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DIVERSITY MAINTENANCE BY INTEGRATION OF MECHANISMS OVER VARIOUS SCALES

Peter Chesson

Research School of Biological Sciences, Australian National University, Canberra ACT 0200 Australia

ABSTRACT

Coral reefs experience temporal and spatial fluctuations in the environment, in the densities of organisms and in the activities of organisms over broad scales. Recent theory implies that fluctuations on any scale can contribute to the maintenance of biological diversity provided limitation of population density can occur on that same scale. Such diversity maintenance requires coupling of fluctuations and density limitation, species differences in their responses to the various levels of fluctuating variables, and life-history or population structure that ameliorates the effects of unfavorable conditions for population growth. In this way, fluctuations permit species to build up in favorable times or places without such gains being canceled by unfavorable conditions at other times or in other places due to unfavorable physical conditions or interactions with other organisms. Though dependent on fluctuations, such mechanisms have many elements in common with more traditional or fluctuation-independent mechanisms; in particular, both sorts of mechanism involve density dependence, and both sorts of mechanism rely on specific ecological differences between species while being strengthened by similarities in average fitnesses between species. Diversity maintenance in reef systems seems most plausibly an integration of such mechanisms over a variety of scales rather than an outcome of mechanisms with no frequency dependence requiring extreme ecological similarity of species.

INTRODUCTION

Coral reefs have some remarkable biological characteristics. They are enormously species rich, and evidence from theoretical models suggest that this species richness may result from other notable features (Chesson and Warner 1981; Warner and Chesson 1985). For example, some species, such as corals, can be very long-lived, and many species may disperse over large distances covering broad environmental gradients. Critical population processes such as larval survival and recruitment may be highly variable in space and time on many scales (Doherty 1983, 1988; Sale 1977, 1984; Harriott and Banks 1995). Such variability on broad ranges of temporal and spatial scales make work in concert with these other life-history characteristics in the maintenance of species diversity (Chesson 1985, 1994; Chesson and Huntly 1993; Kubo and Iwasa 1996). The details of such diversity maintenance in reef systems is the subject of this article. Although the focus here is on species diversity, other work shows that genetic diversity may be maintained in a similar way (Chesson 1985; Gillespie 1991; Ellner and Hairston 1994).

DIVERSITY MAINTENANCE AND DENSITY DEPENDENCE

Ecologists commonly assume that there are two views of diversity maintenance: an equilibrium view, which is associated with traditional diversity maintenance mechanisms such as resource partitioning, segregation of species by habitat or frequency-dependent predation (Chesson and Case 1986), and a nonequilibrium view in which these factors have no role. The idea of equilibrium was originally conceived as a "point equilibrium," i.e. a state of the system at which species densities would remain constant over time unless perturbed by external forces, such as environmental fluctuations. There are many alternatives to point equilibria, ranging from simple deterministic cycles in population density, through chaotic and stochastic fluctuations, to systems that do not persist in the long run. Any of these departures from point equilibrium, excepting the last, permit new ways in which diversity can be maintained. However, there is no necessity that departure from equilibrium has any effect on diversity maintenance. For example, stochastic versions of Lotka-Volterra models have the same predictions as their equilibrium counterparts (Turelli 1981; Chesson 1994).

When departures from equilibrium do introduce new mechanisms of diversity maintenance, as we shall see below, these new mechanisms can act in concert with traditional mechanisms. For example, any two species may coexist partly because they partition resources, and partly because the system fluctuates over time. Thus, it is clear that mechanisms traditionally associated with equilibrium, such as resource partitioning, habitat segregation and frequency-dependent predation, do not rely on equilibrium and can operate in systems that are far from equilibrium much of the time. Thus, they might be called fluctuation-independent mechanisms (Chesson 1994) rather than equilibrium mechanisms.

Recognition that equilibrium is not the issue shifts focus from the equilibrium itself to the forces preventing extinction. Thus, the invasibility approach for stochastic systems was developed (Turelli 1981) with an emphasis on recovery of populations from low density. This approach allows quantification of the strength of diversity maintenance mechanisms via the average rate of recovery, $\bar{r}$, from low density (Chesson and Huntly 1993), which is calculated as the average change in log population size at low density, and is equivalent to the time average of the per capita growth rate of the population. In such calculations, "low density" is any population density low enough for intraspecific density dependence to have negligible effect on population growth.

The theory of $\bar{r}$ involves some complications, but in essence, it can be described as follows. First, if all species are to persist in a community in the long run, they must all have positive $\bar{r}$s (Chesson and Ellner 1989, Chesson and Huntly 1996). Negative or zero values for any species mean that some species must become extinct. However, not all species with zero or negative $\bar{r}$s must become extinct because as extinctions occur, $\bar{r}$s of some remaining species may change from negative or zero values to positive values. In general, in persistent communities, the more strongly positive the $\bar{r}$s are, the more strongly a community is stabilized. For nonpersistent communities, the more strongly negative some $\bar{r}$s are, the more rapidly species disappear from the system.

This approach to diversity maintenance via $\bar{r}$ implicitly involves density dependence. Recovery from low density necessitates a positive value of $\bar{r}$. However, the same positive average growth rate cannot apply at all densities because this would imply indefinite exponential growth of the population. Indeed, the average growth rate for a persisting population is necessarily zero in the long run. Thus, we have positive average growth rates at low density and these must decline to zero and then become negative as densities increase. Such density dependence can be complex, however, departing substantially from the simple direct and instantaneous action depicted in models like the logistic model and Lotka-Volterra competition models. Density dependence affecting $\bar{r}$ may be indirect working through intermediaries such as resources, predators and pathogens, and can be over large temporal and spatial scales with considerable time lags (Chesson 1996). It may also work diffusely over a spatially heterogeneous landscape, or very patchily in space and time so that only in some localities or times is the critical density dependence apparent (Hassell 1987; Chesson 1996).

Some marine systems yield very obvious and quantifiable density dependence(Stimson 1990; Forrester 1995). Others do not reveal strong evidence of density-dependent effects on numbers of individuals(Doherty and Fowler 1994). Nevertheless, it has been suggested that biomass and therefore individual growth may reflect density-dependent interactions(Doherty et al 1988), as might reproductive allocation (Kerrigan and McCormick 1996). Moreover, recent theoretical

results imply that any persistent species must be affected by density dependence even though the system may fluctuate greatly in time and space, and even though the species may have complicated life-history or age structure (Chesson 1996).

In contrast to this approach to diversity maintenance, a number of authors have suggested that diversity can be maintained in situations where all species have $\bar{r}$ approximately equal to zero, and density dependence is of no significance (Huston 1979, 1994; Shmida and Ellner 1984; Hubbell and Foster 1986). The models supporting this view argue that when species are matched closely in competitive ability or when disturbance reduces average population growth rates to very low values, diversity should decay only very slowly. However, Chesson and Huntly (1996) argue that the models on which this argument is based are not robust, and in nature other factors are likely to dominate over this proposed mechanism.

DIVERSITY MAINTENANCE IN A VARIABLE ENVIRONMENT

General models of diversity maintenance now include both density dependence and environmental fluctuations (Chesson 1994). Density dependence is introduced by a *competition parameter*, or in more evocative language, the *competitive response* (Goldberg 1990), measuring the effect on population growth of competition and other negative density-dependent effects such as cannibalism and density-dependent predation (sometimes called "apparent competition" Holt 1977). The competitive response measures the total effect of density dependence both within and between species. For example, in a system in which reproduction is affected by competition, the competitive response may be defined as the ratio of per capita reproduction without competition to per capita reproduction with competition, or more commonly, the log of this value. Correspondingly, to measure the effects of the environment and its fluctuations over time, there is an environmentally-dependent parameter (Chesson 1994), or environmental response (Chesson and Huntly 1996) which measures changes in critical components of per capita population growth due to changes in the environment. The environment is taken to be inclusive of the physical environment and many features of the biological environment so long as these features of the biological environment are not associated with density dependence in the species whose coexistence is in question. For example, density-independent predation could contribute to the environmental response, but density-dependent predation would contribute to the competitive response.

The most important result of Chesson (1994) is that $\bar{r}$, for any given species i in the community, can be partitioned approximately into contributions from different mechanisms of coexistence:

$$\bar{r}_i = \bar{r}_i' - \Delta N + \Delta I \qquad (1)$$

where $\bar{r}_i'$ represents contributions to $\bar{r}$ from fluctuation-independent mechanisms, and ΔN and ΔI represent the effects of fluctuations over time.

Fluctuation-independent mechanisms

Resource partitioning may be an important diversity maintenance mechanism in coral reefs (Anderson et al. 1981), and this mechanism is commonly studied using the Lotka-Volterra competition model. Environmental fluctuations have no effect on $\bar{r}$ in the Lotka-Volterra model (Chesson 1994) and so the ΔI and ΔN terms are zero. However, average environmental responses can affect species coexistence, and in this there is an important lesson. For a simple illustration, consider a special case of the general Lotka-Volterra model.

Assume that competition is symmetric between species so that all interspecific competition coefficients, β, are the same, all intraspecific competition coefficients, α, are the same. Assume also that α and β and are similar in magnitude, then a good approximation to $\bar{r}$ is

$$\bar{r}_i = \bar{r}_i' = \left\{\bar{E}_i - \bar{E}_\cdot\right\} + \frac{b}{n-1}(1 - \beta/\alpha), \qquad (2)$$

where b is the intrinsic rate of increase, n is the number of species in the community, $\bar{E}_i$ is the time-average of the environmental response of species i, and $\bar{E}_\cdot$ is the average of this time average for species i's competitors. The first part, $\bar{E}_i - \bar{E}_\cdot$, may be thought of as a comparison of the average fitness of species i in this system compared with the average fitness of all of its competitors. In the absence of resource partitioning (i.e. with $\alpha = \beta$), the species with the highest average fitness would competitively exclude the other species, and this would occur regardless of environmental fluctuations. However, in the presence of resource partitioning, the interspecific competition coefficient, β, is less than the intraspecific coefficient, α, and the second term in Eq. (2) is positive. If this second term is sufficiently large, it leads to positive values of $\bar{r}$ for all species, meaning that they coexist in the system.

A small ratio of β to α means dissimilarity in resource use. This case can also be thought of as dissimilarity under specific conditions, where the specific conditions are the various resources. The species are dissimilar under these specific conditions as they depend to different degrees on the different resources. Such dissimilarity favors species coexistence. However, dissimilarities in average fitness favor competitive exclusion. These dissimilarities in average fitness can be thought of as dissimilarity on average over all conditions, not the specific conditions of a given resource.

These results show that diversity maintenance is favored by similar fitnesses between species when averaged over all conditions, and dissimilar fitnesses under specific conditions, in agreement with the qualitative conclusions of Abrams (1983). We shall find these same conclusions arising again and again regardless of the diversity maintenance mechanism. Indeed, they appear to be fundamental to species coexistence.

Fluctuation-dependent mechanisms

Temporal environmental fluctuations can lead to a very strong coexistence where species fluctuate in a steady manner over

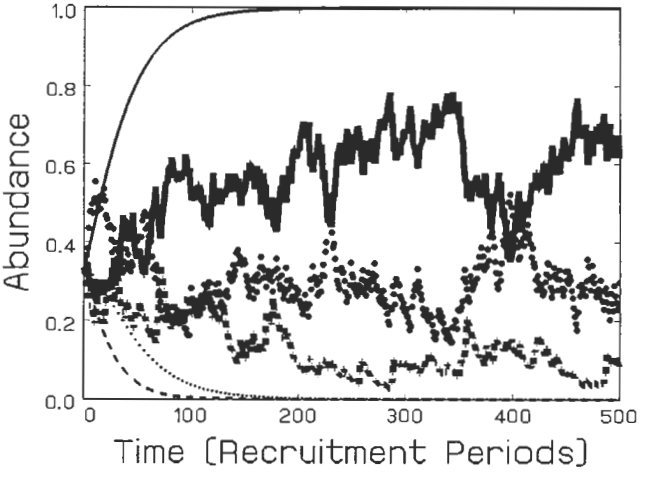

Fig. 1: Simulation of population dynamics of three species competing for space for recruitment. Population densities are represented as fraction of space occupied by that species. The smooth curves correspond to the case where environmental responses have zero variance. Then coexistence is impossible, and the system is dominated by the species with the highest fitness (average environmental response) in that system. With environmentally driven recruitment fluctuations, that are at least partly uncorrelated between species, a stable long-term coexistence is possible. Differences in average fitness are then reflected by different average population densities.

time, showing no tendency toward extinction and always recovering from fluctuations to low densities (Fig. 1). Such stability arises from strong positive values of $\bar{r}$ caused by a large value of ΔI. Paradoxically, such stability depends on the fluctuations in the system, and is quantified by the ΔI term of equation (1), *the storage effect*. The storage effect is the result of the interaction between the fluctuating environmental responses and fluctuating competitive responses.

The storage effect may commonly arise in marine systems from highly variable recruitment (Mapstone and Fowler 1988; Underwood and Fowler 1989; Hughes 1990; Doherty and Fowler 1994), in other words, temporally variable rates of arrival of larvae at a locality where they may settle and mature into adults. The environmental response is the log of the per capita number of larvae seeking to settle on a coral reef at a given time. The competitive response is the log of the ratio of the number of larvae seeking to settle and the actual number settling. Defining δ to the death rate of adults, σ^2 to be the variance over time in the environmental responses, and ρ the correlation between the environmental responses of different species, it follows that

$$\bar{r}_i = \left\{\bar{E}_i - \bar{E}_\cdot\right\} + \frac{(1-\delta)\,\sigma^2}{n-1}(1-\rho) \qquad (3)$$

(Chesson 1994), where $\bar{r}$ is expressed on the timescale of longevity of the adults. The term in braces is $\bar{r}_i'$, and the second term is ΔI, the storage effect.

The most remarkable feature of this equation is involvement of the variance, σ^2, in $\bar{r}$. Variance increases the average recovery rate from low density. It does not merely cause fluctuations, or slow down competitive exclusion. Instead, it has an active role in stabilising species coexistence. This effect, however, depends on differences between species in the way they respond to environmental conditions, as measured by $1 - \rho$. If species respond identically to environmental conditions, then ρ is equal to 1, and ΔI is equal to 0, i.e. there is no storage effect. On the other hand, the smaller ρ is, the stronger the storage effect. The reason is that species gain advantage by responding differently to the environment than other species and thereby reducing the effect of interspecific competition on population growth.

Note that $1 - \rho$ of Eq. 3 corresponds to $1 - \beta/\alpha$ of Eq. 2 in both numerical effect on $\bar{r}$ and in meaning. Both quantify differences between species in their responses to specific conditions. Moreover, both expressions for $\bar{r}$ involve average differences between the environmental responses of the different species, and therefore both support the contention above that diversity maintenance is favored by average similarity in fitnesses between species and dissimilarity between species in their fitnesses under specific conditions. Differences between species in fitness under specific conditions alone, however, do not make a diversity maintenance mechanism. These differences must be linked to competition. In addition, the advantages a species gains under one set of conditions must not be canceled by the disadvantages that it experiences under other conditions. Thus, the storage effect has two other ingredients, which we discuss next.

Covariance between environment and competition

If the arrival of larvae at a reef varies over time in response to environmental conditions, and if space for settlement on the reef is limiting or if density dependent predation limits numbers on a reef ("apparent competition"), then competition or apparent competition will vary with those environmental conditions. In other words, the competitive response will covary with the environmental response. In different settings, an increase in the environmental response might mean higher individual growth rates, for example by larvae after they have settled on a reef, with the consequence that these rapidly growing larvae put more demand on resources such as food or space, at their larger size, or are more attractive to predators. In any of these situations, the competitive response is likely to increase with the environmental response.

The covariance between environment and competition is measured by the standard statistical covariance measure (Chesson 1994) and is invariably density-dependent (Chesson and Huntly 1989). As a species' density gets lower, for example, by chance fluctuation or by experimental manipulation, it causes less competition and the link between a species' environmental response and competition is reduced. Competition will be more affected by the environmental responses of other species in the community, and any correlation between competition and the environmental response of a species will be due to correlations between its environmental response and the environmental responses of other species. If species have the same environmental responses, there is no reason to expect any change in the covariance between environment and competition with density. If species have uncorrelated environmental responses, then the covariance between environment and competition decreases to zero as a species density increases. If species have negatively correlated environmental responses then the covariance between environment and competition becomes negative as a species density approaches zero.

This density-dependent behavior of the covariance between environment and competition means that there are benefits to low density, including the situation when other species are not at low density (i.e. there is an important frequency dependent component to the covariance between environment and competition). As a consequence, when a species is favored by the environment, and is at low density, it need not experience high competition, thus achieving the full benefit of the favorable environmental conditions. In contrast, its competitors at high density do not have such benefits. When they are favored by the environment, they pay the penalty of higher competition.

The covariance between environment and competition enters the storage effect term of expression (3) as $\sigma^2(1-\rho)/(n-1)$, which is the difference between the value of covariance between environment and competition of a species' competitors and its own value at low density. Note that this difference decreases with the number of competitor species because, with an increase in the number of competitors, there is an increase in the chance that the environmental response of a species at low density is similar to that of one or more of its competitors. Thus, it has reduced opportunities for a strong environmental response unhindered by competition.

Note also that covariance between environment and competition does not merely deliver benefits to a species at low density for when a species is disfavored by the environment, it may not receive any reduction in competition. Indeed, it may be unlucky enough to suffer more competition from its competitors. To gain any net benefit from the density-dependent behavior of the covariance between environment and competition, there must also be an *interaction between environment and competition*, which determines how a joint pattern of fluctuations in the environmental and competitive responses is converted into fluctuations in per capita population growth.

Interaction between environment and competition.

Fig. 2 plots per capita population growth as a function of competition for different values of the environmental response. Fig. 2(a) is the situation that occurs in the model of recruitment rate variation discussed above whenever the adult organisms survive for more than one breeding season. The figure assumes that adult survival is relatively insensitive to environment and competition, while recruitment is highly sensitive to these factors. In contrast, in Fig. 2(b), it is assumed adults do not survive for more than one breeding season, or equivalently, that adult survival is just as sensitive to environment and competition as is recruitment.

In Fig. 2(a) the environmental response modifies the effect of the competitive response on population growth, i.e. there is an interaction between the environmental response and the competitive response in their joint determination of the per capita growth rate. For a low value of the environmental response, the competitive response has a relatively weak effect on population growth. This effect

can be interpreted as a buffer against jointly unfavorable environment and competition. In contrast in Fig. 2(b) there is no such effect. The competitive response reduces the growth rate of the population at the same rate regardless of the environmental response.

The density-dependent properties of the covariance between environment and competition discussed above mean that a species at high density experiences the points D and B on these figures, and rarely if ever experiences A and C. A species at low density, however, can experience A and C. In Fig. 2(a), the low density species gains a net benefit from fluctuations between A and C, as the gains from A are much greater than the losses at C. In contrast, in Fig. 2(b) without a buffer against jointly unfavorable environmental and competitive responses, there is no benefit to fluctuations between A and C relative to D and B, and therefore no net benefit from the density dependence of the covariance between environment and competition.

This effect of the interaction between environment and competition is expressed quantitatively in eq.(3) as $(1 - \delta)$,

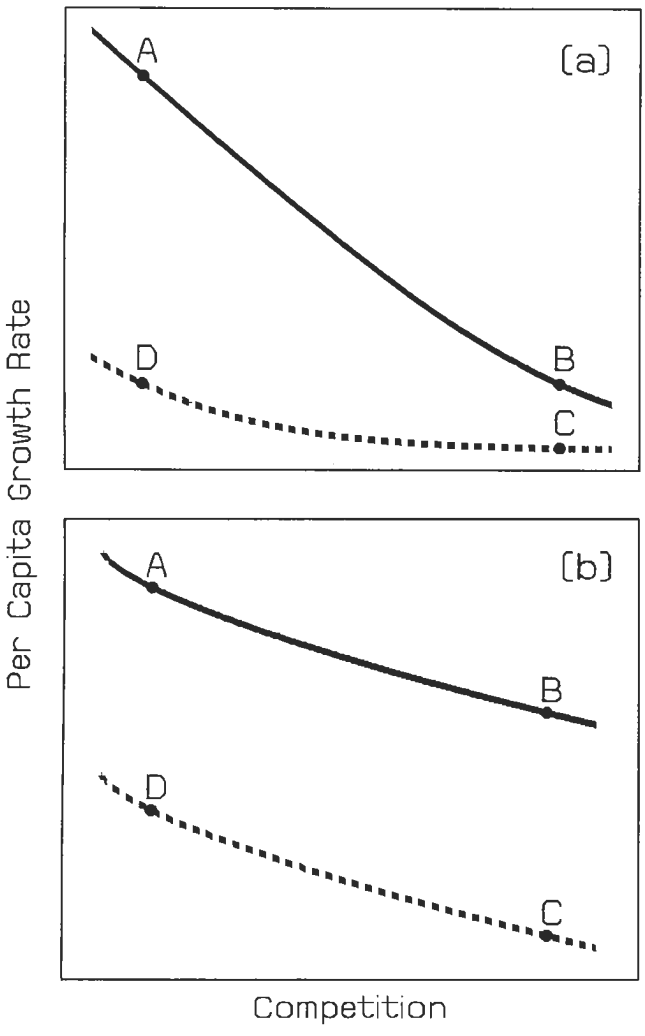

Fig. 2: Per capita population growth as a function of competition (the competitive response) for different values of the environmental response. The solid line is a high environmental response and the dashed line is a low environmental response. (a) Buffered growth rates arising when recruitment is sensitive to environment and competition but adult survival is positive and insensitive. (b) Nonbuffered growth rates arising when adults do not survive more than one breeding season, or have survival just as sensitive as recruitment to environment and competition.

the adult survival rate, which is assumed insensitive to environment and competition. If there is no adult survival or if adult survival is just as sensitive to environment and competition as recruitment, this term is zero and there is no storage effect. With insensitive adult survival, however, the storage effect is proportional to the adult survival rate. The interaction between environment and competition is measured generally as the change in slope between the two curves in Fig. 2(a), relative to the change in the environmental response between the two curves. The storage effect is approximately proportional to this value (Chesson 1994).

Interactions between environment and competition can occur in a variety of ways. The critical feature is that population growth should have a number of contributing components, such as survival and recruitment, with differing sensitivities to environment and competition, and these sensitivities should be correlated, i.e. high sensitivity to competition should go along with high sensitivity to environment (Chesson 1990). The contributing components could be due to different classes of individuals in a population, e.g. in the recruitment variation example considered here, sensitivity of recruitment to competition and the environment could stem from the fragility of larvae and juveniles, while the lower sensitivity of adult survival likely results from the relative robustness of adults. With high fecundities of many marine species, high survival of larvae and juveniles means massive recruitment, but also such survival rates can be enormously variable due to the fragility of larvae, and the high variability of the larval environment. Such heterogeneity provides a buffer to total population growth against unfavorable combinations of environment and competition.

In terrestrial systems, annual plants are buffered by a buried seed bank (Ellner 1984; Chesson and Huntly 1989). The discovery of very long-lived egg banks in freshwater zooplankters (Hairston et al. 1995) opens up the strong possibility that such egg banks may be effective in promoting the storage effect in aquatic animals also. In corals, high longevity, division into autotrophic and heterotrophic ways of making a living, the existence of both vegetative and sexual reproduction, and the variety of phenotypes, may well provide buffering effects of high order.

Coral reefs present spatially heterogeneous environments and many organisms are widespread. Buffering may result from the varying exposure of different sites to environmental and competitive conditions independently of any species differences in distribution patterns. Fish populations are often distributed over a variety of different habitat types including lagoonal and slope environments with the potential for variation in sensitivities to competition and environment. Both corals and agal species can be found distributed over sites on a reef that vary in light intensity, wave exposure, susceptibility to desiccation, sedimentation, and grazing (Birkeland 1977; Brock 1979; Sammarco 1980). Such conditions may lead to an interaction between environment and competition similar to that suggested for understorey herbs in a forest environment (Chesson 1990), buffering environment and competition in space.

HIERARCHIES OF SCALES

Eqs (2) and (3) represent separately the effects of fluctuation-independent and fluctuation-dependent mechanisms. There is no reason why they should not both be present in the same model. For example, larval settlement rates may fluctuate with the environment, but also there may be differences between species in habitat selection, which can be reflected in competition coefficients α and β. Then, if C^* is the equilibrial magnitude of competition, on the timescale of adult longevity

$$\overline{r}_i = \left(\overline{E}_i - \overline{E}_\cdot\right) + \frac{(1 - \beta/\alpha)\,C^*}{n - 1} + \frac{(1 - \delta)\,(1 - \rho)\,\sigma^2 C^*}{n - 1} \qquad (4)$$

(Chesson 1994). In this equation, the first term represents average dissimilarity in fitness, and this term is opposed by two terms measuring dissimilarity in fitness under specific conditions, viz, habitat partitioning and differential res-

ponses a fluctuating environment. Note that these two terms have a similar structure and a similar effect in promoting coexistence.

This similarity between fluctuation-independent and fluctuation-dependent mechanisms is in fact deep (Chessonand Huntly 1993). When viewed on a long timescale, fluctuation-dependent mechanisms can lead to similar population dynamics to fluctuation-independent mechanisms. Indeed, we can think of $\overline{r}_i'$ as including not just fluctuation-independent mechanisms but also fluctuation-dependent mechanisms working on a short timescale, i.e. a timescale less than the unit of time in the *model*. *For example*, suppose the unit of time considered in the model is one year, then the ΔN and ΔI terms of Eq. (1) concern year to year variation, but $\overline{r}_i'$ could incorporate the effects of seasonal variation. Many scales of variation are commonly observed in coral reef systems (Doherty 1983, 1988; Sale 1984; Harriott and Banks 1995), and Eq. (1) shows that these effects can combine over scales, from the scale of seasonal recruitment or growth (Chesson and Huntly 1993; Kubo and Iwasa 1996) to the scale of climate change potentially spanning thousands of years. If covariance between environment and competition, and interaction between environment and competition can exist on a scale, then fluctuations on that scale can contribute to diversity maintenance.

Our discussion has been framed almost entirely in relation to the temporal dimension. However, similar considerations exist for spatial variation (Chesson 1985), including spatial storage effects that rely on habitat segregation. Spatial storage effects can be due to habitat preferences and may be predictable on the basis of fixed features of the habitat such as depth or lagoon versus reef slope locations (Pandolfi 1996). Or alternatively, spatial distributions may be influenced by dispersal of the organisms, which may involve things like interactions between spawning time, currents, storms, movements of larval predators, and larval characteristics (Victor 1986; Pitcher 1988; Hughes et al 1992; Planes et al 1993). Thus, there can be temporally varying spatial patterns of distribution partially uncorrelated between species, or temporally invariant spatial distributions partially uncorrelated between species. Reality is bound to be a mixture of both, but nevertheless, either situation or their combination leads to a spatial version of the storage effect where the emphasis is on fluctuations of environmental responses in space rather than time, and their accompanying covariance with competition.

Environmental responses can be either performance at a site (Comins and Noble 1985; Shmida and Ellner 1984) or arrival of juveniles at a site (Chesson 1985; Roughgarden and Iwasa 1986). With such spatial storage effects, the distribution of the population in space, with populations at least partially out of phase in different localities, provides adequate buffering and does not require high longevity.

The disturbance hypothesis (Connell 1978; Caswell 1978; Hastings 1980) or its more descriptive name, the successional mosaic hypothesis (Chesson and Huntly 1996) has elements in common with both spatial and temporal storage effects. For example, it depends on different species having different fitnesses at different stages of succession at a site, and this must be related to competition (Chesson and Huntly 1996). Moreover, the distribution of the population in space, with different populations at different successional stages, has the effect of buffering unfavorable combinations of environmental and competitive conditions for a species, analogous to the interaction between environment and competition that is required for the storage effect. The presence of natural disturbances of a variety of forms, and the life-history adaptations of some corals (Hughes et al. 1992), and other species, for rapid colonization of disturbed areas, suggests that disturbance may have an important role in diversity maintenance on coral reefs.

DISCUSSION

Paleontological evidence of coral communities suggests that species diversity, indeed, actual species composition, is maintained in coral communities and is stable on timescales as long as 100,000 years (Pandolfi 1996). The theory discussed here suggests that such stability is entirely compatible with, and indeed may well result from, fluctuations and instabilities on shorter timescales (Jackson et al. 1996). Although there has been a tendency in ecology to view density-dependent processes and environmental variability as alternative routes by which diversity may be maintained, theoretical evidence suggests that their interaction is critical. Without density dependence, variability has no importance in the long run. Conversely, variability allows density dependence to act in a way that stabilizes species diversity.

The variability of coral reefs seems to provide strong potential for mechanisms involving interactions between density dependence and variability. The difficulty of measuring density-dependent processes in such variable systems, however, may lead some ecologists to believe that density-dependence is not important on coral reefs(Doherty and Fowler 1994). However, density independence appears unlikely to be a sustainable feature of many species on coral reefs. Instead, it seems more likely that the variable, indirect and often time-lagged nature of density dependence has obscured its understanding. Covariance and interaction between environment and competition provide new ways of thinking about density-dependent processes and variability that could be profitably explored in coral reef studies.

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