with covariances for residents denoted χ_i^{-i} . Involved in these comparisons are the constants, γ_j , which measure the interaction between environment and competition. These constants are negative in the buffered case, emphasized above, where unfavorable combinations of environment and competition are prevented from having strongly negative effects on

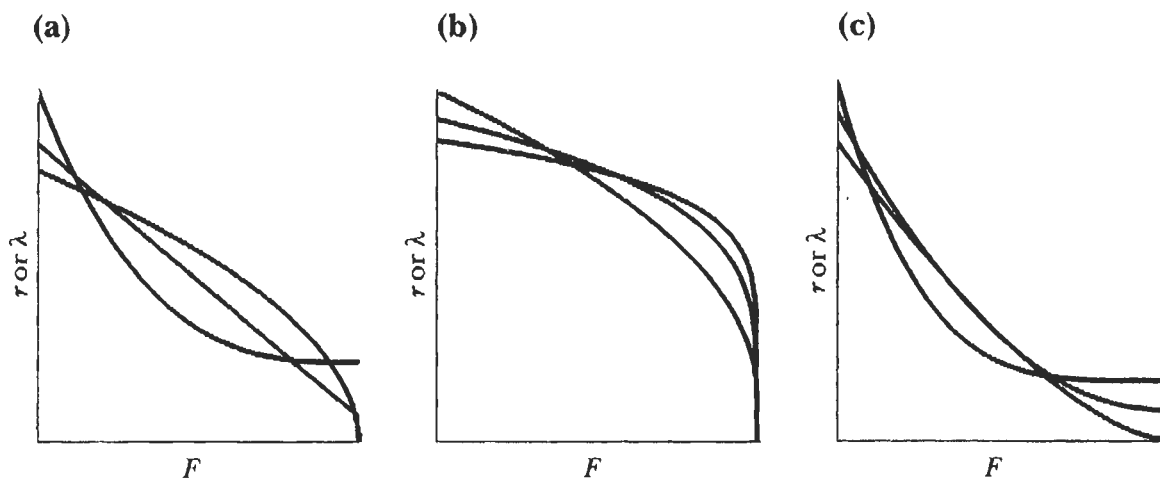
population growth. They are zero in the noninteractive or additive case, which of course leads to a zero storage effect.

The formula in the first row assumes that all species are limited by the same competitive factor. This means that the species are not differentiated by which resources they compete for, or how much they need these different resources, but instead may be differentiated by when and where they use them. The response time constants, $1/b_j$, scale the other quantities in this formula making all comparisons in the same natural units. To understand this formula, it is simplest first of all to assume that the buffering and response time constants are the same for every species. Then the formula for ΔI is directly a comparison of the environment-competition covariance for an invader compared with the average of this covariance for residents. Thus, the weak or negative covariance for an invader compared with the expected positive covariance for residents, multiplied by a negative value of γ , leads to an overall positive storage effect, ΔI . More generally, the relative values of the γ/b terms must be considered too, but the real action in this mechanism is the change in the covariance with the change in state from invader to resident.

The more general formula in the second row embodies essentially the same idea but does not assume the same competitive factor for all species. The constants, q_{is} , however, complicate the covariance comparison. They allow for multiple limiting factors and adjust for unique resource use comparisons for each species pair in that case.

6.4.2. Relative nonlinearity of competition

Different species, even when limited by a common competitive factor, will not necessarily respond in the same way to different amounts of that factor (Armstrong and McGehee 1980; Abrams and Holt 2002; Chesson et al. 2004) (see figure 6.5). For example, consider a guild where each member is limited by the same resource. Some guild members may have a threshold response to the resource, i.e. they show little response to increases in resource density while resources remain scarce (figure 6.5c). Others may have a saturation response: once resource abundances are high, they gain little additional benefit from further increases in resource levels

FIGURE 6.5: Relative nonlinearity of competition


Note: Each panel shows growth rates (r or λ) as a function of a common competitive factor, F , for three species from the same guild. When F is resource shortage, high F represents low levels of resources, and low F represents plentiful resources. In each panel the species have relatively nonlinear responses to F , as measured by differences in their nonlinearity measures, τ . (a) Two species with opposite curvature and a species with a linear response (positive, negative and zero τ). (b) Three species with positive but unequal τ (e.g. different degrees of saturation at high resource abundance). (c) Three species with negative but unequal τ (e.g. different degrees of threshold response to resources).

(figure 6.5b). Yet others may have an essentially linear response: any increase in resource density gives a proportionate increase in the per capita growth rate of the species.

Species coming from these different categories have relatively nonlinear responses to the resource (Chesson 1994, 2000b; Chesson et al. 2004) (see figure 6.5a). If the response of one species is plotted on a graph against the response of another, the graph is some sort of a curve rather than a straight line. The important point is that species with different nonlinear responses will gain unequal benefits as the limiting factor in question increases in abundance. With a limiting resource, fluctuations in the resource will affect different species differently (Armstrong and McGehee 1980; Adler 1990; Chesson 1994, 2000b; Abrams and Holt 2002; Chesson, et al., 2004). A species with a per capita growth rate that is a linear function of a limiting resource sees no long-term effect of fluctuations (figure 6.5a, middle plot). A species with a threshold response has a higher long-term growth rate, \bar{r} , with fluctuations about a given mean resource level than when the resource is fixed at that mean level. Finally, a species with a saturating per capita growth rate as a

function of a resource is better off with a constant resource level than a resource fluctuating about this level as its mean.

Natural communities do not consist of species with just these three discrete types of response to resources, but are instead mixtures of these, and also have other more subtle kinds of nonlinear response. However, due to differences in the natures of their nonlinear responses to resources, different species stand to gain or lose different amounts from the presence of fluctuations in those resources. Nonlinearities in response to resources can increase or decrease fluctuations in those resources. Threshold type responses tend to decrease resource fluctuations, while saturating responses tend to increase resource fluctuations (Chesson et al. 2004). Thus, each type of species tends to reduce the conditions that favor it more, and enhance the conditions that favor a different kind of species. Hence, such relatively nonlinear responses can act as a fluctuation-dependent coexistence mechanism (Armstrong and McGehee 1980).

Quantification of such mechanisms involves first of all defining a measure of nonlinearity. This quantity is τ_j , for species j , and is defined in terms of derivatives of the species per capita growth rate (Chesson 1994). The comparison between species, $\tau_j - \tau_k$, is the relative nonlinearity of species j to species k , and $\tau_i - \bar{\tau}_s^{(i \neq s)}$ is the relative nonlinearity of species i to the average of its competitors. We use the symbol F to indicate the magnitude of the fluctuating competitive factor. This could be a resource, some measure of resource shortage, or it could be the density of a predator, if we are dealing with apparent competition rather than competition. The variance of this competitive factor is to be measured in a resident-invader situation, and the superscript, $\{-i\}$, indicates that species i is in the invader state when this measurement is made.

An informative approximation to the measure of relative nonlinearity, ΔN , derived from Chesson (1994), is given in table 6.2. It is the product of the relative nonlinearity measure, $\tau_i - \bar{\tau}_s^{(i \neq s)}$, and the variance, $\text{var}(F^{(i)})$, of the competitive factor with species i as invader. Unlike ΔI this quantity is always different for different species. In particular, it is negative for all those species with less than average nonlinearity, and positive for all those species with more than average nonlinearity. If the variance of the competitive

factor does not change with the identity of the invader, this mechanism can only modify average fitness differences, and so can only promote coexistence as an equalizing mechanism. As we shall see later, however, when $\text{var}(F^{[-i]})$ does vary with i , relative nonlinearity can be a stabilizing mechanism. It follows the intuitive idea described above. Nonlinearities of residents tend to interact with resources in ways that produce more favorable variances for invaders (Armstrong and McGehee 1980; Chesson 2000b; Chesson et al. 2004). Thus, residents with high values of τ promote high variances, while residents with low values of τ promote low variances. It follows that invaders with low values of τ tend to experience high variance, while those with high τ tend to experience low variance, which is the arrangement promoting positive recovery rates.

Here we have considered only the case where there is a single limiting factor. However, more complex measures of relative nonlinearity exist for multiple competitive factors (Chesson 1994), which, models suggest, may be important in some natural systems. Examples are systems of interacting phytoplankton species com-

TABLE 6.2: Formulae for mechanism measures

Mechanism	Formula	Assumptions
ΔI (storage effect)	$\frac{\gamma_i}{b_i} \chi_i^{[-i]} - \frac{\overline{\gamma_s}}{b_s} \chi_s^{[-i]} \quad (s \neq i)$	Common competitive factor
ΔI	$\gamma_i \chi_i^{[-i]} - \sum_{s \neq i}^n q_{is} \gamma_s \chi_s^{[-i]}$	General case
ΔN (relative nonlinearity)	$(\tau_i - \bar{\tau}^{[s \neq i]}) \text{var}(F^{[-i]})$	Common limiting factor F
$\Delta \kappa$ (fitness-density covariance)	$\frac{\text{cov}_x(\lambda_{ixt}, v_{ixt})}{b_i} - \frac{\overline{\text{cov}_x(\lambda_{sxt}, v_{sxt})}}{b_s} \quad (s \neq i)$	Common competitive factor
$\Delta \kappa$	$\text{cov}_x(\lambda_{ixt}, v_{ixt}) - \sum_{s \neq i}^n q_{is} \text{cov}_x(\lambda_{sxt}, v_{sxt})$	General case

Note: γ_j : buffering coefficient; b_j : sensitivity of species j to a common competitive factor; $\chi_i^{[-i]}$: covariance between environment and competition for an invader species i ; $\chi_s^{[-i]}$: covariance between environment and competition for a resident species s . Superscript $[-i]$: measurement with species i in an invader state. $\bar{\tau}^{[s \neq i]}$: average over all species s , excluding the value i . Values are on the natural scale in the case of a common competitive or limiting factor.

peting for several limiting resources (Huisman and Weissing 2002). Models of such systems often have complex multidimensional nonlinearities, with ample opportunity for important differences between species in these nonlinearities. Thus, when resources fluctuate in these models, important effects on the predicted outcomes of species interactions are to be expected.

6.4.3. Fitness-density covariance

The previous two mechanisms have spatial and temporal versions. Fitness-density covariance, however, is only treated as a separate mechanism in the case of spatial variation. Fitness-density covariance is the covariance in space between the favorability in local conditions for individuals of a species, and their density there (Chesson 2000a; Chesson et al. 2005). The conditions in space are measured by the local fitness, λ_{jxt} , in the discrete-time formulation, and by the per capita growth rate, in continuous-time formulations (Chesson 2000a; Chesson et al. 2005). Population density is measured by the local relative density, which is defined as the ratio of N_{jxt} , the population density of species j , at location x at time t , to \bar{N}_{jt} , the spatial average of this value (the population density at the landscape scale). Thus, the local relative density is $v_{jxt} = N_{jxt} / \bar{N}_{jxt}$, i.e. the local density divided by the density at the landscape level. Thus, this local relative density measures the degree to which the species is concentrated at any particular location, x .

Fitness-density covariance, in general terms, is the covariance in space between local fitness and local density, viz, $\text{cov}_x(\lambda_{jxt}, v_{jxt})$. It turns out to be the difference between the landscape-level fitness, $\tilde{\lambda}_{jt}$, i.e. the average fitness of all individuals of species j , on the landscape, and the spatial average fitness, $\bar{\lambda}_{jt}$, the simple average of λ_{jxt} in space (Chesson et al. 2005). This covariance is important because individuals may often be unevenly distributed in space relative to fitness. If there are more individuals in favorable places than unfavorable places, then fitness-density covariance is positive, indicating that the average fitness in the population is greater than would be obtained if the species were evenly distributed with the same fitness variation over the landscape. On the other hand, if there were more individuals in unfavorable locations, fitness-density covariance would be negative, and in fact the average fitness

of the individuals in a population would be less than the spatial average fitness.

Covariance between fitness and density can have a role in species coexistence because a species at low density has more opportunity to build up in its favorable locations (Chesson 2000a) and this outcome has a major role in coexistence in a variety of spatial models. A species at high density necessarily causes higher competition in the locations where its population is higher than average, reducing fitness there. In the absence of other spatially varying factors, this would lead to negative fitness-density covariance for such species. More generally, fitness-density covariance is simply likely to be less when a species is at high density than when it is at low density. This comparison between high and low densities then applies to species in resident and invader states, promoting recovery from low density and leading to coexistence.

Fitness-density covariance has demonstrated a major role in coexistence in a variety of spatial models (see Bolker and Pacala, 1999; Chesson 2000a; Snyder and Chesson 2003; Snyder and Chesson 2004; Chesson et al. 2005). Table 6.2 gives the quantitative measure, $\Delta\kappa$, of fitness-density covariance as a coexistence mechanism. It consists of simple covariance comparisons between the invader and residents, with the usual weighting factors.

6.5. The community average approach

The quantification of coexistence mechanisms above involves a number of complications. Often the mechanism is most easily understood in terms of how the conditions encountered by an individual species change between its resident and invader states. However, the mechanism quantifications above all involve comparisons between a species as an invader and other species as residents. Second, each of these comparisons involves constants whose different values for different species complicate the interpretation. Not so obvious is the fact that each of the quantities, ΔI , ΔN , and $\Delta\kappa$, in general has a particular value for each particular species. Thus, each of them really should be given a subscript i to indicate its species dependence. That a given mechanism may affect different spe-

cies to different extents, or even in different ways, highlights the fact that these mechanisms need not be purely stabilizing in action, but may modify average fitness differences too.

The formula for ΔN most clearly exhibits an average-fitness difference modifying role. There, the comparison of τ values shows that it will be negative for some species and positive for others. Indeed, without preexisting average fitness differences to equalize, stable coexistence is impossible with this mechanism alone (Chesson 1994, 2000b). Thus, for relative nonlinearity to allow stable coexistence in the absence of other mechanisms, it must have both equalizing and stabilizing roles. However, fitness difference modification can arise also with the storage effect. For instance, in the perennial model with temporal recruitment variation (model 4 of table 6.1), and a single competitive factor, differences between species in adult survival rate lead to an asymmetrical storage effect, which is given in natural units approximately as:

$$\Delta I_i = \sigma^2 \left\{ \frac{(1 - \rho) \bar{s}_j^{(j \neq i)}}{n - 1} + \rho (\bar{s}_j^{(j \neq i)} - s_i) \right\} B \quad (6.16)$$

(Chesson 2003), where ΔI is given a subscript here to emphasize that it is different for different species. Here, $\bar{s}_j^{(j \neq i)}$ is the simple average of resident adult survival rates, while $\bar{s}_j^{(j \neq i)}$ is an average weighted by mean juvenile abundance. The constant B reflects the nature and intensity of competition. Of most significance, $\bar{s}_j^{(j \neq i)} - s_i$ makes ΔI potentially seriously asymmetric, depending on the correlation, ρ , between species over time in recruitment rates. Thus, the component $\sigma^2 \rho (\bar{s}_j^{(j \neq i)} - s_i) B$ of ΔI modifies average-fitness differences and equalizes average-fitness differences, or exacerbates them, depending on the circumstances.

If ΔI in formula (6.16) is averaged over species, its fitness difference modifying component vanishes, and we are left with:

$$\bar{\Delta I} = \sigma^2 \left\{ \frac{(1 - \rho) \hat{s}}{n - 1} \right\} B \quad (6.17)$$

where \hat{s} is another weighted average of the adult survival rates of all species. Except for the fact that \hat{s} is an average, this result is identical to the formula for the ΔI value for individual species when they do not differ in adult survival rate. The difference

$\Delta I_i - \bar{\Delta}I$ is a modifier of average-fitness differences. In this way, the individual species ΔI_i partitions into a stabilizing component, $\bar{\Delta}I$, which is positive and the same for all species, and an average-fitness difference modifying component, $\Delta I_i - \bar{\Delta}I$ (Chesson 2003). The stabilizing component, $\bar{\Delta}I$, is referred to as the community average measure of the mechanism, as it is an average over species of the natural unit measures of the mechanism for the individual species, ΔI_i . For example, consider adding the storage effect to a situation with a preexisting mechanism obeying expression (6.1) above, then expression (6.1) in natural units changes to:

$$\bar{r}_i \approx k'_i - \bar{k}' + A' \quad (6.18)$$

where $A' = A + \bar{\Delta}I$, and is the combined stabilizing effect of the storage effect and the preexisting mechanism, while $k'_i - \bar{k}' = k_i - \bar{k} + \Delta I_i - \bar{\Delta}I$ is the modified fitness comparison.

Table 6.3 gives community-average measures for each of the three variation-dependent coexistence mechanisms. These measures are available at the present time only in the special case where there is common competitive factor. An important feature of both the storage effect and fitness-density covariance, however, is that the critical comparisons are now within species and are direct comparisons of the functional components of the mechanisms without intervening constants. Thus, for the storage effect, we see that for each species, covariance between environment and competition is compared between the invader state, χ_j^{i-j} , and the resident-state average, $\overline{\chi_j^{i-j}}^{(i \neq j)}$, with the average being over each other species i in the invader state. For fitness-density covariance, $\bar{\Delta}\kappa$, the formula consists of direct comparisons of fitness-density covariance in the invader- and resident-state average, for each species. Relative nonlinearity, however, is a little more complex, involving covariance over species of the species' competitive nonlinearity, τ_i , and the variance in the competitive factor for the species in the invader state.

The differences, $\Delta I_i - \bar{\Delta}I$, $\Delta N_i - \bar{\Delta}N$ and $\Delta \kappa_i - \bar{\Delta}\kappa$, each modify the k_i of expression (6.1) as exemplified for the storage effect above. A note of caution here is that it is not always a simple matter of adding a mechanism to a system without changing something else about the system. For example, when the storage effect is intro-

TABLE 6.3: Community-average measures

Mechanism	Formula
$\bar{\Delta I}$	$\frac{1}{n} \sum_{j=1}^n \frac{\gamma_j}{b_j} \left(\chi_j^{(-j)} - \overline{\chi_j^{(-i)}}^{(i \neq j)} \right)$
$\bar{\Delta N}$	$\frac{n}{n-1} \text{cov}_i (\tau_i, \text{var}(F^{(-i)}))$
$\bar{\Delta \kappa}$	$\frac{1}{n} \sum_{j=1}^n \frac{1}{b_j} \left(\text{cov}_x^{(-j)} (\lambda_{jx}, v_{jx}) - \overline{\text{cov}_x^{(-i)} (\lambda_{jx}, v_{jx})}^{(i \neq j)} \right)$

Note: As for table 6.2, and cov_i meaning covariance over species i , with i running through all guild members, 1 to n . In each case a single competitive factor is assumed, and measurements are all expressed on the natural scale.

duced into a system by adding environmental variation, separate variance effects modify the k 's independently of the storage effect contributions, as we shall see below. However, such effects do not alter the primary message here of the stabilizing roles of the community-average measures, and the average-fitness difference modifying roles of the residuals $\Delta I_i - \bar{\Delta I}$, $\Delta N_i - \bar{\Delta N}$ and $\Delta \kappa_i - \bar{\Delta \kappa}$.

A notable feature of these community-average measures for the storage effect, and fitness-density covariance, is their involvement of direct comparisons of the functionally important components of the mechanism. A critical component of the storage effect, for example, is the change in environment-competition covariance between invader and resident states. This is also the component in most doubt, as the other important component, buffered population growth, is often known from the life histories of the organisms. Given buffered population growth, the community-average measure shows that if each species has a higher resident-state covariance than invasion-state covariance, an overall stabilizing outcome must occur, without the need to determine the actual values of the γ 's and sensitivities to competition. A similar feature applies to fitness-density covariance. In summary, these community-average measures show that the stabilizing properties of the storage effect and fitness-density covariance arise from density dependence of the relevant covariances, as the mechanisms are understood intuitively.

The community-average relative nonlinearity measure, $\bar{\Delta N}$, is also instructive in how the mechanism has stabilizing effects. Because ΔN contributes to \bar{r}_i with a negative sign (equation 6.3), we see that negative covariance between nonlinearity and competitive-factor variance leads to a stabilizing effect. It is indeed a negative relationship between nonlinearity and variance that intuitively leads to stability by this mechanism, expressed in the community-average measure by negative covariance. However, studying variance alone, without detailed knowledge of the constants, τ , cannot reveal this stabilizing role, making relative nonlinearity potentially more difficult to study than the storage effect and fitness-density covariance. It is also important to note that the strong asymmetries between species in the species-specific relative nonlinearity measures, ΔN , mean that this mechanism has difficulty permitting the coexistence of more than two species in the absence of another stabilizing mechanism (Chesson 1994). In essence, the fitness difference modifying components tend to dominate the stabilizing effects. However, in conjunction with other mechanisms, relative nonlinearity can potentially have an important equalizing role facilitating the stable coexistence of many species.

6.6. How these measures can be used for hypothesis testing

The statistical expression of these mechanism measures expresses their functional components quantitatively. Thus, it ought to be possible to demonstrate mechanism functioning by measuring the appropriate quantities, and applying statistical tests to these measurements. We consider two different circumstances where approaches to testing these ideas have been worked out, and to some degree are already in application.

6.6.1. Testing the storage effect

With the storage effect, density dependence of covariance between environment and competition emerges as the key functional component. Testing for this density dependence in the appropriate circumstances becomes a strong test of the mechanism. With

the community-average measure, the density in question is intraspecific density, varied between invader and resident states. Ideally, these measurements would be done for all species in a competitive guild, or for a suitable sample of them. Ideally, also, one would like to know the buffering constants γ and the sensitivities to competition, b , for then one could estimate the full magnitude of the mechanism. More generally, one would like to know the coefficients q_{is} for the case where a single limiting factor cannot be assumed (see table 6.2 page 149).

As remarked above, however, knowledge that buffering occurs, i.e. that the constants γ are negative, might often be inferred by knowledge of the life histories of the organisms. In those circumstances, demonstrating an increase in covariance between invader and resident states makes it clear that the storage effect is functioning in the system and ought to promote coexistence. The confidence in this conclusion is greater in the case of a single competitive factor where the community-average measure exists. However, even a simple demonstration of covariance between environment and competition itself is of value, and has been completed for a number of plant communities by Anna Sears (Sears 2004; Sears and Chesson 2007), for without covariance between environment and competition, there can be no storage effect.

How do we choose the environmental response to perform such tests? While the present theory forces us to choose just one component of fitness to define the environmental response, it is best to choose one that a) seems most likely to give covariance between environment and competition, b) appears to have a low or negative correlation between species, and c) will be associated with buffered population growth. Such an environmental response is a good candidate for driving a strong storage effect. Above, growth of a plant over a single growing season was the example of choice. It has merit in plant community ecology for understanding the storage effect as a spatial mechanism. As mentioned above, dispersal in space essentially guarantees buffered population growth, and standard neighborhood competition studies can be modified to measure covariance between environment and competition (Sears 2004; Sears and Chesson 2007). Species removals can be used to mimic invader and resident states. Without maintaining removals for a

number of years before taking the measurements, these would not be true invader and resident states, but should be useful approximations.

6.6.2. Testing mechanisms in combination: the recruitment variation hypothesis

In nature, it is reasonable to expect several mechanisms to be operating in any system. Indeed, it is quite likely that in the presence of environmental fluctuations, all of the fluctuation-dependent mechanisms discussed here would be present. The ideas above allow each of them to be studied separately, and their separate contributions understood. Sometimes, however, it is their combined effect that is of interest, especially if it forms a homogeneous hypothesis in its own right. That is the case with the hypothesis that recruitment fluctuations promote species coexistence in marine and forest systems (Chesson 2003). Storage effect theory in some circumstances predicts that population growth rates will be more variable in the invader state than in the resident state (Chesson and Huntly 1989). In recruitment variation models, this is a reflection of higher recruitment variation. So our task here is to understand coexistence in terms of variation in recruitment rates over time.

We restrict discussion to temporal variation. The environmental response is per capita recruitment to the adult population in the absence of competition, normally measured on a log scale. We shall assume just a single competitive factor, namely, the resource or resource combination needed for recruitment to the adult populations. In many applications this is assumed to be space for marine organisms to settle, or for perennial plants to grow. Chesson (2003) includes a constant α_j to allow recruitment of each species to be uniquely sensitive to competition. This constant makes the formulae look more complicated without materially affecting the results. Thus, for clarity it is omitted in the discussion here.

Both relative nonlinearity of competition, and the storage effect, potentially affect species coexistence when recruitment fluctuates over time. In addition, the per capita growth rate, r_{jp} , is in general a nonlinear function of the environmental response. When the environmental response varies, even with competition held fixed, the long-term growth rate is affected due to the statistical phenomenon

termed *nonlinear averaging* or Jensen's inequality (Chesson et al. 2005). As a consequence, average-fitness differences are modified, but no stabilizing effects occur that are not already accounted for by the storage effect and relative nonlinearity. Specifically, the average-fitness measure, k_j , takes the form:

$$k_j = \mu_j + \frac{1}{2} s_j \sigma_j^2 \quad (6.19)$$

where μ_j is k_j without recruitment variation, s_j is the adult survival rate and σ_j^2 is the variance over time in the environmental response. Thus, we see variance in the environmental response increases average fitness by an amount that depends on the adult survival rate (see Chesson 2003).

The general expression for invasion is the usual one, expression (6.3), which gives $\bar{r}_i = \bar{r}'_i - \Delta N + \Delta I$, with $\bar{r}'_i = k_i - \bar{k}$. The storage effect, relative nonlinearity, and the term $\frac{1}{2} s_j \sigma_j^2$, combine here to give an approximate natural-unit recovery rate equal to:

$$\bar{r}_i \approx \mu_i - \bar{\mu} + \frac{1}{2} \left\{ s_i \text{var}(R'_i) - \overline{\text{var}(R'_r)}^{(r \neq i)} \right\} \quad (6.20)$$

where species i is in the invasion state, and the species designated r are residents and R'_j is ln recruitment. Expression (6.20) is thus equal to the fitness comparison in the absence of recruitment fluctuations, plus a comparison of variances. The variance comparison, however, is complicated by the presence of the adult survival rate, or adult survival divided by a_j in the more general case. Thus, the recovery rate of species i is not necessarily given a boost by having more variable recruitment than residents if its adult survival rate is too low compared with that of residents.

A clearer outcome is found using the community average approach. The quantity A is necessarily equal to $\bar{\Delta I} - \bar{\Delta N}$ because the storage effect and relative nonlinearity are the only mechanisms present. Now rearranging formula (28) of Chesson (2003), we find that:

$$A = \bar{\Delta I} - \bar{\Delta N} \approx \frac{1}{2n} \sum_{j=1}^n s_j \left\{ \text{var}(R'_j{}^{(i \neq j)}) - \overline{\text{var}(R'_j{}^{(i)})}^{(i \neq j)} \right\} \quad (6.21)$$

Thus, we see that there is a net stabilizing effect of recruitment variation if each species as invader has higher recruitment variance

than it has on average when a resident with some other species in the invader state. The more general case with differing sensitivities of the species to competition comes to the identical conclusion, but with s_j/a_j replacing s_j here (Chesson 2003). In answer to our questions, higher recruitment variance in the invader state does promote stable coexistence. Stable coexistence implies that A is positive, but from expression (6.21), we can only say on weighted average over species that we would expect higher recruitment variance in the invader state if the species coexist stably. An especially attractive feature of these formulae, which ought to facilitate tests in nature, is that the separate environmental or competitive responses do not appear here. These results simply involve the combined response, R'_j , the natural log of per capita recruitment in the presence of competition.

To test these ideas, ideally resident and invader states need to be created experimentally or observed naturally. In those systems for which long time series are available, natural observations equivalent to invader states seem feasible (Chesson 2003). In other cases, experimental manipulation might be used to approximate resident and invader states. The details of such designs, however, would be highly system dependent, with small sessile or sedentary organisms permitting the most promising designs. In general, a spatial version of this idea would be simpler for experimental studies because the driving variation, occurring spatially, is observable on a short timescale. However, techniques might be developed for spatially mimicking temporal patterns.

An alternative is to seek predictions applicable to resident species. According to Chesson (2003), smaller values of μ_j should be associated with higher values of $s_j \text{var}(R'_j)/a_j$ among resident species, but knowledge of the various constants μ_j , s_j and a_j might prove troublesome. In some, but not all circumstances (Chesson 2003), μ_j is positively related to resident mean density. Thus, a small value of μ_j places species j in a state similar to an invasion state. Also, a_j turns out to be 1 for the lottery and similar competition models (Chesson 2003). Moreover, in long-lived species, the survival rates, s_j , will all be near 1. Circumstances like these were exploited by Kelly and Bowler (2002) to test the idea that recruitment variation promotes diversity in tropical forests.

6.7. Discussion

The measures presented here, by giving quantitative expression to the functional components of the mechanisms, both elucidate their essential features and provide a route to testing them in especially powerful ways. Although some realistic experimental designs have been sketched for implementing these ideas, much more needs to be done to develop realistic designs for a range of different systems. Along with experimental designs, statistical tests and confidence intervals for these measures are needed, although some are already available and have been applied in studies of neighborhood competition in plants (Sears 2004; Sears and Chesson 2007).

The measures given here are in most cases approximations. Depending on the circumstances, they may not provide accurate measures of the strength of the given mechanism. However, this fact does not invalidate cautious use for understanding mechanism functioning, because these functional expressions, although approximations, capture mechanism functioning as it is more generally understood. In some cases, the expressions are exact (Chesson 2000a), and further exact expressions, extending approximate forms, are under development.

The focus here has been on fluctuation-dependent (Chesson 1994) or variation-dependent (Chesson 2000a) mechanisms. The reason is that the theory of such mechanisms has been developed in statistical form in a way that reveals their functioning. However, statistical formulation is also available for traditional resource partitioning models (Chesson 1990; Haygood 2002) providing the potential for devising tests of mechanism functioning for fluctuation-independent mechanisms also.

Quantification of mechanisms can go beyond testing the functioning of a given mechanism in a particular system to the comparison of the contributions of different mechanisms to coexistence in that system. Here, the recovery rate from low density, and the community stabilization term, A , involve additive contributions from different mechanisms. The overall values of these quantities thus represent the joint effects of the various contributing mechanisms. Moreover, these mechanisms can be further partitioned into con-

tributions from different temporal or spatial scales (Chesson and Huntly 1993). In principle, different mechanisms can be assessed in any given system, their combined contributions to coexistence calculated, and their separate contributions compared. Thus, the analysis of species coexistence need not be restricted to single-mechanism explanations. The oft-given appeal to pluralism in the study of diversity maintenance need not go unheeded.

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