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A Quantitative Genetic Model of r - and K -Selection in a Fluctuating Population

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ABSTRACT: We analyze a stochastic quantitative genetic model for the joint dynamics of population size N and evolution of a multi-dimensional mean phenotype \bar{z} under density-dependent selection. This generalizes our previous theories of evolution in fluctuating environments to include density-dependent (but frequency-independent) selection on quantitative characters. We assume that appropriate constraints or trade-offs between fitness components exist to prevent unlimited increase of fitness. We also assume weak selection such that the expected rate of return to equilibrium is much slower for \bar{z} than N . The mean phenotype evolves to a stationary distribution around an equilibrium point \mathbf{z}_{opt} that maximizes a simple function determined by ecological parameters governing the dynamics of population size. For any \bar{z} , the expected direction of phenotypic evolution is determined by the additive genetic covariance matrix \mathbf{G} and the gradient of this function with respect to the mean phenotype. For the theta-logistic model of density dependence, evolution tends to maximize the expected value of N^θ .

Keywords: quantitative genetics, r - and K -selection, density-dependent selection, fluctuating selection, environmental stochasticity, population dynamics.

Introduction

Most classical population genetics theory either assumes constant population size or allows for population growth but assumes that the relative fitnesses of genotypes are independent of population density. Under these circumstances, evolution increases the density-independent growth rate of log population size, or mean Malthusian fitness \bar{r} . In continuous time, the rate of evolution of \bar{r} in a constant environment is given by Fisher's (1930) fundamental theorem $d\bar{r}/dt = \mathbf{G}_{rr}$, where \mathbf{G}_{rr} is the additive genetic variance of r . This classical theory ignores two important sources of demographic and evolutionary

change in natural populations: environmental stochasticity, which causes random fluctuations in population size, and density regulation of population size, which induces density-dependent feedbacks in the population dynamics. In a fluctuating environment without any density dependence, the long-run growth rate $s = \bar{r} - \sigma_e^2/2$, where σ_e^2 is the temporal environmental variance in r , has been used as a fitness measure (e.g., Turelli 1981; Tuljapurkar 1982; Metz et al. 1992, 2008). The long-run growth rate of a rare allele or genotype determines whether it can successfully invade a large population in a fluctuating environment (Turelli 1981; Tuljapurkar 1982; Gillespie 1991; Charlesworth 1994). Lande (2007, 2008) extended these results further, showing that although the expected evolution maximizes the population's long-run growth rate, the valid measure of a genotype's or phenotype's relative fitness in a fluctuating environment at shorter time scales is its Malthusian fitness in the average environment minus the environmental covariance of its fitness with the population growth rate.

Density-dependent selection occurs when genotypic fitnesses respond differently to changes in population size. If the fitnesses of all genotypes have the same response to environmental change, the relative fitnesses remain constant and selection is density independent. In continuous time models, changes in relative fitness are measured by additive changes in Malthusian fitness.

In a constant environment, MacArthur (1962) showed that for a simple model with logistic density regulation, evolution maximizes the equilibrium population size, or carrying capacity K . This is true regardless of the form of density regulation. This result was later extended to include models of age structure (Charlesworth 1994) and frequency-dependent selection (Nagylaki 1992). MacArthur and Wilson (1967) thus suggested that selection should favor increased population growth rate at small population sizes (r -selection), whereas at large population sizes selection should result in increased carrying capacity

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(K -selection). This implies that in a population of fluctuating size, a trade-off must exist between r - and K -selection such that r -selection prevails when the population size is small compared to K and K -selection dominates when the population is near or above K (MacArthur and Wilson 1967; Pianka 1970, 1972; Roughgarden 1971; MacArthur 1972; Gilpin et al. 1976; Felsenstein 1979; Boyce 1984; Mueller 1997, 2009). Trade-offs between major components of fitness have been comprehensively reviewed by Roff (2002).

Ecologists have long understood that evolution in response to the trade-off between r - and K -selection depends on the magnitude of fluctuations in population size caused by environmental variation (Gadgil and Solbrig 1972). The first models of r - and K -selection in continually fluctuating environments were deterministic models of seasonal fluctuations or stochastic one-locus models (Roughgarden 1971; Turelli and Petry 1980) with asexual inheritance as in MacArthur's (1962) original model. Tanaka (1996) used a quantitative genetic model to demonstrate by means of stochastic simulations that large noise introduced by non-selective removal of individuals promoted r -selection. This culminated in Lande et al.'s (2009) model, which produced the general result that, averaged over the stationary distribution of population sizes N , evolution maximizes the expected value of a simple function of population size rather than population size itself. Use of a haploid or asexual model of inheritance facilitates the derivation of such results because different genotypes constrained by genetic and ecological trade-offs each have their own stationary distribution of population size. Thus, the stable evolutionary equilibrium consists of a population with no polymorphism. For the theta-logistic form of density dependence (Gilpin et al. 1976; Lande et al. 2003) with a constant parameter θ , evolution maximizes $E(N^\theta) = sK^\theta/r = [1 - \sigma_e^2/(2r)]K^\theta$, the average of N^θ over the stationary distribution of population size N (Lande et al. 2009). This is a function of basic ecological parameters: the intrinsic rate of increase of the population in the average environment r , the carrying capacity in the average environment K , and the environmental variance σ_e^2 in the population growth rate. For small environmental variance, $s/r = 1 - \sigma_e^2/(2r)$ is approximately 1 and $E(N^\theta) \approx K^\theta$ so that evolution maximizes K^θ and hence K , as in MacArthur's (1962) model for a constant environment. For large environmental variances, large values of r and s are favored. Similarly, for large values of θ , large r is favored for only very large environmental variances such that density regulation is not significant until the population is close to K . Thus, for a genetic trade-off between r and K , the magnitude of the environmental variance determines the resolution of the conflicting selection pressures on r and K . Generally, for a set of possible combinations of r , K ,

and σ_e^2 that all vary genetically, evolution maximizes the above function of all three parameters.

Lande et al.'s (2009) results were derived from a simple haploid or asexual model of inheritance. However, most traits of interest to ecologists and evolutionary biologists are quantitative polygenic characters influenced by numerous genes and environmental effects that tend to remain polymorphic, allowing continuous adaptation to environmental fluctuations.

Here we extend the above results to quantitative characters in a sexual population by generalizing the model of Lande (2007) for evolution of a vector of correlated characters in a fluctuating environment. This model gives the joint process for mean character and log population size as a diffusion. We derive a maximization principle analogous to the result of Lande et al. (2009) by analyzing expected phenotypic evolution averaged over stationary distribution of population size for a given mean phenotype, assuming weak selection such that the expected rate of return to equilibrium is much faster for N than for \bar{z} . The analysis is based on the simple observation that under density-dependent (but frequency-independent) selection, the dynamics of the total population size takes the same functional form as it does for the fitness of each phenotype, although with different parameters. For example, if the fitness of each phenotype follows the theta-logistic model of density dependence, then the expected dynamics of N is also theta logistic.

Lande's Stochastic Quantitative Genetic Model

We now give a short presentation of the model and main results of Lande (2007), modified to incorporate density-dependent selection. Let \mathbf{z} be a (column) vector of phenotypic characters for an individual with a multivariate normal distribution $p(\mathbf{z})$ in the population, with mean $\bar{\mathbf{z}}$ and covariance matrix \mathbf{P} among individuals. The breeding values are assumed to be normal with the same mean, and the additive genetic covariance matrix \mathbf{G} is assumed to be maintained by mutation and recombination. Time is assumed to be continuous and measured in generations. For simplicity, both \mathbf{P} and \mathbf{G} are assumed to be constant.

We consider a large population where the number of individuals with phenotypes in the range \mathbf{z} to $\mathbf{z} + d\mathbf{z}$ is $n(\mathbf{z})d\mathbf{z}$, corresponding to a total population size $N = \int n(\mathbf{z})d\mathbf{z}$ with phenotypic distribution $p(\mathbf{z}) = n(\mathbf{z})/N$. Generations overlap, but the rates of mortality and reproduction are assumed to be independent of age so that age structure can be ignored. Lande (2007) assumed that the Malthusian fitness of phenotype \mathbf{z} takes the form $r(\mathbf{z}) - g(N)$ (correcting a misprint of n instead of N in Lande 2007), allowing for density regulation of the population but excluding density-dependent selection. Here we allow the Malthusian fit-

ness of each phenotype to have a more general form incorporating density-dependent selection, $m(\mathbf{z}, N)$. The total population size N is assumed to remain large enough that demographic stochasticity and random genetic drift may be disregarded. Environmental stochasticity is described by the density-independent infinitesimal covariance between the changes in $n(\mathbf{y})$ and $n(\mathbf{z})$ due only to selection, $c(\mathbf{y}, \mathbf{z})n(\mathbf{y})n(\mathbf{z})$. Extending the derivation of Lande (2007) as explained in appendix A, we find that the infinitesimal mean and variance of N are $\tilde{m}(\bar{\mathbf{z}}, N)N$ and $\sigma_e^2(\bar{\mathbf{z}})N^2$, respectively, where

$$\begin{aligned}\tilde{m}(\bar{\mathbf{z}}, N) &= \int p(\mathbf{z})m(\mathbf{z}, N)d\mathbf{z}, \\ \sigma_e^2(\bar{\mathbf{z}}) &= \iint p(\mathbf{y})p(\mathbf{z})c(\mathbf{y}, \mathbf{z})d\mathbf{y}d\mathbf{z}.\end{aligned}$$

Here $\sigma_e^2(\bar{\mathbf{z}})$ is the environmental variance in N . Notice that \tilde{m} and σ_e^2 depend on $\bar{\mathbf{z}}$ through the distribution $p(\mathbf{z})$. Transforming the diffusion for N (Karlin and Taylor 1981) to the natural log scale $\ln N$ has infinitesimal mean

$$\frac{1}{dt}E[d\ln N|N, \bar{\mathbf{z}}] = \tilde{m}(\bar{\mathbf{z}}, N) \quad (1)$$

and variance

$$\frac{1}{dt}\text{Var}[d\ln N|N] = \sigma_e^2(\bar{\mathbf{z}}), \quad (2)$$

where $\tilde{m}(\bar{\mathbf{z}}, N) = \bar{m}(\bar{\mathbf{z}}, N) - (1/2)\sigma_e^2(\bar{\mathbf{z}})$ is the stochastic growth rate (infinitesimal mean on the log scale) of the population for a given population size and mean phenotype. The infinitesimal mean for $\bar{\mathbf{z}}$ is

$$\frac{1}{dt}E[d\bar{\mathbf{z}}|\bar{\mathbf{z}}, N] = \mathbf{G}\nabla\tilde{m}(\bar{\mathbf{z}}, N). \quad (3)$$

Here $\nabla = (\partial/\partial\bar{z}_1, \partial/\partial\bar{z}_2, \dots, \partial/\partial\bar{z}_k)^T$ is the gradient with respect to $\bar{\mathbf{z}}$, where T denotes matrix transposition and k is the dimension of \mathbf{z} . So rather than by the gradient of the deterministic growth rate in the deterministic model (Lande 1982), the expected evolution in a fluctuating environment under density-dependent (but frequency-independent) selection is given by the selection gradient of the stochastic growth rate in equation (1). The infinitesimal covariance matrix for $\bar{\mathbf{z}}$ is

$$\begin{aligned}&\frac{1}{dt}\text{Cov}[d\bar{\mathbf{z}}, d\bar{\mathbf{z}}^T] \\ &= \mathbf{G}\mathbf{P}^{-1}\text{Cov}[c(\mathbf{y}, \mathbf{z}), (\mathbf{y} - \bar{\mathbf{z}})(\mathbf{z} - \bar{\mathbf{z}})^T]\mathbf{P}^{-1}\mathbf{G}.\end{aligned} \quad (4)$$

Here $c(\mathbf{y}, \mathbf{z})$ is a scalar, while $(\mathbf{y} - \bar{\mathbf{z}})(\mathbf{z} - \bar{\mathbf{z}})^T$ is a $k \times k$ matrix so that the covariance in the formula is a $k \times k$ matrix with elements that are the covariances between

$c(\mathbf{y}, \mathbf{z})$ and the corresponding element $(\mathbf{y} - \bar{\mathbf{z}})(\mathbf{z} - \bar{\mathbf{z}})^T$. The covariances refer to \mathbf{y} and \mathbf{z} being independent with marginal distributions $p(\mathbf{z})$ so that their joint distribution is $p(\mathbf{y})p(\mathbf{z})$. As pointed out by Lande (2007), this covariance matrix measures an aspect of the curvature of the environmental covariance function $c(\mathbf{y}, \mathbf{z})$ between phenotypes (Lande and Arnold 1983).

Finally, defining $\tilde{c}(\mathbf{z}) = \int c(\mathbf{y}, \mathbf{z})p(\mathbf{y})d\mathbf{y}$, the infinitesimal covariance between $\ln N$ and $\bar{\mathbf{z}}$ is

$$\frac{1}{dt}\text{Cov}[d\ln N, d\bar{\mathbf{z}}|\bar{\mathbf{z}}, N] = \mathbf{G}\mathbf{P}^{-1}\text{Cov}[\tilde{c}(\mathbf{z}), \mathbf{z}]. \quad (5)$$

Here $\tilde{c}(\mathbf{z})$ is a scalar and \mathbf{z} a column vector so that $\text{Cov}[\tilde{c}(\mathbf{z}), \mathbf{z}]$ is a column vector with elements that are the covariances between $\tilde{c}(\mathbf{z})$ and the corresponding component \mathbf{z} , with all covariances referring to the distribution $p(\mathbf{z})$.

If all phenotypes are equally affected by fluctuations in the environment, then $c(\mathbf{y}, \mathbf{z})$ and $\tilde{c}(\mathbf{z})$ are constants σ_e^2 (independent of $\bar{\mathbf{z}}$) and all covariances in equations (4) and (5) are zero. Evolution is still nevertheless stochastic, driven by fluctuations in N .

Maximization Principle for Density-Dependent Selection in a Fluctuating Population

We now specify the form of density-dependent selection as

$$m(\mathbf{z}, N) = r(\mathbf{z}) - \gamma(\mathbf{z})g(N), \quad (6)$$

where $g(N)$ is an increasing function of N . For theta-logistic density regulation, $g(N) = N^\theta$. Thus, although density regulation is determined by total population size N , phenotypic fitnesses at low population size, $r(\mathbf{z})$, and strength of density dependence governed by $\gamma(\mathbf{z})$ vary among phenotypes. Hence, we write

$$\tilde{m}(\bar{\mathbf{z}}, N) = \bar{s}(\bar{\mathbf{z}}) - \bar{\gamma}(\bar{\mathbf{z}})g(N), \quad (7)$$

where $\bar{s}(\bar{\mathbf{z}}) = \bar{r}(\bar{\mathbf{z}}) - (1/2)\sigma_e^2(\bar{\mathbf{z}})$, with $\bar{r}(\bar{\mathbf{z}}) = \int r(\mathbf{z})p(\mathbf{z})d\mathbf{z}$ and $\bar{\gamma}(\bar{\mathbf{z}}) = \int \gamma(\mathbf{z})p(\mathbf{z})d\mathbf{z}$. The function $\bar{s}(\bar{\mathbf{z}})$ is the long-run growth rate of the population in the absence of density regulation. With these assumptions, the expected evolution in equation (3) takes the form

$$\frac{1}{dt}E[d\bar{\mathbf{z}}|\bar{\mathbf{z}}, N] = \mathbf{G}[\nabla\bar{s}(\bar{\mathbf{z}}) - g(N)\nabla\bar{\gamma}(\bar{\mathbf{z}})]. \quad (8)$$

We further assume that weak selection ensures slow changes in $\bar{\mathbf{z}}$ compared to fluctuations in N , that is, that the expected rate of return to equilibrium is much slower for $\bar{\mathbf{z}}$ than $\ln N$. From the infinitesimal mean of $\ln N$ in equation (1), solving for $E d\ln N = 0$, it follows that

$E[g(N)|\bar{z}] = \bar{s}(\bar{z})/\bar{\gamma}(\bar{z})$. After averaging over the distribution of N given \bar{z} , we find the expected response is

$$\begin{aligned} \frac{1}{dt} E(d\bar{z}|\bar{z}) &= \mathbf{G} \left[\nabla \bar{s}(\bar{z}) - \frac{\bar{s}(\bar{z})}{\bar{\gamma}(\bar{z})} \nabla \bar{\gamma}(\bar{z}) \right] \\ &= \bar{\gamma}(\bar{z}) \mathbf{G} \nabla \left[\frac{\bar{s}(\bar{z})}{\bar{\gamma}(\bar{z})} \right]. \end{aligned} \quad (9)$$

The first form of equation (9) separates the expected selection in a fluctuating environment into two terms, the density-independent term of Lande (2007), $\nabla \bar{s}(\bar{z})$, and a density-dependent term, $-\bar{s}(\bar{z}) \nabla \ln \bar{\gamma}(\bar{z})$. Provided that the stochastic density-independent growth rate is positive (so that the population can persist), the second term is negative, showing that selection acts to decrease the strength of density dependence. The expected evolution of the mean phenotype is therefore governed by the function

$$Q(\bar{z}) = \frac{\bar{s}(\bar{z})}{\bar{\gamma}(\bar{z})} = \left[1 - \frac{\sigma_e^2(\bar{z})}{2\bar{r}(\bar{z})} \right] g(K(\bar{z})), \quad (10)$$

where $K(\bar{z})$ is the carrying capacity, or stable equilibrium, of the total population in the average environment, given by $g(K(\bar{z})) = \bar{r}(\bar{z})/\bar{\gamma}(\bar{z})$. The function $Q(\bar{z})$ plays an analogous role to the mean fitness of the population in models lacking density-dependent selection (Lande 2007). But in equation (9), with density-dependent selection, the rate of evolution is also proportional to the strength of density dependence in the population growth rate, $\bar{\gamma}(\bar{z})$.

Although the full joint stochastic process for \bar{z} and $\ln N$ is complicated, some important general conclusions can still be reached when parameter restrictions or trade-offs ensure the existence of an equilibrium in the sense that the joint dynamics of N and \bar{z} achieves a stationary distribution. Because this is a stochastic model in \bar{z} as well as N , one cannot find a function of \bar{z} that is maximized by long-term evolution as in the haploid (asexual) model of Lande et al. (2009). Although that model includes stochastic fluctuations in population size, it considers a constant value of z defining r , K , and σ_e^2 only as an evolutionarily stable strategy that cannot be invaded by any other phenotype. In our model of a sexual population, phenotypic and genetic variation always exists, and we assume that genetic variances and covariances are maintained such that \mathbf{G} is constant. Thus, there is no particular function of \bar{z} that is maximized by evolution, because stochastic fluctuations in population size in combination with density-dependent selection always generate temporal changes in \bar{z} . However, because the process is initiated with a given mean phenotype and population size, the joint distribution of (\bar{z}, N) is determined at future times by the properties of the joint process. Accordingly, the parameters of these future joint distributions, such as their

means and variances, are subject to deterministic temporal changes.

We now write $\delta Q(\bar{z}) = Q(\bar{z} + E d\bar{z}) - Q(\bar{z})$ for the evolution of $Q(\bar{z})$ induced if the change in \bar{z} was as expected during dt . This quantity is $\delta Q(\bar{z}) = \nabla Q(\bar{z})^T E d\bar{z}$, which in combination with equation (9) yields

$$\frac{1}{dt} \delta Q(\bar{z}) = \bar{\gamma}(\bar{z}) \nabla Q(\bar{z})^T \mathbf{G} \nabla Q(\bar{z}) \geq 0.$$

Hence, under the expected evolution of \bar{z} toward \mathbf{z}_{opt} , $Q(\bar{z})$ always increases and is maximized at $\bar{z} = \mathbf{z}_{\text{opt}}$, where $\nabla Q(\bar{z}) = 0$ and the expected evolution stops. Under suitable constraints ensuring that a stationary distribution of \bar{z} exists, \mathbf{z}_{opt} is then a natural measure of its location. The dynamics of $Q(\bar{z})$ based on simulation of the joint diffusion for \bar{z} and N is illustrated in figure 1.

Appendix C shows that the dynamics of $\ln N$ depends on \bar{z} only to the second order in $\Delta \bar{z} = \bar{z} - \mathbf{z}_{\text{opt}}$ and $\Delta g(N) = g(N) - \bar{s}(\bar{z})/\bar{\gamma}(\bar{z})$. Therefore, under stationary fluctuations in \bar{z} and N , the unconditional expectation of $g(N)$ is approximately the expectation of $g(N)$ when \bar{z} is kept constant at \mathbf{z}_{opt} (corresponding to $\mathbf{G} = 0$). Hence, the stationary distribution of $\ln N$ is the distribution maximizing $Eg(N)$ to this order of approximation. The function $Q(\bar{z})$ is at any time less than or equal to its maximum, so its mean value as well as $Eg(N)$ is always smaller than but close to $Q(\mathbf{z}_{\text{opt}})$.

Numerical Example

The assumption of a trade-off is required, because otherwise the evolution of the mean phenotype would always increase \bar{r} and decrease $\bar{\gamma}$, that is, there will always be selection for large \bar{r} and large K . The empirical foundation for such a relationship between $r(z)$ and $\gamma(z)$ among phenotypes within a population is difficult to assess due to lack of empirical evidence (Newton 1998; Bonenfant et al. 2009), but trade-offs have been demonstrated in laboratory experiments (Mueller 1997, 2009).

As a simple example, we consider a one-dimensional character z and the logistic dynamics of N , that is, $g(N) = N$. The environmental variance is constant, σ_e^2 , while r and γ vary among individuals according to their phenotype z . The density-dependent component of Malthusian fitness is assumed to be a decreasing function of the phenotype, for example, body size, $r(z) = r_0(1 - e^{\alpha(z-z_0)})$ with $\alpha > 0$, which cannot exceed r_0 . To reflect an intraspecific trade-off between r and γ , the strength of density dependence is assumed to decrease with increasing z as $\gamma(z) = \gamma_0 e^{-\beta z}$, where $\beta > 0$. The corresponding mean functions are $\bar{r}(\bar{z}) = r_0(1 - e^{\alpha(\bar{z}-z_0)+\alpha^2 P/2})$ and $\bar{\gamma}(\bar{z}) = \gamma_0 e^{-\beta \bar{z} + \beta^2 P/2}$, where P is the phe-

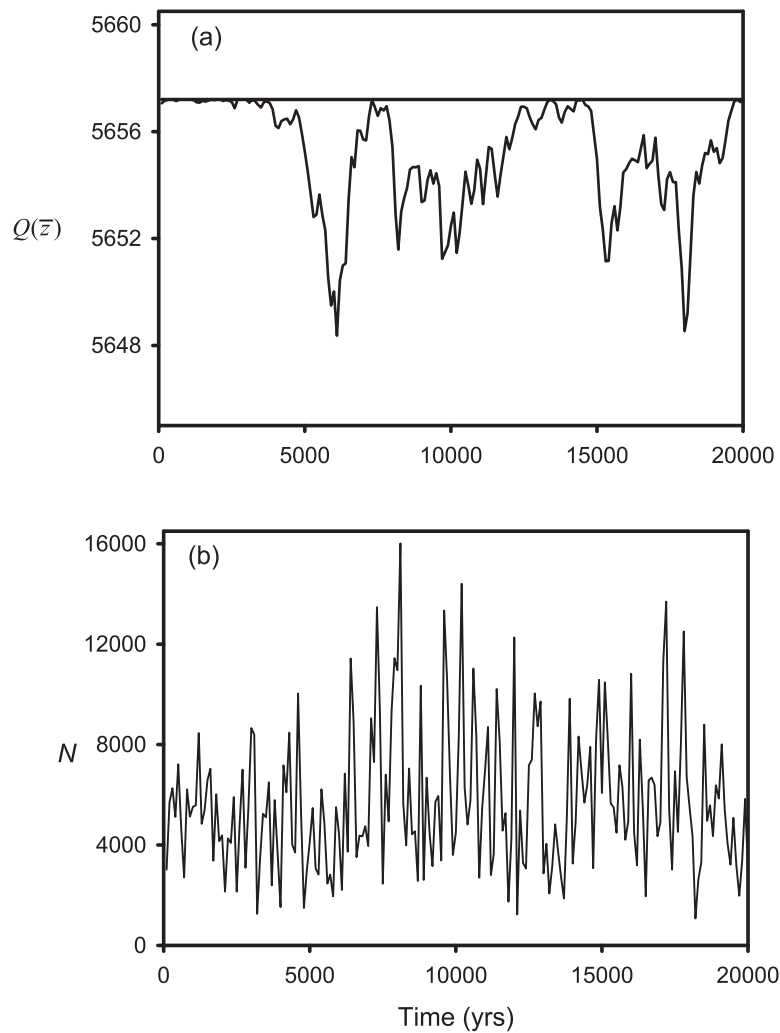


Figure 1: Small temporal fluctuations in function $Q(\bar{z})$ and its maximum (horizontal straight line; a). Corresponding large fluctuations in population size over the same time period (b). Model is the numerical illustration defined in “Numerical Example,” with parameters $z_0 = 200$, $r_0 = 0.1$, $\sigma_c^2 = 0.01$, $\alpha = 0.003$, $\beta = 0.01$, $P = 100$, $G = 50$, and $\gamma_0 = 0.00001$.

notypic variance. Thus, $\bar{s} = \bar{r} - \sigma_c^2/2$ and $\bar{\gamma}$ depend on \bar{z} in such a way that $Q = \bar{s}/\bar{\gamma}$ has a unique maximum at

$$z_{\text{opt}} = z_0 + \alpha^{-1} \ln \left[\frac{(r_0 - \sigma_c^2/2)\beta}{r_0(\alpha + \beta)} \right] - \frac{\alpha P}{2},$$

with corresponding mean parameter $r_{\text{opt}} = (\alpha r_0 + \beta \sigma_c^2/2)/(\alpha + \beta)$, which increases with increasing environmental noise. Figure 2a shows examples of $E(d\bar{z}/dt)$ plotted against \bar{z} for four different values of σ_c^2 . The rate of change in the mean character \bar{z} is greater in more stochastic environments. Furthermore, the value of \bar{z} maximizing $Q(\bar{z})$ is smaller for larger environmental variance (fig. 2b). Figure 3 shows simulations

of the same process with the same parameters over a long time interval and the mean \pm SD for the corresponding stationary distribution of \bar{z} computed by the first-order approximation given in appendix B. The variance of this stationary distribution and the temporal autocorrelation in \bar{z} are both large under large environmental stochasticity. Evolution “tries” to maximize the function $Q(\bar{z})$ (fig. 1a), but stochastic effects always kick it back to values slightly below the optimum (not more than about 0.2% below the maximum in the example shown). Finally, in this example, population fluctuations are rather large (varying from about 1,000 to 16,000 individuals) and much faster than fluctuations in \bar{z} (fig. 1b), in accordance with the assumption of weak selection.

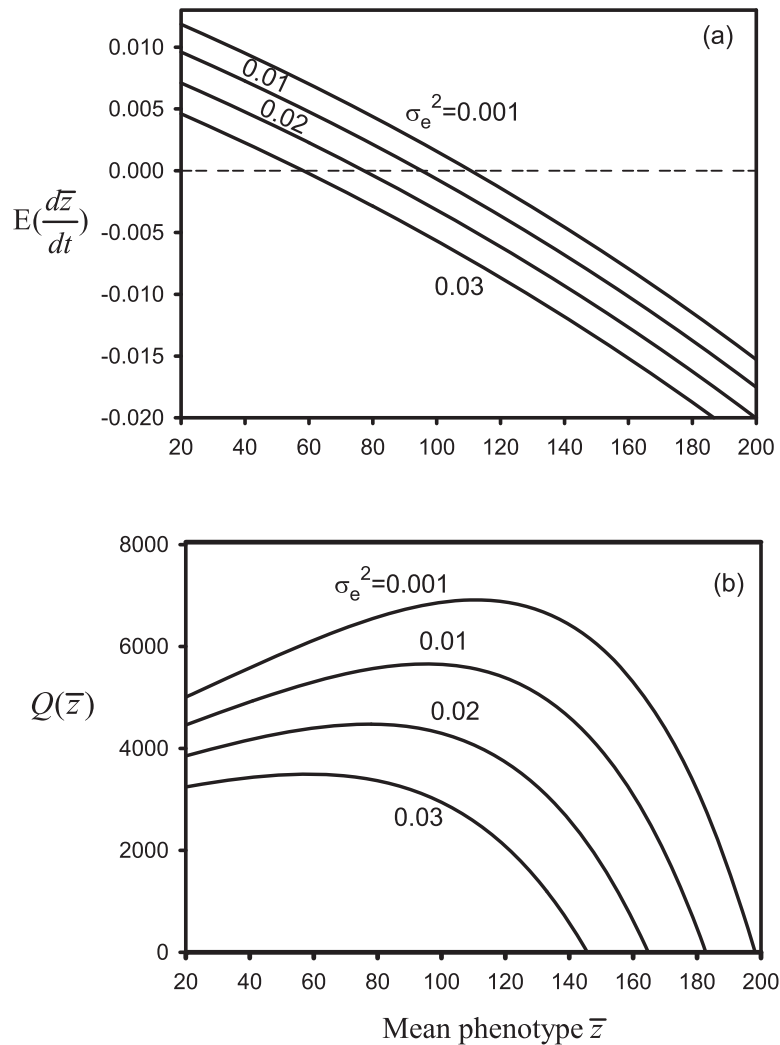


Figure 2: Expected change in mean phenotype $E(d\bar{z}/dt)$ versus \bar{z} (a). Model and parameters other than σ_e^2 are as in figure 1. Function $Q(\bar{z})$ for the same model and parameters (b). Both graphs show the same four different values of the environmental variance σ_e^2 , which is assumed to have no genetic variation.

In figure 4a, $EQ(\bar{z}) \approx EN$ is shown as functions of σ_e^2 for different values of G , keeping the heritability G/P constant. As a further illustration, we also analyze the deviation between $EQ(\bar{z})$ and the maximum $Q(z_{\text{opt}})$. This is most easily done by studying the process $\ln Q = \ln \bar{s} - \ln \bar{\gamma}$. In appendix B, we have derived the first-order approximation to the stationary variance of \bar{z} in the univariate case with constant σ_e^2 . Then, we have approximately

$$\ln Q(z_{\text{opt}}) - E \ln Q(\bar{z}) \approx -\frac{1}{2} (\ln Q)'' \text{Var}(\bar{z}), \quad (11)$$

where the second derivative, which is negative, is evaluated at z_{opt} . Figure 4b shows this deviation as a function of σ_e^2 for the same values of G and P used in figure 4a.

Discussion

Here we show that the expected evolution of the mean phenotype \bar{z} under density-dependent selection, subject to appropriate constraints on components of fitness, approaches the value z_{opt} maximizing $Q(\bar{z})$ (eq. [10]). For the theta-logistic form of density dependence $g(N) = N^\theta$, we have $Q(\bar{z}) = \{1 - \sigma_e^2(\bar{z})/[2\bar{r}(\bar{z})]\}K(\bar{z})^\theta$. Under the theta-logistic model, this implies that evolution approximately maximizes EN^θ (Lande et al. 2009). In general $Q(\bar{z})$ depends on the mean phenotype through three ecological parameters— $\bar{r}(\bar{z})$, $K(\bar{z})$, and the environmental variance in population growth rate $\sigma_e^2(\bar{z})$ —that govern the stochastic dynamics of N . These ecological parameters,

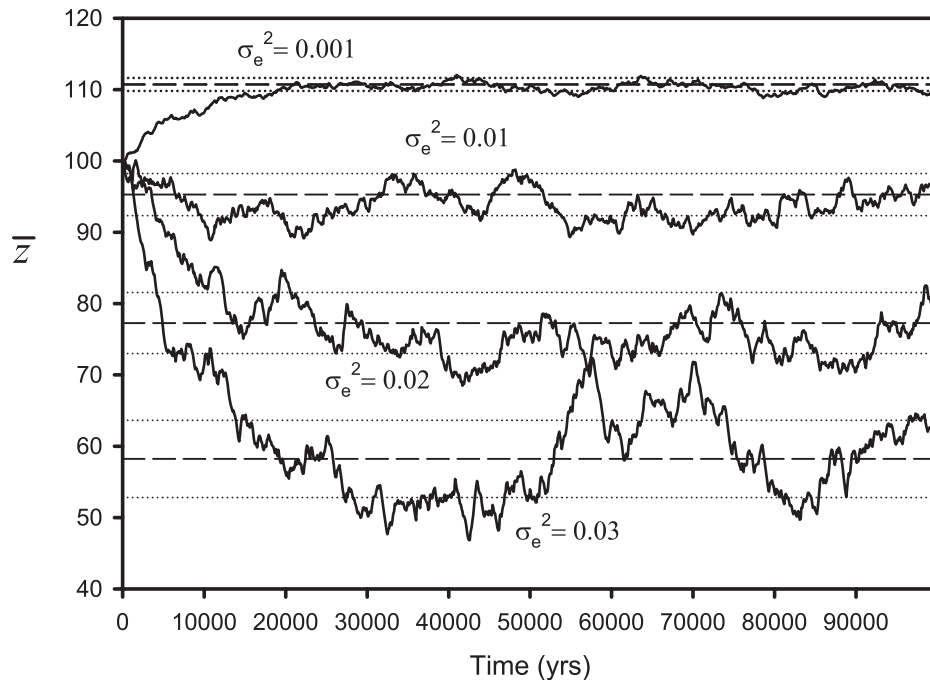


Figure 3: Simulation of \bar{z} for each of the four values of environmental variance in figure 1 and mean values \pm SD computed by the approximations to the stationary distribution derived in appendix B. Model and parameters are as in figure 2.

which are averaged over the population, are functions of \bar{z} . However, z_{opt} will not be reached as a final value because of fluctuations in the mean phenotype caused by stochastic density-dependent selection driven by fluctuating population size (fig. 1). This causes stochastic evolution of the mean phenotype toward a stationary distribution around z_{opt} (fig. 3).

In our quantitative genetic model, we assume that genetic variation is maintained by mutation and recombination. This differs from the haploid model of Lande et al. (2009), in which a single genotype finally becomes fixed. The results derived from these two models have striking similarities but also some differences. We find that the function Q maximized by evolution has the same form as that given by Lande et al. (2009) except with the (r, K, σ_e^2) for a fixed genotype replaced by their population values, depending not only on \bar{z} but also on the genetic and phenotypic variation. Thus, evolution no longer leads to fixation because we assume that polygenic variation is always maintained in the population, which therefore continually evolves in response to stochastic fluctuations in population density (fig. 3).

Our assumption of weak selection implies that $Q(\bar{z})$ approximately equals the expected value $E[g(N)|\bar{z}]$ of the density-dependent function $g(N)$ averaged over the stationary distribution of N for a given \bar{z} . We have shown that the expected evolution of \bar{z} toward z_{opt} always increases

$Q(\bar{z})$. However, stochastic density-dependent selection continually perturbs the mean phenotype away from z_{opt} (fig. 1a). The dynamics of N under weak selection is almost unaffected by \bar{z} in the neighborhood of z_{opt} . Consequently, $Q(\bar{z})$ will always remain close to its maximum under the stochastic evolution of \bar{z} , as illustrated in figures 1a and 4b. Thus, in the joint stationary distribution of \bar{z} and N , $Eg(N) \approx E[g(N)|\bar{z}]$ so that evolution approximately also maximizes $Eg(N)$ unconditionally.

One of the most interesting properties of $Q(\bar{z})$ is the information it contains about the balance between *r*- and *K*-selection in a fluctuating population. In a constant environment ($\sigma_e^2 = 0$), the mean phenotype evolves to z_{opt} , and evolution maximizes $N = K$, as shown by MacArthur (1962). This occurs for any form of density regulation $g(N)$. In a stochastic environment ($\sigma_e^2 > 0$), population size as well as mean phenotype will fluctuate. A stationary distribution could be achieved by some combination of stabilizing selection on \bar{z} toward maximum *r* and *K* and minimum σ_e^2 or, alternatively, by a trade-off among them involving antagonistic selection on \bar{z} . In the haploid model of Lande et al. (2009), large environmental variance in population growth rate leads to evolution toward fixation at a large intrinsic growth rate *r*, in agreement with previous results for deterministic seasonal environmental fluctuations and analysis of stochastic, diploid, one-locus models (Roughgarden 1971; Turelli and Petry 1980). In

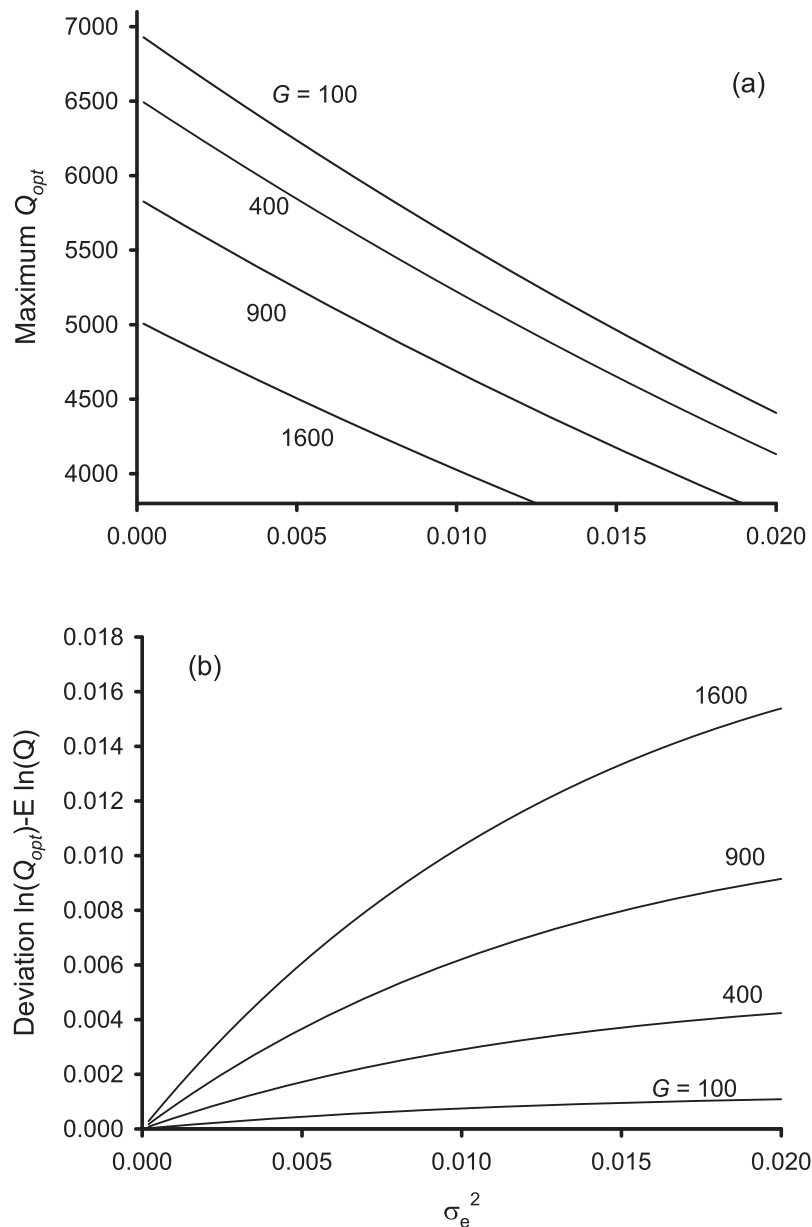


Figure 4: Maximum Q_{opt} of $Q(\bar{z}) \approx EN$ as a function of the environmental variance σ_e^2 for different values of the additive genetic variance G under constant heritability $h^2 = G/P = 0.3$ (a). Corresponding deviation between the maximum $\ln(Q_{opt})$ of $\ln Q$ and the expected value $E \ln(Q)$ calculated from equation (11) and the first-order approximation to the stationary variance of \bar{z} derived in appendix B (b). Model and other parameters are as in figure 1.

our quantitative genetic model, one would have to analyze the effect of environmental noise on the balance between r - and K -selection in each case separately by studying how $Q(\bar{z})$ is affected by changes in the environmental covariances $c(y, z)$ that define $\sigma_e^2(\bar{z})$. However, $Q(\bar{z})$ is the same as the function maximized by the fixed type in the haploid model, with the modification that r , K , and σ_e^2 are replaced by their population values. The general conclusions on the

balance between r - and K -selection are therefore equivalent for the haploid and diploid models. In the quantitative genetic model, increasing environmental noise produces expected evolution toward larger values of $\bar{r}(\bar{z})$ and $\bar{s}(\bar{z})$. Estimating the functions $c(y, z)$, $r(z)$, and $\gamma(z)$ is a difficult task that will require large long-term data sets and new statistical methods.

Our analysis of density-dependent selection in a fluc-

tuating environment excludes frequency dependence of phenotypic fitnesses, which would violate the basic gradient formulation of evolutionary dynamics in equation (3) (Wright 1969). Frequency-dependent selection often arises in models of sexual selection and asymmetric resource competition within species (e.g., Lande 1976, 1980; Goldberg and Lande 2006). Our assumption of white environmental noise analyzed as a diffusion process also excludes environmental cycles, major catastrophes, and large fluctuations in population size, which would require further analyses (Lande et al. 2003). This excludes several interesting biological phenomena, such as seasonality and other periodic environmental and catastrophic changes as well as yearly population changes of more than about 30%, which would require more specific analyses (Lande et al. 2003). However, no evidence for significant environmental autocorrelations was found in the dynamics of several populations of large mammals (Morris et al. 2011; Engen et al. 2013).

We have shown that conditioned on the current evolutionary state of a population, expected evolution is toward maximizing a simple function of basic ecological parameters that are functions of the mean phenotype \bar{z} . Thus, the most general question that can be answered about the long-term evolution of population dynamics not conditioned on genetic and evolutionary parameters is how much on average a population deviates from what it is expected to maximize, averaged over the stationary distribution of \bar{z} and N (figs. 1a, 4b). Figure 1a shows how $Q(\bar{z})$ fluctuates, approaching its maximum but always being reduced by stochastic effects so as to remain slightly below it.

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APPENDIX A

Derivation of the Joint Diffusion for Mean Phenotype \bar{z} and Population Size N

The mean phenotype before selection is $\bar{z} = \int zp(z)dz$, where $p(z) = n(z)/N$ and $N = \int n(z)dz$. Adopting the notation of Lande (2007), we find that the distribution of phenotypes after selection (weighting the phenotypes by their Malthusian fitnesses) during dt is $p^*(z) = p(z) +$

$dp^*(z)$ and that the infinitesimal change in mean phenotype after selection is $d\bar{z}^* = \int zdp^*(z)dz$ with expectation $Ed\bar{z}^* = \int zEdp^*(z)dz$.

The infinitesimal change due to selection on $p(y) = n(y)/N$, $p(z) = n(z)/N$, and N (before sexual recombination and reproduction) can be found from the transformation formulas for a multivariate diffusion (Karlin and Taylor 1981). However, $p(z)$ is not a diffusion process, because mutation, segregation, and recombination are assumed to maintain approximate normality of the distribution of breeding values and phenotypes, keeping the additive genetic and phenotypic covariance matrices \mathbf{G} and \mathbf{P} constant. Thus, $p(z)$ is assumed to maintain approximately its normal shape, while the mean phenotype \bar{z} evolves. For notational simplicity, the phenotype distribution is denoted $p(z)$, suppressing the parameters \bar{z} and \mathbf{P} .

The infinitesimal covariance between the change in $n(z)$ and N due to selection alone is $\int c(y, z)n(y)n(z)dy = N^2 \int c(y, z)p(y)p(z)dy = N^2 \bar{c}(z)p(z)$, while the infinitesimal variance of N is $N^2 \int c(y, z)p(y)p(z)dydz = N^2 \sigma_c^2(\bar{z})$. Replacing $r(z)$ with $m(z, N)$ in the transformation leads to no more changes in the formulas of Lande (2007) than replacing $r(z)$ with $m(z, N)$ in all infinitesimal moments. As an illustration of these replacements, we give the derivation of the infinitesimal change in $p(z)$ caused by selection only. With μ_n and μ_N as the infinitesimal means of n and N , respectively, and ν_{nn} , ν_{nN} , and ν_{NN} as the covariances, the infinitesimal mean of p^* is

$$\begin{aligned} \mu_p &= \frac{1}{dt} Edp^*(z) \\ &= \frac{\partial p}{\partial n} \mu_n + \frac{\partial p}{\partial N} \mu_N \\ &\quad + \frac{1}{2} \frac{\partial^2 p}{\partial n^2} \nu_{nn} + \frac{1}{2} \frac{\partial^2 p}{\partial n \partial N} \nu_{nN} + \frac{1}{2} \frac{\partial^2 p}{\partial N^2} \nu_{NN} \end{aligned}$$

With the derivatives worked out and the infinitesimal moments inserted, we find the infinitesimal mean of the phenotype frequency $p(z)$ due to selection alone to be

$$\mu_p = p(z)[m(z, N) - \bar{m}(\bar{z}, N) + \sigma_c^2(\bar{z}) - \bar{c}(z)].$$

This is the same as equation (9a) in Lande (2007), with Lande's $r(z)$ and \bar{r} (independent of N) replaced by the density-dependent parameters $m(z, N)$ and $\bar{m}(\bar{z}, N)$, respectively. The rest of the derivation is exactly as in Lande (2007), with the same simple substitution of functions producing the modified version of Lande's equation (10c) for the expected response to \bar{z} :

$$\begin{aligned}\frac{1}{dt}E(d\bar{z}|\bar{z}) &= \mathbf{G} \frac{\partial \tilde{m}(\bar{z}, N)}{\partial \bar{z}} \\ &= \mathbf{G} \nabla \tilde{m}(\bar{z}, N).\end{aligned}$$

The higher moments of the joint diffusion for \bar{z} and N are not affected by the above substitution, so equations (4) and (5) presented in the main article are equivalent to equations (11) and (12) in Lande (2007).

APPENDIX B

Approximation to the Joint Stationary Distribution of N and \bar{z}

Linearization

To further illustrate the theory, we now assume that the environmental noise is nongenetic so that $\sigma_e(\bar{z})$ is a constant σ and consider a univariate character z . Under moderate environmental noise, the joint process can then be analyzed by linearization around $N = K_{\text{opt}}$ and $\bar{z} = z_{\text{opt}}$, where subscript “opt” in general denotes functions evaluated at $\bar{z} = z_{\text{opt}}$. This leads to a bivariate Ornstein-Uhlenbeck process for $(\ln N, \bar{z})$.

Generally, the process $\ln N$ is affected by the process \bar{z} , and \bar{z} is affected by $\ln N$. However, while the effect of $\ln N$ on the character process is strong because $g(N)$ defines the complete noise in that process, the opposite is not the case. The main noise in $\ln N$ is defined by $\sigma_e(\bar{z})$, while the noise components determined by stochastic fluctuations in \bar{z} are small. Actually, using the first-order approximation around the joint equilibrium for $\ln N$ and \bar{z} , we find that the dynamics of $\ln N$ is not at all affected by \bar{z} . This is because the derivative of $d(\ln N)$ with respect to \bar{z} is the expected response in \bar{z} , which is zero by definition of the joint equilibrium giving $(\bar{z} - z_{\text{opt}})$ a zero first-order term in the model for $\ln N$.

We derive the linear model by linearizing $g(N)$ in $\ln N$, the equilibrium point $N = K_{\text{opt}}$, and $z = z_{\text{opt}}$ for the stochastic model, which is given by $g(K_{\text{opt}}) = (r_{\text{opt}} - \sigma^2/2)/\gamma_{\text{opt}}$. The linear approximation for the dynamics of $\ln N$ is, accordingly,

$$\begin{aligned}d(\ln N) &= -\gamma_{\text{opt}} g'(K_{\text{opt}}) K_{\text{opt}} (\ln N - \ln K_{\text{opt}}) dt \\ &\quad + \sigma dB(t),\end{aligned}$$

where g' is the derivative of g . Defining the corresponding variable with zero mean, $x = \ln N - \ln K_{\text{opt}}$, we find the linearized dynamics to be

$$dx = -axdt + \sigma dB(t),$$

where $a = \gamma_{\text{opt}} g'(K_{\text{opt}}) K_{\text{opt}}$. Assuming theta-logistic population regulation (Lande et al. 2003), we find $a = \theta r_{\text{opt}}$.

The first-order approximation to the equation for the mean character is

$$d\bar{z} = -b(\bar{z} - z_{\text{opt}}) - G_{zz} \tilde{\gamma} \Delta g(N),$$

where $b = -G_{zz}(\bar{z}' - \tilde{\gamma}'' s_{\text{opt}}/\gamma_{\text{opt}})$ and $\Delta g(N) = g(N) - \bar{g}$. Here all first and second derivatives, denoted by superscripts single prime and double prime, respectively, are evaluated at $z = z_{\text{opt}}$. Linearizing as before, we obtain

$$\begin{aligned}g(N) &\approx g(K_{\text{opt}}) + g'(K_{\text{opt}}) K_{\text{opt}} (\ln N - \ln K_{\text{opt}}) \\ &= \frac{s_{\text{opt}}}{\gamma_{\text{opt}}} + g'(K_{\text{opt}}) K_{\text{opt}} x.\end{aligned}$$

Inserting this, we obtain a linearized equation for \bar{z} . Using $y = \bar{z} - z_{\text{opt}}$, we find the equation for y is

$$dy = -bydt + \eta xdt,$$

where $\eta = -G_{zz}(d\gamma/dz)g'(K_{\text{opt}})K_{\text{opt}}$. The derivative is evaluated at z_{opt} .

Solution of the Linear Model

The set of linear stochastic differential equations is now

$$dx_t = -ax_t dt + \sigma dB(t),$$

$$dy_t = -by_t dt + \eta x_t dt,$$

where t denotes time and $B(t)$ is a standard Brownian motion with $E[dB(t)] = 0$ and $\text{Var}[dB(t)] = dt$. The solution of this system is a linear function of the noise process $dB(t)$. Furthermore, positive a and b make the joint system stationary, and the solution is a two-dimensional Ornstein-Uhlenbeck process with zero expectation. Accordingly, the complete solution is determined by the second-order moments $c_{xx}(t) = \text{Cov}(x_u, x_{u+t})$, $c_{xy}(t) = \text{Cov}(x_u, y_{u+t})$, $c_{yx}(t) = \text{Cov}(y_u, x_{u+t})$, and $c_{yy}(t) = \text{Cov}(y_u, y_{u+t})$, where $t > 0$.

The process x_t is a one-dimensional Ornstein-Uhlenbeck process with solution $c_{xx}(t) = e^{-at}\sigma^2/(2a)$. By the stationarity, we have $\text{Var}(y_t) = \text{Var}(y_t + dy_t)$. Following the equation for dy_t , we have $\text{Var}(y_t) = \text{Var}[y_t(1 - bdt) + \eta x_t dt]$. If we ignore terms of order dt^2 , the right side equals $(1 - 2bdt)\text{Var}(y_t) + 2\eta \text{Cov}(x_t, y_t)$, giving us $c_{yy}(0) = c_{xy}(0)\eta/b$. Using the same technique for $\text{Cov}(x_t, y_t)$ and given that $dB(t)$ is independent of x_t and y_t by definition, we have

$$c_{xy}(0) = \frac{\eta}{a+b} c_{xx}(0) = \frac{\sigma^2 \eta}{2a(a+b)}$$

and consequently

$$\text{Var}(y_i) = c_{yy}(0) = \frac{\sigma^2 \eta^2}{2ab(a+b)},$$

$$\rho_{xy} = \text{corr}(x_i, y_i) = \sqrt{\frac{b}{a+b}}.$$

By the same method, we further find $c_{yy}(t+dt) = (1-bdt)c_{yy}(t) + \eta c_{yx}(t)dt$, giving us the differential equation

$$c'_{yy}(t) = -bc_{yy}(t) + \eta c_{yx}(t).$$

Proceeding with the same technique, we also find

$$\begin{aligned} c'_{yx}(t) &= -ac_{yx}(t) \\ &= -bc_{xy}(t) + \eta c_{xx}(t) \\ &= -bc_{xy}(t) + \frac{e^{-at}\eta\sigma^2}{(2a)}. \end{aligned}$$

With the boundary conditions given by $c_{yx}(0) = c_{yx}(0)$ and $c_{yy}(0)$ derived above, the final solution yields for $b \neq a$

$$c_{xx}(t) = \frac{\sigma^2 e^{-at}}{2a},$$

$$c_{yx}(t) = \frac{\sigma^2 \eta e^{-at}}{2a(a+b)},$$

$$c_{xy}(t) = \frac{\sigma^2}{2a(b-a)}(e^{-at} - e^{-bt}) + \frac{\sigma^2 \eta e^{-bt}}{2a(a+b)},$$

$$c_{yy}(t) = \frac{\sigma^2 \eta^2}{2(b^2 - a^2)} \left(\frac{1}{a} e^{-at} - \frac{1}{b} e^{-bt} \right).$$

For $b = a$, we find

$$c_{yx}(t) = \frac{\sigma^2 e^{-at}}{2a} \left(t + \frac{\eta}{2a} \right),$$

$$c_{yy}(t) = \frac{\sigma^2 \eta^2 e^{-at}}{4a^2} \left(t + \frac{1}{a} \right).$$

APPENDIX C

Dynamics of $\ln N$ near z_{opt}

Although evolution will not exactly maximize $Eg(N)$ unconditionally, that is, when averaged over the joint stationary distribution of \bar{z} and N , it will be approximately maximized because the dynamics of $\ln N$ is practically unaffected by \bar{z} near z_{opt} . To see this, we expand the infinitesimal mean of $\ln N$ in \bar{z} at z_{opt} . Illustrating this for a one-

dimensional z , writing $\Delta\bar{z} = \bar{z} - z_{\text{opt}}$, and using $\nabla Q(z_{\text{opt}}) = 0$, we derive to the second order

$$\begin{aligned} \frac{1}{dt} E d \ln N &= \left[\bar{s} - \bar{\gamma} g(N) - \bar{\gamma}' \Delta g \Delta \bar{z} \right. \\ &\quad \left. - \frac{1}{2} (\bar{s}'' - \bar{\gamma}'' \bar{s} / \bar{\gamma}) (\Delta \bar{z})^2 \right], \end{aligned}$$

where superscripts single prime and double prime denote first and second derivatives, respectively, and all functions are evaluated at $\bar{z} = z_{\text{opt}}$. Assuming that σ_e^2 is constant or depends weakly on \bar{z} near z_{opt} and can be approximated by $\sigma_e^2(z_{\text{opt}})$, it appears that no first-order terms remain, leaving only the second-order term $-\bar{\gamma}' \Delta g \Delta \bar{z} - (1/2)(\bar{s}'' - \bar{\gamma}'' \bar{s} / \bar{\gamma})(\Delta \bar{z})^2$. This also occurs in the multidimensional case.

Using our first-order approximation to $\Delta g(N)$, we can write the second-order noise term as $G_{zz}^{-1}(\eta xy + by^2)$, which has expectation $G_{zz}^{-1}[-\eta c_{xy}(0) + bc_{yy}(0)]$. Inserting the expressions for $c_{xy}(0)$ and $c_{yy}(0)$ derived in appendix B then shows that the expected value of this noise term is zero to this order of approximation.

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“Crouch’s Cove, Casco Bay, Maine ... The whole island is at present covered with a growth of spruce trees (*Abies nigra*), excepting a narrow strip on the seaward side, and on this, at the southerly end of the island, are several shell-heaps of different sizes ... The shells are mostly deposited evenly, but here and there are raised into small knolls, and all are covered with turf.” From “An Account of Some *Kjækkenmæddings*, or Shell-Heaps, in Maine and Massachusetts” by Jeffries Wyman (*American Naturalist*, 1868, 1:561–584).