Short-term Instabilities and Long-term Community Dynamics

Peter Chesson and Nancy Huntly

Competition in a temporally variable environment leads to sequences of short-term instabilities that in some cases are the mechanism of long-term coexistence; in other cases they promote long-term instability. Recent work associates long-term stability with a positive relationship between environmental and competitive effects and with population growth rates that are buffered against jointly unfavorable environmental and competitive events. Buffered growth rates arise from population subdivision over life-history stages, microenvironments or phenotypes. A distinct but related mechanism of long-term stability relies on population growth rates that are nonlinear functions of competition. New ways of understanding and investigating species diversity follow from these results.

Although it is recognized that the stability of an ecological community depends on the temporal scale on which it is viewed, it is not well-appreciated that in some systems long-term stability may be a consequence of short-term instabilities. As viewed here, long-term stability is the tendency of a community to recover from extreme perturbations of the densities of any of its component species[1]. Short-term instabilities are trends on a short time-scale that would lead to extinctions if extrapolated into the future (Box 1). We review models that demonstrate the potential for short-term instabilities to contribute to long-term coexistence of species, and we discuss data that are consistent with these models.

As an introduction to these ideas, first consider the claim often made for terrestrial plant communities that all species have similar resource requirements, and that the number of distinct resources is far less than the number of species. According to classical ecological theory such systems should be unstable: some species should show trends to extinction. However, in nature the environment varies from year to year, and such trends to extinction could occur for different species in different years because the optimal environmental conditions for growth, reproduction or seedling establishment may vary among species[2].

The long-term trend for any one species results from all its yearly, short-term trends. How short-term trends combine, however, depends on the biology of the species. In the presence of features such as long-lived iteroparous adults or dormant seeds that survive through unfavorable periods and buffer population decline, all species can show long-term trends to increase from low density. Thus, the community can be stable on a long time-scale, even though the conditions in any year are unstable and if sustained would lead to extinction of some species (Fig. 1).

Ideas such as these have had a long development, beginning with verbal arguments based on observations of planktonic communities[3] and terrestrial plant communities[2]. A critical component of these arguments is that environmental conditions must favor different species at different times. More recently, mathematical models have shown that short-term instabilities may promote long-term stability, have no long-term consequences, or promote long-term instability, depending on specific biological traits such as life histories[4].

The earliest models of competitors in fluctuating environments[5] made no attempt to include specific life-history traits. Turelli[6] determined that short-term instabilities in these models did not appreciably affect long-term coexistence. The importance of life histories was soon recognized, and several different models were able to show long-term stability from short-term instabilities[7–9]. These models all involved the 'storage effect'[10] – the idea that long-lived life-history stages (adults of many species, dormant seeds, cysts or other resting stages) buffer population decline under unfavorable environmental or competitive conditions.

More generally, buffers to population decline, and the opposite concept, 'amplifiers', result when life-history stages that are present simultaneously are affected differently by environmental and competitive factors[4,7,11]. Recently, it has been understood that buffering and amplification can result from physiology[10,12], behavior[11,12], and

Box 1. Stability

Following Chesson and Case[1], we define a community as stable if the constituent species recover from perturbations to low density. This concept can be applied on different time-scales. On a long time-scale, stability means that the abundance of any species will show a long-term increasing trend following a natural or artificial perturbation to low density.

On a short time-scale we are concerned with instability. Instability means that a species should decrease from low density situations. Extrapolation to the future under constant conditions predicts extinction. However, the necessity to deal with low density on a short time-scale is a problem if the system does not visit low density during the short period of interest. Thus we adopt a more restricted definition of short-term instability as being a trend on a short time-scale that would lead to species extinctions if extrapolated to the future under constant environmental conditions.

The definitions of 'short' and 'long' time-scales are deliberately left vague because they will depend on the system. Figure 1 depicts a particular example where the short time-scale is a year and contains one full cycle of reproduction and death. A long time-scale is about five to many years. The figure is the output of a model of two annual plant species competing in a fluctuating environment.

Examination of Fig. 1 shows that there are many years in which one species increases simultaneously with a decrease in the other species. These situations are short-term instabilities in which the increasing species would eventually dominate and the decreasing species would become extinct if the environment were held constant. Such situations are not the only short-term instabilities, however, for the model is constructed so that every year one species gains relative to the other species even if both are increasing or decreasing. Measuring such relative changes requires more information than the crude changes in densities over time given in the figure.

Figure 1 also demonstrates long-term stability: whenever a species drops sufficiently below its mean density, there is an average upward trend over the next several years. As a consequence, both species remain in the system and there is no long-term tendency for either to be eliminated.

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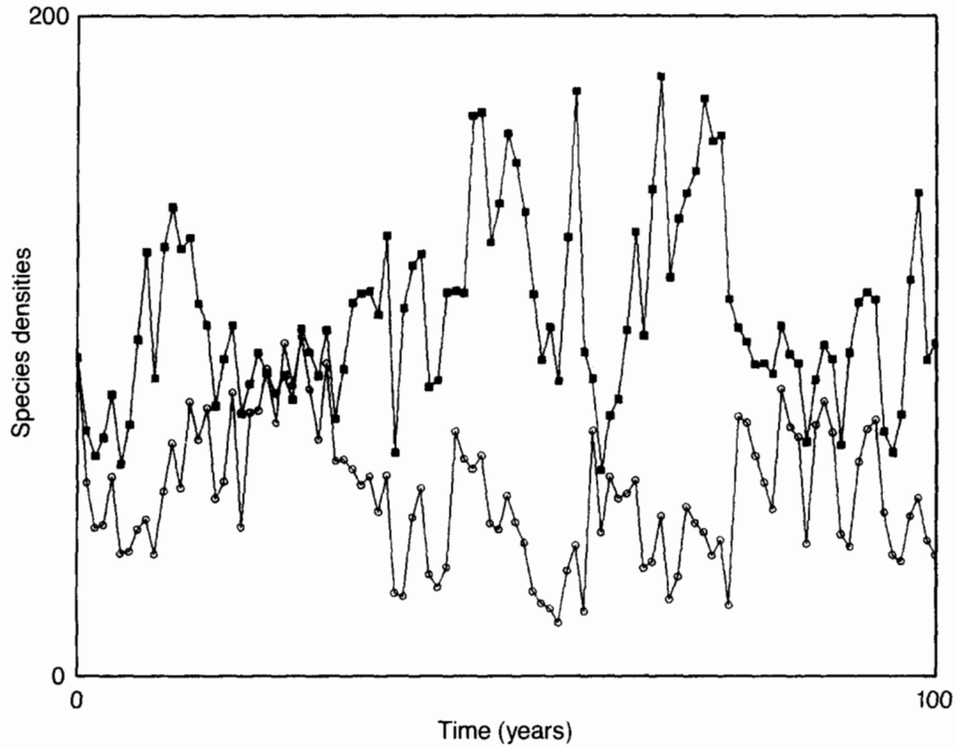

Fig. 1. Simulation of the annual plant model of Box 2 (Eqn 2), with competition coefficients, α_{ij}, equal to 1, seed survival rates, s_i, equal to 0.9, and independent rectangular variation in seed germination, E_i, over the range 0 to 1. The species represented by black squares has maximum seed yield, Y_i, of 100 and is the competitive dominant. The other species has maximum seed yield of 80.

heterogeneity within a population due to phenotypic variation and spatial patchiness[4]. Buffering and amplification are central to the effects of short-term instabilities on long-term community dynamics. A clear picture of their roles is now emerging[4,12]; we consider this next.

Models and mechanisms

There are several different ways in which short-term instabilities lead to long-term stability. We give here an account of one of these sufficient to give the flavor of them all. Box 2 defines a general model of competition in an environment that varies randomly through time. If we assume that a species has similar effects on interspecific and intraspecific competitors, then the model is unstable for any environmental conditions, and fluctuations of the environment over time create a sequence of short-term instabilities. Three important concepts link the short and long time-scales.

1. *Covariance between environment and competition*

Environmental factors have both direct effects on organisms and indirect effects that occur because the environment modifies the amount of competition[11]. We define environmental favorability through the direct environmental effect and measure it by a density-independent, but environmentally dependent, population parameter such as a birth rate, juvenile survival rate or seed germination rate.

An increase in environmental favorability for abundant species is assumed to result in increased competition, for example due to higher density or biomass. This increased competition is an indirect effect of the environment[4]. The simplest examples of such covariance between environment and competition are provided by organisms competing for space[7]. In this case, the total supply of space is often fixed, but the number of organisms competing for it depends on reproduction and juvenile survival, which depend on the environment. Thus, environmental favorability for an abundant species can be expected to have positive correlation or *positive covariance* with competition. An important consequence of positive covariance is that better environmental conditions for abundant species are at least partially offset by higher competition.

2. *Differential responses to the environment*

We shall assume that different species in a community do not respond to the environment in exactly the same way – species differ in their optimal environments. Although their environmental responses may be similar (all species may experience good periods simultaneously), they must not be identical.

Such differential responses to the environment imply that the covariance between environmental favorability and competition declines as a species' density decreases (Fig. 2). This occurs because, as its density declines, a species contributes a decreasing amount to total competition in the multispecies system. Consequently, fluctuations in environmental favorability for a species at low density are less frequently offset by changes in competition. At low density, a species experiences more extreme conditions (situations in which environment and competition are both unfavorable or both favorable) than at high density.

3. *Subadditive growth rates*

Many organisms have traits that tend to buffer the effects of jointly unfavorable environmental and competitive conditions while not preventing advantage being taken of jointly favorable conditions[11]. Consider the example of an annual plant in which population size is the number of seeds in the soil after seed release. The environmentally dependent parameter is the fraction of seeds germinating in a year, and competition for resources occurs among growing seedlings[8,11].

If nongerminating seeds have low mortality in the seed bank, little population change occurs when few seeds germinate. Moreover, it matters little whether the low number of germinating seeds have successful reproduction. Competition (which comes mostly from species that did not have low germination) has very little effect on overall population growth. The graph of population growth against competition (Fig. 3b, lower curve) is almost flat.

On the other hand, if many seeds germinate, seed production from these germinating seeds greatly affects population growth. Low competition results in good seed yields and a high population growth rate, while high competition

leads to poor seed yields and low population growth. In this case, population growth responds strongly to competition (Fig. 3b, upper curve).

The weaker effect of competition in an unfavorable environment compared with a favorable environment is called subadditivity[4,11]. Subadditivity implies that population growth is buffered against jointly unfavorable combinations of environment and competition, while jointly favorable combinations permit strong population growth.

Long-term stability

As shown above, jointly favorable combinations of environment and competition occur more when a species is at low density than at high density. Consequently, at low density the frequency distribution of fluctuations in the growth rate has a pronounced upper tail that is not present in high-density situations (Fig. 4). Jointly unfavorable combinations of environment and competition are more prevalent at low density too, but the buffering effect of subadditivity prevents severe reductions in the growth rate. Thus, the growth rate frequency distribution at low density is skewed relative to that at high density and has a higher mean.

These results imply that the sign of the average growth rate of a competitive subordinate can become density-dependent in the presence of environmental fluctuations. A species that has negative growth rates at all densities under constant environmental conditions can have positive average growth rates at low density and negative average growth rates at high density, when the environment fluctuates. Positive average growth rates at low density mean a long-term tendency to increase from low density. It follows that environmental fluctuations can give all species a long-term tendency to increase from low density, resulting in a system with long-term stability[1]. This long-term stability depends on short-term instabilities: although there may be an average competitive dominant, each species must be dominant under some environmental conditions. Long-term stability also depends on subadditivity and the magnitude of the covariance between environment and competition. Indeed, the average growth rate at low density can be shown to increase approximately with the product of measures of subadditivity, covariance, and fluctuations in dominance[4].

This result can be viewed within a classical context. Differential responses to the environment that affect competition permit species to have temporal niches. But it is important to appreciate that temporal niches are not effective without subadditivity. Subadditivity prevents population gains achieved under favorable conditions from being eliminated by poor conditions at other times.

The models reviewed here also have implications for natural selection. If specialization can permit a species to be superior to an average competitive dominant under particular environmental conditions, then such specialization may allow a species to have a long-term increasing trend from low density and should be selected. In addition, models similar to those discussed here have been applied within a species to show that genetic polymorphisms can be maintained by environmental fluctuations[13].

Are the critical features – 1, 2 and 3 above – found in nature? Others have focused on the evolution of traits that reduce the fluctuations of individual populations, such as iteroparity[14], dormancy[15], extended diapause[16], seed polymorphisms[17] and dispersal[18]. The theory discussed here adds a new perspective. These commonly occurring traits also introduce subadditive effects in multispecies competition models and buffer joint negative effects of environment and competition.

The literature is less supportive of positive covariance between environment and competition. In part, this stems from the lack of focus on mechanisms of competition. Thus, it is not clear how tightly environmental and competitive effects are linked. There are, however, well-documented examples where favorable conditions for a species at some stage in its life cycle lead to severe competition at a later stage[19–21]. Unless environmental factors have direct effects on the availability of resources that mediate competition, environmental

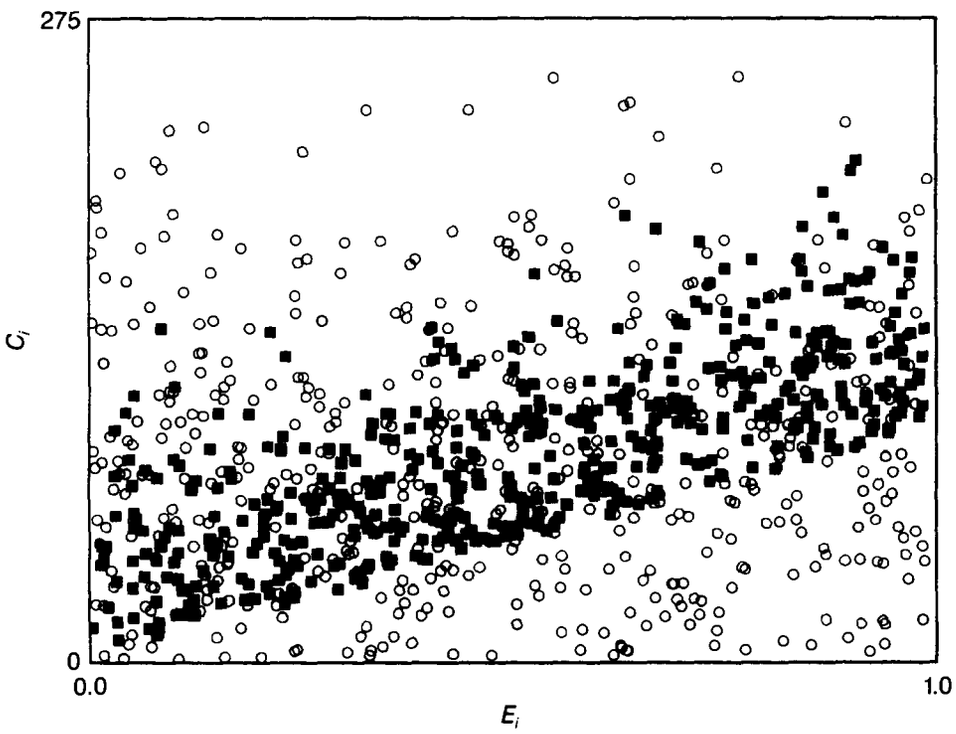

Fig. 2. Scatter plots of the environmentally dependent parameter (E_i) against the competitive parameter (C_i) for a species at low density (open circles) and the same species at high density (filled squares) in the presence of an interspecific competitor. The data are generated from the same model as Fig. 1, for the competitively subordinate species held at 0 (low density) and 100 (high density).

Box 2. Community models for temporally variable environments

Many models of competitive interactions in a temporally variable environment can be put in the form

$$\ln X_i(t+1) - \ln X_i(t) = g_i(E_i, C_i) \quad (1)$$

where $X_i(t)$ is the population density of species i at time t, and $g_i(E_i, C_i)$ is the growth rate of log population size for the period t to $t+1$ – it equals 'r' of demography and is referred to here as the growth rate. The growth rate depends on an environmentally dependent parameter, E_i, and a competitive parameter, C_i, which are assumed to vary over time and therefore can be written as $E_i(t)$ and $C_i(t)$. C_i summarizes the effects of all forms of competition (interspecific and intraspecific) on the growth rate of species i.

A particular example is a model of annual plants with a seed bank[8,11], where

$$g_i(E_i, C_i) = \ln[s_i(1 - E_i) + Y_i E_i / C_i] \quad (2)$$

E_i is the germination fraction, s_i is the yearly survival rate of ungerminated seeds, and Y_i is the seed yield from a seed germinating in the absence of competition. C_i specifies the reduction in seed yield due to competition, which is assumed to be related to total seed germination. A plausible form for a two-species system is

$$C_i = 1 + \alpha_{i1} E_1 X_1 + \alpha_{i2} E_2 X_2 \quad (3)$$

where the α_{ij} are competition coefficients. Note that C_i is an increasing function of E_1 and E_2, and hence will give positive covariance between environment and competition.

Additive models are defined by the fact that the growth rate can be expressed as a function of E_i minus a function of C_i:

$$g_i(E_i, C_i) = A_i(E_i) - B_i(C_i) \quad (4)$$

One can think of this as meaning that environmental and competitive factors have independent effects on the growth rate. However, C_i may still covary with E_i.

The stochastic analogues of the Lotka–Volterra competition model[6] are perhaps the best-known models that have the form (4). In addition, the annual plant model above is additive if survival in the seed bank is zero ($s_i = 0$, for example due to seed predation), for then Eqn (2) becomes

$$g_i(E_i, C_i) = \ln Y_i E_i - \ln C_i \quad (5)$$

Additive models can also be recognized by graphing $g_i(E_i, C_i)$ against C_i for different values of E_i. This gives the parallel curves of Fig. 3a. Such parallelism shows that the effect of competition, which may be thought of as the slope of $g_i(E_i, C_i)$ as a function of C_i, does not depend on the value of E_i.

Survival of ungerminated seeds in model (2) ($s_i > 0$) gives the converging growth rates of Fig. 3b, showing that the effect of competition on the growth rate is less when the environment is poor, i.e. when there is a low germination fraction. Such growth rates are called subadditive; they buffer population growth against jointly unfavorable environmental and competitive conditions.

Superadditive growth rates are depicted in Fig. 3c, in which greater sensitivity to competition is found when environmental conditions are poorer. In essence, the effects of a poor environment and competition are amplified when they occur together. This arises in the model (2), for example, when the survival rate of ungerminated seeds is the environmentally dependent parameter.

favorability and competition should always have positive covariance.

A range of possibilities for short-term instabilities

Environmental and competitive factors may also have superadditive effects on population growth rates (Fig. 3c), thereby amplifying population decline under unfavorable environmental and competitive conditions. Examples include some cases of environmental dependence of resource uptake rates[11] and environmental dependence of adult death rates[4]. If environmental and competitive effects covary positively in these situations, environmental fluctuations will disfavor a species at low density. Instead of promoting long-term stability, environmental fluctuations may lead to long-term instability, causing competitive exclusion[11]. If the covariance between environmental favorability and competition is negative, however, superadditivity promotes long-term stability. Subadditivity with negative covariance promotes long-term instability.

There are yet other ways in which short-term instabilities may modify long-term community dynamics. These have been studied in both deterministic[22,23] and stochastic[24] models. Models in which competitive and environmental factors are additive may still predict long-term stability if competitive factors are nonlinearly related among different species. For example, species may depend on the same resource but have differently shaped curves describing their harvesting ability at different resource densities (Fig. 5). Short-term instabilities again can combine to produce stability in the long run. Just as with nonadditive models, however, there are situations in which instability can be promoted.

Although the effects of nonadditivity and nonlinearity are broadly similar, the situations in which they affect long-term stability are different. In the case of nonadditivities, different species may respond identically to competition, but must show differences in their responses to the environment. For nonlinearities to affect long-term stability, species must differ in their responses to competition (Fig. 5).

The effects of fluctuations in additive linear systems

As stressed above, either nonadditive effects of environmental and competitive factors, or nonlinearity of the competitive factors themselves, are essential for short-term instabilities to lead to long-term stability. However, environmental fluctuations are sometimes viewed as delaying competitive exclusion in systems that are additive and linear[3]. In additive linear systems, with species limited by the same factor, there is always an average competitive dominant that excludes all other species[11]. Whenever there is appreciable average dominance, the rate of competitive exclusion reflects differences between species in the mean of an environmentally dependent measure of competitive ability. The long-term rate of competitive exclusion does not depend on fluctuations in this measure. This is true even when environmental fluctuations make competition sporadic in occurrence[11,25].

These results may be interpreted as meaning that environmental variability has no effect on the rate of competitive exclusion in additive linear systems. However, it might also be argued that environmental variability can prevent significant average dominance because the environment never stays in the optimal state for any species. In this case, however, environmental variation will lead to a random walk to extinction and the rate of competitive exclusion will increase steadily with environmental variance, unless the pertinent environmental variation is regular in occurrence, e.g. seasonal variation which does not lead to a random walk.

It also has been argued that environmental unpredictability should promote convergence of the ecological requirements of species, making them more or less equal[26,27]. This implies that species should be limited by the same, possibly composite, factor. Only in the unlikely event that species are also demographic equals, so that there is no average competitive dominance, will this permit any long-term coexistence. Such communities do not have long-term stability as defined here, and have

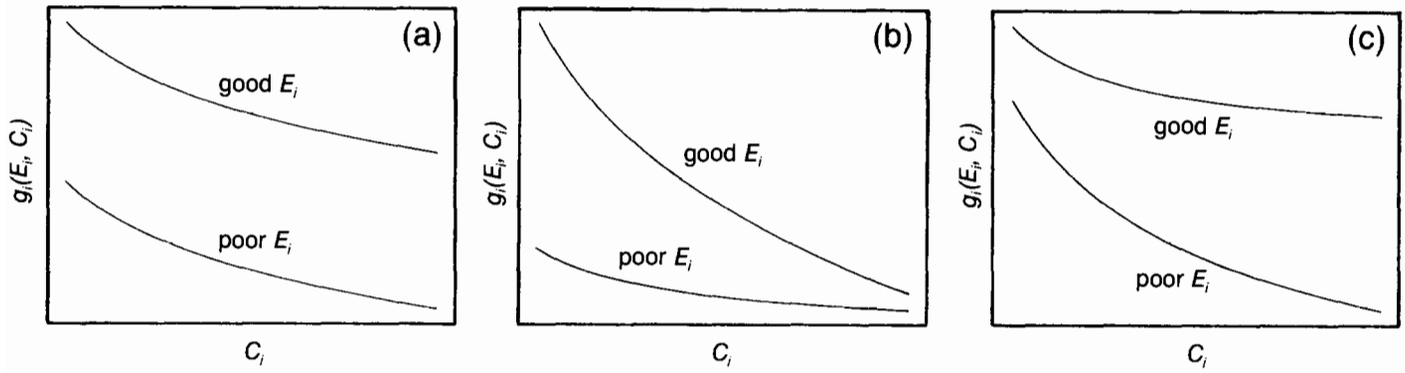

Fig. 3. Population growth rates, $g_i(E_i,C_i)$ (changes in log population size in one unit of time), as a function of competition, C_i, for different values of the environmentally dependent parameter, E_i. The situations depicted are (a) additive, (b) subadditive, and (c) superadditive.

diversity and species composition determined by speciation rates, migration rates and historical factors[1]. This argument for ecological convergence, though appealing for the unlikely case of species that are affected by abiotic and biotic factors in additive and linear ways, does not apply in systems with subadditive growth rates and positive covariance between environment and competition. As discussed above, in such systems selection should favor different responses to environmental conditions, which should permit a species to coexist stably with its competitors.

Examples in nature

Many plant ecologists share the view that the high species diversity characteristic of many plant communities results from nonequilibrium processes[2], which we have called short-term instabilities. Grubb[2] focuses attention on the importance of differential recruitment in time and space, especially environmental requirements for seed production and seedling establishment. These environmental requirements, which Grubb calls the 'regeneration niche', define 'environmental favorability' in the mathematical theory we discuss.

Numerous observations suggest that the processes modeled in this mathematical theory contribute to the diversity of plant communities. Relative abundances and reproductive outputs of species within steppe, tundra, prairie, grassland and desert fluctuate greatly from year to year, and many of these fluctuations in germination, vegetative growth or reproduction have been correlated with environmental conditions such as rainfall and temperature[2,9,28–32].

An example in which a particular environmental factor has been identified as contributing to short-term shifts in relative population growth is the series of changes in relative abundance of blue grama grass (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) that occurred in North American prairie during and after the droughts of the 1930s and 1950s[29]. Blue grama increased at the expense of buffalo grass throughout the drought years, but declined with the resurgence of buffalo grass following the resumption of higher rainfall. A second case in which environmental factors are identified involves desert perennials. The age structure of three populations of succulents has been linked directly to year-to-year variations in rainfall that allow or preclude establishment of seedlings[33]. Desert annual species differ in their germination responses to rainfall patterns[32,34], and may provide a third example.

In these examples, the perennating stages (which may be either seed banks or vegetative storage pools, above or below ground) have the potential to buffer populations against the effects of unfavorable fluctuations in environment and competition. Thus population growth rates should be subadditive.

New directions

This theory poses several questions that are amenable to empirical investigation, but have not been closely examined. First, how do environmental factors cause fluctuations in population growth rates, and in what ways do species differ in their responses to environmental fluctuations and to competition? Second, how do environmental factors affect competition, thus causing covariance between environment and competition? Finally, what sources of nonadditivity and nonlinearity are present? How do responses to environment and competition vary among age or stage classes, phenotypes, or subpopulations in distinct microhabitats? As reviewed elsewhere[4,35], these important elements can be measured quantitatively so that the magnitude of the predicted stabilizing effect can be estimated.

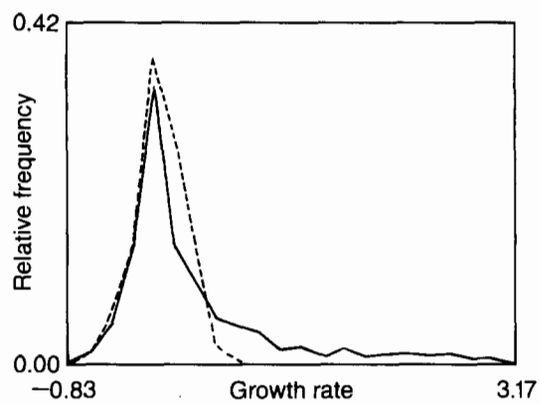

Fig. 4. Data from Fig. 2 converted by the appropriate subadditive growth rate function into frequency distributions of growth rate fluctuations over time. The solid line represents low density, the dashed line represents high density.

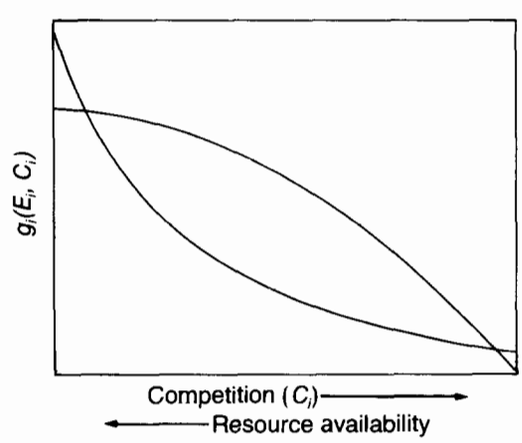

Fig. 5. Population growth rates, $g_i(E_i,C_i)$, as a function of competition or resource availability. The curves for two different species have distinctly different nonlinear responses to competition and resource availability. In particular, they are relatively nonlinear because neither one can be changed into the other by linear transformation of the ordinate.

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50 Years of Studying the Scarlet Tiger Moth

David A. Jones

A growing number of long-term studies in plant and animal ecological genetics is now rewarding the patience, perseverance and perspicacity of those involved. A handful have involved work spanning 30 years and more, with an initial major impact on the way the study of population biology has developed. It is 50 years since investigation of the medionigra *form of the scarlet tiger moth began, and in spite of very low allele frequencies and population numbers the* medionigra *allele persists in the original population. It is only by such long-term studies that we will be able to obtain more than just a cursory understanding of what really happens in natural populations of plants and animals.*

In 1938, E.B. Ford and R.A. Fisher began a study of the day-flying moth *Panaxia (Callimorpha) dominula* L. – the scarlet tiger moth – in the 7 ha calcareous fen between Cothill and Dry Sandford, southwest of Oxford, England. At the time of Ford's death, in January 1988, the colony had been the subject of research for 50 years. This long-term study is worth reassessing, for it consists of some superb field and laboratory work that established the first examples of:

(1) sophisticated mark–release–recapture experiments;
(2) controlled translocation experiments with insects;
(3) estimates of relative fitness of all stages in the life cycle;
(4) negative assortative mating in insects;
(5) the observation in laboratory selection experiments of evolution of dominance in opposite directions, anticipating the same evolutionary changes in nature;
(6) the determination of food-plant preferences in peripheral populations.

In addition, it was the work of Sheppard and Cook[1] on *Panaxia* that showed most forcefully the importance of including frequency-dependent selection in even the simple models of population genetics. The immediate consequence was the removal of genetic load as a major stumbling block to the understanding of the maintenance of genetic polymorphism.

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Early work at Cothill Fen

The site at Cothill was well known to collectors earlier in the century because two variants of the moth occurred there. While an undergraduate at Oxford, Ford visited the colony in the July of 1921, but failed to find either variant. At that time neither had been named, nor was anything known about their genetics. By 1942 the variants were called *medionigra* and *bimacula*[2], and they showed a clear pattern of inheritance[3], although there was considerable variation in the phenotype depending upon the temperature at which larvae and pupae were raised[4]. The typical form (*dominula*) and *bimacula* are the homozygotes, while *medionigra* is the heterozygote for the allele pair involved (Fig. 1).

Revisiting the colony in 1936 and in 1938, Ford noticed several specimens of *medionigra*. He concluded that *medionigra* must have increased in frequency since 1921, and on examining reliable data he estimated that the *medionigra* form had occurred at a maximum frequency of 2.4% before 1929[5]. Until that time almost no research had been done on any natural population of animals or plants in which a change in allele frequency with time had been observed, and so it seemed to Ford that an ideal opportunity was at hand. He and Fisher began the study in 1938.

In Britain the scarlet tiger moth lives in colonies and has one generation per year, the adults flying in

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