Optimal Recombination Rate in Fluctuating Environments

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ABSTRACT

The optimal recombination rate which maximizes the long-term geometric average of the population fitness is studied for a two-locus haploid model, assuming that the fitnesses of genotypes AB , Ab , aB and ab are $1 + s(t)$, $1 - s(t)$, $1 - s(t)$, and $1 + s(t)$, respectively, where $s(t)$ follows various stationary stochastic processes with the average zero. With positive recombination, the polymorphism is stably maintained at both loci. After an initial transient phase, the dynamics are reduced to one dimension, and are analyzed for (i) weak selection limit, (ii) strong selection limit, and (iii) selection with two state Markovian jump. Results are: (1) If the environmental fluctuation has a predominant periodic component, r_{opt} is approximately inversely proportional to the period irrespective of selection intensity. (2) If the fluctuation is a superposition of many periodic components, the one with the longest period is the most effective in determining r_{opt} because the genetic dynamics cannot track very quick fluctuations (*low pass filter* effect). (3) If the power spectrum density is decreasing with the frequency, as in pink, or $1/f$ noises, r_{opt} is small when selection is weak, and increases with the selection intensity. Numerical calculation of the genetic dynamics of a recombination modifier supports all these predictions for the evolutionarily stable recombination rate.

ONE of the most exciting subjects in theoretical population biology is the evolution of sex and recombination. In spite of numerous studies since FISHER (1930) (e.g., MULLER 1964; CROW and KIMURA 1965; MAYNARD SMITH 1971, FELSENSTEIN 1974; FELSENSTEIN and YOKOYAMA 1976; STROBECK, MAYNARD SMITH and CHARLESWORTH 1976; HAIGH 1978), no final consensus exists on what is the main evolutionary determinant of recombination rate.

One hypothesis assumes that the evolutionary advantage of sex and recombination is the adaptation to changing environment (MAYNARD SMITH 1968; SLATKIN 1975; LEVIN 1975; WILLIAMS and MITTON 1973; CHARLESWORTH 1976; CHARLESWORTH, CHARLESWORTH and STROBECK 1977; HAMILTON 1980). Suppose that environmental fluctuation switches fit genotypes, and that recombination between currently fit genotypes produces ones which do not fit in the current environment but will fit in the future. Then a population with some recombination would have an advantage in the new environment over the one without recombination. On the other hand, too frequent recombination is deleterious because it breaks down currently fit genotypes. Therefore, there must be an optimal (or evolutionarily stable) recombination rate which depends on the persistent time of environmental fluctuation, as shown by CHARLESWORTH's (1976) computer simulation of the genetic dynamics of a recombination modifier.

In this paper, we study the optimal recombination rate between two loci under environments fluctuating

with various temporal structure. Two simplifying assumptions we adopt in the analytical work are: (1) The evolutionarily stable recombination rate is the one which maximizes the long-term geometric average of population mean fitness. (2) The fitnesses of genotypes fluctuate in a highly symmetric way, so that the polymorphism at both loci is stably maintained without additional processes. Then we numerically calculate the genetic dynamics of a recombination modifier, and confirm the predictions on the evolutionarily stable recombination rate.

Model

We first consider a population of haploid organisms living in a temporally fluctuating environment with nonoverlapping generations, and focus on two loci each with two segregating alleles (A and a ; B and b). We denote the frequencies of the four genotypes, AB , Ab , aB and ab , by X_1 , X_2 , X_3 and X_4 , respectively; and the fitness of the j th genotype in the t th generation by $1 + S_j^t$ ($j = 1, 2, 3$ and 4).

Let $\tilde{X}_i^t$ be the frequency of i th genotype after selection. For $i = 1, 2, 3, 4$, we have:

$$\tilde{X}_i^t = (1 + S_i^t)X_i^t / W_t, \quad (1a)$$

where W_t is the population mean fitness defined by

$$W_t = \sum_{j=1}^4 (1 + S_j^t)X_j^t. \quad (1b)$$

The genotype frequencies are then changed by recombination, as

$$X_i^{t+1} = \tilde{X}_i^t - rh_i D_i, \quad (1c)$$

with

$$h_1 = -h_2 = -h_3 = h_4 = 1,$$

TABLE 1

Fitnesses of each genotype in the t th generation assumed in the model

Genotype	Fitness	Frequency
AB	$1 + s_t$	X_1^t
Ab	$1 - s_t$	X_2^t
aB	$1 - s_t$	X_3^t
ab	$1 + s_t$	X_4^t

Selection coefficient s_t fluctuates over generations with mean zero.

where D_t is the linkage disequilibrium in the t th generation,

$$D_t = \bar{X}_1^t \bar{X}_4^t - \bar{X}_2^t \bar{X}_3^t, \quad (1d)$$

and r is the recombination rate between the two loci.

In the following, we focus our attention on the sign change of epistasis by assuming $S_1^t = S_4^t = s_t$ and $S_2^t = S_3^t = -s_t$, where s_t varies in time with average zero. Then, the selection favors genotypes AB and ab in some generations, and Ab and aB in other generations (Table 1). Recombination is able to produce genotypes which will fit in the future environment but not in the current one. This special fitness regime was first proposed by STURTEVANT and MATHER (1938). Although MAYNARD SMITH (1978) questioned the plausibility, this is the simplest case demonstrating the advantage of recombination in a fluctuating environment, and it may have typical characteristics common to more general cases.

The geometric average of the population mean fitness is:

$$\bar{W} = \lim_{n \rightarrow \infty} (W_1 W_2 \cdots W_n)^{1/n}, \quad (2)$$

which equals the long-term average rate of population growth. In the evolution of a parameter of the genetic system, such as recombination rate, the geometric average fitness (2) calculated for each parameter value often gives a measure for the rate of increase of the modifier genes controlling the parameter (LEVINS 1968; LEWONTIN and COHEN 1969; KARLIN and MCGREGOR 1974), and thereby tend to be maximized as evolutionary consequences although not always (GILLESPIE 1981). In this paper, to concentrate on the relation between the evolution of recombination rate and the way the environment fluctuates, we adopt the simplifying assumption: the recombination rate which maximizes the geometric average of population fitness (2) is the one to be attained through evolution.

The Malthusian parameter m_t is the per capita rate of net population growth, and equals the fitness W_t minus 1: $m_t = W_t - 1$, whose arithmetic average is related to $\bar{W}$ as:

$$\begin{aligned} \bar{W} &= \exp \left[\lim_{n \rightarrow \infty} (1/n) \sum_{i=1}^n \log(1 + m_i) \right], \\ &\approx \exp \left[\lim_{n \rightarrow \infty} (1/n) \sum_{i=1}^n m_i \right], \end{aligned} \quad (3)$$

provided that m_i is small. Therefore the long-term geometric average of the population fitness is related to the long-term arithmetic average of the Malthusian parameter by $\bar{W} = \exp(\bar{m})$.

From equation (1), the change of genotype frequency X_i in a generation is

$$X_i^{t+1} - X_i^t = [(1 + h_i s_t)/W_t - 1]X_i^t - r h_i D_t, \quad (4)$$

where we put $S_i^t = h_i s_t$. If neither selection coefficient s_t nor recombination rate r is very large, the difference equation

(4) can be approximated by a differential equation:

$$dX_i/dt = (h_i s(t) - m)X_i - h_i r D, \quad (5)$$

with a continuous time parameter t , where $i = 1, 2, 3$ and 4. Malthusian parameter is $m = W - 1 = \sum_i h_i s(t)X_i$. Since continuous time dynamics are mathematically more tractable than the corresponding discrete time dynamics, we begin our analysis with equation (5) instead of equation (1), except for the case of extremely strong selection.

Another way to derive a continuous time model equation (5) is considering overlapping generation model (KIMURA, 1956).

By noting the relation $\sum_{j=1}^4 X_j = 1$, we can rewrite equation (5) as a three-dimensional dynamical system of $X = X_1 + X_4$, $Y = X_1 - X_4$ and $Z = X_2 - X_3$:

$$dX/dt = 2s(t)X(1 - X) - 2rD, \quad (6a)$$

$$dY/dt = [s(t) - s(t)(2X - 1)]Y, \quad (6b)$$

$$dZ/dt = [-s(t) - s(t)(2X - 1)]Z, \quad (6c)$$

where linkage disequilibrium is $D = [2X - 1 - Y^2 + Z^2]/4$. The temporal average of $s(t)$ is assumed to be zero. The long-term average Malthusian parameter $\bar{m}$ of the population is

$$\bar{m} = \lim_{T \rightarrow \infty} (1/T) \int_0^T s(t)[2X(t) - 1]dt. \quad (7)$$

In the following, we examine the maximization of $\bar{m}$, the long term arithmetic average of the Malthusian parameter.

As shown in APPENDIX A, for any initial condition, both $Y(t)$ and $Z(t)$ tend to zero as t increases, provided that the average Malthusian parameter $\bar{m}$ is positive. In addition the positivity of $\bar{m}$ holds in the neighborhood of $Y = Z = 0$. Hence, a closed invariant set $\{(X, Y, Z); 0 \leq X \leq 1 \text{ and } Y = Z = 0\}$ of the dynamics (6) is attracting (GUCKENHEIMER and HOLMES 1983). Moreover, the invariant set is globally attracting, as confirmed numerically in all the cases examined in the following. After a transient period, the dynamical system (6) therefore is approximated by the one-dimensional system:

$$dX/dt = 2s(t)X(1 - X) + r(1/2 - X), \quad (8)$$

and $Y = Z = 0$.

In the following, we study the optimal recombination rate r_{opt} which maximizes the long-term average Malthusian parameter (7), for various ways the selection coefficient $s(t)$ fluctuates with time.

Linear analysis

If the magnitude of selection coefficient $s(t)$ is sufficiently smaller than the recombination rate r , equation (8) can be linearized around $X = 1/2$ which is the equilibrium for $s(t) = 0$. The equation for the small deviation $U(t) = X(t) - 1/2$ is:

$$dU/dt = s(t)/2 - rU, \quad (9)$$

where we neglect second order terms with respect to $U(t)$.

We first consider the simplest case in which $s(t)$ is a sinusoidal function: $s(t) = A \cos(kt)$, where A and k are the amplitude and the frequency of the environmental fluctuations of selection coefficient. By integrating equation (9) and neglecting terms which damp out as t grows, we have the asymptotic solution of $X(t)$ and from this the long-term average Malthusian parameter (7):

$$\bar{m} = \frac{A^2 r}{2(r^2 + k^2)}. \quad (10)$$

FIGURE 1.—The optimal recombination rate (r_{opt}) in an environment fluctuating with a single predominant period. Horizontal axis is the period T . The solid curve indicates the optimal recombination rate r_{opt} for weak selection calculated by equation (11); the broken curve, that for the strong selection limit given by equation (24). The bars show the intervals with which the evolutionarily stable recombination rate exists, obtained by computer simulation of recombination modifier dynamics (Table 2). Bars with open circles ($\circ$), $s = 0.05$, linked modifier; bars with open squares ($\square$), $s = 0.5$, linked modifier; and bars with closed squares ($\blacksquare$), $s = 0.5$, unlinked modifier.

Since equation (10) attains its maximum at $r = k$, the optimal recombination rate r_{opt} which maximizes $\bar{m}$ under the constraint $0 \leq r \leq 1/2$ depends on the period T_0 ($= 2\pi/k$) as:

$$r_{\text{opt}} = \begin{cases} 2\pi/T_0, & \text{if } T_0 \geq 4\pi, \\ 1/2, & \text{if } T_0 \leq 4\pi. \end{cases} \quad (11)$$

Thus, if the environment fluctuates slowly (large T_0), the optimal recombination rate is small, i.e., tight linkage is optimal, and is inversely proportional to the period T_0 . On the other hand, in an environment fluctuating quickly (period T_0 is shorter than 12.6 times average generation time), the optimal recombination rate is 0.5, the maximum value, indicating no linkage between the loci.

Figure 1 illustrates the optimal recombination rate given by formula (11) together with the evolutionarily stable recombination rate obtained numerically by the genetic dynamics of a recombination modifier, which we will explain later.

Spectrum of environmental fluctuation

More generally $s(t)$ may be some superposition of sinusoidal fluctuations with different periods and amplitudes:

$$s(t) = \int_0^\infty [A(k) \sin kt + B(k) \cos kt] dk, \quad (12)$$

where $A(k)$ and $B(k)$ are the weights for the fluctuation of period $2\pi/k$. The power spectrum density (see, for example, NISBET and GURNEY 1982) of $s(t)$ is defined by

$$f(k) = [A(k)^2 + B(k)^2]/2, \quad (13)$$

which indicates the importance of the fluctuation component with period $2\pi/k$.

According to standard calculations, we can derive the asymptotic solution of the linearized system (9) and then the long-term average of Malthusian parameter from equations (7), (12) and (13), and $X = 1/2 + U$, as

$$\bar{m} = \int_0^\infty \frac{rf(k)}{r^2 + k^2} dk. \quad (14)$$

Note that if a single predominant component of frequency k_0 exists in the environmental fluctuation, the power spectrum density is approximated by: $f(k) = (A^2/2)\delta(k - k_0)$, where $\delta(\cdot)$ is the Dirac's delta function, and equation (14) becomes equation (10) of the previous section.

Low pass filter effect

Equation (14) states that the long-term average Malthusian parameter $\bar{m}$ is the integral of the power spectrum density $f(k)$ multiplied by a weighting factor $r/(r^2 + k^2)$. The factor decreases monotonically with k and is very small for k much larger than r —it operates on $f(k)$ as a “low pass filter” which selectively filters out high frequency components of the environmental fluctuation.

Therefore, if the fluctuation consists of several components of different frequencies, those of lower frequencies (i.e., longer periods) have stronger effects on the population mean fitness, and hence on the optimal recombination rate.

For example, Figure 2 illustrates the case in which the fluctuation has two components of frequencies k_1 and k_2 ($k_1 < k_2$), such as the tidal and the annual periods. Since the power spectrum is: $f(k) = A^2\delta(k - k_1) + B^2\delta(k - k_2)$, the average Malthusian parameter is:

$$\bar{m} = A^2r/(r^2 + k_1^2) + B^2r/(r^2 + k_2^2). \quad (15)$$

According to both numerical and analytical calculations, if A^2 and B^2 are of the same order of magnitude, i.e., the two components are comparable in strength, then the Malthusian parameter (15) is unimodal as a function of r , with the peak very close to k_1 (the smaller of the two frequencies), which is the optimal recombination rate under an environment fluctuating purely with the longer period component.

The magnitude of the shorter period component must be far stronger for both components to be similarly influential to the optimal recombination rate in the face of low pass filter effect. Then $\bar{m}$ is a bimodal function of r . Figure 2 illustrates a jump of the optimal recombination rate when the relative importance of two components changes gradually. The optimal recombination rate is exclusively regulated by the longer period component until its relative importance becomes as low as $1/125$ of the shorter period component.

The low pass filter effect also explains why the optimal recombination rate for periodic $s(t)$ is determined only by the basic period, and is insensitive to the “shape,” which is determined by harmonics of higher frequencies.

As to the optimal recombination rate for the general power spectrum pattern, we prove the following propositions in Appendix B.

Proposition 1. *The optimal recombination rate is between the minimum and the maximum frequencies of environmental fluctuation: $k_{\min} \leq r_{\text{opt}} \leq k_{\max}$.*

Proposition 2. *If $f(k)$ is a decreasing function of k , then $\bar{m}(r)$ is a decreasing function of r , as far as linear analysis is applicable.*

Many examples of random noise observed in nature have a decreasing power spectrum $f(k)$, including “ $1/f$ noise” and “pink noise” (NISBET and GURNEY 1982). Hence we may call them “noisy” fluctuations. For instance, the power spectrum of pink noise is $f(k) = A^2(2/\pi)a/(a^2 + k^2)$, where a (>0) is the autocorrelation. From equation (14), we have:

$$\bar{m} = A^2/(a + r), \quad (16)$$

which is, in fact, monotonically decreasing with r .

Proposition 2 seems to conclude that “zero recombination” is optimal for noisy fluctuation of selection. However, the conclusion is based on the linearized system (9) which is

FIGURE 2.—Low pass filter effect. Upper figures illustrate selection coefficient $s(t)$ fluctuating with time t having two strong components of different frequencies ($k_1 = 0.01$ and $k_2 = 0.5$), for various ratios of the relative importance of the components ($A^2/B^2 = 1/5$ in (A), $1/25$ in (B), and $1/125$ in (C)). Lower figures show the long-term average Malthusian parameter $\bar{m}$ (plotted as the ratio to the maximum value $\bar{m}_0$) versus recombination rate r when $s(t)$ fluctuates as shown in upper figures [calculated by equation (15)]. Even if the lower frequency component is much weaker than the higher frequency component, it is more influential in determining the optimal recombination rate (in (A) and (B)), due to the low pass filter effect of the genetic dynamics. In (C), we further reduce the relative importance of the longer period component, and the r_{opt} which attains the peak Malthusian parameter $\bar{m}_0$ jumps to the one corresponding to the higher frequency (shorter period) component.

valid only for r sufficiently larger than the selection intensity $|s|$. Therefore, Proposition 2 rather tells us that the optimal r is very small—at most of the same order of magnitude as $s(t)$ if the power spectrum is monotonically decreasing.

These results suggest that not all kinds of environmental fluctuation make a large recombination rate advantageous; rather the fluctuation must have a significant periodic component. The following proposition confirms this conjecture:

Proposition 3. *If $f(k)$ locally increasing at $k = 0$ so that:*

$$f(k) \geq f(0) + ck, \quad (0 \leq k \leq \delta), \quad (17)$$

for some $c > 0$ and $\delta > 0$, then $m(r) > m(0)$ holds for sufficiently small $r > 0$.

In contrast to noisy fluctuation with a decreasing power spectrum, a power spectrum $f(k)$ increasing with k around $k = 0$ indicates some “orderly” structure of fluctuation, though its period may be blurred. Then, there exists an optimal recombination rate which is positive, according to Proposition 3.

Strong selection limit

If selection is not weak, the nonlinearity of the dynamics causes interaction between modes of different periods; thus the linear analysis in the last section fails.

Here we consider the other extreme, a strong selection limit, in which the selection coefficient $s(t) = \pm 1$, indicating that genotypes under their unfavorable environment have

zero viability or null fertility. If selection is very strong, we can no longer use the continuous time models such as equations (6) and (7). Instead we start with the discrete time model as follows.

Under the strong selection assumption, we have

$$X'_1 = X'_4, \quad \text{and} \quad X'_2 = X'_3, \quad \text{for } t > i_0, \quad (18)$$

for any initial condition, where i_0 is the generation when the first environmental change occurs. This is because all the genotypes in the $(i_0 + 1)$ th generation are produced from recombination between the preexisting genotypes which themselves are doomed to vanish in the new environment. This is the extreme example of the general tendency that both $Y(t) = X_1 - X_4$ and $Z(t) = X_2 - X_3$ in equation (6) tend to zero as t increases.

We assume that, in each generation, natural selection and recombination occur in that order. Let $X_t = X'_1 + X'_4$, and let $\tilde{X}_t$ be the corresponding quantity after selection and before recombination. Then we have the recursion equations (for $t > i_0$):

$$\tilde{X}_t = (1 + s_t)X_t/W_t, \quad (19a)$$

$$X_{t+1} = \tilde{X}_t + r[1/2 - \tilde{X}_t] \quad (19b)$$

where $W_t = 1 + s_t(2X_t - 1)$. We combine these two as:

$$X_{t+1} = r/2 + (1 - r)(1 + s_t)X_t/[1 + s_t(2X_t - 1)]. \quad (20)$$

In this strong selection limit, X_{t+1} is determined simply by

the value of s_t as:

$$X_{t+1} = \begin{cases} 1 - r/2, & \text{if } s_t = 1, \\ r/2, & \text{if } s_t = -1, \end{cases} \quad (21)$$

regardless of the value of X_t . Consequently, the population fitness in the $(t+1)$ th generation, W_{t+1} , is given by

$$W_{t+1} = 1 + s_{t+1}(2X_{t+1} - 1) = \begin{cases} 2 - r, & \text{if } s_{t+1} = s_t, \\ r, & \text{if } s_{t+1} \neq s_t. \end{cases} \quad (22)$$

First we consider a periodic environment, so that either $s_t = +1$ or $s_t = -1$ holds during successive τ generations, i.e., the duration τ is the number of generation during which s_t remains the same. Then the long-term average of the geometric mean fitness is

$$\begin{aligned} \bar{W} &= \exp \left[\lim_{n \rightarrow \infty} (1/n) \sum_{t=1}^n \log W_t \right] \\ &= \exp \left[(1/\tau) \log(r) + (1 - 1/\tau) \log(2 - r) \right]. \end{aligned} \quad (23)$$

By setting the derivative of (23) with respect to r be zero, we conclude that the optimal recombination rate r_{opt} which maximizes (23) is inversely proportional to the duration τ :

$$r_{\text{opt}} = \begin{cases} 2/\tau, & \text{if } \tau \geq 4, \\ 1/2, & \text{if } \tau \leq 4, \end{cases} \quad (24)$$

because of the constraint of $r \leq 1/2$. Noting that the duration τ equals half the period, this formula gives a result numerically similar to the weak selection case (11) (see Figure 1), but r_{opt} is smaller in (24) than in (11).

The same analysis applies to a nonperiodic environment. Actually, the optimal recombination rate in the strong selection limit is determined only by the average number of environmental changes in the long time interval. For instance, in jump-type Markovian processes with transition rate p per generation:

$$P(s_{t+1} = \pm 1 | s_t = \mp 1) = p, \quad (25)$$

the optimal recombination rate is given by equation (24) where τ equals the relaxation time $1/p$; i.e., $r_{\text{opt}} = 2p$.

A Markovian jump type process has a power spectrum density which monotonically decreases with the frequency, because it is the discrete time version of pink noise. For weak selection fluctuating with such a power spectrum, the optimal recombination rate must be small, as shown by Proposition 2 of the previous section. However, in the strong selection limit, r_{opt} may be large when the relaxation time is sufficiently short. The optimal recombination rate under "noisy" fluctuations therefore depends greatly on the selection intensity. This result contrasts with the case of periodic fluctuations in which the optimal recombination rate is similar between the two extremes of selection intensity: weak and strong selection limits.

Two-state Markovian jump selection

If natural selection is mildly strong, neither analysis developed in the last two sections is applicable. Here we examine a particular class of environmental fluctuations for which the optimal recombination rate can be analytically derived for wide range of selection intensity.

We assume that the selection coefficient $\{s(t); -\infty < t < \infty\}$ is a "two-valued stationary Markov process," i.e., $s(t)$ takes one of the two distinct values $\pm s$, and randomly jumps between them with a transition rate p :

$$P(s(t + \Delta t) = \mp s | s(t) = \pm s) = p\Delta t + o(\Delta t). \quad (26)$$

FIGURE 3.—Optimal recombination rate when the selection coefficient jumps between $\pm s$ with transition rate p . The long-term average Malthusian parameters $\bar{m}$ is calculated by numerical integration of equation (28), for various values of the parameters. The optimal recombination rate r_{opt} is obtained for each pair of parameters p and s fixed. This figure illustrates the relationship between r_{opt}/s and p/s (●, $s = 0.01$; ○, $s = 0.1$; ▲, $s = 0.5$, and □, $s = 1.0$). Data points are on a single curve irrespective of the magnitude of s . The solid curve represents the harmonic mean formula (29b); the broken line, the geometric mean formula (29a).

where Δt is small. Since the rate of state change is p , the autocorrelation of $s(t)$ decays as $\exp(-pt)$. The inverse $1/p$ is the relaxation time; the average duration of each environment. The stochastic process $\{X(t); 0 \leq t < \infty\}$ is then defined as the solution of a stochastic differential equation (8). Although $\{X(t); 0 \leq t < \infty\}$ by itself is non-Markovian, the vector-valued stochastic process $\{(X(t), s(t)); 0 \leq t < \infty\}$ is Markovian.

This process is mathematically equivalent to the one locus two allele model with mutation and stochastic selection analyzed by MATSUDA and ISHII (1981) if we replace mutation by recombination. The exact solution for the stationary joint distribution of X and s is known [equation (3.7) in MATSUDA and ISHII 1981] as:

$$\phi(X, \pm s) = \begin{cases} C \left[\frac{(A - X)(X - b)}{(X - a)(B - X)} \right]^Q / |F_{\pm}|, & \text{for } b < X < A, \\ 0, & \text{for } 0 < X < b, A < X < 1, \end{cases} \quad (27)$$

where $F_{\pm}(X) = \pm 2sX(1 - X) + r(1/2 - X)$; A and a are the two roots of quadratic equation $F_+(X) = 0$; B and b , those of $F_-(X) = 0$; $Q = p/\sqrt{4s^2 + r^2}$; and C , a normalizing factor. The mean Malthusian parameter (7) of the population is

$$\bar{m} = \int_b^A \frac{r(2X - 1)^2}{2X(1 - X)} \Phi(X) dX, \quad (28)$$

where $\Phi(X) = \phi(X, +s) + \phi(X, -s)$.

Given the parameters s (selection intensity) and p (transition rate of environment), the Malthusian parameter $\bar{m}$ is calculated by numerical integration of equation (28) for various values of r , and the optimal recombination rate r_{opt} is obtained as a function of s and p . Figure 3 illustrates the results. If we change the time unit for the above system, the three rate parameters, r_{opt} , s , and p , are multiplied by the same factor. Since any relationship among r_{opt} , p and s must remain valid under such an alteration, the ratio r_{opt}/s must be a function of p/s , independent of the absolute values of s , as shown in Figure 3. The optimal recombination rate never exceeds the selection intensity. It is approximately half of the harmonic mean of s and p when the ratio p/s is

TABLE 2
Evolutionarily stable recombination rate for periodical fluctuation

τ	$r_{\text{opt weak}}$	$r_{\text{opt strong}}$	Linked modifier		Unlinked modifier
			$s = 0.05$	$s = 0.5$	$s = 0.5$
1	0.488	0.50	$0.45 < r_E < 0.50$	$0.48 < r_E < 0.50$	$0.48 < r_E < 0.50$
2	0.458	0.50		$0.48 < r_E < 0.50$	$0.48 < r_E < 0.50$
3	0.420	0.50		$0.48 < r_E < 0.50$	$0.48 < r_E < 0.50$
4	0.382	0.50		$0.48 < r_E < 0.50$	$0.46 < r_E < 0.48$
5	0.347	0.40	$0.46 < r_E < 0.50$	$0.44 < r_E < 0.48$	$0.34 < r_E < 0.38$
10	0.231	0.20	$0.26 < r_E < 0.30$	$0.20 < r_E < 0.24$	$0.12 < r_E < 0.14$
25	0.111	0.08	$0.10 < r_E < 0.14$	$0.06 < r_E < 0.10$	$0.02 < r_E < 0.04$
50	0.059	0.04	$0.05 < r_E < 0.07$	$0.03 < r_E < 0.05$	$0.0 < r_E < 0.01$

τ : duration of each environment (half period); s : selection intensity; r_{opt} : the optimal recombination rate given by equation (11) for weak selection limit and equation (24) for strong selection limit. The interval including the evolutionarily stable recombination rate is given both for linked ($r_0 = 0$) and unlinked ($r_0 = 0.5$) modifiers.

larger than 1; but for small p/s , it is approximately half of the geometric mean of s and p :

$$r_{\text{opt}} \sim \begin{cases} 0.5\sqrt{sp}, & p < s, \\ 0.5(2sp/(s+p)), & p > s. \end{cases} \quad (29a)$$

$$(29b)$$

Given the transition rate p , the optimal recombination rate monotonically increases with the selection intensity s . In the limit of weak selection, equation (29b) states that the optimal recombination rate is as small as the selection intensity s , as suggested by Proposition 2.

When p/s is smaller than 0.01, numerical integration of (28) is technically very difficult. K. ISHII (personal communication) observed that, for p/s as small as 10^{-4} , r_{opt} becomes proportional to p .

Numerical analysis of modifier dynamics

In the foregoing analysis, we have assumed that the recombination rate which maximizes the long-term geometric average of the population fitness (r_{opt}) is the one to be evolved. In this section, we numerically examine the genetic dynamics of a recombination modifier to determine whether or not the optimal recombination rate can be obtained as an evolutionary consequence of modifier dynamics, and to check the predicted dependence of the evolutionarily stable recombination rate on the temporal structure of environmental fluctuation.

Consider an additional locus M with two alleles m_1 and m_2 , controlling the recombination rate between two selected loci A and B . The recombination rate is determined by the diploid genotype: genotypes m_1m_1 , m_1m_2 and m_2m_2 realize the recombination rate r_1 , $(r_1 + r_2)/2$ and r_2 , respectively. The loci A , B and M are linearly arranged on the map in this order, and the recombination rate between modifier M and locus B is r_0 . We then examine which of the modifier alleles will spread for various temporal structures of the environmental fluctuation.

For most cases, there exists a unique evolutionarily stable recombination rate r_E : if r_1 and r_2 are both larger or both smaller than r_E , after many (about 10^3 to 10^5) generations, the allele giving the recombination rate closer to r_E becomes quasifixed (its frequency becomes larger than 99%). If instead r_E is between r_1 and r_2 , the polymorphism of two alleles is stably maintained. Hence we expect that after repeated events of invasion and replacement of various modifier alleles, the recombination rate between A and B would evolve toward r_E .

In some cases, however, the system shows bistability: there

are two recombination rates both of which are evolutionarily stable against alleles showing slightly different recombination rates.

Tables 2 to 4 show the interval that includes the evolutionarily stable recombination rate r_E (estimated by simulations of genetic dynamics, see APPENDIX C for details) and the optimal recombination rate r_{opt} (derived theoretically in the preceding sections).

Fluctuation with a single period

The results for the case of periodically fluctuating selection are listed in Table 2 and illustrated in Figure 1. The evolutionarily stable recombination rate r_E is accurately predicted by the optimal recombination rate r_{opt} given by equation (11) for the weak selection limit and by equation (24) for the strong selection limit in Table 2. The r_E monotonically decreases with the period of environmental fluctuation. It is relatively insensitive to the magnitude of the selection coefficient: r_E is similar for $s = 0.5$ and $s = 0.05$, but r_E for strong selection tends to be smaller than that for weak selection, as predicted by r_{opt} . The r_E is also insensitive to the linkage between the modifier and the selected loci: it is similar for completely linked ($r_0 = 0$) and unlinked ($r_0 = 1/2$) modifiers, though the latter tends to be smaller.

This case is the same as the genic modifier model studied by CHARLESWORTH (1976) except that he assumed diploid genetics with marginal overdominance at both selected loci. CHARLESWORTH reported that r_E was small both for very short periods of fluctuation and for very long periods, and is the highest for an intermediate period. This conclusion is different from ours and can be explained by that he calculated modifier evolution only for several hundred generations—we numerically followed his genic modifier model of diploid systems much longer (about 10^4 generations) and obtained the monotonic decrease of r_E with the environmental period.

Fluctuation with two strong components

Table 3 shows the results for the case in which the fluctuation of the selection coefficient is the superposition of two periodic components. If the two components are comparable in strength, the evolutionarily stable recombination rate is very close to the optimal one for the fluctuation only with the longer period component; hence the low pass filter effect works in modifier genetic dynamics. If the relative importance of the long-period component decreases as low as $(A^2/B^2)^{1/25}$ of the short-period one, the system becomes bistable; i.e., two recombination rates corresponding to the shorter and longer periods are both stable with

TABLE 3
Low pass filter effect

A	B	
0.1	0.0	$0.006 < r_E < 0.008$
0.1	0.1	$0.006 < r_E < 0.008$
0.05	0.1	$0.006 < r_E < 0.008$
0.02	0.1	$0.006 < r_{E1} < 0.01, 0.34 < r_{E2} < 0.38^a$
0.005	0.1	$0.35 < r_E < 0.45$
0.0	0.1	$0.38 < r_E < 0.42$

Evolutionary stable recombination rate for the case when the selection coefficient is a superposition fluctuating with two components: $s(t) = A \sin(0.01t) + B \sin(0.5t)$. The long-term average Malthusian parameter is shown in Figure 2.

^a The domain of attraction for r_{E1} : $0.0 \leq r < 0.1$; that for r_{E2} : $0.1 < r \leq 0.5$.

respect to the invasion of a modifier, showing a slightly different recombination rate. As A^2/B^2 decreases further, the equilibrium with the lower recombination rate disappears and the one with the higher recombination rate becomes globally stable. Thus the jump of the evolutionarily stable recombination rate, predicted by the corresponding optimization model (Fig. 2), is demonstrated by the modifier genetic dynamics (Table 3).

Noisy fluctuation

Table 4 illustrates the results for the case in which the selection coefficient fluctuates with pink noise, realized by Markovian jump processes. Again the r_E can be approximated by equation (29) for the optimal recombination rate. The evolutionarily stable recombination rate is small for weak selection and increases with the magnitude of the selection coefficient. The contrast between sensitive dependence of r_E on the selection intensity for noisy fluctuation and insensitive dependence for orderly fluctuation is thus confirmed.

For pink noise fluctuation, we observe that the strength of linkage between the modifier M and the selected locus B does not affect r_E much, but r_E tends to be smaller for unlinked modifiers ($r_0 = 1/2$) than for tightly linked ones ($r_0 = 0$) especially when $r_{opt} < 0.05$.

In short, all the important features of the evolutionarily stable recombination rate in fluctuating environments, predicted theoretically by the optimization model, are thus confirmed by the evolutionary dynamics of a recombination modifier.

DISCUSSION

For the simplest models of evolution in a temporally changing environment, life history traits which maximize the geometric average population fitness are the ones to be evolved (LEVINS 1968; LEWONTIN and COHEN 1969). With sophisticated analysis, KARLIN and MCGREGOR (1974) demonstrated that the evolutionary consequences of modifier gene dynamics often maximize the geometric average of the population fitness, but not always (e.g., GILLESPIE 1981 for mutation modifier).

According to our numerical analysis, the optimization model works very well in predicting how the evolutionarily stable recombination rate depends on the temporal structure of environmental fluctuation—all the predictions derived from the optimization model also hold for the evolution of modifier dynamics.

CHARLESWORTH (1976) claimed that significant evolution of a high recombination rate requires strong linkage between the modifier and one of the selected loci, and hence considered it as demonstrating a limitation of the optimization approach. However, our computer simulation shows that, although the evolution rate is slower for unlinked modifiers than for linked ones, the evolutionarily stable recombination rate r_E for unlinked modifiers can be high: it is close to the maximum value (0.5) for cyclic fluctuation with a short period ($\tau = 1 \sim 4$); hence it is not very different from r_E for linked modifiers, both for our haploid

TABLE 4
Evolutionarily stable recombination rate for fluctuation with Markovian jump model

s	$\tau(=1/p)$	r_{opt} Eq. (34)	r_{opt} strong	Linked modifier	Unlinked modifier
0.5	2	0.250 ^H	0.50	$0.48 < r_E < 0.50$	$0.48 < r_E < 0.50$
	3	0.204 ^G	0.50	$0.32 < r_E < 0.36$	$0.26 < r_E < 0.30$
	4	0.177 ^G	0.50	$0.24 < r_E < 0.26$	$0.16 < r_E < 0.20$
	5	0.158 ^G	0.40	$0.18 < r_E < 0.22$	$0.12 < r_E < 0.14$
	10	0.112 ^G	0.20	$0.10 < r_E < 0.14$	$0.05 < r_E < 0.06$
	25	0.071 ^G	0.08	$0.05 < r_E < 0.07$	$0.01 < r_E < 0.02$
	50	0.05 ^G	0.04	$0.02 < r_E < 0.04$	$0.0 < r_E < 0.01$
0.05	2	0.045 ^H			
	3	0.043 ^H		$0.04 < r_E < 0.05$	$0.01 < r_E < 0.02$
	4	0.042 ^H		$0.04 < r_E < 0.06$	$0.0 < r_E < 0.01$
	5	0.040 ^H		$0.03 < r_E < 0.04$	$0.0 < r_E < 0.01$
	10	0.034 ^H		$0.02 < r_E < 0.04$	$0.0 < r_E < 0.01$
	25	0.022 ^G		$0.02 < r_E < 0.03$	$0.0 < r_E < 0.01$
	50	0.016 ^G		$0.01 < r_E < 0.02$	$0.0 < r_E < 0.01$

s : selection intensity; $\tau = 1/p$: relaxation time; r_{opt} : optimal recombination rate calculated by equation (29a) (geometric mean formula, indicated by G), and by (29b) (the harmonic mean formula, by H); also r_{opt} of the strong selection limit is given by equation (24). The intervals including the evolutionarily stable recombination rate r_E are given both for linked ($r_0 = 0$) and unlinked ($r_0 = 0.5$) modifiers.

model (Table 2) and for CHARLESWORTH's diploid overdominance model. The r_E tends to be smaller for unlinked modifiers than for linked ones: the difference becomes significant when the optimization model predicts a small recombination rate ($r_{\text{opt}} < 0.05$), both for periodic and noisy fluctuations (Tables 2 and 4). Hence, the concept of the optimal recombination level for a given environment works better than CHARLESWORTH (1976) concluded.

The main simplifying assumption adopted in this paper is the special way the fitnesses of the four genotypes correlate (Table 1). Since the average fitnesses of the two segregating alleles are exactly the same for both loci, the polymorphisms at both loci are stably maintained, as proved in APPENDIX A. But the result of our analysis should be of no biological importance if a slight fitness difference between alleles could break the genetic polymorphism, which is necessary for the advantage of recombination to manifest itself.

Fortunately, we can prove (see APPENDIX A) that a protected polymorphism is structurally stable for the deterministic fluctuation of $s(t)$ with a positive recombination rate—polymorphisms at both loci should be maintained for any perturbation of sufficiently small magnitude. Intuitively speaking, this is because recombination, associated with the temporal fluctuation of epistasis, contributes genetic variation by producing two currently nonfit genotypes with equal frequencies, and thus reduces the unbalance between allele frequencies. The numerical analysis of the dynamics (1) with small perturbations, explained in APPENDIX A, supports the stabilizing effect of recombination, and further suggests that the effect is strongest for an intermediate r which produces a sufficiently positive advantage measured by $\bar{m}$.

Therefore, in a haploid *two-locus* model of changing environment, a polymorphism can be structurally stable: this makes a sharp contrast with the one-locus haploid model, in which neither random nor systematic fluctuations of selection coefficient can make a polymorphism structurally stable—quasifixation is certain if there is no mutation (KIMURA, 1954; GILLESPIE, 1973).

However, the above mechanism for polymorphism is not effective if the fitness difference between alleles is large. Then the polymorphism needs to be maintained by additional processes, such as mutation-selection balance, frequency dependent selection, or heterotic interaction in diploid genotypes. We may examine the optimal recombination rate in these more general systems in which we consider processes responsible for polymorphism. The advantage of recombination may possibly have a similar relation with the temporal structure of environmental fluctuation (*e.g.*, the power spectrum of selection) to what the present

model concludes. For example, CHARLESWORTH's (1976) recombination modifier model with marginal overdominance, which helps maintain the genetic variation, shows very similar results to the haploid model we studied, according to our numerical analysis.

Another shortcoming of our model is the assumption of a two-locus genetic system, instead of a polygenic system with many loci controlled by also many recombination modifiers. SLATKIN and LANDE's (1976) model for the evolution of niche width under changing environment seems to have some analogy to the polygenic model of the evolution of recombination, if we assume that a larger within-family variance of traits is produced by a higher recombination rate.

In spite of these potential problem with the underlying genetic system, our analysis has its value in revealing new aspects of the evolution of recombination rates under various ways the environment fluctuates. The results are summarized as:

First, if the environment fluctuates periodically, the optimal recombination rate is approximately inversely proportional to the period, both in weak and strong selection limits. We expect that this result holds also for selection of intermediate intensity, and conjecture that the optimal recombination rate is relatively insensitive to the magnitude of selection in the *orderly* (or approximately periodic) fluctuation of the environment. The average Malthusian parameter $\bar{m}$ for the model equation (8), in which $s(t)$ alternates between s and $-s$ with the duration τ for each value, is obtained by equation (3.6) of ISHII, MATSUDA and OGITA (1982, p. 341) with the necessary replacement of parameters. The numerical calculation of their result supports an insensitive dependence of the evolutionarily stable recombination rate on the selection intensity s .

Note that the period in the model is measured by the number of generations. Therefore, if we compare several organisms having different generation times growing under the same periodic environment, the optimal recombination (per generation) rate should increase with the generation time. According to (11), if the generation time is as long as a tenth of the environmental period, r_{opt} is the maximum value 0.5, which is realized when the two loci are located on different chromosomes or far apart on the same chromosome.

Second, if the environmental fluctuation includes several components of different periods, the one with the longest period is the most important, because the genetic dynamics cannot track quick environmental changes and hence skip high frequency components selectively (low pass filter effect). The effect is more important when selection is weak. Effectiveness of low frequency components would explain that the optimal recombination rate is small when the environmental fluctuation is noisy, *i.e.*, the power spectrum is a de-

creasing function of the frequency. The optimal recombination rate for periodic fluctuation is determined only by the basic period irrespective of the shape of fluctuation which is given by harmonics of high frequency. In a similar vein, temporal fluctuation with a period shorter than the generation time of organisms has negligible effect on the optimal recombination rate because of the averaging.

If the environment has two dominant components of fluctuation (for example, tidal and annual periods), and if the one with shorter period is so strong that even after the filtering by the demographic dynamics the strength of the two components are comparable, then the optimal recombination rate may discontinuously change at some point as the relative strength of the two components changes continuously. This suggests a possible dichotomy of genetic systems differing in the fraction of sexual reproduction when life history parameters gradually change.

Third, if the environmental fluctuation is *noisy*, showing a decreasing power spectrum pattern, the optimal recombination increases with the selection intensity. Specifically in pink noise, r_{opt} is close to one half of the harmonic average of the selection intensity (s) and the environmental transition rate (p), when $p > s$ and is half of their geometric average when $p < s$. In the noisy processes, the duration of each environment has a large variance so that there are many short runs of the same environment as well as long ones. When selection is weak, the genetic dynamics slowly track environmental shifts, not responding to short runs; hence very long runs of the same environment that occasionally appear make a high recombination rate disadvantageous. However, as the selection intensity increases, the system becomes able to respond to shorter runs of each environment; hence the optimal recombination becomes larger, until finally both short and long runs are equally important in determining the optimal recombination, so that the average environmental duration decides the optimal value, as in the strong selection limit.

The evolutionary advantage of recombination has been previously discussed in the context of the benefit of sexual reproduction. Possible factors favoring sexual reproduction in the face of meiotic cost (MAYNARD SMITH 1978) include (1) acceleration of the accumulation rate of favorable mutant genes by combining separately created ones into the same genome (FISHER 1930; CROW and KIMURA 1965; MAYNARD SMITH 1971; FELSENSTEIN 1974; FELSENSTEIN and YOKOYAMA 1976; STROBECK, MAYNARD SMITH and CHARLESWORTH 1976), (2) protecting a population from irreversible accumulation of deleterious mutations (MULLER 1964; HAIGH 1978), (3) frequency dependent selection favoring rare types caused either by intraspecific competition or via host-parasite and

predator-prey interactions (WILLIAMS and MITTON 1973; LEVIN 1975; MAYNARD SMITH 1976; HAMILTON 1980), and (4) the switching over of genotypes in temporal or spatial fluctuations of environment (SLATKIN 1975; CHARLESWORTH 1976; CHARLESWORTH, CHARLESWORTH and STROBECK 1977; HAMILTON, HENDERSON and MORAN 1981). In this paper we have developed the last hypothesis.

The model we studied in this paper is based on only one of several hypotheses on the evolutionary advantage of recombination, which are equally plausible at the present stage. After detailed examination of each possible mechanism, as we did in the paper, we will then be at a stage to evaluate the relative importance of different mechanisms for the evolutionary advantage of recombination, and will be able to answer why sexual reproduction is so prevalent in nature.

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APPENDIX A

In the following, we first prove that the 3-dimensional dynamics (6) are effectively described by the 1-dimensional dynamics (8), and then we show that a protected polymorphism is structurally stable.

Lemma 1. Both variables $Y(t)$ and $Z(t)$ in equations (6) tend to zero for any initial condition, provided that the long-term average of the Malthusian parameter (7) is positive.

Proof. Equation (6b) can be rewritten as

$$dY/dt = k(t)Y, \quad (\text{A1})$$

where $k(t) = s(t) - s(t)[2X(t) - 1]$. According to (7), when the average of $s(t)$ is zero, we have $\lim_{T \rightarrow \infty} (1/T) \int_0^T k(t)dt = -\bar{m}$. For an arbitrary small positive number $\delta > 0$, we have

$$|Y(t)| < |Y(0)| \exp(-(\bar{m} - \delta)t) \quad (\text{A2})$$

for sufficiently large t . Hence if $\bar{m}$ is positive, $Y(t)$ exponentially converges to zero as t grows infinitely large. Similarly, from (6c), we can derive that $Z(t)$ goes to zero as t grows. Here, $-\bar{m}$

is called the “Lyapunov exponents” of variables $Y(t)$ and $Z(t)$; which govern their asymptotic behavior as $Y(t) \sim \exp(-\bar{m}t)$ and $Z(t) \sim \exp(-\bar{m}t)$. The positivity of $\bar{m}$, therefore, implies that both $Y(t)$ and $Z(t)$ exponentially decrease with the asymptotic rate $\bar{m}$ as t increases for any initial condition. Thus we proved Lemma 1.

Lemma 2. Long-term average Malthusian parameter $\bar{m}$ is positive in the neighborhood of $Y = Z = 0$.

Proof. First, we note that $Y(t) = Z(t) = 0$ holds for all t if we start with the initial condition $Y(0) = Z(0) = 0$. Therefore $\{(X, Y, Z); 0 \leq X \leq 1, Y = Z = 0\}$ is an invariant set of the dynamics (6). Now we examine whether the invariant set is attracting or not. Since D in (6a) depends on Y and Z only through second order terms, we can neglect them in the neighborhood of $Y = Z = 0$. Letting $U = X - 1/2$, the system then becomes

$$dU/dt = 2s(t)[1/4 - U^2] - rU, \quad (\text{A3})$$

together with equation (A1) for Y and a similar one for Z . Using (A3), the integrand of equation (7) is

$$2s(t)U(t) = [U/g(U)]dU/dt + rU^2/g(U), \quad (\text{A4})$$

where $g(U) = 1/4 - U^2$ is positive because $|U| < 1/2$ from definition. Then equation (7), the long-term average of the Malthusian parameter, is

$$\bar{m} = \lim_{T \rightarrow \infty} (1/T) \log[g(U(0))/g(U(T))]/2 + \lim_{T \rightarrow \infty} (1/T) \int_0^T rU(t)^2/g(U(t))dt. \quad (\text{A5})$$

Since the first term of (A5) vanishes, we conclude $\bar{m} > 0$.

Combining Lemma 2 with Lemma 1, we conclude that $Y(t)$ and $Z(t)$ converge to zero in the neighborhood of $Y = Z = 0$, i.e., the line segment $\{(X, Y, Z); 0 \leq X \leq 1, Y = Z = 0\}$ is a locally attracting invariant set (GUCKENHEIMER and HOLMES, 1983). Therefore, the dynamical system is effectively described by the one-dimensional equation (8) if both $Y = X_1 - X_4$ and $Z = X_2 - X_3$ are sufficiently small initially.

We numerically confirmed $\bar{m} > 0$ holds for any initial condition, and that the invariant set is in fact globally attracting— Y and Z converge to zero with time and the system becomes one-dimensional. The same tendency is emphasized in the strong selection limit, in which $X_1 = X_4$ and $X_2 = X_3$ hold for all the generations after the first environmental change.

Given that $Y(t)$ and $Z(t)$ converge to zero, we prove that the polymorphism is protected at both loci as follows: Let us consider the reduced dynamics (8) in the neighborhoods of $X = 0$ and $X = 1$, as:

$$dX/dt = r/2, \quad X \neq 0, \quad (\text{A6a})$$

$$dX/dt = -r/2, \quad X \neq 1 \quad (\text{A6b})$$

where small terms (of higher order with respect to X and $(1 - X)$, respectively) are neglected. We can conclude from (A6) that $X(t)$ must stay away from boundaries; i.e., there exists a positive constant $\delta > 0$ so that $\delta < X(t) < 1 - \delta$. Together with $Y(t) = Z(t) = 0$, we conclude that the frequency of any genotype remains positive: $X_i(t) > \delta/2$ ($i = 1, 2, 3$ and 4).

Intuitive justification of the logic supporting the joint polymorphism is as follows: the relation $Y = Z = 0$ indicates $X_1 = X_4$ and $X_2 = X_3$. Suppose that either pair of genotypes (say AB and ab) almost vanishes ($X_1, X_4 \approx 0$), which would imply that the other two exist in about 50% abundance ($X_2, X_3 \approx 0.5$) because the total sum of the four genotypes is 1. Then recombination between the two abundant genotypes would produce

other “vanishing” genotypes, which contradicts the assumption. Therefore no genotype vanishes if Y and Z go to zero for a positive recombination rate.

Structural stability of protected polymorphism

We can further state that polymorphism at both loci is a “robust” property, or structurally stable, in the sense that the system perturbed by small additional terms should also have a protected polymorphism at both loci as long as these terms are sufficiently small. Note that Y and Z in the unperturbed system exponentially converge to zero with negative Lyapunov exponent, $-\bar{m}$, and that X goes neither to 0 nor to 1 along the line segment of $Y = Z = 0$. Under small perturbation, equations (A1) and (A6) have small terms in the right hand sides; then both Y and Z converge to a small neighborhood of $Y = Z = 0$, and X remains away from 0 or 1, implying a protected polymorphism.

To confirm the structural stability of the system, we numerically followed the genetic dynamics (1) adding the perturbation terms $\epsilon_i(t)$ ($i = 1, 2, 3, 4$) to the original fitness fluctuation. The selection coefficient of genotype i in the t th generation was $S_i(t) = h_i s(t) + \epsilon_i(t)$, with $h_1 = -h_2 = -h_3 = h_4 = 1$.

For cases where $s(t)$ fluctuates either periodically or randomly, we examined two types of perturbations: (1) $\epsilon_i(t)$ s are constant with respect to time and are randomly chosen from the interval $[-\epsilon, \epsilon]$. This includes cases of constant fitness difference between alleles. (2) $\epsilon_i(t)$ s are temporally fluctuating noises possibly with some autocorrelations with ϵ magnitude: $\sup_{i,t} |\epsilon_i(t)| < \epsilon$. In both, the values for different genotypes are independent. For each set of parameters, we calculated the number of generations before the frequency of either allele reached 99%, which we regarded as quasifixation. Ten replicates were calculated for each set of parameters, starting at an initial condition randomly chosen from the interval $[0, 1]$. Note that, because of the stochasticity in the initial condition, in Markovian jump selection, or in the perturbation, an allele frequency may exceed 99% in a finite time, even when all the alleles are stochastically protected in the sense of TURELLI (1981).

Results are: (1) for the unperturbed system ($\epsilon = 0$), no allele exceeds 99% in abundance before 10^5 generations, both for periodical ($s = 0.1$, period = 5) and for pink noise ($s = 0.1$, $p = 0.2$) fluctuation. (2) The same is true for the stochastically perturbed system with $\epsilon_i(t)$ fluctuating independently between generations. (3) The polymorphism is more vulnerable to temporally constant perturbations than fluctuating ones: For the case where $s(t)$ fluctuates with period $\tau = 5$, magnitude $s = 0.1$, and perturbation $\epsilon = 0.001$, no allele was quasi-fixed before 10^5 generations for $r = 0.5$, while quasifixation occurred within several thousand generations for $r = 0$. For pink noise, with $s = 0.1$, $\epsilon = 0.001$, and $p = 0.2$ ($\tau = 5$), no allele exceeded 99% before 10^5 generations in 6 out of 10 runs for $r = 0.01$; in contrast, quasifixation occurred between 10^3 and 10^4 generations in most (9 out of 10) cases for $r = 0$, and it also occurred before 10^3 generations in 7 out of 10 runs for $r = 0.5$. The last result is plausible because the convergence of Y and Z toward zero, which is a key step in the above proof of the maintenance of polymorphism, is caused by the negative Lyapunov exponent, $-\bar{m}$; hence the effect of recombination to protect the polymorphism is larger for intermediate r near r_{opt} , which results in a sufficiently positive $\bar{m}$, rather than too small or too large r .

APPENDIX B

In the following, we prove Propositions 1, 2 and 3 on the relationship between the optimal recombination rate and the power spectrum of environmental fluctuation.

Proof of Proposition 1: Differentiating equation (14) with

respect to r , we immediately have

$$\frac{\partial \bar{m}}{\partial r} = \int_0^\infty \frac{k^2 - r^2}{[r^2 + k^2]^2} f(k) dk \quad (\text{B1})$$

$$= \int_{k_{\min}}^{k_{\max}} \frac{[k - r][k + r]}{[r^2 + k^2]^2} f(k) dk,$$

and hence

$$\frac{\partial \bar{m}}{\partial r} \begin{cases} > 0, & \text{if } r < k_{\min}, \\ < 0, & \text{if } r > k_{\max}. \end{cases} \quad (\text{B2})$$

Since $\bar{m}$ increases monotonically with r for $r < k_{\min}$, and decreases for $r > k_{\max}$. We conclude that the optimal recombination rate, which maximizes $\bar{m}$ defined by equation (14), must lie in the range of $k_{\min} \leq r_{\text{opt}} \leq k_{\max}$.

Proof of Proposition 2: For any r_1 and r_2 satisfying $r_1 < r_2$, we have

$$\bar{m}(r_1) - \bar{m}(r_2) = \int_0^\infty \frac{f(r_1 X) - f(r_2 X)}{1 + X^2} dX > 0, \quad (\text{B3})$$

from (14), because $f(r_1 X) > f(r_2 X)$ holds for a decreasing function $f(x)$. Hence we conclude that $\bar{m}(r)$ is monotonically decreasing with r .

Proof of Proposition 3: First we note that

$$\begin{aligned} \bar{m}(0) &= \lim_{r \rightarrow 0} \int_0^\infty \frac{r f(k)}{r^2 + k^2} dk = \lim_{r \rightarrow 0} \int_0^\infty \frac{f(rX)}{1 + X^2} dX \\ &= \int_0^\infty \frac{f(0)}{1 + X^2} dX \\ &= \pi f(0)/2. \end{aligned} \quad (\text{B4})$$

On the other hand, $\bar{m}(r)$ can be estimated using the assumption (17), as

$$\begin{aligned} \bar{m}(r) &= \int_0^\infty \frac{f(rX)}{1 + X^2} dX \geq \int_0^{\delta/r} \frac{[f(0) + c r X]}{1 + X^2} dX \\ &= f(0) \text{Arctan}(\delta/r) + (c r/2) \log(1 + \delta^2/r^2). \end{aligned} \quad (\text{B5})$$

Then we have

$$[\bar{m}(r) - \bar{m}(0)]/r \geq f(0) [\text{Arctan}(\delta/r) - \pi/2]/r + (c/2) \log(1 + \delta^2/r^2). \quad (\text{B6})$$

As r tends to zero, the first term in the right-hand side of (B6) converges to $-f(0)/\delta$, and the second term diverges to positive infinity. Therefore for sufficiently small r , $\bar{m}(r) - \bar{m}(0)$ is positive.

APPENDIX C

Here we illustrate how to determine the location of evolutionarily stable recombination rate with an example of periodic fluctuation with the selection coefficient $s = 0.05$, the period $\tau = 25$, and the tight modifier linkage ($r_0 = 0$). We calculated the case of $r_1 = 0$ and $r_2 = 0.05$, starting from the population in which two modifiers (m_1 and m_2) are equally abundant. Computer run showed that m_2 increases, and in about 1000 generations it occupied more than 99% of the whole population. In the next run with $r_1 = 0.05$ and $r_2 = 0.10$, we again obtained the quasifixation of the modifier m_2 for the higher rate; hence the evolution toward a higher recombination rate. In contrast, if both r_1 and r_2 are larger, say $r_1 = 0.4$ and $r_2 = 0.5$, the allele for the smaller recombination rate (m_1) became fixed, indicating the evolution toward smaller recombination rate occurs. By calculations for various pairs of r_1 and r_2 , we saw that the allele for the higher recombination rate wins if both r_1 and r_2 are

smaller than 0.10, but the allele for the lower rate wins if both are larger than 0.14. For the case of $r_1 = 0.10$ and $r_2 = 0.14$, we observed a stable polymorphism of m_1 and m_2 maintained even after 10,000 generations. From these results, we concluded that the evolutionarily stable recombination rate, r_E is between 0.10 and 0.14. By similar procedures, we determined

the intervals listed in Tables 2–4. If we use a smaller difference between r_1 and r_2 , we can specify r_E with a higher precision, but the number of generations required for the modifier evolution increases because the natural selection working on the modifier becomes weaker.