

Evolutionary stability under the replicator and the gradient dynamics

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Summary

We unite two general models for evolutionary change under the forces of selection, mutation and reproduction, a genetic model (replicator dynamics) and a cultural model (gradient dynamics). Under the assumption of normality, we find that the mean and variance dynamics are essentially identical under the two models and we relate these to the ESS and convergence stability conditions.

Keywords: evolutionary stability; gradient dynamics; quantitative genetics; replicator dynamics

Introduction

Many biological characters of interest are quantitative; their values range over a continuum of possible states rather than a set of discrete states. Although emphasis tends to be placed on characters that have a genetic basis, characters that are determined largely by learning rather than genetics are also of interest (e.g. cultural characters). In both cases, what is usually of ultimate interest is an understanding of how the frequency distribution of the character evolves over time and a determination of those population configurations that are in some sense stable (e.g. evolutionarily stable; Maynard Smith and Price, 1973; Maynard Smith, 1982). After all, it is such stable frequency distributions that we can expect to observe most often.

The aim of this paper is to unite two quite general models for evolutionary change: a model for genetic evolution (the replicator dynamic) and a model for cultural evolution (the gradient dynamic). For each case, one can imagine the character distribution of the population changing as a result of two processes. First, the distribution will change as the population adapts either genetically or behaviourally to its present circumstances. Second, there is an element of mutation whereby the population is infused with new genetic variation during genetic evolution, or individuals undergo random behavioural drift during cultural evolution. Thus both the replicator and the gradient evolutionary dynamics are composed of a selection and a mutation component.

The genetic model describes evolution of the genotypic value of a trait determined additively in a diploid sexual population at a large number of independent loci under the joint forces of selection, mutation and reproduction. The cultural model is intended to model the cultural evolution of a behavioural trait in a population with overlapping generations under transmission by learning or imitation, and random drift.

The mathematical connection between the two evolutionary models becomes clear once we derive equations for the evolution of the mean and variance in each case. One of our principal findings is that the mean and variance dynamics are essentially identical in both models under the assumption that the population distribution is normal and under this condition we formulate the stability conditions for a stable equilibrium under these dynamics.

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We compare the stability conditions so obtained to the classic conditions for evolutionary stability in monomorphic evolutionary models, in particular the ESS condition of Maynard Smith and Price (1973) and its extension to the CSS of Eshel and Motro (1981). We show that a consideration of dynamical stability in the replicator or gradient dynamics can give us a better understanding of the roles played by these stability conditions. For example, it is roughly true that the ESS condition (Equation 26, below) corresponds to the equilibrium of the variance of the distribution, and the CSS extension (Equation 27, below) corresponds to the stability of the mean.

For our derivative notation, we use subscripts to denote partial derivatives with respect to character variables x and μ , and superscript 'dot' to denote the time derivative. Thus \dot{f}_x or \dot{f}_{xx} or $\dot{f}_{x\mu}$ denote first and second partial derivatives of any function $f = f(x, \mu)$ and \dot{f} is the rate of change of f in evolutionary time.

The genetic model – the replicator dynamic

The following is our notation:

- $x = \sum x_i$ is the character where the sum is over the $2n$ allelic values which determine x – the maternal and the paternal values at each of n loci.
- $p_i(x_i)$ is the marginal density function of x_i , assumed normal. We assume that the x_i are independent random variables – this will be a good approximation if linkage and selection are weak and mating is random (Turelli and Barton, 1990; Burger, 1991).
- \bar{x}_i is the mean of x_i and $\mu = \sum \bar{x}_i$ is the mean of x .
- V is the variance of x .
- $W = W(x)$ is the fitness of x . Generally, we will assume frequency dependence, specifically that W depends also on μ : $W = W(x, \mu)$. \bar{W} is mean fitness.
- $W_i(x_i)$ is marginal fitness of the i th allelic value.
- α_i is the mutation rate of the i th allelic value, and $\alpha = \sum \alpha_i$ is the genome-wide mutation rate.
- $u_i(\xi)$ is the probability density that a single mutation of x_i will increase it by an amount ξ . We assume that mutation has no preferred direction, so that the distribution $u_i(\xi)$ has mean 0.
- v_i is the variance of the distribution $u_i(\xi)$, and $v = \sum \alpha_i v_i / \alpha$ is the average variance of a mutational jump.

The replicator dynamic for the distribution of allelic values at the i th locus is:

$$\dot{p}_i(x_i) = p_i(x_i)(W_i(x_i) - \bar{W}) + \alpha_i \left[\int_{-\infty}^{\infty} u_i(\xi) p_i(x_i - \xi) d\xi - p_i(x_i) \right] \quad (1)$$

where the first term measures the effect of selection and the second term the effect of mutation. If fitness measures rate of offspring production, and offspring genotype is given by average parental genotype, then the rate of change of the character density due to selection should be proportional to $W - \bar{W}$. The second term in Equation (1) expresses the difference between flow of mutant values into x_i , and the flow away from x_i . Equation (1) first appeared in Kimura (1965) for a multi-locus model with a 'continuum of alleles' at each locus (Crow and Kimura, 1964). Kimura assumed a quadratic fitness W , and in his analysis assumed mutations of small effect (small v). Burger (1991) has studied the evolution of the moments of p under this model. The selection term was introduced into the ESS literature by Taylor and Jonker (1978), and studied by Zeeman (1980) and Hofbauer *et al.* (1979). Maynard Smith (1982) normalized the selection term by dividing by \bar{W} (in discrete time), but the unnormalized version allows the magnitude of W to affect the speed of evolution.

Under the dynamic (1), \bar{x}_i changes according to the equation:

$$\dot{\bar{x}}_i = \text{cov}(x_i, W_i) \quad (2)$$

This represents the effect of selection; since $u_i(\xi)$ has mean zero, the mutation term in Equation (1) has no effect on the mean of x_i . Equation (2) is the continuous analogue of the fundamental equation for the selection differential discovered independently by Robertson (1966), Li (1967) and Price (1970). If we sum over the components of x (Appendix A8), the evolution of the character mean follows:

$$\dot{\mu} = \text{cov}(x, W) = \bar{W}(E_W(x) - \mu) = \bar{W}S \quad (3)$$

and the evolution of the character variance (Appendix A10) follows:

$$\dot{V} = \bar{W}(\text{var}_W(x) - V) + \alpha v \quad (4)$$

where E_W denotes expectation and var_W denotes variance with respect to the distribution Wp/\bar{W} of the 'selected' population. S is the selection differential of quantitative genetics and is defined by Equation (3). The last term in Equation (4) assumes that mutation occurs independently at each locus. We note that Equations (3) and (4) do not require p_i to be normal, nor do they require x_i to be independent.

The cultural model – the gradient dynamic

We use the same notation, except that x has only one component. The gradient dynamic is:

$$\dot{p} = -V(W_x p)_x + \alpha \left[\int_{-\infty}^{\infty} u(\xi) p(x - \xi) d\xi - p(x) \right] \quad (5)$$

The selection term has been introduced into the ESS literature by D. Friedman and J. Yellin (submitted). A heuristic for the expression is to suppose that an x -individual has a small probability of moving its phenotype in the direction in which fitness is increasing, and this probability is proportional to the fitness gradient at x . This expression is also used to model fluid flow under a pressure gradient or the motion of organisms towards sites of higher nutrient concentration (Edelstein-Keshet, 1988, section 9.4). The integral term measures behavioural drift.

Under this dynamic, the rates of change of the mean μ and the variance V of the p -distribution are given by (Appendix A21, A23):

$$\dot{\mu} = VE(W_x) \quad (6)$$

and

$$\dot{V} = 2VE[(x - \mu)W_x] + \alpha v \quad (7)$$

Equations (6) and (7) do not require p to be normal.

Normality of the population distribution

It is interesting that under the assumption of normality of $p(x)$, the equations for $\dot{\mu}$ and \dot{V} are, except for a multiplicative constant, identical for the two dynamical systems. Indeed, if p is normal, then both systems (3, 4) and (6, 7) can be rewritten as (Appendix A26–A32):

$$\dot{\mu} = VE(W_x) \quad (8)$$

and

$$\dot{V} = kV^2 E(W_{xx}) + \alpha v \tag{9}$$

where we take $k = 1$ for the replicator dynamic and $k = 2$ for the gradient dynamic. That is, under the action of selection, the population mean evolves at the same rate for the two dynamics, but the selection component of the variance changes twice as fast in the gradient dynamic as in the replicator dynamic.

There are different lines of argument for why p might often be expected to remain normal. First, if W is a quadratic function of x (Equation 20 below – this corresponds in discrete time to the important case of Gaussian fitness), then it is easily argued (Lande, 1976) that selection preserves normality in both dynamic Equations (1) and (5). This is not true for the effects of mutation, but it will be approximately true if the effect of each mutation is small and Kimura's (1965) approximation (Equation 32) is valid (Turelli, 1984; Bulmer, 1989). Second, for the genetic model with arbitrary fitness function, random mating can be expected to restore normality in each offspring generation provided selection is weak (Burger, 1991). Third, Turelli and Barton (1994) have recently shown that the assumption of normality gives remarkably accurate predictions for the change of mean and variance, even if selection is strong and generates substantial deviations from normality.

Stability of equilibria

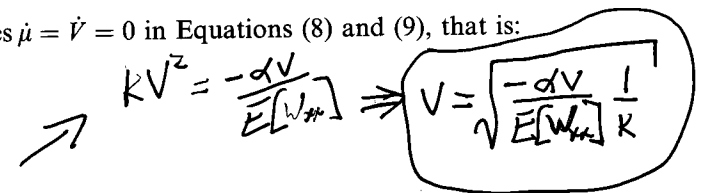
Here we assume that an equilibrium exists and look at the conditions that allow it to have stable mean and variance. This is always a necessary condition for the stability of the equilibrium, but under the assumption of normality it will also be sufficient. We remark that Burger (1986) has shown that an equilibrium of the one-locus Equation (1) will always exist if W is quadratic (Equation 20).

The equilibrium requires $\dot{\mu} = \dot{V} = 0$ in Equations (8) and (9), that is:

$$E(W_x) = 0 \tag{10}$$

and

$$E(W_{xx}) = -\alpha v / kV^2 \tag{11}$$



and this will be stable when the Jacobian matrix

$$M = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} = \begin{bmatrix} d\dot{\mu}/d\mu & d\dot{\mu}/dV \\ d\dot{V}/d\mu & d\dot{V}/dV \end{bmatrix} \tag{12}$$

is stable; that is, when both eigenvalues of M have negative real part. Standard conditions for this are (Edelstein-Keshet, 1988, p. 142):

$$m_{11} + m_{22} < 0 \tag{13}$$

and

$$m_{11}m_{22} - m_{12}m_{21} > 0 \tag{14}$$

For the system (8, 9), matrix (12) has the form (Appendix A33–A44):

$$M = \frac{V}{2} \begin{bmatrix} 2E(W_{xx} + W_{x\mu}) & E(W_{xxx}) \\ 2kVE(W_{xxx} + W_{x\mu x}) & 5kE(W_{xx}) + kVE(W_{xxx}) \end{bmatrix} \tag{15}$$

If, in the stability analysis, we focus only on μ and forget about V , then the stability condition, from the upper-left corner of M , is simply

$$E(W_{xx} + W_{x\mu}) < 0 \tag{16}$$

Thus $W_{xx} + W_{x\mu}$ controls the stability of the population mean. If we focus only on V , the stability condition, from the lower-right corner of M , is

$$5E(W_{xx}) + VE(W_{xxx}) \quad (17)$$

Equation (11) tells us that $E(W_{xx})$ must be negative at an equilibrium, but (17) says that for this to be stable we need slightly more. Using (13) and (14), we can formulate the conditions that the system be stable in both variables at once, but we will not bother to record these. They simplify rather nicely however, in the important special case that W is quadratic in x .

The case of quadratic W

Suppose that fitness W has the mathematical form:

$$W(x, \mu) = ax^2 + bx + c \quad (18)$$

where a , b and c can depend on μ . In this case, conditions (10) and (11) give an equilibrium as the solutions $\mu = \mu^*$, $V = V^*$ to the equations:

$$\mu = \frac{-b}{2a} \quad (19)$$

and

$$2akV^2 = -\alpha v \quad (20)$$

and such solutions will exist when $a < 0$. The matrix M in (15) now has the form:

$$M = \frac{V}{2} \begin{bmatrix} 2E(W_{xx} + W_{x\mu}) & 0 \\ 2kVE(W_{xx\mu}) & 5kE(W_{xx}) \end{bmatrix} \quad (21)$$

This is triangular, and the eigenvalues lie on the diagonal, so that the conditions that the system be stable are simply that the diagonal elements be negative. These can be written:

$$2a + 2\mu a_\mu + b_\mu < 0 \quad (22)$$

and

$$a < 0 \quad (23)$$

These stability conditions are, of course, local, but the equilibrium can be seen to be globally stable. Indeed, if W has the form (18) with $a < 0$, then at the equilibrium (μ^*, V^*) provided by (19, 20), the function

$$L(\mu, V) = \frac{1}{2} [(\mu - \mu^*)^2 + (V - V^*)^2] \quad (24)$$

is a Lyapounov function for the system (8, 9). Observe that

$$\begin{aligned} \dot{L} &= (\mu - \mu^*)\dot{\mu} + (V - V^*)\dot{V} \\ &= (\mu - \mu^*)(2a\mu + b)V + (V - V^*)(2akV^2 + \alpha v) \\ &= (\mu - \mu^*)(2a\mu - 2a\mu^*)V + (V - V^*)(2akV^2 - 2akV^{*2}) \\ &= 2a[V(\mu - \mu^*)^2 + k(V + V^*)(V - V^*)^2] \end{aligned}$$

Since $a < 0$, this is negative everywhere except at $(\mu, V) = (\mu^*, V^*)$.

Relation to the standard ESS theory in a monomorphic population

The standard ESS conditions for a continuous trait x to have a stable equilibrium at a value $x = \mu$ is to require, first of all, that a population fixed at μ cannot be invaded by a rare deviant strategy, and this requires that $W(x, \mu)$ be a maximum in x at $x = \mu$. Local sufficient conditions for this are:

$$W_x = 0 \quad (25)$$

and

$$W_{xx} < 0 \quad (26)$$

Second, we require that in a population fixed at a value μ' different from μ , mutants will be selected which tend to move the population mean in the direction of μ . This is Eshel's (1983) CSS extension, and the local condition for this is:

$$W_{xx} + W_{x\mu} < 0 \quad (27)$$

Equation (25) is called the equilibrium condition, and it compares with (6), which says that a normal population has a stationary mean when $E(W_x) = 0$. Condition (26) is the local maximum condition, and it is analogous to, but less prescriptive than, condition (11) for an equilibrium in the population variance. Condition (27) compares with (16) for the population mean to be stable by itself. Conditions (25)–(27) are all evaluated at the equilibrium $x = \mu$.

Condition (26) is generally called the ESS condition (Eshel, 1983), but it was called δ -stability by Taylor (1989). Condition (27) was called m -stability by Taylor (1989) and convergence stability by Christiansen (1991). Eshel (1983) defines a CSS as an equilibrium at which both (26) and (27) hold.

If W is quadratic in x , then W_{xx} and $W_{xx} + W_{x\mu}$ are both equal to their expected values, and so the monomorphic stability conditions (26) and (27) are equivalent to the stability of the system (8) and (9) – since this is given by the stability of the matrix (21). An example of such a fitness function is described in the Discussion.

Phenotypic evolution in the replicator dynamics

In the biological scenario modelled by the replicator dynamics, fitness is actually a function of phenotype z , but the dynamics of the genotype x are simpler than those of z (since x is what is inherited by the offspring), and it is the x -dynamics which give the same pattern for the evolution of μ and V as the gradient dynamics. In the simplest model:

$$z = x + e$$

where e is the environmental deviation, assumed normal and independent of x , with density function $\phi(e)$ with mean 0 and variance τ . If we let $\hat{W}(z)$ denote the fitness of z , then the genotypic fitness W is given by:

$$W(x) = \int \hat{W}(z)\phi(z-x)dz$$

and this is what is used in the x -equation (1). Then the dynamics of z can be obtained from those of x .

Discussion

Constructing a dynamic

Taper and Case (1992), in their discussion of different modelling approaches to evolutionary stability, describe the quantitative genetics approach as 'unquestionably the most realistic genetic

description with the fewest constraining assumptions', and it is, in their opinion, 'the standard by which to judge the success of the other two approaches' (the ESS and the CSC – co-evolutionary stable community). We would agree. By giving ourselves a population distribution, we can observe more of the effect of selection than simply how it changes the mean; we can also calculate its effect on the spread of the distribution. In fact, a nice feature of the normal distribution is that it is entirely specified by its mean and variance, so that we get a complete description of the population dynamics with a two-variable system.

Of course, there is the question of how the dynamics should be constructed from the fitness function, and the answer to that lies in deciding exactly how the fitness is to work. When fitness measures number of offspring, and these are genetically identical to the parent, the standard replicator dynamic (Equation 1) seems appropriate. When fitness measures ability to attract local adherents, the gradient dynamic (Equation 5) might apply. The interesting result is that both these systems provide essentially the same dynamics for the mean and variance in a normal population (Equations 8 and 9).

Mutational effects

If mutation has a small effect – that is, if the variance v of $u(\xi)$ is small – then the integral in (1) and (5) can be approximated by the second derivative of p :

$$\int_{-\infty}^{\infty} u(\xi)p(x - \xi)d\xi - p(x) \cong \frac{v}{2}p_{xx} \quad (28)$$

This was the approximation used by Kimura (1965). A similar approximation was used by Fisher (1937) to model the spread of a gene in a spatially distributed population; here p is the allele frequency and x is the spatial variable. Fisher studied the case in which the selection term is independent of x and is logistic in p . A guide to the interesting history of this version of the equation can be found in Edelman-Keshet (1988, section 10.6). The second-derivative term is also found in the one-dimensional diffusion equation, where p is, for example, the concentration of a gas (Edelman-Keshet, 1988, section 9.4), and in the one-dimensional heat equation, where p is temperature.

Turelli (1984) argued that the amount of variation observed in natural populations makes it unlikely that the assumption of small mutational jumps is valid, and proposed an alternative 'house-of-cards' approximation for the mutation term (Kingman, 1978):

$$\int_{-\infty}^{\infty} u(\xi)p(x - \xi)d\xi - p(x) \cong \alpha [u(x) - p(x)] \quad (29)$$

which assumes that the allelic value of a mutation is independent of its previous value. Bulmer (1989) provides a good discussion of these issues. One nice mathematical property of Kimura's approximation (28) is that it preserves normality of p if $W(x)$ is quadratic.

Comparison with the static ESS conditions

In the ESS literature, there has been some attention paid to the relative significance of the two monomorphic stability conditions (26) and (27). We have suggested that the behaviour of the dynamic Equations (8) and (9) can give us a better understanding of the significance of the role played by these two conditions. For example, from Equations (11) and (16) we can see that (26) has to do with the equilibrium of the variance and (27) has to do with the stability of the mean. As another example, it turns out that in an inclusive fitness argument, (27) can be checked (Taylor, 1989) but (26) cannot – and the question is raised whether we can generally expect (27) to be

enough. In other words, might we have an equilibrium which satisfied (27) but not (26), and if so what would it look like and how would the population behave near such a point? At such an equilibrium, if the population mean changed a small amount, the effect of selection on local mutants would be to restore the mean to its equilibrium value (since $W_{xx} + W_{x\mu} < 0$), but, on the other hand, for a population exactly at equilibrium, selection would favour local mutants on either side (since $W_{xx} > 0$). One has a feeling that the effect would be that the population mean should be stable, but that the success of mutants on either side of the mean should cause the variance to grow. This is exactly what is predicted by conditions (16) and (9) when $E(W_{xx} + W_{x\mu}) < 0$ and $E(W_{xx}) > 0$.

An example of an equilibrium at which $W_{xx} + W_{x\mu} < 0$ but $W_{xx} > 0$ is found in the resource exploitation model of Abrams *et al.* (1993). Here, the trait x can be thought of as measuring individual foraging intensity, and the resource density, R , is a decreasing function of the population mean μ :

$$R = 1/(a + \mu)$$

Assume that the individual consumption rate is xR , and fecundity b is proportional to the square of this. If we include a death rate which is proportional to x , we get the quadratic fitness:

$$W(x, \mu) = (xR)^2 - dx$$

It is easy to check that when $2ad > 1$, we have an equilibrium at which $W_{xx} > 0$ and $W_{xx} + W_{x\mu} < 0$. Abrams *et al.* (1993) call this a stable local minimum – in effect, W has a minimum in x , but is stable in μ .

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References

- Abrams, P.A., Matsuda, H. and Harada, Y. (1993) Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* **7**, 465–487.
- Bulmer, M.G. (1989) Maintenance of genetic variability by mutation–selection balance: A child's guide through the jungle. *Genome* **31**, 761–767.
- Burger, R. (1986) On the maintenance of genetic variation: Global analysis of Kimura's continuum-of-alleles model. *J. Math. Biol.* **24**, 341–351.
- Burger, R. (1991) Moments, cumulants and polygenic dynamics. *J. Math Biol.* **30**, 199–213.
- Christiansen, F.B. (1991) On conditions for evolutionary stability for a continuously varying character. *Am. Nat.* **138**, 37–50.
- Crow, J.F. and Kimura, M. (1964) The theory of genetic loads. In *Proceedings of the XIth International Congress of Genetics* **2**, 495–505.
- Edelstein-Keshet, L. (1988) *Mathematical Models in Biology*. Random House, New York.
- Eshel, I. (1983) Evolutionary and continuous stability. *J. Theor. Biol.* **103**, 99–111.
- Eshel, I. and Motro, U. (1981) Kin selection and strong evolutionary stability of mutual help. *Theor. Pop. Biol.* **19**, 420–433.
- Fisher, R.A. (1937) The wave of advance of advantageous genes. *Ann. Eugen.* **7**, 355–360.
- Friedman, D. and Yellin, J. (submitted). Evolving landscapes for population games.
- Hofbauer, J., Schuster, P. and Sigmund, K. (1979) A note on evolutionary stable strategies and game dynamics. *J. Theor. Biol.* **81**, 609–612.

- Kimura, M. (1965) A stochastic model concerning the maintenance of genetic variability in quantitative characters. *Proc. Nat. Acad. Sci USA* **54**, 731–736.
- Kingman, J.F.C. (1978) A simple model for the balance between selection and mutation. *J. Appl. Prob.* **15**, 1–12.
- Lande, R. (1976) The maintenance of genetic variability by mutation in a polygenic character with linked loci. *Genet. Res. Camb.* **26**, 221–235.
- Li, C.C. (1967) Fundamental theorem of natural selection. *Nature, Lond.* **214**, 505–506.
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Maynard Smith, J. and Price, G.R. (1973) The logic of animal conflict. *Nature* **246**, 15–18.
- Price, G.R. (1970) Selection and covariance. *Nature, Lond.* **227**, 520–521.
- Robertson, A. (1966) A mathematical model of the culling process in dairy cattle. *Anim. Prod.* **8**, 95–108.
- Taper, M.L. and Case, T.J. (1992) Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* **46**, 317–333.
- Taylor, P.D. (1989) Evolutionary stability in one-parameter models under weak selection. *Theor. Pop. Biol.* **36**, 125–143.
- Taylor, P. and Jonker, L. (1978) Evolutionarily stable strategies and game dynamics. *Math. Biosci.* **40**, 145–156.
- Turelli, M. (1984) Heritable genetic variation via mutation–selection balance: Lerch's zeta meets the abdominal bristle. *Theor. Pop. Biol.* **25**, 138–193.
- Turelli, M. and Barton, N.H. (1990) Dynamics of polygenic characters under selection. *Theor. Pop. Biol.* **38**, 1–57.
- Turelli, M. and Barton, N.H. (1994) Genetic and statistical analyses of strong selection on polygenic traits: What me, normal? *Genetics* **138**, 913–941.
- Zeeman, E.C. (1980) Population dynamics from game theory. In *Global Theory of Dynamical Systems*, pp. 471–496. Lecture Notes in Mathematics, Vol. 819. Springer, Berlin.

Appendix

To simplify notation, in each of the subsections below we use \int for $\int_{-\infty}^{\infty}$ and $E[F(x)]$ denotes the expected value of F , i.e. $E[F] = \int Fpdx$. We also make use of the following identities:

If p is normal with mean and variance μ and V , and F is a function of x and μ , then:

$$p_x = -p_\mu = -\frac{(x - \mu)}{V}p \quad (\text{A1})$$

$$\int (x - \mu)^2 Fpdx = V \cdot E[F] + V^2 \cdot E[F_{xx}] \quad (\text{A2})$$

$$\int (x - \mu) Fpdx = V \cdot E[F_x] \quad (\text{A3})$$

Equation (A1) can be verified by direct computation. To verify (A2), note:

$$\int (x - \mu)^2 Fpdx = -V \int (x - \mu) Fp_x dx \quad (\text{by [A1]}) \quad (\text{A4})$$

$$= V \int [(x - \mu)F]_x p dx \quad (\text{int. by parts}) \quad (\text{A5})$$

$$= V \int Fp dx + V \int (x - \mu) F_x p dx \quad (\text{A6})$$

Using (A1) in the second term and integrating by parts yields:

$$\int (x - \mu)^2 Fpdx = VE[F] + V^2 E[F_{xx}] \quad (\text{A7})$$

Equation (A3) can be verified with the procedure used for Equation (A2).

Now we derive the replicator and gradient dynamical equations for the mean and variance (i.e. (3, 4) and (6, 7)).

Replicator dynamics

$\dot{\mu}$: From (2) we have $\dot{\bar{x}}_i = \text{cov}[x_i, W_i]$ and it follows that:

$$\dot{\mu} = \sum_i \dot{\bar{x}}_i = \sum_i \text{cov}[x_i, W_i] = \sum_i \text{cov}[x_i, W] \quad (\text{A8})$$

$$= \text{cov}[x, W] \quad (\text{A9})$$

\dot{V} : We have:

$$\frac{d\text{var}[x_i]}{dt} = \frac{d}{dt} \int (x_i - \bar{x}_i)^2 p_i dx_i \quad (\text{A10})$$

$$= -2\dot{\bar{x}} \int (x_i - \bar{x}_i) p_i dx_i + \int (x_i - \bar{x}_i)^2 \dot{p}_i dx_i \quad (\text{A11})$$

The first term of (A11) is zero and using Equation (1) for \dot{p}_i in the second term gives:

$$\int (x_i - \bar{x}_i)^2 (W_i - \bar{W}) p_i dx_i + \alpha_i \left[\int (x_i - \bar{x}_i)^2 \int u_i(\xi) p_i(x_i - \xi) d\xi dx_i - \int (x_i - \bar{x}_i)^2 p_i dx_i \right] \quad (\text{A12})$$

The mutation term in (A12) (the second term) can be reduced as follows. First, changing the order of integration in the double integral gives:

$$\alpha_i \left[\int u_i(\xi) \int (x_i - \bar{x}_i)^2 p_i(x_i - \xi) dx_i d\xi - \text{var}[x_i] \right] \quad (\text{A13})$$

Using a change of variable, $z_i = x_i - \xi$ gives:

$$\alpha_i \left[\int u_i(\xi) \int (z_i + \xi - \bar{x}_i)^2 p_i(z_i) dz_i d\xi - \text{var}[x_i] \right] \quad (\text{A14})$$

which reduces as

$$\alpha_i \left[\int u_i(\xi) \int [(z_i - \bar{x}_i)^2 + 2\xi(z_i - \bar{x}_i) + \xi^2] p_i(z_i) dz_i d\xi - \text{var}[x_i] \right] = \quad (\text{A15})$$

$$\alpha_i \left[\int u_i(\xi) [\text{var}[x_i] + 0 + \xi^2] d\xi - \text{var}[x_i] \right] = \quad (\text{A16})$$

$$\alpha_i v_i \quad (\text{A17})$$

Using this result in (A12) gives:

$$\frac{d\text{var}[x_i]}{dt} = \bar{W}(\text{var}_W[x_i] - \text{var}[x_i]) + \alpha_i v_i \quad (\text{A18})$$

Now by independence of the allele frequency distributions and mutation across loci,

$$\dot{V} = \sum_i d\text{var}[x_i]/dt \quad (\text{A19})$$

$$= \bar{W}(V_W - V) + \alpha v \quad (\text{A20})$$

which is Equation (4).

$$E[x^2] = V_x + \bar{x}^2$$

Gradient dynamics

Because the mutation term in the gradient dynamics (5) is identical to that of the replicator dynamics (1) by dropping the subscript i , we need only consider the selection term to derive the equations for $\dot{\mu}$ and \dot{V} .

$\dot{\mu}$: Using (4) we have:

$$\dot{\mu} = \int x \dot{p} dx = -V \int x [W_x p]_x dx \quad (\text{A21})$$

$$= VE[W_x] \quad (\text{int. by parts}) \quad (\text{A22})$$

\dot{V} : We have:

$$\dot{V} = -2\dot{\mu} \int (x - \mu) p dx + \int (x - \mu)^2 \dot{p} dx \quad (\text{A23})$$

$$= -V \int (x - \mu)^2 [W_x p]_x dx + \alpha v \quad (\text{by [5]}) \quad (\text{A24})$$

$$= 2VE[(x - \mu)W_x] + \alpha v \quad (\text{int. by parts}) \quad (\text{A25})$$

Now we show that if p is normal with mean and variance μ and V , then both the replicator dynamics (3, 4) and the gradient dynamics (6, 7) can be written as (8, 9) with $k = 1$ or 2 respectively.

Replicator dynamics

$\dot{\mu}$: First note that (A9) can be written as:

$$\dot{\mu} = \int (x - \mu)(W - \bar{W}) p dx \quad (\text{A26})$$

$$= VE[W_x] \quad (\text{by [A3]}) \quad (\text{A27})$$

\dot{V} : From (A20) we have:

$$\dot{V} = \bar{W}(V_W - V) + \alpha v \quad (\text{A28})$$

$$= \int (x - \mu)^2 (W - \bar{W}) p dx + \alpha v \quad (\text{A29})$$

$$= V^2 E[W_{xx}] + \alpha v \quad (\text{by [A2]}) \quad (\text{A30})$$

Gradient dynamics

We need only consider the dynamics of the variance, since (6) is identical to (8). Therefore, using (7) we have:

$$\dot{V} = 2V \int (x - \mu) W_x p dx + \alpha v \quad (\text{A31})$$

$$= 2V^2 E[W_{xx}] + \alpha v \quad (\text{by [A3]}) \quad (\text{A32})$$

Now we derive the entries of the Jacobian matrix (15) using Equations (8) and (9):

$$d\dot{\mu}/d\mu : \frac{d}{d\mu} \left[V \int W_x p dx \right] = V \left[\int W_{x\mu} p dx + \int W_x p_\mu dx \right] \quad (\text{A33})$$

and using (A1) in the second term of (A33) and integrating this term by parts gives:

$$= V \cdot E[W_{x\mu} + W_{xx}] \quad (\text{A34})$$

$$d\dot{\mu}/dV : \frac{d}{dV} \left[V \int W_x p dx \right] = E[W_x] + V \int W_x p_V dx \quad (\text{A35})$$

$$= 0 + \frac{1}{2V} \int (x - \mu)^2 W_x p dx \quad (\text{A36})$$

since the first term of (A35) is zero at equilibrium by (10), and therefore

$$= \frac{1}{2} \int W_x p dx + \frac{1}{2} V \int W_{xxx} p dx \quad (\text{by [A2]}) \quad (\text{A37})$$

$$= \frac{1}{2} V E[W_{xxx}] \quad (\text{by [10]}) \quad (\text{A38})$$

$$d\dot{V}/d\mu : \frac{d}{d\mu} \left[kV^2 \int W_{xx} p dx + \alpha v \right] = kV^2 \left[E[W_{xx\mu}] + \int W_{xx} p_\mu dx \right] \quad (\text{A39})$$

and using (A1) in the second term of (A39) and integrating by parts gives:

$$= kV^2 E[W_{xx\mu} + W_{xxx}] \quad (\text{A40})$$

$$d\dot{V}/dV : \frac{d}{dV} \left[kV^2 \int W_{xx} p dx + \alpha v \right] = 2VkE[W_{xx}] + V^2 k \int W_{xx} p_V dx \quad (\text{A41})$$

$$= 2VkE[W_{xx}] + \frac{1}{2} k \int (x - \mu)^2 W_{xx} p dx \quad (\text{A42})$$

and from (A2):

$$= 2VkE[W_{xx}] + \frac{1}{2} VkE[W_{xx}] + \frac{1}{2} V^2 kE[W_{xxxx}] \quad (\text{A43})$$

$$= \frac{5}{2} VkE[W_{xx}] + \frac{1}{2} V^2 kE[W_{xxxx}] \quad (\text{A44})$$