

COEXISTENCE MEDIATED BY RECRUITMENT FLUCTUATIONS: A FIELD GUIDE TO THE STORAGE EFFECT

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In this paper we discuss ways of testing the hypothesis that recruitment fluctuations promote species coexistence in communities of long-lived organisms (Chesson and Warner 1981). The hypothesis was originally formulated for two species that compete for a common limiting resource such as attachment sites or territories. Strict resource limitation means that one species increases at the expense of the other, and competitive exclusion is favored. Exclusion can be prevented, however, if two conditions prevail. First, environmental conditions must vary, resulting in fluctuating recruitment rates. This can confer on low-density species a high potential for occasional relative increases in population size. Second, adults must be able to survive over periods of poor recruitment, such that the population declines only slowly during these periods. Under these conditions, a species tends to recover from low densities, and competitive exclusion is opposed.

The major element in such coexistence is the fact that a strong recruitment produces a cohort of adults that survives over a number of potential reproductive periods. This high adult survival limits the losses that occur whenever recruitment fails. Indeed, in the presence of overlapping generations and fluctuating recruitment rates, the average population growth rate is more strongly affected by the benefits of favorable periods than by the costs of unfavorable periods. We refer to this phenomenon as the *storage effect* because strong recruitments are essentially stored in the adult population, and are capable of contributing to reproduction when favorable conditions return.

Persistence of a species by means of the storage effect is exemplified by herring in the North Sea. These herring enter the fishery when they are 3 yr old; in 1907 such 3-yr-old fish made up the vast majority of the total catch. In the following year, the majority of fish were 4 yr old, and this extraordinary year class continued to sustain the major portion of the fishery until 1913, when it still made up 65% of the total catch (Hjort 1914). This sort of pattern is true for many fisheries: when natural mortality rates are low, the persistence of one or a few strong year classes can maintain stocks over many reproductive periods. If the adults have

high fecundity, even a few individuals are capable of producing a strong year class when environmental conditions are favorable. Low adult death rates allow such strong year classes to persist through time until a favorable recruitment period occurs. Some storage of strong year classes occurs whenever generations overlap, but its effectiveness is reduced if adult death rates are high.

The idea that organisms somehow can store the periods of good recruitment is not a new one. Various authors have described storage in resting stages (e.g., the "seed bank" of Harper 1977; see also Lloyd and Dybas 1966). The key element added here is that this storage can contribute strongly to species coexistence when resources are limiting and recruitment fluctuates.

We stress that the storage effect demonstrates coexistence in what has been called a closed equilibrium system (Caswell 1978; Connell 1978). In more descriptive terminology, it is a system without spatial heterogeneity, and coexistence is not a transient phenomenon: neither species ever becomes extinct. In our lottery model (Chesson and Warner 1981), the storage effect is the only mechanism promoting coexistence. Thus, the storage effect can be viewed as an alternative to other hypotheses of coexistence such as intermediate disturbance that maintains spatial heterogeneity, niche differentiation, or frequency-dependent mortality (for references, see Connell 1978). In its present form, however, the storage idea is overly seductive. It is liable to be used either as a last-resort explanation after attempts to demonstrate other hypotheses have failed or as an unsupported and convenient explanation without benefit of critical testing.

For this reason, we ask here if the proposed mechanism can be realistically expected to operate in natural systems, and if so, whether it is possible to differentiate it from other hypotheses of coexistence. First, we review some recent work that shows our original model to be part of a general class of models, all of which include the storage effect. Taking a somewhat different approach, we then consider aspects of the environment and the life history traits of organisms that would tend to foster coexistence, and mention some communities in which recruitment variability is likely to be playing a role in coexistence. Next, we discuss how the storage mechanism might be distinguished from others in a field situation, both quantitatively and qualitatively. Finally, we suggest extensions of the storage concept to include the storage at other stages of the life cycle (e.g., in seed banks) and the effects of resource storage within an organism.

THE LOTTERY MODEL

Sale (1977, 1978) envisioned a community in which individuals, once settled, cannot be displaced by any other individuals regardless of species. Once a particular site becomes vacant through mortality of the previous occupant, allocation is random, on a first-come, first-served basis. Thus, the species compete for space through production of dispersing young, and in our model (Chesson and Warner 1981) the probability that an individual of a particular species will occupy a site is equal to that species' proportion of the total population of dispersing forms that survive to the settling stage. This proportion depends on the number and fecundity of individuals contributing to the population of dispersing forms, relative to the same parameters for the other species. In this simple case, we assume there

are always sufficient young to fill all available spaces. The birth rate of a species, as used here, includes juvenile mortality and may be defined as the per capita number of offspring surviving to the settling stage during one unit of time.

Environmental variability is represented by variation in the per capita birth or death rates of the species. We found that when no variability exists, two species cannot coexist unless the ratio of the birth and death rates is the same for both species, which is unlikely and evolutionarily unstable. This is true whether or not the generations overlap, that is, whether or not all sites become available each generation. One species dies out and the other species increases to occupy all available space.

With the addition of environmental variability, the outcome remains the same for nonoverlapping generations, i.e., when there is no storage effect. Competitive exclusion involves the following important features: as a species increases in numbers, its percentage of increase during favorable periods decreases because of space limitation. The percentage of change in the ratio of densities of the two species, under given environmental conditions, is the same at all densities, however. Thus, a highly favorable period for a species at high density results in a large percentage decrease for the other species.

The situation changes entirely when, in addition to environmental variability, there are overlapping generations. In this case, no matter how high the abundance of a species, and no matter how favorable a period it has, it cannot depress the population of the other species by any more than the amount set by the adult death rate of that species.

As in the case of nonoverlapping generations, the percentage increases that occur during favorable periods for a species are greatest at low density. This is because the amount of space available for colonization by new recruits does not vary greatly with population density and is, therefore, larger in relation to population size for a species at low density. Thus, at low density, relatively large increases in population size are possible; and such increases do occur when the species experiences highly favorable periods. Overlapping generations ensure that the gains made during favorable periods are not lost immediately when an unfavorable period occurs. Thus, each species can increase from low density by having only some periods when it is favored.

In this setting, it is possible for competitively unequal species to coexist. For instance, one of the species may tend to have much stronger recruitments during favorable periods than the other species, but the two can coexist provided the inferior species still has favorable periods when it recruits strongly at the expense of the superior species.

It should be noted that the storage effect is essential to coexistence here. Variable recruitment is essential so that both species have favorable periods, and overlapping generations are necessary so that the gains made during favorable periods are not immediately lost in the next unfavorable period.

MODELS DEMONSTRATING THE STORAGE EFFECT

The storage effect has now been shown to promote coexistence in a variety of models (Chesson 1983, 1984; Ellner 1984; Shmida and Ellner 1984). We review

here the results coming from these different models within the framework of a general model of a multispecies community.

Let $X_i(t)$ be the size of the adult population of species i at time t , then

$$X_i(t + 1) = [1 - \delta_i(t)]X_i(t) + R_i(t)X_i(t) \quad (1)$$

where $\delta_i(t)$ is the per capita adult death rate and $R_i(t)$ is the per capita rate of recruitment to the adult population. Generally,

$$R_i(t) = f_i[\mathcal{E}(t), X_1(t), \dots, X_k(t)] \quad (2)$$

where f_i is some function, $\mathcal{E}(t)$ is a vector of environmental variables, and $X_1(t), \dots, X_k(t)$ are the population densities of the k species in the system. For instance, in the multispecies lottery model (Chesson 1983, 1984)

$$R_i(t) = S(t) \cdot B_i(t) / \sum_{j=1}^k B_j(t) X_j(t) \quad (3)$$

where $S(t)$ is the amount of space available from adult death and the $B_i(t)$ are density-independent birth rates. These birth rates are assumed to fluctuate with the environment and so $\mathcal{E}(t) = [B_1(t), B_2(t), \dots, B_k(t)]$. We emphasize, however, that in the analysis below no particular form is assumed for $R_i(t)$. In most of our discussion we shall assume for simplicity that the $\delta_i(t)$ are constant. The quantitative details of our results do change if the $\delta_i(t)$ are allowed to vary (Chesson and Warner 1981), but the qualitative conclusions do not, provided that under all conditions the $\delta_i(t)$ have a low probability of being near 1, i.e., generations must always be overlapping.

To see if species i will persist in the system, we need to study the instantaneous growth rate (the change in log population size from one time to the next), i.e.,

$$\log X_i(t + 1) - \log X_i(t) = \log [1 - \delta_i + R_i(t)]. \quad (4)$$

Species i will tend to increase from low density if the time average of (4), when species i is at low density, is positive. Thus, we conclude that species i will persist if

$$E \log [1 - \delta_i + R_i(t)] > 0, \quad (5)$$

where E means the theoretical mean value, and is calculated in the limit as the density of species i tends to 0. Requirement (5) is the invasibility criterion for persistence (Turelli 1978). It can be written in the alternative form

$$E \log [1 - \delta_i + \delta_i \rho_i(t)] > 0 \quad (6)$$

where $\rho_i(t) = R_i(t)/\delta_i$. Note that if $\rho_i(t) > 1$, recruitment exceeds death and species i increases from time t to time $t + 1$. Equivalently, if $\log \rho_i(t) > 0$, species i increases, whereas if $\log \rho_i(t) < 0$, species i decreases. The quantity $\log \rho_i(t)$ will fluctuate with time but its value at any time can be used as a measure of the favorability of the environment for the growth of species i at that time.

With the above definitions, it is shown in Chesson (1983) that the persistence condition (6) will be satisfied whenever

$$E(\log \rho_i | \rho_i > 1) > c(\delta_i) P(\rho_i < 1) / P(\rho_i > 1) \quad (7)$$

where the quantity $c(\delta_i) = -\log(1 - \delta_i)/\delta_i$ and is near 1 for small δ_i . The value $E(\log \rho_i | \rho_i > 1)$ is the theoretical mean of $\log \rho_i(t)$ for periods during which species i is increasing (i.e., $\rho_i(t) > 1$, or equivalently $\log \rho_i(t) > 0$) and is evaluated for species i in the limit as density approaches 0. Since $\log \rho_i$ measures the favorability of the environment for species i , the left-hand side of condition (7) measures the "mean benefit" enjoyed by the species during favorable periods. In the terminology of gambling, the ratio of probabilities $P(\rho_i < 1)/P(\rho_i > 1)$, for favorable versus unfavorable periods, can be called the "odds of an unfavorable period." Thus for species with low adult death rates we can summarize condition (7) as follows: A species will persist provided that, at low density, its mean benefit during favorable periods is greater than the odds of an unfavorable period.

Condition (7) is actually highly conservative in the sense that persistence will occur under a much broader range of conditions, but it is adequate for our present illustrations. The critical aspect demonstrated here is that the benefits gained in favorable periods are of far greater importance than the costs incurred during unfavorable periods. In fact, persistence can occur as long as favorable periods convey sufficient benefit (given their frequency), independently of how costly the unfavorable periods might be. This is the storage effect.

The ways in which storage affects growth and stability of a single species have been studied in detail by others (Murphy 1968; Schaffer and Gadgil 1975; Hastings and Caswell 1979; Goodman 1984). Our concern here is not with single species, but with coexistence of the different species in a community.

The fact that a species can persist simply by doing well in certain favorable periods provides a mechanism of coexistence of negatively interacting species. Species may harm one another by depressing recruitment rates. If the environment varies, however, some species may be advantaged at some times and others at other times. For instance, if species A has an especially good period for reproduction, but other species do not reproduce proportionately as well, then competition among juveniles will result in a high recruitment for species A and low recruitments for other species. Alternatively, competition for resources for reproduction may occur among adults, and if competitive ability fluctuates at this level, then recruitment rates will fluctuate also. These fluctuations mean that each species can have periods when it recruits well, even in the presence of strong competition, and thus coexistence can occur by the storage effect.

Note, however, that the storage effect requires that competition among adults should not greatly influence adult survival. It is precisely this relative protection of adult survival from competition, and from fluctuations in the environment, that results in effective storage of strong recruitments in the adult population. These strong recruitments then can be used to produce more strong recruitments when favorable conditions return.

These ideas have been explored in a variety of specific examples of the general model. The multispecies lottery model (Chesson 1983, 1984) shows that recruitment fluctuations can promote coexistence in multispecies assemblages. Other variations have (1) allowed competition among prerecruitment juveniles (Chesson 1983); (2) permitted spatial heterogeneity of various kinds (Chesson 1985; Shmida and Ellner 1984); and (3) removed the assumption that space is always in short

supply (Chesson 1983). All of these models have the property that coexistence is favored by the storage effect if recruitment for the different species tends to peak at different times. While these models all involve competition for space, another class of models that includes quite general forms of competition comes to essentially the same conclusions (Chesson 1983, 1984). At least theoretically, the storage effect promotes coexistence under very general circumstances.

WHAT FOSTERS COEXISTENCE?

We focus now on the within- and between-species characteristics that should promote coexistence according to the models of the storage effect reviewed above. The within-species characteristics (low mortality, high and age-correlated fecundity, and environmental sensitivity in the young) permit a species to have positive average growth at low density when faced with varying conditions for life. The between-species characteristics (similarity of reproductive rates and differential responses to the environment) ensure that these varying conditions permit each species to have periods favorable to recruitment. We stress that the presence of these features does not verify the hypothesis of coexistence by the storage effect; it simply increases the likelihood that the storage effect will be a significant factor.

Within-Species Characteristics

Low adult mortality.—The longer adults live, the less the population will decline over a series of low-recruitment periods. Low adult mortality also increases the probability that when a favorable period does occur, enough adults will be present to provide a sufficient number of young to take advantage of the available habitat. If adult life spans are short, the storage effect will be very weak. Indeed, if adults survive for no more than one recruitment period, there is no storage effect in our model. Coexistence is then less likely, and for many of the extensions mentioned above it is impossible.

The adult mortality rate is measured relative to the rate of reproductive events. Thus, any adult that lives long enough to engage in many reproductive periods is a likely candidate for the storage effect. Large trees and corals are obvious examples of appropriate species, but storage could also be important for much shorter-lived species that reproduce often. Many coral reef fishes, for example, spawn on a daily basis throughout the year (Warner and Robertson 1978), and thus an adult is present over hundreds of potential recruitment periods even though it may live for only a few years.

The storage effect can also be achieved through diapause: reproduction can cease without the adult population being substantially reduced over a long time period.

Fecundity that increases with adult age.—In many species, including most fishes and perennial plants, fecundity increases with the size of the individual, and growth is indeterminate. In such species, adult biomass is an appropriate measure of the population's reproductive potential, and the rate of attrition of adult

biomass, combining both growth and adult death, is a more appropriate parameter than the adult death rate, δ_a . In this setting, a low rate of attrition of adult biomass enhances the storage effect, just as low adult mortality enhances the storage effect when fecundity is independent of age. Moreover, an increase in fecundity with age can act to compensate for a high adult death rate.

High reproductive rate.—If an adult individual can produce large numbers of potential recruits, many of which do survive to adulthood during a favorable period, then the population can withstand longer and more severe periods when recruitment is sharply reduced. Thus, the storage effect will apply best for organisms with the potential for high fecundity.

When the reproductive rate is lower, storage is still present but its effectiveness is reduced. For example, a species with low fecundity must either live a long time or not have recruitment reduced greatly during unfavorable periods if it is to increase from low density.

Environmental sensitivity.—High reproductive rates can have an additional effect. A large clutch size is often related to less energy being devoted to each individual young. This leads to a probable lowering of average individual fitness for the offspring (Smith and Fretwell 1974), and these smaller young may be less able to compensate for environmental fluctuations. This can magnify the variance in realized recruitment, and should foster coexistence. In other words, under the same environmental conditions, a group of highly fecund species should show more variability in recruitment rates than species with low fecundity, and thus be more likely to coexist.

Between-Species Characteristics

Competitive differentials.—As outlined in the next section, species are more likely to coexist if they have similar *average* reproductive rates and competitive abilities, because less environmental variability is required for their coexistence. In general, if one species has an overall lower average reproductive rate and competitive ability, then it is more quickly and more often driven to rarity, it recovers less strongly when favored, and the periods in which it is actually favored become less common.

Differential responses to the environment.—Not surprisingly, when the peaks of reproduction occur for different species at different times, coexistence is fostered because a species can take full advantage whenever a favorable recruitment interval corresponds to its reproductive peak, little diluted by the effects of other species. (For a similar idea, see Grubb 1977.) It is important to note that coexistence is fostered even if separation of breeding or recruitment peaks is based on arbitrary stimuli unrelated to individual growth or survival (Leigh 1982). Moreover, such stimuli can be predictable stimuli such as day length, or less predictable characteristics like temperature and moisture. In fact, different species may respond in the same way to an environmental stimulus and still have separate reproductive peaks if they have different time lags in their responses to the environment, as has been suggested for some perennial plants (Harper 1977).

Differential responses to the environment may, in some cases, be looked upon

as a kind of temporal partitioning of resources, but as the lottery model demonstrates, overlapping generations are an important feature if such temporal partitioning is to lead to coexistence.

Environmental Characteristics

What sorts of environments lead to the within-species characteristics? Long life and high fecundity are the key elements of a bet-hedging strategy (Stearns 1976; Warner 1980). That is, when the environment for adults is predictable in time and space (leading to high and relatively invariant adult survival), but juvenile survival is low and fluctuating (the latter is represented in the model as recruitment variability), reproductive effort should be low and adults consequently long-lived (reviewed in Stearns 1976; Goodman 1984). Thus, reproduction is spread over many time periods, a few of which may be favorable.

Individuals with low reproductive effort do not necessarily have low fecundity, however, because the partitioning of energy available for reproduction may respond to different selective pressures (Smith and Fretwell 1974). If the fitness of the young depends on size (e.g., if they must engage in direct competition for new sites with other young), then large young and a consequent low clutch size should be most adaptive. On the other hand, if habitat becomes available unpredictably in time and space, and at a relatively low rate, being able to disperse to such habitat may be much more important than competitive ability. In this case, dispersal of many young is at a premium, and organisms with finely partitioned reproductive effort should be favored.

To summarize, the environment that appears most conducive to eliciting life history characteristics that foster coexistence by the storage effect is one that is relatively benign and permanent for established adults, but where young encounter and secure a new site by chance rather than direct competition with other young. Alternatively, the ability of adults to undergo diapause and to reproduce facultatively in response to changes in the environment can eliminate the need for a continuously benign situation.

Note that we do not claim that the within-species characteristics arose as an evolutionary response to interspecific competition and resource limitation. Although this may occur, our point here is that these characteristics foster species coexistence, regardless of their evolutionary source.

Several communities consist of species that possess life histories similar to those described above. As mentioned above, both trees and corals are often long-lived, and they can have relatively high fecundity. In the tropics, both of these groups exist in highly diverse communities. Although a few differences in niche utilization can be demonstrated, and a few fugitive species have been identified, the numbers of species are still staggering (Connell 1978). High temporal variability in reproduction and recruitment has been well documented for plant species in general and trees in particular (Grubb 1977; Harper 1977; Hubbell 1980). For the case of tropical forests, recruitment of a particular species can be massive but infrequent (Connell et al. 1984). Thus, it is highly possible that the storage effect is contributing significantly to coexistence in these cases.

Communities of tropical reef fish form another group in which the storage effect may be important. Adult life spans encompass many potential recruitment periods (see above), and recruitment itself has often been shown to be highly variable (e.g., Luckhurst and Luckhurst 1977; Russell et al. 1977; Victor 1983). Many sessile marine invertebrates also have been found to have these essential properties for the storage effect (Butler and Keough 1981; Keough 1983; Caffey 1985; Underwood and Denley 1984). Moreover, the storage effect has been postulated to explain coexistence of soft-bottom marine invertebrates (Woodin and Yorke 1975) and coexistence of *Eucalyptus* spp. in Australian sclerophyll forests (Comins and Noble 1985).

DISTINGUISHING THE STORAGE EFFECT FROM OTHER MECHANISMS OF COEXISTENCE

Although the storage effect increases the likelihood of coexistence, it does not preclude the operation of other mechanisms that, in particular circumstances, might be more important, e.g., intermediate disturbance, succession, frequency-dependent mortality, niche differentiation, etc. While the basis for a sound approach to science is to formulate and distinguish among alternative hypotheses, natural systems are rarely so easily categorized. We suspect that the storage mechanism will often act in concert with other mechanisms of coexistence. Therefore, we first address the question of whether the recruitment variability measured in a particular system would be adequate to ensure coexistence. Recognizing that other mechanisms may also be operating in a particular community, we then give a method for estimating the contribution that storage is making toward persistence. Finally, we take the more classical approach of casting the storage effect as a distinct and qualitatively testable alternative hypothesis.

How Much Variability Is Sufficient for Coexistence?

It must be emphasized that in our model the relevant variation is that which occurs at low density. Thus the discussion below assumes that all quantities are measured for low-density situations. The problem of defining low density and measuring parameters for that situation is discussed in detail in the next section.

For the two-species lottery model, Chesson and Warner (1981, fig. 1) determined the variance of $\log \rho_i$ necessary for positive boundary growth rates and hence coexistence, assuming that $\log \rho_i$ is normally distributed and the death rates of the two species are equal. The figure thus gives the conditions for coexistence in such a model. The figure also can be used for the more general models discussed above by using the following rules: (1) a species will always persist if $E \log \rho_i > 0$; (2) if $E \log \rho_i$ is negative, consult the figure to determine if the boundary growth rate is positive, given the death rate and the mean variance of $\log \rho_i$.

For small death rates and arbitrary distributions for $\log \rho_i$, the approximate persistence criterion

$$E\rho_i > 1 \quad (8)$$

TABLE 1
 HYPOTHETICAL EXAMPLE OF TESTING FOR SUFFICIENT VARIABILITY FOR COEXISTENCE IN THE
 TWO-SPECIES LOTTERY MODEL

ENVIRON- MENTAL CONDITIONS	POPULATION PARAMETERS				PROBABILITY OF OCCURRENCE
	B_1	B_2	ρ_1	ρ_2	
Type 1	0.5	2	0.25	4	1/3
Type 2	3	1	3	1/3	1/3
Type 3	2	0.5	4	1/4	1/3
	Mean of ρ_i when > 1		3.5	4	
	Probability (p) that $\rho_i > 1$		2/3	1/3	

NOTE.—The criterion is $E\rho_i > 1/p$; since $3.5 > 3/2$ and $4 > 3$, there is sufficient variability for both species to persist.

is useful (Chesson and Warner 1981). Using this, one can gain an intuitive feeling for the amount of variation necessary for coexistence, as follows. Criterion (8) implies that a species will persist if the mean of ρ_i during favorable periods is greater than $1/p$, where p is the probability of occurrence of a favorable period. Thus, for example, in the two-species lottery model, species i will persist if the value of the ratio $(B_i/\delta_i)/(B_j/\delta_j)$, measured during favorable periods for i , is greater than $1/p$. Given sufficient variability, this can be true for both species. There is a similar interpretation in the multispecies model (Chesson 1984), in which the weighted averages of the parameters for the other species are used in place of B_j and δ_j . (The weights in this case are the other species' densities.) A representative test using hypothetical data is given in table 1.

These statements apply when death rates are small, and they are conservative in that case, since they make no allowance for any successful reproduction in periods when the species is not favored. When reproduction is moderately successful in the unfavorable periods, there is less need for high reproduction during favorable periods. That is, the nearer the value of $\log \rho_i$ is to zero, the less variation there needs to be for coexistence. In the extreme case of $E \log \rho_i = 0$ and constant death rates, any variation at all in $E \log \rho_i$ will lead to persistence of species i . For the two-species lottery model, this means that if species are similar in average recruitment and death rates, very little temporal variation is necessary for coexistence. Thus, for cases when appreciable reproduction occurs during unfavorable periods, the persistence criterion applied in table 1 is inappropriate and the more exact criterion (8) should be used.

What Is the Contribution of the Storage Effect toward Persistence?

Since the mean instantaneous population growth rate at low density is the chief determinant of persistence, one way of identifying the importance of storage to persistence is to partition this growth rate into components contributed by various phenomena. The storage effect comes from the interaction between overlapping generations and variation in the parameter ρ , which is the per capita recruitment

rate divided by the adult death rate. If we can remove the variation in ρ to give some mean value, which we shall denote by $\bar{\rho}$, then the quantity

$$\frac{1}{n} \sum_{j=1}^n \log[1 - \delta(j) + \delta(j)\bar{\rho}] \quad (9)$$

will represent that part of the mean instantaneous growth rate that does not involve the storage effect, and

$$\frac{1}{n} \sum_{j=1}^n \log[1 - \delta(j) + \delta(j)\rho(j)] - \frac{1}{n} \sum_{j=1}^n \log[1 - \delta(j) + \delta(j)\bar{\rho}] \quad (10)$$

is the contribution resulting from the storage effect. We use a sample mean in (9) and (10) rather than the theoretical expected value because we expect the quantities to be calculated from actual observations of recruitment and adult mortality in a population. We must expect that δ will be variable; while this suggests defining $\bar{\rho}$ as a conditional mean, given δ , it is not feasible in practice given the quantities of data currently available.

Removal of variation in ρ to obtain $\bar{\rho}$ is a problem. Clearly, we need some mean value of ρ , but our results will very much depend on whether we take the usual arithmetic, the geometric, the harmonic, or some other mean. The geometric mean seems most appropriate here because the geometric mean of ρ would describe population growth if generations were not overlapping (so that there would be no storage effect):

$$X(t + 1) = (\bar{\rho})^t X(0) \quad (11)$$

where $\bar{\rho}$ is the geometric mean of $\rho(0), \rho(1), \dots, \rho(t - 1)$

$$\left(\bar{\rho} = \left[\prod_{j=1}^{t-1} \rho(j) \right]^{1/t} = e^{\overline{\log \rho}} \right).$$

The result (11) also provides a partial justification for finding an average of ρ , which combines R and δ , rather than the plausible alternative of averaging R separately. Using the geometric mean for $\bar{\rho}$ means that quantity (10) will often be positive, so that storage often has a positive contribution to persistence. The more desirable but less practicable definition of $\bar{\rho}$ as a geometric mean conditional on δ would always give a positive storage component, as one might expect from the arguments given here. With the present definition of $\bar{\rho}$, however, a negative storage effect can arise from a strong negative correlation between δ and ρ (see example below).

If this analysis yields a positive nonstorage component (9), then one can conclude that factors other than storage are sufficient to explain persistence. If quantity (9) is negative, but the sum of (9) and (10) is positive, then we must conclude that storage is necessary for persistence. To demonstrate then that the storage effect is a likely mediator of coexistence, it also must be shown that competition is occurring and that recruitment is negatively correlated across different species.

In practice, one of the major problems with calculating these components of the mean instantaneous growth rate is that ρ is properly measured only at low population densities. A precise rule for deciding on the bottom range of population densities for use in the calculation of ρ is not easy to find, but it is possible to give some rough guidelines. In a histogram of observed population densities one can often find a lower tail. Population densities in this tail presumably have a tendency for positive growth that prevents the population from heading even lower toward extinction. Thus the lower tail represents the appropriate bottom range for evaluation of expressions (9) and (10). The shape of the histogram may present a clear choice for the beginning of the lower tail; if it does not, we offer the arbitrary suggestion that the maximum frequency in the tail should be no more than one-half the modal frequency. For times when $X(t)$ belongs to the bottom range but $X(t + 1)$ does not, the values of δ and ρ for the time interval $(t, t + 1)$ must still be included in the averages (9) and (10) to avoid bias.

Data that cover a sufficient number of reproductive periods are difficult to find. One of the best examples of a long-term study of population size, mortality, and recruitment is Svane and Lundälv's (1982) 10-yr study of the ascidean *Boltenia echinata*. During that period, *Boltenia* underwent rather large fluctuations in population size, allowing an analysis of the contribution of storage to persistence (table 2). Comparisons of quantities (9) and (10) at low densities of the two populations studied shows that storage has a minimal effect on instantaneous growth rate in this species. In fact, *Boltenia* nearly always (8 of 9 instances) enjoyed very high recruitment immediately after periods of low density, so that (in the period studied, at least) there was no need for storage to maintain the population over a series of unfavorable periods.

In contrast, analysis of eight biweekly intervals for the daily-spawning coral-reef fish *Thalassoma bifasciatum* (see table 3) gave a storage contribution to

TABLE 2

POPULATION PARAMETERS FOR THE ASCIDEAN *Boltenia echinata* FROM THE ROCKY SUBTIDAL OF SWEDEN

Observational Data	Sheltered Population	Exposed Population
No. of 6-mo time periods	19	19
Range and mean (in parentheses) of estimated population densities (individuals/m ²)	10–200 (51.6)	10–150 (39.7)
No. of periods used in analysis	5	4
Range of estimated population densities in periods used (individuals/m ²)	10–19	10–28
$\bar{\rho}$ (range)	4.86 (.08–29.66)	3.73 (1.27–6.60)
Range of δ_i	.035–.371	.048–.625
Nonstorage contribution to growth rate (quantity [9])	.368	.627
Storage contribution to growth rate (quantity [10])	.036	–.056

NOTE.—Data are estimated from Svane and Lundälv 1982, figs. 2, 3. Recruitment and mortality samples were taken every 2 mo. Since growth studies indicate that recruits reach maturity in about 5 mo, three successive 2-mo samples were combined for this analysis. Population densities were estimated for the beginning of each 6-mo period.

TABLE 3

POPULATION PARAMETERS FOR THE BLUEHEAD WRASSE, A CARIBBEAN CORAL-REEF FISH (*Thalassoma bifasciatum*), DURING A PERIOD OF LOW POPULATION DENSITY

Observational Data	
No. of periods (wks) used in analysis	8
Range of population sizes	73-142
\bar{p} (range)	1.34 (.05-93.00)
Range of δ_i	.010-.207
Nonstorage contribution to growth rate (quantity [9])	.028
Storage contribution to growth rate (quantity [10])	.036

NOTE.—Weekly measurements of population size, settlement, and death were made on two small reefs off the coast of Panama from June 30 to November 1, 1981.

population growth rate of 0.028, versus 0.036 for the nonstorage contribution. Recruitment in this species is highly variable (Victor 1982, 1983), and individuals participate in hundreds of reproductive events over their life spans, so we might expect storage to play an important role in persistence.

In both of these studies, much recruitment probably occurred as a result of dispersal of larvae from places outside the study area, and the nonstorage components in the growth rates may well reflect such immigration. Although the analysis above can be used to estimate the importance of the storage effect to the persistence of a species in a local area, with external populations taken as given, it cannot be used to draw conclusions about persistence of the species within its overall habitat. For that, it is necessary to take a time series of estimated total population sizes, death rates, and recruitment rates for an area large enough to have most new recruits born within the area.

It will be highly interesting to see the contribution of storage to persistence in other species, whether on a local scale or on the more global scale suggested above. Obtaining a long enough series of data to apply the above techniques will be a problem, however, especially because only the bottom range of population densities is to be used. In some cases it may be possible to augment the data at low densities. For example, this can be done if there is a known or hypothesized relationship between the critical rates, $\delta_i(t)$ and $R_i(t)$, applying at low density and measurable environmental factors. Alternatively, there may be some relationship between these rates at higher densities and the corresponding rates at low density. For instance, if the two-species lottery model is hypothesized, then dividing the observed value of $R_i(t)$ by $R_j(t)/\delta_j$ (the ratio of the recruitment rate to the adult death rate for the other species) gives the value of $R_i(t)$ that would apply at low density under the same environmental conditions. In this way, one can generate a series of estimated $R_i(t)$ values for low densities from observations made at any density. Calculating (9) and (10) from such estimated data then tests the storage effect within the more specific context of the lottery model.

It is important to note that inaccuracy in the estimation of the death rates and recruitment rates as a result of sampling error will tend to bias the estimates (9) and (10). This sampling error must be kept small in relation to the true variation in

ρ and δ , or else the bias must be corrected (Cox and Hinkley [1974] review several methods).

A more serious problem with these techniques is an intrinsic aspect of their nonexperimental nature. For example, observing the predation on a particular species in nature indicates the direct effects of predation on the species' growth rate, but it does not include the indirect effects resulting from predation by the same predators on the species' competitors. Without taking into account these indirect effects, it is impossible to predict the outcome for the species when its predators are removed. In a similar way, (9) and (10) indicate the direct effect of storage, but not any associated indirect effects. For instance, (9) and (10) may say that a species depends on the storage effect for persistence, but the removal of variability (see below) may not lead to the species' extinction if there is a greater direct negative effect on a competitor through this elimination of variability.

For these reasons, attempts to carry out a quantitative assessment of the contribution that storage makes toward coexistence may generally be unsatisfactory. Storage can operate completely independently of other mechanisms, of course, so it can be cast as a distinct alternative and tested as such.

Is the Storage Effect Necessary for Coexistence?

Connell (1978) has provided a convenient summary of several hypothetical mechanisms of coexistence, and has outlined some of the experimental protocols necessary to sort among them, so they need not be detailed here. Techniques involving transplantation, exclusion of predation or disturbance, removals, and alterations of density can help to identify situations in which compensatory mechanisms have a strong effect on coexistence. If no compensatory effects can be demonstrated and thus succession or intermediate disturbance appear unlikely, then the most convincing qualitative evidence for the storage effect would be to show that extinctions occur with a reduction in recruitment variability. That is, particular species have the advantage with relatively constant recruitment, and other species are driven to extinction. This is a simple prediction in theory, but manipulations of recruitment rates are technically difficult, and the very nature of the storage mechanism implies that the waiting time to extinction under relatively constant conditions may be quite long.

Since the storage effect depends on both recruitment variability and long adult life span, an alternative manipulation would be to uniformly increase adult mortality rates. This reduces the storage effect, with a predicted loss of some species (at least temporarily) from the observed community. The contrast with other mechanisms of coexistence is especially strong here, since a reduction in adults present could reduce competition and/or increase the opportunities for fugitive species. These latter effects can act to increase species diversity under the intermediate disturbance and successional hypotheses, respectively. If the key to local species coexistence is simple niche differentiation, then neither reduction of recruitment variability nor uniform increases in adult mortality rates should be expected to lower diversity.

By definition, a niche-differentiated species enjoys a competitive advantage for

one or a few habitats or resources. Under the worst of conditions, the species may exist only as a few adults in favorable habitats. If these individuals eventually are able to take advantage of a favorable period, the species may expand well beyond the limits of optimal habitat. Indeed, for the majority of the time, most individuals in a species will be found sharing habitats with other species who also have had periods of expansion in the past (see Dale 1978). Our models of the storage effect show that the existence of a refuge is not necessary for continued coexistence, but it certainly would help by providing a lower average death rate at lowest densities.

Since natural disturbance has been implicated in the maintenance of diversity in several communities, it is important to point out the effects of such disturbance on the storage mechanism. If increases in disturbance simply raise the mean rate of recruitment, diversity should remain unchanged; but since increases in disturbance often result in increases in adult mortality, diversity may be reduced because of less overlap of generations. Only if the disturbance increases variation in recruitment rates will diversity be increased.

Stochastic versus Deterministic Community Regulation

We have shown that the storage mechanism can be a testable alternative hypothesis for species coexistence. The mechanism does not require any specific differences in competitive ability of adults, mean recruitment rate of young, or niche requirements among the coexisting species. In fact, the existence of such differences will not prevent storage from operating, and we expect that storage will occur to some extent in most communities. That is, both quantities (9) and (10) will be positive, and the storage mechanism will be particularly important in facilitating recovery of a species after a long series of unfavorable periods.

For example, a quiescent interlude in a successional community represents an unfavorable period for early successional types, because no new space for recruitment is being created. If these early successional species are true fugitives with high reproductive efforts and low competitive ability, such a quiescent period may threaten extinction. If they are not affected by other species within the adult community, however, and are simply unable to recruit into occupied areas (the "toleration" model of succession, see Connell and Slayter 1977), then the adults form a reserve for future colonization when conditions change. Essentially, this is the storage effect in action.

It has been stated recently that an appropriate way to distinguish stochastically regulated communities from those governed by some deterministic process is by the persistence of structure among the latter sorts of communities (Grossman 1982; Grossman et al. 1982). In this case, structure is defined by the proportional abundances of the constituent species. This is intuitively appealing, since a general conception of stochastically regulated communities is one in which species abundances fluctuate widely. This need not be so, however. Indeed, for long-lived species that coexist by the storage effect, adult population numbers need not fluctuate in an extreme manner even though recruitment may be highly variable, for the variance of adult population size is approximately proportional to the adult death rate (Chesson 1982, 1984). Thus, for long-lived organisms, the

relative abundances of adults of the different species may remain constant on a time scale that is very long compared with the mean lifetime of an adult individual.

We emphasize that stochastic fluctuations are an essential component of coexistence in the above case, even though adult population sizes may not fluctuate greatly. Thus, persistence of structure can be a characteristic of both deterministic and stochastically regulated communities. In a community modeled by Chesson (1982), recruitment to the adult population fluctuates in the most extreme manner possible, but as an outcome of the storage effect these fluctuations do not translate into comparable fluctuations at the level of the adult population. In situations where there is, say, a 50% or greater chance of no favorable periods during the lifetime of an individual, however, then wide fluctuations in adult populations can be expected also. It follows that a thorough knowledge of the distribution and effect of recruitment variability is needed before the persistence-of-structure criterion can be deemed appropriate for distinguishing between stochastic and deterministic regulation of communities. Grossman (1982) has provided a beginning in this direction by examining the age structures of the constituent populations. If stable relative adult abundances are being produced in the context of fluctuating recruitment, the size of age classes should not decrease monotonically with age. Monotonic age structure argues against the importance of recruitment fluctuations.

POSSIBLE EXTENSIONS OF THE STORAGE IDEA

Although the models and discussion above have centered on adults, any stage in the life cycle, except postreproductive stages, are candidates for a storage effect. Provided the stage is reasonably long-lived and can withstand unfavorable periods, it may lead to storage of the effects of favorable periods and, therefore, may promote coexistence. For example, Ellner (1984) has shown that seed banks can permit coexistence by a storage effect in a model of an annual plant community.

Storage may also occur within an individual. Animal or plant species that build reserves of nutrients or energy in their bodies, and compete for these resources, may be able to coexist by a storage effect. For example, if reproductive output is directly related to nutrient or energy reserves of an individual, then the total reserves of the population may take the place of the adult population in the equations above, with the variable acquisition of resource by the species taking the place of variation in recruitment. If these equations are to be translated unmodified into this new setting, with $X_i(t)$ representing the total amount of resource stored by the population of species i , then it must also be assumed that resource acquisition will depend on the total resource currently stored by the population, not the population size. Moreover, substantial reinterpretation of some of the equations will be necessary in this new setting. The other extreme, in which resource acquisition by the population depends on population size, not the amount of stored resource, requires additional equations to describe the system.

The idea of a storage effect involving resources rather than individuals is essentially niche partitioning in time, but with an important addition of storage of

the resource in the population. Storage means that summation will occur over different conditions of resource availability with the likely consequence that favorable periods will have more important effects than unfavorable periods.

Gray and Schlesinger (1983) have reported nutrient storage, in the presence of variable acquisition rates, in the leaves of the evergreen shrub *Ceanothus megacarpus*. Although it is not clear that this species competes for nutrients with other species, Gray and Schlesinger suggested that this nutrient storage allows it to be an effective competitor for space with the coastal sage scrub species *Salvia leucophylla* during periods of low nutrient supply. Unlike *Ceanothus*, *Salvia* shows strong growth responses to high nutrient supply, and may well be an effective competitor for space at such times. Thus in this example, nutrient storage in one species, but not the other, essentially leads to fluctuating recruitment rates and may lead to a storage effect at the level of recruitment.

SUMMARY

For most species, a changeable environment creates a situation in which recruitment varies considerably from one breeding season to the next. If adults survive well, an occasional favorable recruitment can sustain population numbers over long periods. In effect, the gains made in favorable periods are stored in the adult population. Storage is particularly important when the species is at low densities, because then the potential population growth rate is very high if a favorable period occurs. Our past work showed that the storage mechanism could lead to coexistence of two species in lottery competition for space, as long as generations overlapped and there was sufficient variation in recruitment (Chesson and Warner 1981). This was true even if one species had an average competitive advantage. The storage model also operates when more than two species are competing, when resources renew independently of population sizes, and when not all the resource is used. It also operates in simple Lotka-Volterra systems in which adults do not compete directly with juveniles.

The field ecologist is faced with the more practical problem of determining whether the storage mechanism is operating in a particular system. Species with relatively long lives and high fecundities are most likely to enjoy the benefits of the storage effect. Environments that theoretically elicit these life history characteristics are relatively benign and permanent for established adults, but are such that births and/or juvenile survivorship vary widely. Trees and many marine organisms are examples of species with the proper life histories, and storage may be important in maintaining the high diversity of these communities.

The storage mechanism is capable of independently maintaining species coexistence, and we provide some suggestions on how to distinguish qualitatively the operation of storage from alternative mechanisms. We expect, however, that storage will make some positive contribution toward species persistence in nearly all communities, and we give a method for estimating empirically how large that contribution is.

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