

# Density-dependent selection in a random environment: An evolutionary process that can maintain stable population dynamics

(ecological genetics/*r*-selection/chaos/stochastic approximations)

MICHAEL TURELLI AND DOUG PETRY

Department of Genetics, University of California, Davis, California 95616

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**ABSTRACT** A theoretical analysis of natural selection is presented in which fitnesses depend on population density and randomly varying environmental processes. The theory is based on a general, heuristic analysis of a pair of coupled, nonlinear, stochastic difference equations that describe the joint dynamics of allele frequencies and population size. Four main conclusions emerge from the investigation of a particular class of models: (i) growth rates at low population densities tend to increase; (ii) individual selection, given sufficient genetic flexibility, will mold growth rates at higher densities so that in spite of *i*, stable deterministic population dynamics are maintained; (iii) "more fit" genotypes cannot be simply characterized—in particular, the mean population size need not be increased; and (iv) genetic polymorphisms can be maintained in both haploid and diploid organisms.

The connection between population dynamics and natural selection was central to Darwin's theory of evolution. Yet it is only within the past 20 years that a theory of selection has been developed in which fitnesses depend on population density (1-7). Because unpredictable environmental variation is an intrinsic part of nature, another important recent development is the incorporation of random fluctuations into relative fitnesses and population growth rates (see refs. 8 and 9 for reviews). This paper explores models that merge these two lines of investigation by letting fitnesses depend on both population density and random processes. One model of this sort was recently analyzed by Heckel and Roughgarden (10). Using an approximate analytical approach developed by Turelli (11) as a refinement of his technique (12), we will examine a more general class of models. The questions considered are: (i) how does individual selection act on population parameters that govern the stability of deterministic population dynamics, (ii) what characterizes "more fit" genotypes, and (iii) under what conditions are "protected polymorphisms" (13) maintained? The answer to (i) is shown to be strikingly model-dependent, but general conclusions emerge for a particular class of models. The answers to (ii) and (iii) differ significantly from the standard deterministic results.

The usual formulation of density-dependent selection at a diallelic locus is as follows. Assume that generations are discrete, denote the alleles by  $A_1$  and  $A_2$ , and let  $p_t$  denote the frequency of  $A_1$  at some specified stage of the life cycle (usually zygote or prereproductive adult) in generation  $t$ . Let  $N_{ij,t}$  denote the number of  $A_iA_j$  individuals at the censused life stage in generation  $t$ ; and let  $N_t = N_{11,t} + N_{12,t} + N_{22,t}$ , the total popu-

lation size. Denoting the (absolute) fitness of genotype  $A_iA_j$  by  $w_{ij}(N_t)$ , the recursions of interest are

$$p_{t+1} = p_t[p_t w_{11}(N_t) + q_t w_{12}(N_t)]/\bar{w}(N_t), \quad [1]$$

$$N_{t+1} = N_t \bar{w}(N_t), \quad [2]$$

in which  $q_t = 1 - p_t$  and  $\bar{w}(N_t) = p_t^2 w_{11}(N_t) + 2p_t q_t w_{12}(N_t) + q_t^2 w_{22}(N_t)$ . We assume that neither allele is completely dominant, that the  $w_{ij}$ 's are nonnegative, decreasing, differentiable functions with  $w_{ij}(0) > 1$ , and that recursion 2 has a locally stable equilibrium for each fixed  $p$ . The solution of  $w_{ij}(N) = 1$  is denoted  $K_{ij}$ . It has been shown under these assumptions (5, 7, 14) that, except for models yielding zero fitnesses, the qualitative outcome of selection is governed solely by the  $K_{ij}$ 's and selection maximizes the equilibrium population size. (See refs. 7 and 14 for precise descriptions of the maximization, ref. 15 for clarification of its biological import, and refs. 16-18 for the implications of relaxing the constraints on the  $w_{ij}$ 's.) In particular, if  $K_{11} < K_{12} < K_{22}$ , the population will evolve toward monomorphism for  $A_2$ ; whereas if  $K_{12} > K_{11}, K_{22}$ , a stable polymorphism will result. These results are easily motivated by observing that if the population is initially monomorphic for  $A_2$  and has achieved ecological equilibrium so that  $N_t = K_{22}$ , the dynamics of a mutant  $A_1$  allele would be approximately

$$p_{t+1} = p_t w_{12}(K_{22})/w_{22}(K_{22}) = p_t w_{12}(K_{22}). \quad [3]$$

Thus  $A_1$  would increase if and only if  $K_{12} > K_{22}$ . This boundary analysis will be generalized below to include stochastic effects.

In constant-environment models of populations with stable dynamics, selection does not act directly on parameters such as intrinsic growth rates that determine the local stability of and rate of return to the population-size equilibrium but not its position. In these models, such parameters could be subject to evolutionary modification only through pleiotropic effects of alleles controlling the  $K_{ij}$ 's. However, the direction of evolutionary change cannot be specified *a priori* because it would depend on the nature of the pleiotropy. Plausible arguments can be made for both positive and negative correlations between intrinsic growth rates and carrying capacities (cf. refs. 2 and 15). The evolution of intrinsic growth rates and other stability-determining parameters has important ecological and evolutionary implications. As several recent papers have pointed out (e.g., ref. 19), the task of understanding population dynamics in nature will be exceedingly complex if the relevant growth laws are not stable but intrinsically chaotic or cyclical with long periods. However, empirical studies that have fit simple growth curves to data have almost invariably yielded

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parameter estimates corresponding to stable population dynamics (20–22). Thomas *et al.* (21) have proposed group selection as a possible explanation. As shown below, the observed stability can also be accounted for by individual selection.

The key finding of the Heckel and Roughgarden (10) random environment study was that for a particular model, the stability-determining growth rate parameter,  $r$ , came under direct evolutionary control. They found that if genotypes differed only in their  $r$  values, selection would favor the genotype with the lowest  $r$ , so that  $r$  would tend to evolve toward zero. Our analysis will show that this prediction is not robust. In fact, for a large class of models  $r$  is selected upward. However the evolution of a second stability-determining parameter can counter the effects of ever-increasing  $r$  and maintain stable population dynamics. If the evolution of this parameter is constrained by pleiotropic effects, evolutionary increase of  $r$  can lead to unstable dynamics.

### A GENERAL MODEL AND APPROXIMATE BOUNDARY ANALYSIS

The heuristic boundary analysis of Eq. 3 will be extended to account for environmental fluctuations in the fitnesses  $w_{ij}$ . Let  $z_{ij,t}$  denote a vector-valued, stationary stochastic process with  $E(z_{ij,t}) = 0$  that models the environmental variation experienced by genotype  $A_iA_j$ . The second order moments of these processes will be generically denoted  $\sigma^2$ . Assume that the fitness of  $A_iA_j$  in generation  $t$  can be expressed as  $w_{ij}(N_t, z_{ij,t})$ , that the functions  $w_{ij}(N, 0)$  satisfy the conditions specified in the review of the deterministic theory presented above, and that the bivariate functions remain nonnegative and are differentiable. The recursions 1 and 2 generalize to the stochastic equations

$$p_{t+1} = p_t[p_t w_{11}(N_t, z_{11,t}) + q_t w_{12}(N_t, z_{12,t})] / \bar{w}_t, \quad [4]$$

$$N_{t+1} = N_t \bar{w}_t \quad [5]$$

with  $\bar{w}_t = p_t^2 w_{11}(N_t, z_{11,t}) + 2p_t q_t w_{12}(N_t, z_{12,t}) + q_t^2 w_{22}(N_t, z_{22,t})$ .

We conjecture that if  $A_1$  is a new mutant, Eq. 4 can be approximated by

$$p_{t+1} = p_t w_{12}(N_t, z_{12,t}) / w_{22}(N_t, z_{22,t}), \quad [6]$$

and the dynamics of  $N_t$  can be approximated by the stationary solution of

$$N_{t+1} = N_t w_{22}(N_t, z_{22,t}), \quad [7]$$

corresponding to the long-term stochastic behavior of a population monomorphic for  $A_2$ . We also conjecture that Eqs. 6 and 7, together with the analogous equations with the roles of  $A_1$  and  $A_2$  reversed, can provide necessary and sufficient conditions for the existence of a stable polymorphism. Two assumptions underly the latter conjecture. The first is that the stochastic dynamics of a polymorphic population would ultimately produce the configuration described by Eqs. 6 and 7 so that  $A_1$  must be able to increase in frequency according to them in order to be maintained. The second is that no additional information relevant to evaluating  $P(p_t \rightarrow 0 \text{ as } t \rightarrow \infty)$  is contained in the fully nonlinear system 4, 5. We cannot rigorously justify these assumptions, but computer simulations support predictions based on them (see ref. 23 for a similar analysis of two-dimensional diffusion processes).

In addition, partial support comes from the corresponding density-independent theory. Note that if the population process  $N_t$  can be described by a stationary solution of Eq. 7, Eq. 4 is equivalent to a density-independent model of selection in a

random environment. As shown heuristically by Gillespie (24) and rigorously by Karlin and Liberman (25),  $p_t$  will be repelled from zero and allele  $A_1$  will be “protected” if and only if  $E[\ln w_{12}(N_t, z_{12,t})] > E[\ln w_{22}(N_t, z_{22,t})]$ . This criterion follows directly from Eq. 6. Stationarity of  $N_t$  with respect to Eq. 7, implies that  $E[\ln w_{22}(N_t, z_{22,t})] = 0$ . Hence the conjectured condition for protection of the  $A_1$  allele reduces to

$$E[\ln w_{12}(N_t, z_{12,t})] > 0 \quad [8]$$

in which  $E$  denotes expectation taken with respect to the joint stationary distribution of  $N_t$  and  $z_{12,t}$  and the distribution of  $N_t$  determined by Eq. 7.

In most circumstances, it will be impossible to compute analytically the expectation in 8, and approximations or numerical evaluations, or both will be required. We will outline a general approximation technique (see ref. 11 for details). The approximation assumes that the level of environmental variation is sufficiently low that terms of order  $\sigma^n$  for  $n \geq 3$  can be ignored. To simplify the notation, we will drop the second subscript in the expressions that follow; thus,  $w_{12}(N_t, z_{12,t})$  will be written as  $w_1(N_t, z_{1,t})$ . This notation emphasizes the fact that our boundary analysis is equivalent to the analysis of a haploid model with  $A_2$  an established genotype and  $A_1$  a rare mutant.

To approximate  $E[\ln w_1(N_t, z_{1,t})]$ , introduce the variable  $n_t = (N_t - K_2)/K_2$  and expand  $\ln w_1(N_t, z_{1,t})$  in a Taylor series about  $(K_2, 0)$ .  $E(n_t)$  and  $E(n_t^2)$  are of order  $\sigma^2$  (11). Hence, assuming that the means of terms of the form  $n_t^a z_{1,t}^b$  for  $a + b \geq 3$  are of order  $\sigma^3$  or smaller, one can obtain an approximation for 8 valid to order  $\sigma^2$  by ignoring terms involving third and higher-order partial derivatives. The resulting approximation for  $E[\ln w_1(N_t, z_{1,t})]$  depends only on  $E(n_t)$ , the variance-covariance matrix of  $(n_t, z_{1,t})$ , and  $w_1$  and its first- and second-order partial derivatives at  $(K_2, 0)$ . We will consider here only the case in which the noise processes  $z_{i,t}$  are nonautocorrelated so that only  $E(n_t^2)$  and  $E(n_t)$  must be approximated. Any scheme of cross-correlation is allowed. With the assumption that the deterministic dynamics of the resident genotype are stable,  $E(n_t^2)$  can be obtained to order  $\sigma^2$  by linearizing Eq. 7 about  $(K_2, 0)$ . To approximate  $E(n_t)$ , recall that the assumption of stationarity of  $N_t$  with respect to Eq. 7 implies that  $E[\ln w_2(N_t, z_{2,t})] = 0$ . Repeating the second order Taylor series approximation yields a linear equation for  $E(n_t)$  in terms of  $E(n_t^2)$  and the variance-covariance matrix of  $z_{2,t}$ .

In the applications of the next section, the  $w_i$  depend on only two noise processes,  $z_{i,t}$  and  $z'_{i,t}$ . Their standard deviations will be denoted  $\sigma_i$  and  $\sigma'_i$  and their correlation  $\rho_i$ . The approximations described above imply that to order  $\sigma^2$

$$\begin{aligned} E[\ln w_1(N_t, z_{1,t}, z'_{1,t})] = & \ln w_1 \\ & + (K_2^2/2)(D_{NN}w_1 - cD_{NN}w_2)E(n_t^2) \\ & + (\sigma_1^2 D_{zz}w_1 - c\sigma_2^2 D_{zz}w_2)/2 + [(\sigma'_1)^2 D_{z'z'}w_1 \\ & - c(\sigma'_2)^2 D_{z'z'}w_2]/2 \\ & + (\rho_1\sigma_1\sigma'_1 D_{zz'}w_1 - c\rho_2\sigma_2\sigma'_2 D_{zz'}w_2), \quad [9] \end{aligned}$$

in which  $D_{xy}w_i = \partial^2 \ln w_i / \partial x \partial y$ ;  $c = (\partial \ln w_1 / \partial N) / (\partial \ln w_2 / \partial N)$ ,  $E(n_t^2) = [(d\sigma_2)^2 + (d'\sigma'_2)^2 + 2dd'\rho_2\sigma_2\sigma'_2] / (1 - \lambda^2)$ ,  $d = \partial w_2 / \partial z$ ,  $d' = \partial w_2 / \partial z'$ ,  $\lambda = 1 + K_2(\partial w_2 / \partial N)$ , and all of the functions are evaluated at  $(K_2, 0, 0)$ . If the right hand side of Eq. 9 is positive, we expect that allele  $A_1$  will be protected—i.e.,  $P(p_t \rightarrow 0 \text{ as } t \rightarrow \infty) = 0$ . If it is negative, by analogy to the density-independent theory we expect that the equilibrium  $p_t = 0$  will be attracting—i.e.,  $p_t$  will tend to converge to zero when near it (see ref. 25).

If no noise is present, the right hand side of Eq. 9 reduces to  $\ln w_1$ , whose sign would determine the fate of  $A_1$  in a deter-

ministic environment. Because of the additional terms,  $K_1 > K_2$  is neither necessary nor sufficient for allele  $A_1$  to be protected, and any parameters that enter the partial derivatives of the  $w_i$  will come under selection. However, the intensity of selection is on the order of  $\sigma^2$  (note that the quantities  $D_{NN}$  are proportional to  $K^{-2}$ ). It is reassuring that if the genotypes  $A_1A_2$  and  $A_2A_2$  have identical fitness functions and experience identically distributed environmental perturbations, the right hand side of Eq. 9 reduces to zero. Thus, as expected under neutrality, the rare allele tends to neither increase nor decrease. This also shows that our analysis is inappropriate for models involving complete dominance.

## RESULTS AND DISCUSSION

To focus on the evolution of stability-determining parameters that come under direct selection only when population fluctuations are considered, we will investigate several stochastic analogs of

$$N_{t+1} = N_t G[(N_t/K)^\theta] \quad [10]$$

in which  $G(0) = 1 + r$ ,  $G(1) = 1$ ,  $G(x) > 0$ , and  $G'(x) < 0$ . We will concentrate on three specific cases:  $G(x) = \max[0, 1 + r(1 - x)]$ ,  $G(x) = \exp[\ln(1 + r)(1 - x)]$ , and  $G(x) = (1 + r)/(1 + rx)$ . These will be referred to as the linear, exponential, and hyperbolic models, respectively. Each is a discrete-time analog of  $dN/dt = rN[1 - (N/K)^\theta]$  (cf. refs. 26 and 27). The linear and exponential forms have been fit to *Drosophila* data by Mueller (22) and Thomas *et al.* (21), respectively. Their work provided the motivation for considering this class of models. Unlike the logistic model, which corresponds to  $\theta = 1$ , and various multi-parameter growth models such as those proposed by Schoener (28) and Hassell (29), this model has two separate parameters,  $r$  and  $\theta$ , that govern the shape of population trajectories without modifying the equilibrium population size. The importance of this flexibility will become clear below. The local (and presumably global) stability of  $K$  is governed jointly by  $r$  and  $\theta$  according to the eigenvalues  $\lambda = 1 - \theta r$ ,  $\lambda = 1 - \theta \ln(1 + r)$ , and  $\lambda = 1 - \theta r/(1 + r)$ , corresponding to the linear, exponential, and hyperbolic models, respectively. For Eq. 10,  $\lambda = 1 + \theta G'(1)$ .

For a given deterministic model, stochasticity can be incorporated in various ways. Because the biological mechanisms that produce these recursions and determine their parameters are not specified, the manner of incorporation of noise can only metaphorically reflect specific biological processes. We will consider two extremes. The first corresponds to stochastic fluctuations in the species' limiting resource and is modeled by replacing  $K$  in Eq. 10 by  $K(1 + z_t)$  with  $z_t > -1$ . [One can multiply  $1/K$  by  $(1 + z_t)$  without modifying the conclusions below.] In this context,  $E(z_t^2) \equiv \sigma_K^2$  is the square of the coefficient of variation of  $K$ . This formulation of density-dependent growth in a random environment has been repeatedly used in theoretical ecology (e.g., refs. 9, 12, 30, 31). Nevertheless, there are certainly stochastic environmental factors that can affect individual survival rates and thereby population growth rates in a density-independent fashion. These can be modeled by multiplying the per capita growth rate,  $G$ , in Eq. 10 by  $(1 + z_t)$  with  $z_t > -1$ . Here  $E(z_t^2) \equiv \sigma_G^2$  is the square of the coefficient of variation of the per capita growth rate. Actual environmental events such as temperature and rainfall fluctuation would almost certainly not fit neatly into either of these categories but rather would contribute to both. Hence, we suggest that a more reasonable representation of a "random environment" than either the purely density-dependent or the density-independent extremes is to simultaneously consider both. A mathematical

assumption that is critical to several of the predictions below is that the level of environmental noise does not affect the arithmetic mean growth rate and  $K$  value (or, alternately, the value of  $K^{-1}$ ). This convention coincides with the standard interpretation of "average". It implies that as the level of environmental fluctuations increases, the geometric mean growth rate and  $K$  value decrease, leading to a decrease in the (arithmetic) mean population size.

**Evolution of Population Parameters.** The selection pressures acting on the stability-determining parameters can be isolated by determining the fate of a rare mutant that has the same deterministic equilibrium and experiences the same level and pattern of environmental variation as the resident type but differs slightly in its  $r$  or  $\theta$  values, or both (cf. ref. 32). Applying the approximation 9 to the general model 10 with noise in both  $K$  and  $G$  shows that the mutant, denoted with subscript 1, should succeed or fail according to whether

$$\begin{aligned} \theta_1 \theta_2 \{ \theta_1 G'_2 [(G'_1)^2 - G''_1 - G'_1] - \theta_2 G'_1 [(G'_2)^2 \\ - G''_2 - G'_2] \} (1 - 2\theta_2 G'_2 \omega) \\ - \theta_2 G'_2 (2 + \theta_2 G'_2) (\theta_2 G'_2 - \theta_1 G'_1) \quad [11] \end{aligned}$$

is positive or negative. In [11],  $G'$  and  $G''$  are evaluated at 1; and

$$\omega = \rho \left( \frac{\sigma_K}{\sigma_G} \right) + \left( \frac{\sigma_K}{\sigma_G} \right)^2 \quad [12]$$

with  $\rho$  denoting the level of cross correlation between the fluctuations in  $K$  and  $G$ . Note that for any level of cross-correlation,  $\omega \geq -1/4$ . Almost all of the results reported below follow from [11]. The critical assumptions on which its biological usefulness hinges are: (i) that the models examined are sufficiently accurate descriptions of population dynamics and (ii) that specific patterns of pleiotropy do not prevail that link the values of  $r$  and  $\theta$  either positively or negatively to each other or to  $K$  and  $\sigma^2$ , which are also under selection. If these assumptions hold, natural selection should drive parameter values in the direction predicted by [11]. When only a single parameter is varied, we will refer to the predicted results as "univariate evolution". To illustrate the sensitivity of the predictions to the model used, we present a progression of results beginning with univariate evolution of  $r$  with noise in either  $K$  or  $G$  and ending with general results that follow from [11].

Because the dependence of  $G'(1)$  and  $G''(1)$  on  $r$  cannot be specified in general, [11] yields no general prediction for the univariate evolution of  $r$ . Table 1 shows the results for our specific models. Extremely diverse predictions emerge. For the linear model with noise in  $K$ , the prediction  $r \downarrow 0$  parallels that of Heckel and Roughgarden (10) for a linearized version of this model with  $\theta = 1$ . However, if noise is added to  $G$  rather than to  $K$ , selection drives  $r$  toward  $1/\theta$ . Results for the exponential model can be obtained analytically without recourse to the approximations of the previous section whenever the stochastic model possesses a stationary distribution with  $E \ln N_t < \infty$  (see ref. 11 for details). Noise in  $K$  leaves  $r$  as a neutral parameter, just as it is in the deterministic theory. With noise in  $G$ , on the other hand,  $r$  evolves upward and even can be selected into the region corresponding to deterministic chaos. Although our approximate analysis requires  $|\lambda| < 1$  for the resident genotype, the parameter values of the rare mutant need not satisfy this constraint. Thus, although our analysis cannot predict whether an initially unstable population ( $\lambda < -1$ ) will evolve stability, it can predict whether an initially stable population will gradually evolve parameter values yielding instability.

For the hyperbolic model,  $r$  is expected to increase whether noise is added to  $K$  or to  $G$ . As  $r \rightarrow \infty$ ,  $\lambda \rightarrow 1 - \theta$ , which can be

Table 1. Univariate evolution of  $r$  and  $\theta$  in stochastic analogs of Model 10 with noise in either  $K$  or  $G$

	Linear		Exponential		Hyperbolic	
	$K$	$G$	$K$	$G$	$K$	$G$
$r$	$\downarrow 0$	$\frac{1}{\theta}$	Neutral	$\uparrow$	$\uparrow$	$\uparrow$
$\lambda_r$	$\uparrow 1$	$\rightarrow 0$	—	$\downarrow$ (chaos)	$\downarrow 1 - \theta$	$\downarrow 1 - \theta$
$\theta$	$\downarrow 0$	$\rightarrow \frac{2}{1 + 2r}$	$\downarrow 0$	$\rightarrow \frac{2}{1 + \ln(1 + r)}$	$\downarrow 0$	$\rightarrow 2$
$\lambda_\theta$	$\uparrow 1$	$\rightarrow 1 - \frac{2r}{1 + 2r}$	$\uparrow 1$	$\rightarrow 1 - \frac{2 \ln(1 + r)}{1 + \ln(1 + r)}$	$\uparrow 1$	$\rightarrow 1 - \frac{2r}{1 + r}$

any value less than one. Thus, literally *any* prediction can be obtained concerning the evolutionary dynamics of  $r$  and  $\lambda$ . Moreover, these approximate analytical predictions are supported by computer simulations. In contrast to this diversity, all three models give the same predictions for the univariate evolution of  $K$  and  $\sigma^2$ .  $K$  tends to increase as expected from the density-dependent deterministic theory, and  $\sigma^2$  tends to decrease as expected from the density-independent stochastic theory (24).

Once the parameter  $\theta$  is introduced, even if only to provide increased flexibility for data fitting, it is artificial to regard it as a constant that cannot be modified by selection.  $\theta$  can be estimated and, as demonstrated by Mueller (22), there is likely to be intrapopulation genetic variation for its value. Hence, in principle, it can respond to selection. However, as stated earlier, predictions from [11] concerning its evolution will only be meaningful if it can be genetically disentangled from the other parameters under selection. This can only be determined empirically. With this caveat, we will examine its univariate evolution. The results for models with noise in  $K$  or  $G$  are summarized in Table 1. Unlike the predictions for  $r$ , clear patterns appear. With only noise in  $K$ , selection always acts to reduce  $\theta$  toward zero, pushing  $\lambda$  toward one. This holds for Eq. 10 whenever  $c(G) \equiv [G'(1)]^2 - G'(1) - G''(1) > 0$ , as it is for the linear, exponential, and hyperbolic models. In contrast, whenever  $c(G) > 0$  and noise is added only to  $G$ ,  $\theta$  is selected toward a positive constant that depends on the model, and the corresponding eigenvalue, denoted  $\hat{\lambda}_\theta$ , satisfies  $|\hat{\lambda}_\theta| < 1$ . This result is generalized below.

In the presence of correlated noise in  $K$  and  $G$ ,  $r$  evolves upward for both the exponential and hyperbolic models. For the exponential model, this eventually would lead to instability if  $\theta$  remained fixed; for the hyperbolic model, instability can result only if  $\theta > 2$ . For the linear model,  $r$  evolves toward  $\hat{r}_\theta = [-1 + \sqrt{1 + 4\omega}]/2\theta\omega$ , with  $\omega$  defined by [12]. For  $\omega > 0$ , the corresponding eigenvalue always lies between zero and one. For the general model 10, if  $c(G) > 0$  and  $\omega > -1/4$  selection pushes  $\theta$  toward

$$\hat{\theta}_G = \frac{(G')^2 + c(G) - \sqrt{[(G')^2 + c(G)]^2 + 16(G')^2 c(G)\omega}}{4G'c(G)\omega} > 0, \tag{13}$$

and the corresponding eigenvalue,  $\hat{\lambda}_\theta$ , satisfies  $|\hat{\lambda}_\theta| < 1$ . If  $\omega > 0$  and  $G''(1) \leq -G'(1)$ , which is satisfied by the linear model for all  $r > 0$ , by the exponential for  $0 < r \leq e - 1$ , and by the hyperbolic for  $0 < r \leq 1$ ,  $\hat{\lambda}_\theta > 0$ . Thus for this broad class of models, evolution of  $\theta$ , based solely on individual selection, emerges as a potential evolutionary mechanism capable of

maintaining stable population dynamics. For the linear model, evolution of  $r$  can also maintain stability.

Because of the complexity of expression 11 when both  $r$  and  $\theta$  vary, the joint evolution of these parameters has not been completely characterized for any of our models. However, an interesting result follows from examining the direction of selection along a particular slice of  $(r, \theta)$  space. If the rare type has the same eigenvalue [i.e., the same value of  $\theta G'(1)$ ] as the resident, [11] has the same sign as  $\theta_1^2 G''_1(1) - \theta_2^2 G''_2(1) + (\theta_2 - \theta_1)(1 - \lambda)$ . Because this expression is generally not equal to zero, it shows that  $\lambda$  by itself does not determine the outcome of selection. When applied to the linear model, for which  $G''(1) = 0$ , it shows that selection favors lower  $\theta$  and higher  $r$ . Thus, in the linear model with noise in both  $K$  and  $G$ , there is selection for ever higher intrinsic growth rates, just as there is in the exponential and hyperbolic models. This selection pressure, which is proportional to  $\sigma^2$ , can be viewed as additional support for and quantification of the proposal that high intrinsic growth rates are favored in uncertain environments. Although the underlying models are quite different, this result parallels the “ $r$ -selection” reported in refs. 4, 16, and 33 and implicit in the two-species analysis of ref. 23.

**Characterization of Fitness and Conditions for Polymorphism.** As originally emphasized by MacArthur (1),  $K$  plays the role of fitness in the standard deterministic theory of density-dependent selection. Natural candidates for a stochastic analog are the arithmetic, geometric, and harmonic mean population size. These can be approximated by  $K[1 + E(n_t)]$ ,  $K[1 + E(n_t) - \text{Var}(n_t)/2]$ , and  $K[1 + E(n_t) - \text{Var}(n_t)]$ , respectively. By comparing the conditions for these quantities to increase with conditions for a rare mutant to increase, one finds that univariate evolution of  $r$ ,  $K$ , or  $\sigma$  leads to the increase of all three means. However, none of them need be increased by univariate evolution of  $\theta$  or multivariate evolution. Thus, as conjectured by Slatkin and Maynard Smith (34), there is no simple characterization of “more fit” genotypes. In spite of the counterexamples, preliminary numerical investigations suggest that all three means “usually” increase under selection, just as  $\bar{w}$  does in deterministic two-locus theory (35).

Because of the large number of parameters, many conditions can be provided under which these models maintain polymorphisms. The most surprising is that a haploid polymorphism can exist with two genotypes that differ only in their  $\theta$  values (cf. ref. 16). Naturally, because of the convergence result 13, the  $\theta$  values must lie on opposite sides of  $\hat{\theta}_G$ . There are two especially interesting classes of diploid polymorphisms. If  $c(G) > 0$ , the general model 10 with noise in both  $K$  and  $G$  will produce a stable polymorphism whenever the heterozygotes experience less environmental variation than either homozygote (cf. ref. 24). In addition, for all three specific models, poly-

morphisms can be maintained with heterozygotes intermediate but alternate homozygotes favored with respect to  $r$  and  $K$ . Thus pleiotropic "tradeoffs" of the type frequently discussed in evolutionary ecology can also provide a basis for the maintenance of genetic variation (cf. refs. 4 and 16).

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