

Ecological Character Displacement in a Variable Environment

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Received March 7, 1989

We analyzed a simple genetic model of ecological character displacement in a fluctuating environment. Character states of two identical, competing species were determined by a single-gene, two-allele model. In each generation, the carrying capacity of different segments of a uniform resource spectrum fluctuated randomly. Inter- and intraspecific exploitation competition reduced fitnesses of similar genotypes. In contrast to demographic models of niche shift, this genetic model led to a high average overlap of species in a variable environment. However, for moderate or small environmental fluctuations, character distributions of the two species diverged significantly and rapidly. Results were nearly identical for a model of environmental fluctuations that incorporated resource "crunches." These models were sensitive to the intrinsic rate of increase of the competing species: divergence was substantially slower at small values of r . Nevertheless, most simulations of this simple genetic model suggest that interspecific competition can lead to significant divergence, even in a moderately fluctuating environment. © 1991 Academic Press, Inc.

The phenotypes of ecologically similar species sometimes diverge in sympatric populations. Character displacement (Brown and Wilson, 1956) refers to those cases in which selection for reduced interspecific competition leads to phenotypic divergence. Selection for an avoidance of hybrid matings may also cause displacement (Bossert, 1963; Levin, 1986), but will not be considered here.

There have been many mathematical treatments of phenotypic divergence, and it is useful to distinguish between genetic and demographic models. Genetic models of character displacement describe an evolutionary shift in the mean and/or variance of phenotypes of competing species (e.g., Bulmer, 1974; Crozier, 1974; Slatkin, 1980). Selection favors phenotypes

that do not overlap too much with competitors, leading to a divergence of populations and a reduction in phenotypic overlap. These models are sensitive to the amount of within- and between-phenotype variance (Taper and Case, 1985), whether or not resources are completely utilized (Milligan, 1985), and to the symmetry of resource use between species (Slatkin, 1980).

Demographic models of niche shifts (*sensu* Abrams, 1986) describe phenotypic divergence in terms of the assembly of communities via colonization and extinction. The mean and variance of resource use (and hence, of phenotypes) do not evolve, and divergence occurs through competitive exclusion of species with high overlap (e.g., MacArthur and Levins, 1967; May and MacArthur, 1972; May, 1974; Roughgarden, 1976; Lawlor and Maynard Smith, 1976). These models are sensitive to the form of the competition coefficient (Abrams, 1975), the assumption of a common equilibrium among species, and whether the competitors are viewed as residents or as invading colonists (Turelli, 1978a). Abrams (1986) analyzed both models under a two-consumer-two-resource scenario, and Milligan (1986) considered a hybrid model that incorporates both a genetic basis for phenotypes and colonization by invading species.

In spite of this variety of theoretical approaches, the genetic models of character displacement all assume that the environment of the competing species is temporally constant. In other words, the available resource spectrum does not vary through time. Environmental stochasticity has been incorporated into demographic competition models (May and MacArthur, 1972; May, 1974; Turelli, 1978a) and into single-species models of the evolution of niche width (Slatkin and Lande, 1976; Roughgarden, 1979), but not into genetic models of character displacement.

An analysis of character displacement models that include environmental stochasticity is timely because there is currently a debate over the importance of competition in variable environments (Wiens, 1977; Schoener, 1982, 1984; Walter *et al.*, 1984). Wiens (1977, 1986) suggests that, in a variable environment, populations are often well below their carrying capacities. Except during occasional resource "crunches," natural selection for the avoidance of competition is weak. Schoener (1982, 1984) argues that a sudden increase in available resources will not necessarily reverse earlier directional selection for character displacement. Both sides seem to agree that a realistic analysis of competition must take into account fluctuating resource availability.

In this study, we analyze the behavior of a one-gene, two-allele model of character displacement in a fluctuating environment. Our simulation study addresses three questions: (1) How are the mean and variance of phenotypic overlap affected by temporal variation in the carrying capacity of the environment? 2) Is the time required to reach equilibrium overlap

increased or decreased in a variable environment? 3) Lastly, are the results sensitive to the particular form of the competition equation or the pattern of temporal variation in carrying capacity?

MATERIALS AND METHODS

Life Cycle

For each of two competing species, we assume a randomly mating population of infinite size with non-overlapping generations. Inter- and intraspecific exploitation competition reduce the fitnesses of different genotypes each generation. The two species use resources identically, and inter- and intraspecific competitive effects are symmetric.

Character Inheritance

We assume that character states are determined entirely by a single gene with two alleles, resulting in three different genotypes (AA, Aa, and aa). The resource spectrum is assumed to be a one-dimensional, uniform distribution divided into contiguous, equivalent segments 1, 2, and 3, which are used exclusively by genotypes AA, Aa, and aa, respectively. For species (*i*), the population is composed of the three genotypes (*j*). g_{ij} is the fraction of the population of species (*i*) comprised of genotype (*j*), so that

$$\sum_{j=1}^3 g_{ij} = 1.0. \quad (1)$$

Let $P_{1A,t}$ equal the frequency of the A allele in the population of species 1 at time *t*. Following Wright (1955):

$$P_{1A,t+1} = \frac{(P_{1A,t})^2 W_1 + (P_{1A,t})(1.0 - P_{1A,t}) W_2}{(P_{1A,t})^2 W_1 + (P_{1A,t})(1.0 - P_{1A,t}) W_2 + (1.0 - P_{1A,t})^2 W_3}. \quad (2)$$

We now require frequency-dependent fitness functions that incorporate both intra- and interspecific competition for a given genotype. The simplest linear function is

$$W_j = 1.0 + r \left(1.0 - \sum_{i=1}^2 g_{ij} \right). \quad (3)$$

r is the intrinsic rate of increase. This formulation is similar to Roughgarden's (1971) density-dependent selection models that are based on the logistic growth equation for a single species. In our model, *K* is analogous to a genotype frequency of 1.0, and g_{ij} is analogous to *N*/*K*. For

a given genotype, fitness decreases below 1.0 as competing populations exceed carrying capacity ($g_{ij} > 1.0$).

However, there are important differences between our model and Roughgarden's (1971) single-species selection models. Roughgarden's (1971) model operates on density-dependence; whereas our model operates on frequency-dependence. A density-dependent version of Eq. (3) behaved similarly to our frequency-based model. Second, the error term in Eq. (4) would need to be present in the denominator of g_{ij} for exact correspondence with the logistic equation. However, our goal was not to model the logistic equation, but to provide a simple competition model that incorporates temporal stochasticity in available resources.

Note that the fitness of individuals of species 1, genotype j is reduced by both intraspecific (g_{1j}) and interspecific (g_{2j}) competition among individuals of the same genotype. Competition between genotypes is not incorporated into this model.

Next, we introduce an error term, e_j , that represents random variation in the carrying capacity of the environment for genotype j :

$$W_j = 1.0 + r \left(1.0 + e_j - \sum_{i=1}^2 g_{ij} \right). \quad (4)$$

e_j is a standard, uniform variate with a mean of zero, so that the random fluctuations in the environment are "white noise" (May, 1974), with no serial autocorrelation.

We used Eqs. (2) and (4) to track changes in allelic frequencies for both species through time. The model assumes random mating, so genotype frequencies each generation were calculated from the Hardy-Weinberg equation. Genotype frequencies were scaled to mean fitness each generation, and W_j was set to 0.0 if it ever became negative.

To test the sensitivity of the model to the assumption of a linear fitness function, we considered three alternative formulations to Eq. (4). Each of these non-linear fitness functions is derived from a variant of the logistic growth equation (Hutchinson, 1978):

$$W_j = 1.0 + r \left(1.0 + e_j - \left(\sum_{i=1}^2 g_{ij} \right)^2 \right). \quad (5)$$

Equation (5) is a quadratic form derived from Gilpin and Ayala (1973).

$$W_j = 1.0 + \frac{(r)(1.0 + e_j - \sum_{i=1}^2 g_{ij})}{(1.0 + e_j + \sum_{i=1}^2 g_{ij})}. \quad (6)$$

Equation (6) is a hyperbolic form derived from Smith's (1963) modification of the logistic growth curve for freshwater cladoceran populations.

$$W_j = r \left(\exp \left((\ln(2)) \left(1.0 + e_j - \sum_{i=1}^2 g_{ij} \right) \right) \right). \quad (7)$$

Equation (7) is an exponential form derived from the Ricker equation (1954) of population growth.

All of these equations are decreasing functions of $\sum_{i=1}^2 g_{ij}$. For the deterministic version of each equation (range of $e_j = 0.0$), W_j approaches 2.0 as the competing populations approach 0.0 ($\sum_{i=1}^2 g_{ij} = 0.0$), and W_j approaches 1.0 as the competing populations approach carrying capacity ($\sum_{i=1}^2 g_{ij} = 1.0$).

Models of Environmental Variation

For each set of simulations, we fixed the range of e_j from a minimum of 0.1 to a maximum of 1.0. If the range of $e_j = 1.0$, then the carrying capacity of the environment can fluctuate between 0.0 and 2.0 in a single generation. If the range of $e_j = 0.1$, then carrying capacity fluctuates between 0.9 and 1.1. For each of the four fitness functions (Eqs. (4) through (7)) we analyzed three models of temporal resource fluctuation:

(1) *Independent Fluctuations*. The carrying capacities of the three resource classes fluctuate independently of one another each generation.

(2) *Resource Crunch Model*. This model is the same as model 1 (independent fluctuations), except that each generation there is a 0.10 probability of a resource crunch. In a resource crunch, all three resource spectra fall to 10% of carrying capacity. Thus, during a crunch, $e_1 = e_2 = e_3 = -0.9$. In non-crunch generations, environmental stochasticity corresponds to normal background "noise" in the availability of resources. Although there are many ways that resource crunches could be simulated, we believe this scenario captures the essence of Wiens' (1977) model.

(3) *Central Resource Constant*. The two extreme resource classes fluctuate independently, but the central resource remains constant. Thus, $e_2 = 0.0$, so that heterozygotes of both species utilize a constant resource.

Measurement of Phenotypic Overlap

Most theoretical studies have measured niche separation as d/w , the ratio of the distance between resource utilization peaks (d) to the standard deviation of resource utilization (w) (May and MacArthur, 1972). However, this measure would not be informative in our analyses of only three resource classes. Therefore, we chose to use a familiar measure

of niche overlap to quantify the overlap of phenotypes of species 2 on species 1:

$$\alpha = \frac{\sum_{j=1}^3 [(g_{1j})(g_{2j})]}{\sum_{j=1}^3 [(g_{1j})^2]} \quad (8)$$

This is equivalent to the competition coefficients in MacArthur and Levins (1967). Of course, there are many other ways to measure overlap (Levins, 1969; Schoener, 1974), but this index allows for comparisons of relative overlap under different models. For all models, the initial allele frequencies were $P_{1A,1} = 0.75$ and $P_{2A,1} = 0.50$ in the two species populations. These frequencies generated a starting alpha of 0.7457 (Table I).

Table I shows the initial genotype frequencies, and illustrates the effects of inter- and intraspecific competition for the deterministic case. In the absence of interspecific competition, both species converge to an identical genotype distribution, with the heterozygote being most common. In the presence of interspecific competition, each species specializes on one end of the resource spectrum, and the most common genotype is the corresponding homozygote. Divergence in this model is due primarily to interspecific, rather than intraspecific competition.

Equilibrium Conditions

We considered the two species populations to have reached an evolutionary "equilibrium" when we would measure no further consistent changes in alpha. We used a moving average of alpha for 10 consecutive generations to measure changes in overlap. Using the deterministic case (Eq. (4); range of $e_j = 0.0$), we established equilibrium as the time in generations for which:

$$|\bar{\alpha}_{t-9,t} - \bar{\alpha}_{t-10,t-1}| < 0.0004 \quad (9)$$

TABLE I

Effects of Intra- and Interspecific Competition on Genotype Frequencies and Equilibrium Overlap for the Deterministic Model (Eq. 3) with $r = 1.0$

	G_1 (AA)	G_2 (Aa)	G_3 (aa)	alpha
Initial conditions	S_1 .5625 S_2 .2500	.3750 .5000	.0625 .2500	.7457
Intraspecific competition	S_1 .2697 S_2 .2697	.4615 .4615	.2697 .2697	1.0000
Intra- and interspecific competition	S_1 .6220 S_2 .0447	.3333 .3333	.0447 .6220	.3333

For the deterministic case, this yielded an alpha of 0.333, reached in 31 generations. The equilibrium overlap was stable, and was reached no matter what the initial genotype frequencies. The only exception to this equilibrium occurred if the initial genotype distributions were identical between species. In this case the distributions did not change and measured overlap remained at 1.0. However, this equilibrium was unstable, and the system converged to an overlap of .333 if the genotype frequencies of either species were perturbed.

As a check on the equilibrium criterion, we compared simulation results (model 1; range of $e_j=0.8$) to a series that ran first for 100 generations. Average alpha values were identical to two decimal places and variances were identical to one decimal place. The moving average difference had to be lowered to achieve stable overlap values at small r .

Simulation Procedures

Simulations were first written in CP/M interpreted BASIC on a Kaypro (1984) PC, then converted to Turbo PASCAL 5.0 and run on an IBM Model 40. Each generation, we tracked genotype frequencies for 100 generations beyond the point at which Eq. (9) was first satisfied. We recorded the number of generations to equilibrium and the mean overlap (Eq. (8)) for the 100 generations following equilibrium. We also recorded the final value of alpha for the generation at the end of each simulated run. The distribution of alpha values showed some left-handed skewness, but could be reasonably described by a Gaussian curve. Therefore, we used the standard deviation of the final alpha values as a measure of variability in overlap. Final values of alpha from different runs were used to estimate the standard deviation of overlap at equilibrium. We ran 100 simulations for each range of e_j from 0.0 to 1.0, incremented by 0.1. We repeated this series for the four population equations (Eqs. (4) through (7)) under each of the three models of environmental variation.

RESULTS

We begin with a discussion of results obtained when $r = 1.0$. The average time to equilibrium was usually less than 100 generations for most fitness functions and models of environmental variation (Fig. 1). Independent resource fluctuations (model 1) led to a small increase in the amount of overlap at equilibrium compared to a deterministic model (Fig. 2a). The standard deviation of overlap also increased as a function of environmental noise (Fig. 3a). The four fitness functions were quite similar in their behavior, although non-linear models (Eqs. (5) through (7)) usually generated lower means and standard deviations of overlap. The resource

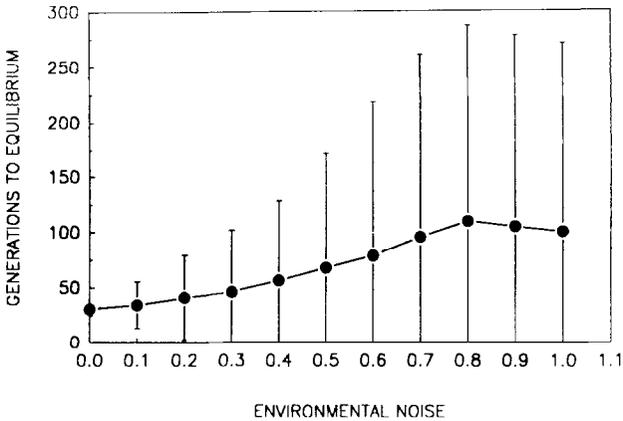


FIG. 1. Average time in generations to reach equilibrium. The average \pm two standard deviations is shown for 100 simulations of the linear fitness function (Eq. (4)) under the model of independent resource fluctuations (model 1) ($r = 1.0$).

crunch model (model 2) generated overlap means (Fig. 2b) and standard deviations (Fig. 3b) that were virtually indistinguishable from those generated by the independent fluctuations model (model 1).

When the central resource was held constant (model 3), overlap showed more of an increase with environmental stochasticity, and the four population equations diverged at the highest levels of noise (Fig. 2c). The hyperbolic fitness function (Eq. (6)) generated the largest overlap, and the exponential fitness function (Eq. (7)) generated the smallest overlap. The standard deviation of overlap was reduced in the central resource crunch model and the model of independent fluctuations (Fig. 3c).

The behavior of these population models was very sensitive to the intrinsic rate of increase, r (Roughgarden, 1975; Turelli, 1978a). r is a measure of the responsiveness of the population to changes in carrying capacity (Roughgarden, 1975). We simulated Eq. (4) with smaller values of r and found that the time to reach equilibrium increased by a factor of roughly $1/r$ (Table II). A second consequence of reducing r is that it acts as a scalar and also reduces e_j , the amount of environmental stochasticity (Feldman and Roughgarden, 1975). Thus, at small r , the populations reached a lower equilibrium overlap. However, the behavior of the model under the different scenarios of environmental fluctuations, and for the four fitness functions, was not sensitive to r .

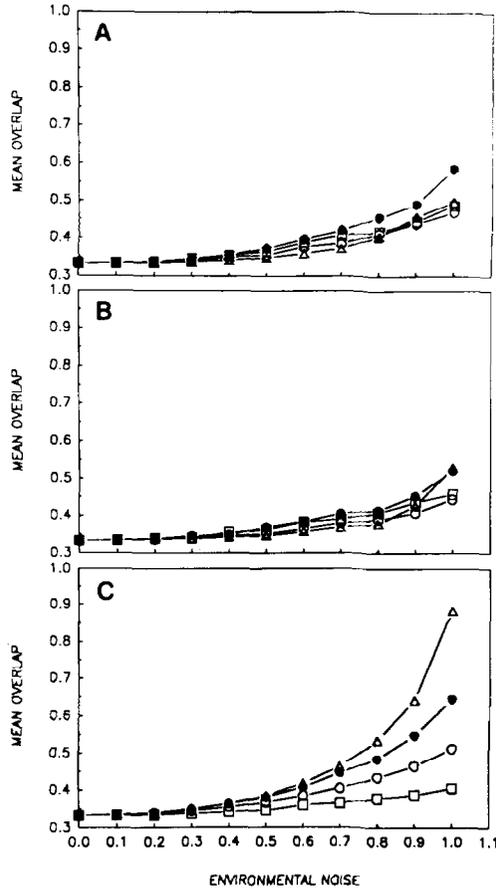


FIG. 2. Average overlap as a function of increasing environmental variation. Overlap is measured as α (Eq. (8)), and environmental noise is measured as the range of e_j (for the deterministic case, the range of $e_j = 0.0$). Each point is the average of 100 population runs, for which the mean overlap was calculated for 100 generations after equilibrium was reached. Closed circle = linear fitness function (Eq. (4)); open circle = quadratic fitness function (Eq. (5)); open triangle = hyperbolic fitness function (Eq. (6)); open square = exponential fitness function (Eq. (7)). Figure 2a = independent resource fluctuations; Fig. 2b = resource crunch model; Fig. 2c = central resource held constant.

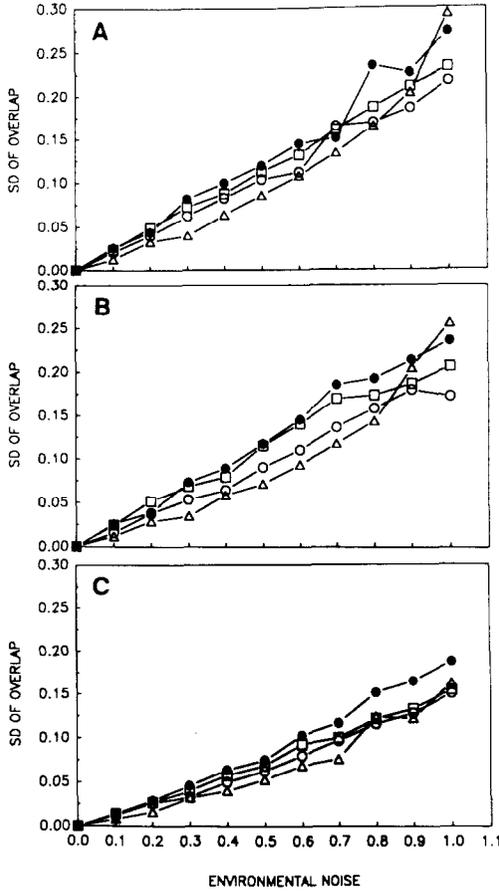


FIG. 3. Standard deviation of overlap as a function of increasing environmental variation. Each point is the average of 100 standard deviations calculated for 100 generations after equilibrium was first reached. Symbols and models as in Fig. 2.

TABLE II

Effects of Varying r on the Number of Generations to Equilibrium and the Equilibrium Overlap Achieved (Eq. 4)

Range of e_j	$r = 1.0$		$r = 0.5$		$r = 0.1$	
	alpha	equilibrium time	alpha	equilibrium time	alpha	equilibrium time
0	.3333	31	.3333	46	.3333	252
0.1	.3350	35	.3340	42	.3357	200
0.5	.3737	68	.3588	55	.3444	301
1.0	.4907	105	.4137	70	.3517	371

DISCUSSION

For these simple genetic models, environmental variation increases overlap between competing species. This increase contrasts sharply with the decrease in overlap that is predicted by some of the demographic models of niche shift (May and MacArthur, 1972; May, 1974; but see Turelli, 1978a). Although overlap increases with environmental variation, low or moderate levels of stochasticity (range of $e_j < 0.4$) do not affect average overlap very much. Even in a moderately fluctuating environment, competition between species should lead to strong divergence of sympatric populations. The increased overlap of competitors in a variable environment is in accord with Wien's model. However, even under models of strong environmental fluctuations, both species exhibited substantial divergence, as Schoener has argued.

The results of these models were sensitive to variation in r , the intrinsic rate of increase. At high values of r ($r = 1.0$), populations rapidly achieved carrying capacity, so they diverged quickly even in the face of fluctuating resources. At low values of r ($r = .10$), populations diverged so slowly that competition was not an important force in the short run. Nevertheless, these models were quite robust to the form of the fitness function, the pattern of environmental fluctuation, and the strength of the stochastic forces. The results suggest that competing species may diverge under a variety of scenarios of resource fluctuation.

Of course, a stochastic environment will make it difficult to evaluate displacement from a single measurement of overlap because confidence intervals for point estimates of overlap are large (Fig. 4). Nevertheless, if

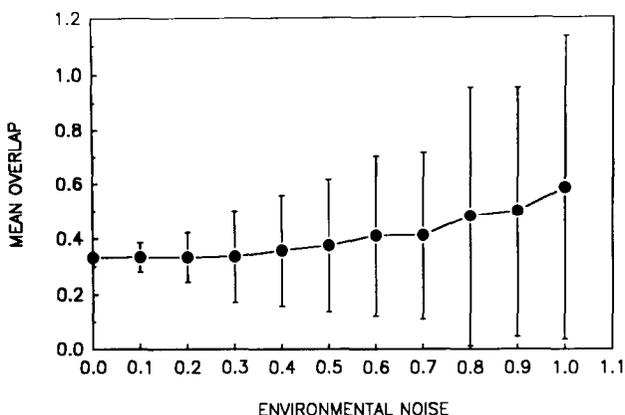


FIG. 4. Variability about point estimates of overlap. The average \pm two standard deviations is shown for point estimates of overlap measured 100 generations after equilibrium was reached.

fluctuations are small or moderate (range of $e_j < 0.4$), divergence of the two populations from an initial state of high overlap should be detectable.

Comparisons with Other Models

It is instructive to briefly review the behavior of demographic models of niche shifts and genetic models of character displacement in constant and variable environments. In a constant environment, there is no effective limit to similarity in the demographic models (May and MacArthur, 1972; May, 1974), and hence no divergence of competing species. However, the greater the overlap between species, the more restricted the range of carrying capacities that allow for coexistence (May, 1974). In contrast, most genetic models predict divergence of competitors in a constant environment (e.g., Crozier, 1974; Bulmer, 1974; Milligan, 1985), as long as there are some constraints on the phenotypic variance (cf. Slatkin, 1980; Taper and Case, 1985).

May and MacArthur (1972) considered the behavior of a demographic displacement model (MacArthur and Levins, 1967) in a variable environment. Their analysis suggested that even a small amount of environmental stochasticity leads to a substantial decrease in overlap, although the magnitude of environmental stochasticity has only a weak effect on the magnitude of divergence. However, May and MacArthur's (1972) model contained several biological and mathematical flaws (Feldman and Roughgarden, 1975; Abrams, 1975; Turelli, 1977, 1978a, 1978b). Turelli (1978a) reformulated the model and concluded that weak to moderate stochastic variation in the environment has a very minor effect on limits to similarity.

Turelli's models also showed that increasing stochasticity led to a decrease in overlap (Tables 1-4 in Turelli (1978a); Fig. 3 in May and MacArthur (1972); note that May and MacArthur's (1972) measure of "niche overlap," d/w , is actually a measure of niche separation). The difference in the models was whether the decrease in overlap was substantial (May and MacArthur, 1972) or trivial (Turelli, 1978a). Abrams (1986) describes several niche shift models that may also lead to parallel or convergent displacement.

Thus, a fluctuating environment may cause separation in the niche shift models because it leads to extinction of species that overlap too much in resource use. In contrast, the genetic models we have analyzed here suggest that a fluctuating environment prevents specialization in resource use and leads to increasing overlap between competing species.

Further Considerations

These simulation results must be interpreted cautiously because they incorporate at least two unrealistic assumptions. First, we have assumed

infinite population sizes of both species, so there were no effects of genetic drift or demographic extinction. Extreme resource fluctuations occasionally led to gene fixation and species extinctions, but only when the range of e_j exceeded 1.0. Slatkin (1980) found that, in a constant environment, divergence was affected by the relative densities of the two competing species.

A second limitation of our approach is that we have posited an extremely simple genetic model of character states and resource use. The strong divergence that we found in our models may result from these constraints on phenotypic variance (Slatkin, 1980; Taper and Case, 1985). A multi-locus model of character displacement might not behave the same in a variable environment.

Incorporating demographic and genetic complexity into these models may provide additional insight into the evolution of character displacement in a variable environment.

ACKNOWLEDGMENTS

We thank F. Sonleitner, G. Graves, B. Van Horne, M. Slatkin, D. Simberloff, T. Schoener, J. Wiens and three anonymous reviewers for valuable comments on an early draft of the manuscript.

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