

CHAPTER 8

ENVIRONMENTAL VARIABILITY MODULATES THE INSURANCE EFFECTS OF DIVERSITY IN NON-EQUILIBRIUM COMMUNITIES

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8.1	Abstract	159
8.2	Introduction	160
8.3	Model	162
8.4	Results	165
	8.4.1 Without Immigration ($I_i = 0$)	165
	8.4.2 With Immigration ($I_i = 9.89E - 4$)	165
8.5	Discussion	170
8.6	Acknowledgments	173
8.7	Literature Cited	173
	Appendix 8A	176

8.1 ABSTRACT

Previous theoretical analyses of the relation between diversity and community stability have ignored or greatly simplified the environment. One ubiquitous feature of stochastic environments is the autocorrelation, or long-term memory, that is apparent over multiple time scales. We analyze a model of nonequilibrium resource competition and show how environmental autocorrelation can strongly define community stability. Autocorrelated environmental variability can have destabilizing

effects 50 times greater than the stabilizing effects of increasing species richness; this result was exacerbated when we considered a case where increasing species richness had a destabilizing effect on community dynamics. In particular, the interaction between nonlinear resource competition and autocorrelation in the environment alters the magnitude and timing of population and community fluctuations. Increasing the autocorrelation of the environment caused a qualitative shift in community dynamics from a single long-term “steady state”, in which population fluctuations were small and biomass was relatively evenly distributed across all species, to metastable dynamics characterized by periods of relative stability, punctuated by abrupt shifts in species dominance and a highly uneven biomass distribution. Consistent with recent metacommunity theory the addition of immigration stabilized the community. We suggest that increasing autocorrelation, due to climate change, may have hitherto unforeseen destabilizing effects on community dynamics that may compound the effects of ongoing species loss.

Keywords: environmental fluctuations, autocorrelation, diversity, stability, community evenness, resource competition, dispersal.

8.2 INTRODUCTION

Ecological communities are perturbed by environmental fluctuations over a great range of temporal scales (Davis 1986; Levin 1992; Roy et al. 1996; Bennett 1997; Shugart 1998; Dynesius and Jansson 2000). Differential species responses to short and long-term environmental variation ensure that communities are in a constant floral and faunal disequilibrium. The differences between species in their capacity to respond to environmental variation causes some species to track change closely, whilst others respond much more slowly, resulting in time-lagged responses to environmental change occurring over much longer timescales (Davis 1986; Bennett 1997).

The shifts in distribution and abundance that accompany species responses to environmental change can have profound affects upon community structure and functioning (Steele and Henderson 1984; Braswell et al. 1997; McGowan et al. 1998; Hulme et al. 1999; Dynesius and Jansson 2000; Knapp et al. 2002; Stenseth et al. 2002). Recent ecological theory suggests that short-term variation in species abundance may affect the stability of community processes. Specifically, aggregate community processes, such as biomass production, will be stabilized by differences in the magnitude and timing of species responses to the environment, the asynchronous fluctuations at the population level result in a buffering effect at the community level (Doak et al. 1998). Furthermore, increasing species diversity is thought to enhance this buffering effect by increasing the range of species responses to environmental fluctuations (McNaughton 1977; Doak et al. 1998; Hughes and Roughgarden 1998; Ives et al. 1999; Yachi and Loreau 1999; Chesson et al. 2001; Norberg et al. 2001; Ives and Hughes 2002).

Ives and Hughes (2002) define two conditions necessary for a stabilizing effect of increasing species richness. Firstly, the net effect of competition on the variability in population growth rates of component species should be independent of species number (i.e. variability in per capita growth rates should remain the same irrespective of the number of species in the community) and the strength of interspecific competition. Secondly, all species within the community should have approximately equal densities. Although these assumptions are not excessively unrealistic, conditions under which they break down are known. For example, recent experimental tests of this theory (Petchey et al. 2002; Gonzalez and Descamps-Julien 2004) suggest that the variability of population growth rates is not independent of species richness. Furthermore, community abundance distributions are not uniform but rather are typified by the relatively long-term dominance of one or a few species and rare species are maintained by immigration, a characteristic of natural communities that would seem to be the norm rather than the exception (e.g. Rahel 1990; Venrick 1990; Bengtsson 1994).

Another aspect that may limit the generality of recent theoretical results is the observation that the conditions for stability have been based on linearization techniques. The assumptions of the linear approach are that the community must be close-to-equilibrium, that environmental fluctuations are of small amplitude, and that the system must not be close to a bifurcation point. Yet, much of the literature indicates that long-term community dynamics, whether aquatic or terrestrial, are typified by large amplitude fluctuations that are driven by environmental variation (e.g. Willis et al. 1995; Whitlock and Bartlein 1997; Francis et al. 1998; Allen et al. 1999). This apparent inconsistency between theoretical studies and observations suggests that studies of the stability of far-from-equilibrium communities would be worthwhile. We address this issue, and the others raised earlier, by examining whether previous conclusions regarding the stabilizing effect of species diversity are altered by considering large amplitude environmental fluctuations, and in particular, whether the scale of autocorrelation of these fluctuations can affect community stability.

The temporal scaling of environmental variability can be characterized by its frequency structure. For example, temperature fluctuations in marine and terrestrial environments tend to increase in power (variance) at low frequencies (Mandelbrot and Wallis 1969; Steele 1985; Pelletier 2002; Vasseur and Yodzis 2004), by analogy with light such spectra are referred to generically as “red” as opposed to “white” spectra, in which all frequencies have equal variance. The property of increasing power (variance) through time is responsible for the long-term autocorrelation structure, or “memory” typical of many environmental variables. Previous work has identified the temporal scaling of environmental fluctuations as a key factor that may affect many ecological processes. Theory and experiments have demonstrated that extinction probabilities (Ripa and Lunderg 1996; Petchey et al. 1997; Cuddington and Yodzis 1999; Halley and Kunin 1999; Wichmann et al. 2003) as well as various aspects of population (Steele and Henderson 1984; Heino 1998; Morales 1999; Petchey 2000; Gonzalez and Holt 2002; Inchausti and Halley 2002) and community

dynamics (Caswell and Cohen 1995; Ripa et al. 1998; Ripa and Ives 2003; Ripa and Ives, this volume) are dependent upon the autocorrelation in the environment.

To examine whether community stability is affected by the temporal scaling of the environment we adopt a standard resource competition model where species coexistence is fluctuation-dependent (*sensu* Chesson 2000) and is made possible by a storage effect (Lehman and Tilman 2000; Chesson et al. 2001). The buffered population growth generated by this model is also the basis of the stabilizing (insurance) effect of diversity previously reported (Ives et al. 1999; Yachi and Loreau 1999; Chesson et al. 2001; Norberg et al. 2001; Ives and Hughes 2002), what we are concerned with here is establishing how fluctuations in some environmental variable, other than the resource, modulate this buffering effect. Recent work has shown that “opening” a community to immigration can qualitatively alter community dynamics and stability (Holt et al. 2003; Loreau et al. 2003) and so we also study the effect of environmental scaling in the presence of immigration. Consistent with earlier results we show that diversity has a stabilizing effect on community biomass but that the temporal scaling of the environment *is* an important determinant of long-term population and community stability. In particular, we show that reddened environmental fluctuations can generate strong asymmetries in community structure that result in low community stability despite the presence of compensatory fluctuations between species. In addition, to meet the challenge of recent experimental results that suggest a destabilizing role of diversity (Petchey et al. 2002; Gonzalez and Descamps-Julien 2004; Petchey this volume) we analyze a case where the breadth of species’ environmental tolerance (realized niche) is dependent upon species diversity. This follows from the basic expectation that the realized niche of any organism will be smaller than its fundamental niche (environmental tolerance) due to biotic interactions such as competition (Austin et al. 1990). Consistent with experimental results we demonstrate that this assumption can generate a destabilizing effect of increasing species richness. However, over long timescales community stability is still primarily dependent upon the temporal scaling of the environment.

8.3 MODEL

We consider a standard resource competition model and, to provide a comparison with previous work, we follow the parameterization of Lehman and Tilman (2000). The model is written in the following form (see Appendix 8A):

$$\begin{cases} \dot{R} = 1 - R - \sum_{i=1}^N g_i(x) \frac{RB_i}{R+K_i} \\ \dot{B}_i = B_i \left[g_i(x) \frac{R}{R+K_i} - m_i \right] + I_i \quad i \in \{1, 2, \dots, N\} \\ g_i = r_i \exp \left[\frac{1}{2} \left(\frac{x - \tau_i}{w_f / N^\beta} \right)^2 \right] \end{cases} \quad (8.1)$$

where N is the number of species, R is the amount of resource, B_i is the biomass of species i , K_i is the half saturation constant of the resource limitation function of

species i , m_i is the specific mortality rate of species i , I_i is an exogenous constant immigration flow, $x \in [-1, 1]$ is the environmental variable and τ_i is the value of x for which species i has its optimal productivity rate, which falls off as a Gaussian curve away from this value, β is a scaling constant that determines how the width of species environmental tolerance w_f is altered by increasing species richness. Written in this form time is now measured in resource time constant units, providing a relative measure of all the frequencies of the biomass and environmental fluctuations with respect to the resource. For every simulation run the m_i , K_i , w_f and r_i were identical and equal to 0.1, 0.1, 0.2 and 1.0, respectively, and consistent with previous analyses (Lehman and Tilman 2000). We present the four cases of $\beta = 0$ and $\beta = 0.2$, together with $I_i = 0$ and $I_i = 9.90\text{E} - 4$. A $\beta = 0$ assumes that the width of the environmental tolerance (fundamental niche) of each species is unaltered by increasing diversity, whilst a $\beta = 0.2$ assumes a weak monotonic and symmetrical decline in the width of the environmental tolerance with increasing species diversity (i.e. a decline in the realized niche ($w = \frac{w_f}{N^\beta}$) of each species with species addition). $I_i = 0$ assumes that there is no exogenous immigration and is consistent with previous analyses (Lehman and Tilman 2000) whilst $I_i = 9.90\text{E} - 4$ assumes an exogenous immigration flow of 0.01% of the maximal single species density achievable (see Appendix 8A). The additions of β and I_i to this model are new and provide a simple, and plausible, means of studying cases where the addition of species may have negative effect upon community stability (e.g. Petchey et al. 2002; Gonzalez and Descamps-Julien 2004), and the effects of a continuous flow of immigrants (a “mass effect”) from outside the local community (e.g. Schmidha and Wilson 1985). Because of the absence of demographic stochasticity, population biomass can reach very low levels without suffering extinction; the effect of this potentially unrealistic assumption is assessed by studying the effects of immigration that prevents populations from attaining very low levels of biomass.

We vary the environmental variable x as a $1/f$ process (Halley 1996), i.e. a process where the spectrum relating the frequency, f , and power $S(f)$ is of the following form:

$$S(f) \propto \frac{1}{f^\gamma} \quad (8.2)$$

Typically, for natural environmental variables $\gamma \in [0.5, 1.5]$ and they are therefore reddened (e.g. Pelletier 2002). Thus the power (amplitude) is directly proportional to the power γ of the reciprocal of frequency and low frequency dominance engenders the property of increasing variance and a long-term correlation structure.

A $1/f$ time series can be approximated by the following function:

$$x(t) = \sum_{f=1}^{n/2} \frac{1}{f^{\frac{\gamma}{2}}} \sin\left(\frac{2\pi ft}{n} + \theta_f\right) \quad (8.3)$$

where n is the length of the series, f the frequency, t is the time, γ determines the relation between power and frequency and θ_f is a uniform deviate in $[0, 2\pi)$ which

adds random phase to each sine wave. We simulated environmental fluctuations with $n = 512$ and $\gamma \in [0, 2]$, replicate series with the same mean and variance were constructed, and rescaled in the interval $[-1, 1]$, for each simulation run using a method of spectral mimicry (Cohen et al. 1999).

We varied species richness from 2 to 24 and examined population and community stability, in response to changing γ , by extensive numerical simulation. The model was numerically integrated using the Heun algorithm (Quarteroni 1999) with a fixed time step ($dt = 0.02$) for 60,000 units of time, where the first 10,000 were dropped and the statistics calculated on the remaining 50,000. These very long and time-consuming simulations allowed us to assess community stability after the elapse of the transient dynamics, an aspect of the simulation of this model overlooked by Lehman and Tilman (2000). For each of the combinations of N and γ values, 11 independent simulations were conducted and the results were averaged. Both the Heun integrator and the spectral mimicry method were implemented in the Matlab environment.

In keeping with previous studies we adopt a definition of stability based on the temporal variance of population and community biomass. We measure population (PS) and community (CS) stability as the inverse of the coefficient of variation (Lehman and Tilman 2000):

$$PS = \frac{\sum_{i=1}^N \frac{E_t [B_i]}{\sqrt{\text{Var}_t B_i}}}{N} \tag{8.4}$$

$$CS = \frac{E_t \left[\sum_{i=1}^N B_i \right]}{\sqrt{\text{Var}_t \left[\sum_{i=1}^N B_i \right]}}$$

where E_t and Var_t stand for the time average and variance of the argument variable. Furthermore, because previous analyses have identified community evenness as an important factor influencing community stability (Hughes and Roughgarden 1998; Ives and Hughes 2002), we also examine how community evenness (CE), calculated at each instant in time and averaged over each of the replicate simulations, i.e.

$$CE = E_t \left[-\frac{\sum_{i=1}^N p_i \ln(p_i)}{\ln(N)} \right], \quad p_i = \frac{B_i}{\sum_{i=1}^N B_i} \tag{8.5}$$

is altered as a function of N and γ .

8.4 RESULTS

8.4.1 Without immigration ($I_i = 0$)

For a given level of diversity, increasing γ (the relative dominance of low frequencies in the environment) has a large qualitative effect on both population and community dynamics (Figure 8.1). For low values of γ we obtain a single steady state defined by sustained population fluctuations of small amplitude for all species (Figure 8.1 top panels). An increase in γ results in “outbreak” dynamics in which each species increases from rare and dominates the community for relatively brief periods of time (Figure 8.1 middle panels). For $\gamma > 1.0$ we obtain metastable dynamics defined by distinct switches between long steady-states with alternating species dominance (Figure 8.1 bottom panels).

For $\beta = 0$, increasing N reduced mean population biomass (Figure 8.2A) but, because of compensatory population dynamics, it had a weak positive effect on total community biomass that saturated quickly for $N > 2$ (Figure 8.2E). For $\beta = 0.2$, whilst the effects on population biomass are unchanged (Figure 8.2B), community biomass (Figure 8.2F) peaked for $N = 4$ and then declined as N is increased from 2 to 24.

For $\beta = 0$, increasing γ from 0 to 2 reduced population stability eight-fold (Figure 8.2C) and community stability 100-fold (Figure 8.2G). This destabilizing effect of γ was associated with strong alterations in the symmetry of community structure as reflected by the declines in community evenness for $\gamma > 0.2$ (Figure 8.3A). For all levels of γ increasing diversity stabilized fluctuations in community biomass, although this stabilizing effect was small (twofold) compared to the destabilizing (100-fold) effect of the environment described above. Furthermore, the stabilizing effect of diversity saturated at $N > 3$ (Figure 8.2G). Similar effects of increasing γ on population (Figure 8.2D) and community stability (Figure 8.2H) were observed for $\beta = 0.2$. However, for $\gamma > 0.2$ and $\beta = 0.2$ communities were destabilized by increasing N (Figure 8.2H). In general, communities were less stable for $\beta = 0.2$ than $\beta = 0$. In sum, in the absence of immigration, irrespective of the value of β , the destabilizing effects of increasing γ outweighed the stabilizing (or destabilizing) effects of increasing N .

8.4.2 With immigration ($I_i = 9.89E - 4$)

For $\beta = 0$, immigration strongly and qualitatively alters the results for community stability (Figure 8.4G), whilst population stability remains unaltered (Figure 8.4C). The continuous loss of stability described above with increasing γ now only occurs for $N = 2$. For $N > 2$, although community stability still declines 100-fold up to $\gamma = 1.0$, for $\gamma > 1.0$ we obtain a rapid increase in stability such that for $\gamma = 2.0$ the community is more stable than for $\gamma = 0$. Furthermore for $\gamma > 1.5$ there is a strongly stabilizing (100-fold) effect of increasing N from 2 to 3 species, an effect that is

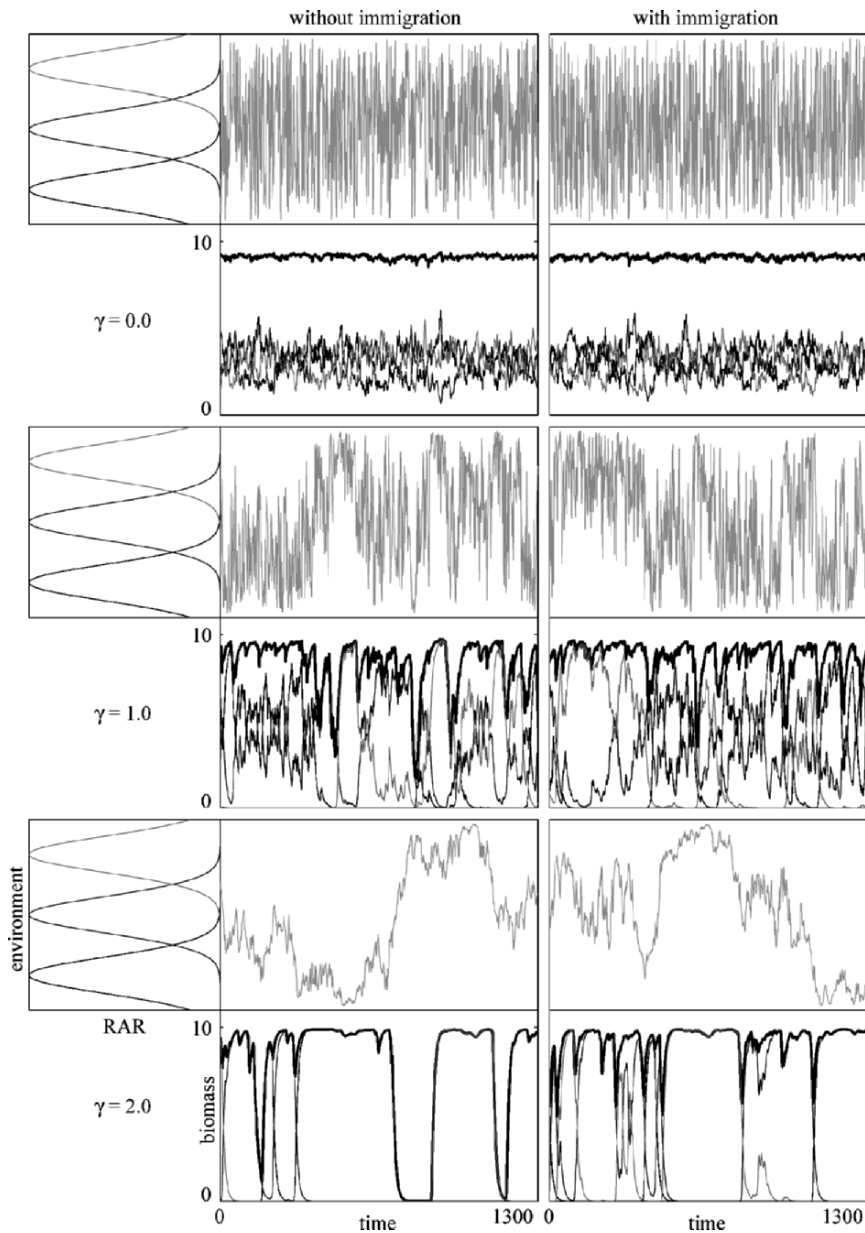


Figure 8.1. Example time series, for the two cases with and without immigration, for the case where $\beta = 0$, and for three levels of $\gamma = 0.0, 1.0$, and 2.0 . Environmental fluctuations are shown in grey. Adjacent to these is shown the niche of each species along the environmental gradient (RAR = resource assimilation rate). The mixed grey lines show the fluctuations in species biomass; the black line depicts the fluctuations in total community biomass.

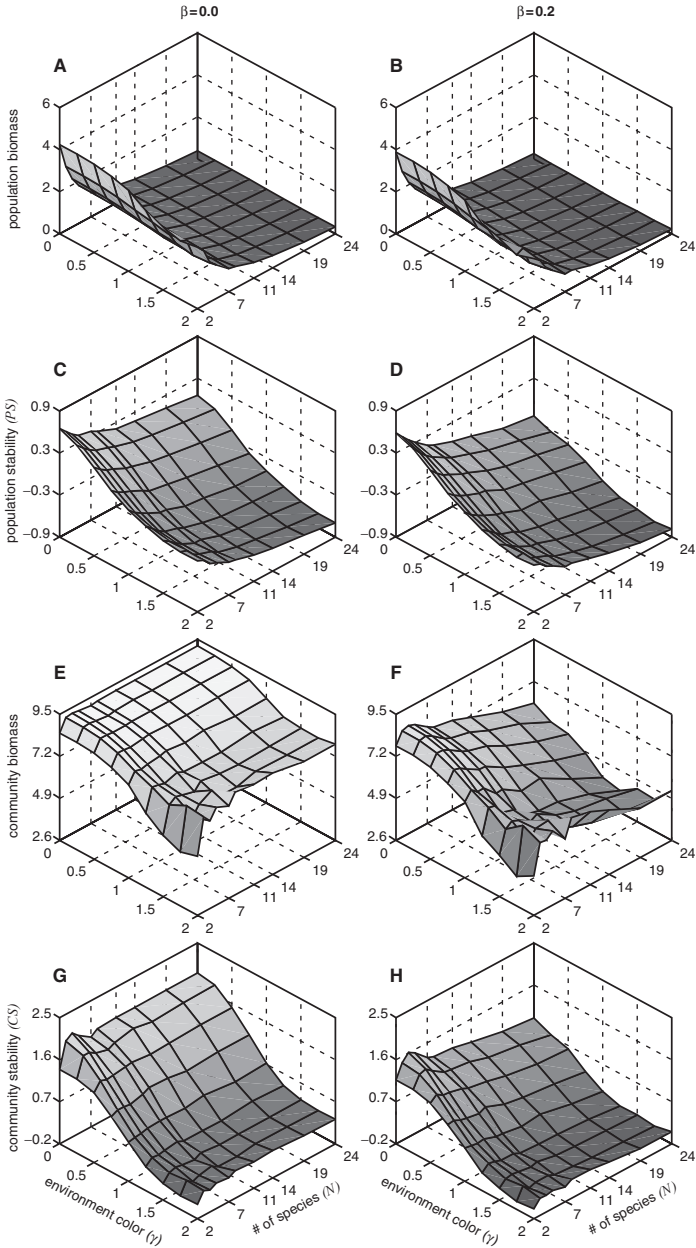


Figure 8.2. Surface plots, for the case without immigration, of mean population (a and b) and community (e and f) biomass and \log_{10} of population (PS , c, and d) and community (CS , g, and h) stability, as a function of species richness (N) and fluctuation spectra (γ), for the two cases of $\beta = 0$ and $\beta = 0.2$, see text for calculation.

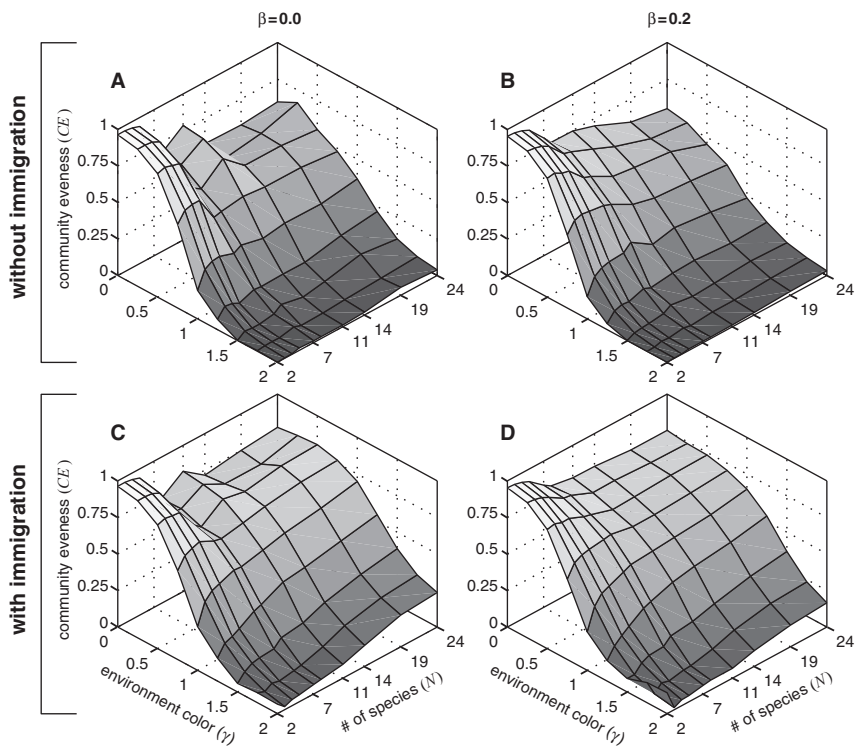


Figure 8.3. Surface plots, for the two cases with and without immigration, of mean instantaneous community evenness CE as a function of (N) and fluctuation spectra (β), for the two cases of $\gamma = 0$ and $\gamma = 0.2$, see text for calculation.

substantially greater than the weaker approximately threefold stabilizing effect of increasing N over the same range for $\gamma < 1.5$.

Immigration has a strong effect on community biomass (Figure 8.4E). The presence of a continuous flow of immigrants (a mass effect) from outside the local community ensures that biomass of any single species never attains the very low levels observed in the absence of immigration. This effect is confirmed by greater community evenness in the presence of immigration, especially for $N > 10$ (Figure 8.3C).

Increasing β from 0 to 0.2 had no noticeable effect on population biomass and stability (Figures 8.4B and D). However, we found a negative effect on community biomass and stability (Figures 8.4F and H) for $0 < \gamma < 1.0$ as N was increased. This effect is no longer apparent for $\gamma > 1.0$ and $N = 4$, resulting in the attenuation of the U-shaped relation between γ and community stability.

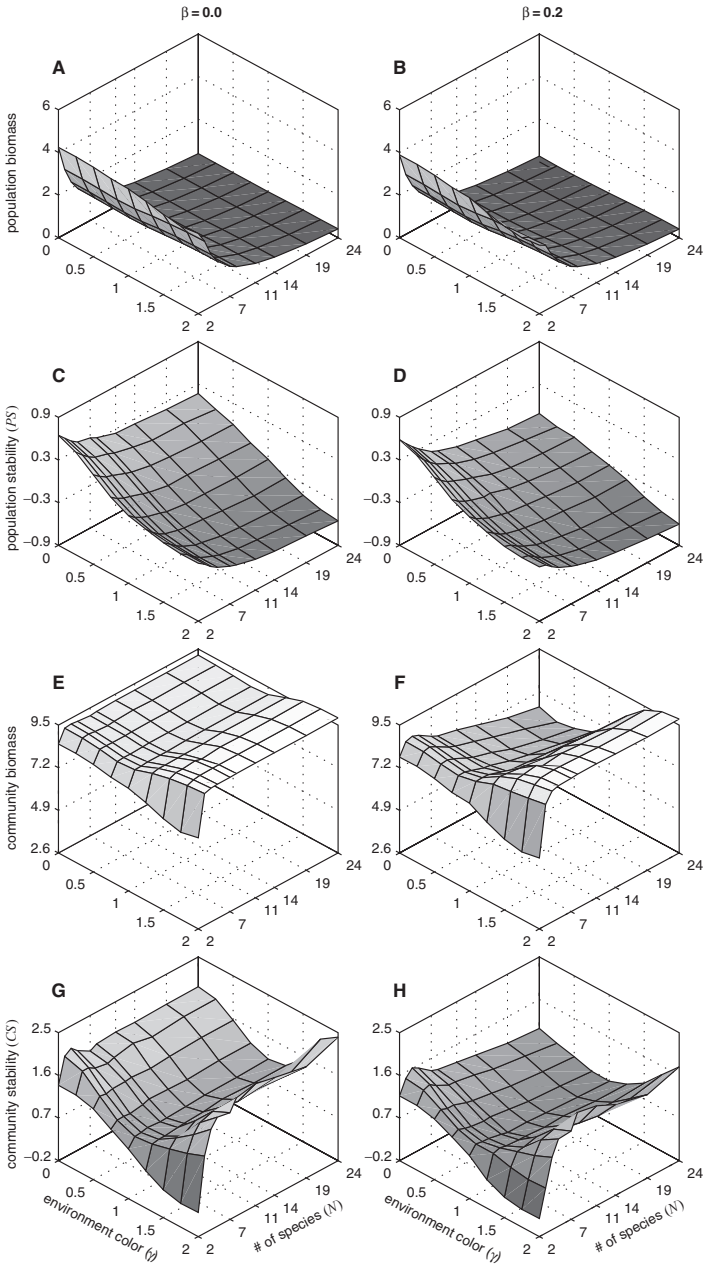


Figure 8.4. Surface plots, for the case with immigration, of mean population (a and b) and community (e and f) biomass and \log_{10} of population (PS, c, and d) and community (CS, g, and h) stability, as a function of species richness (N) and fluctuation spectra (γ), for the two cases of $\beta = 0$ and $\beta = 0.2$, see text for calculation.

8.5 DISCUSSION

The insurance effect is now considered to be the principal mechanism by which diversity may beget stability (McNaughton 1977; Doak et al. 1998; Hughes and Roughgarden 1998; Ives et al. 1999; Yachi and Loreau 1999; Chesson et al. 2001; Norberg et al. 2001; Ives and Hughes 2002). This study extends previous work using this resource competition model (Lehman and Tilman 2000; Chesson et al. 2001) where the stabilizing effects are a direct consequence of the temporal niche differentiation between species. We have shown that under certain realistic patterns of environmental variation the destabilizing effects of the environment were up to 50 times greater than the stabilizing effect of increasing diversity. These results suggest that the temporal structure of the environment may significantly modulate the stabilizing effects of diversity in a manner that has not been fully appreciated to date.

An understanding of our results requires the consideration of three factors: the width of the environmental tolerance (w_f) of each species, the resource assimilation rate (r_i) of each species, and the scale of autocorrelation in the environment (γ). Because w_f and r_i were held constant across species, it is possible to identify the direct effects of increasing γ in the presence and absence of immigration. Increasing γ destabilized total community biomass for three reasons: (1) because it increased population variability, (2) reduced community evenness, and (3) lengthened the interval (lowered the frequency) between compensatory switches in dominance. We consider these effects in turn below.

Increasing the temporal correlation of the environment (increasing γ) is destabilizing in this model because it causes a shift from small amplitude population fluctuations to large amplitude “outbreak” dynamics that substantially reduced population stability (Figures 8.1, 8.2C and D). It is important to note that because the environmental mean and variance was held constant this effect derives only from a change in the autocorrelation of the environment. A destabilizing effect of autocorrelated environmental fluctuations was also reported by Steele and Henderson (1984) and Gonzalez and Holt (2002), although these studies only considered single species populations. Previous theoretical studies (e.g. Roughgarden 1975; Ripa and Ives 2003) have demonstrated that autocorrelated environmental fluctuations can increase the variance of population fluctuations but none have shown the destabilizing effect this can have at the community level (Figures 8.2G and 8.4G and H).

The second result of note is the effect of the environment on community evenness, and the destabilizing affect this has on the community. Low levels of γ (< 0.2) characterize an environment dominated by high frequencies that often changes state and remains within the environmental tolerance of any given species for relatively brief periods of time. Here the short-term fluctuations of the environment cause community biomass to be distributed relatively evenly across several species (high evenness) at any one point in time (Figures 8.1 and 8.3), total biomass never reaches low levels and community stability is maximal. This scenario corresponds most closely to that explored by recent theoretical analyses that have used linear models to study the

effects of diversity on community stability (e.g. Hughes and Roughgarden 1998; Ives and Hughes 2002). This previous work assumed that the variance of the population and community fluctuations is small and community evenness is high (Ives and Hughes 2002), and it is useful that we recover this result for low values of γ (< 0.2). However, by studying the response of a nonlinear model to large and autocorrelated environmental fluctuations we obtained additional results that enrich earlier conclusions. We found that increasing the autocorrelation length of the environment creates large amplitude population and community fluctuations and a low evenness in the biomass distribution across the community. Low evenness precludes the contribution of much of the community to any insurance effect of diversity and this effect of the environment is strongly destabilizing. Ives and Hughes (2002) indicate that low evenness is destabilizing and suggested this might come about by asymmetric interspecific competition. We conclude that autocorrelation in the environment may also be sufficient to create strong unevenness and low stability (see also Gonzalez and Descamps-Julien 2004).

An important feature of autocorrelated environmental fluctuations is the presence of relatively infrequent but abrupt shifts in environmental state (Roy et al. 1996; Alley et al. 2003). Here, this environmental pattern induced a dynamical behavior known as metastability (Galves et al. 1987) in the nonequilibrium dynamics of the community. Metastable dynamics are commonly found in nonlinear systems forced by random variation (Horsthemke and Lefever 1984), and are characterized by the long-term persistence of unstable equilibria and abrupt shifts between unstable equilibria (Galves et al. 1987). In this model, for $\gamma > 1.0$, the abrupt shifts in community biomass are associated with species turnover where the dominant species was almost entirely replaced, typically with a delay (results not shown), by the species optimally adapted to the new prevailing environmental state. Examples of this type of community metastability followed by abrupt reorganization in response to environmental fluctuations can be found in the paleoecology literature, and it has been reported for assemblages as disparate as temperate forests and grasslands, and oceanic foraminifera (e.g. Davis 1986; Tsedakis 1993; Roy et al. 1996; Cannariato et al. 1999).

The major consequence of metastability and abrupt species turnover through time is the strong destabilizing effect at the community level; immigration buffered this effect. Autocorrelated environmental variability resulted in low community evenness that increased the duration of periods of rarity (Steele and Henderson 1984; Caswell and Cohen 1995). In our model immigration stabilized the community in strongly autocorrelated environments ($\gamma > 1.0$) by shortening the recurrence time of rare species, a continuous flow of immigrants maintained the biomass levels of the rare species at a level that allowed rapid recovery as the environment changed state. This result supports the finding of Loreau et al. (2003) that present a similar stabilizing effect of dispersal in source-sink metacommunities. Our results suggest that metastable dynamics may be a common feature of nonequilibrium community dynamics that warrant further study.

Our model, like any other, makes several simplifying assumptions. Clearly, rates of biomass production are not equal across all species in a guild or community, and species are not spaced equally in environmental niche space. The effects of relaxing these assumptions will be reported elsewhere (Gonzalez and DeFeo, unpublished). Furthermore, at very long timescales one might expect to see evolutionary change in the environmental tolerance of component species. With regard to this, Bennett (1997) has argued that millennial-scale climate changes obliterate adaptation to local environments at shorter timescales and that the position and volume of a species' fundamental niche are constrained phylogenetically. In addition, we employed a resource competition model with a single trophic level because recent experiments that employed the same model of resource competition indicate that fluctuation-dependent mechanisms of coexistence may underlie the stabilizing effect of diversity (Descamps-Julien and Gonzalez 2005). Of course all species are embedded in a food web which may alter the results we obtained here. However, Ripa and Ives (Chapter 6, this volume) also report destabilizing effects of environmental autocorrelation on simple food webs using multivariate autoregressive models of multispecies communities. Our results are relevant to recent experimental tests of diversity-stability theory that have demonstrated a destabilizing effect of increasing species richness (Petchey et al. 2002; Gonzalez and Descamps-Julien 2004). For example, Gonzalez and Descamps-Julien (2004) found that increasing species richness destabilized population growth rates. In our model this result was obtained for positive values of β that caused a monotonic decline in the width of a species' niche with increasing species diversity, i.e. a decline in niche width (w_f) with species addition. Mean community biomass and stability declined under this scenario because the total amount of environmental range covered by the community increased less than linearly with the addition of new species. There is little in the literature on the direct effect of interspecific competition on species niche breadth, thus further experimentation is now needed to establish whether this kind of mechanism is sufficient to explain the experimental results cited above.

These results also raise two issues of current conservation concern. Firstly, human-induced climate change may involve not only changes in mean conditions, but also increased autocorrelation of the environment (Wigley et al. 1998). The effect of such change has been ignored in the ecological literature as a potential climate change impact. Our results suggest that increasing environmental autocorrelation may have a strong destabilizing effect on community stability. Secondly, this effect will be compounded by the loss of rare species when the environment is not at their competitive optima (e.g. Jackson and Weng 1999). Palynological evidence suggests that species maladapted to prevailing environmental conditions have persisted in the past at very low densities in regionally dispersed local refugia (Schauffler and Jacobson 2002). Following environmental change these species can spread rapidly and come to dominate the regional community in a matter of generations (Gear and Huntley 1991; Solomon and Kirilenko 1997). Habitat fragmentation is currently threatening the persistence and dispersal capacity of many rare species and hence their likelihood

of contributing to community stability. The results of our model suggest that the interactive effects of climate change (increasing autocorrelation) and the loss of rare species may have hitherto unforeseen consequences for future community stability.

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APPENDIX 8A

Normalization: The resource competition model where each species has its optimal competitive ability at some value of the environmental factor is,

$$\begin{cases} \dot{R} = \alpha(S - R) - \sum_{i=1}^N g_i(x) \frac{Q_i R B_i}{R + K_i} \\ \dot{B}_i = B_i \left[g_i(x) \frac{R}{R + K_i} - m_i \right] & i \in \{1, 2, \dots, N\} \\ g_i = r_i \exp \left[-\frac{1}{2} \left(\frac{x - \tau_i}{w} \right)^2 \right] \end{cases} \quad (8A.1)$$

This model contains $5N + 3$ parameters which do not act independently on the dynamics of the system. Rescaling the state variables and time as:

$$R \rightarrow \frac{R}{S}, \quad B_i \rightarrow \frac{B_i Q_i}{S}, \quad t \rightarrow \alpha t, \quad (8A.2)$$

we obtain,

$$\begin{cases} \dot{R} = 1 - R - \sum_{i=1}^N g_i(x) \frac{R B_i}{R + K_i} \\ \dot{B}_i = B_i \left[g_i(x) \frac{R}{R + K_i} - m_i \right] & i \in \{1, 2, \dots, N\} \\ g_i = r_i \exp \left[-\frac{1}{2} \left(\frac{x - \tau_i}{w} \right)^2 \right] \end{cases} \quad (8A.3)$$

where the new parameters are rescaled as,

$$r_i \rightarrow \frac{r_i}{\alpha}, \quad K_i \rightarrow \frac{K_i}{S}, \quad m_i \rightarrow \frac{m_i}{\alpha}, \quad (8A.4)$$

and the new model has $4N + 1$ independent parameters.

We can also normalize the environmental variable, by supposing x is given by, $x = \bar{x} + \Delta x$, where \bar{x} is the mean value and Δx are the environmental fluctuations which are within the range $[\Delta x_m, \Delta x_M]$. We rescale the variable x , the parameters τ_i , and w with respect to $\Delta x_M - \Delta x_m$, so that x varies between -1 and $+1$ and the width of the environmental tolerance is,

$$w \rightarrow \frac{w}{\Delta x_M - \Delta x_m} \quad (8A.5)$$

We assume τ_i evenly spread across the range of environmental fluctuations, and

$$w = \frac{w_f}{N^\beta} \quad (8A.6)$$

where, w is equivalent to the realized niche width and w_f the fundamental niche. Thus for a $\beta = 0$ we obtain the case typical of the standard model, whilst for $\beta = 0.2$ the width of the environmental tolerance declines monotonically with increasing species diversity.

Finally, we have modified the species i biomass equation as follows:

$$\dot{B}_i = B_i \left[g_i(x) \frac{R}{R + K_i} - m_i \right] + I_i \quad (8A.7)$$

to introduce the effects of a continuous flow (I_i) of exogenous immigrants (a mass effect) from outside the local community. To give a relative measure to the immigration flow, we can set $I_i = p_i \bar{B}_{i,M}$ where $\bar{B}_{i,M}$ is the maximal species density achievable by species i and p_i is a percent measure of the immigration flow with respect to $\bar{B}_{i,M}$. Hence,

$$I_i = \frac{p_i (r_i - m_i + p_i - K_i (m_i - p_i))}{(m_i - p_i) (r_i - m_i + p_i)} \quad (8A.8)$$

which gives $I_i = 9.8989E - 4$ for the parameters at the values mentioned in the text ($m_i = 0.1$, $K_i = 0.1$, and $r_i = 1.0$) and $p_i = 0.01\%$.