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Uniqueness of polymorphism for a discrete, selection-migration model with genetic dominance

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Abstract.

The migration into a natural population of a controlled population, e.g., a transgenic population, is studied using a one island selection-migration model. A 2-dimensional system of nonlinear difference equations describes changes in allele frequency and population size between generations. Biologically reasonable conditions are obtained which guarantee the existence and uniqueness of a polymorphic equilibrium in the cases of complete dominance and no dominance in fitness. This model may provide some useful information about the migration of transgenes into a natural population.

§1. Introduction

Migration and natural selection are two evolutionary processes that are important determinants of genetic composition and demographic properties of populations [3]. Effects produced by the interaction of these factors can significantly influence genetic variability in populations as well as affect mean population fitness. Here we study the impact of these two agencies within the framework of a one-island migration model. In this context, genes and individuals are viewed as migrating from a large donor population into an island or receiving population in which density-dependent selection takes place. Based upon this model, we describe the changes in allele frequency and population size that occur over generations in an island population in terms of a system of two-dimensional difference equations. With certain assumptions this system is applicable to the investigation of the fate of a transgene that has migrated into a nontargeted natural population. Considered

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in this light, a population composed of individuals genetically modified through transgenics is understood to be the donor population, and a natural population is viewed as the island or recipient population. In this paper we demonstrate that a unique polymorphic equilibrium exists for this system when density-dependent fitness is regarded to be under the control of a single genetic locus with alleles expressed according to either a complete dominance or a no dominance mode [1].

The one-island model studied here could potentially be used to explore incorporation of transgenes into natural tree populations. In forest biology, there is much concern about ecological consequences that might result from such gene transfer. As a case in point, genetic engineering is being seriously considered as a method for improving wood properties of loblolly pine (*Pinus taeda*), a timber tree grown extensively in the southeastern United States and several South American countries (see Sedjo [7]). This biotechnology has the potential to produce trees with greater quantities of useful fiber and fiber that can more efficiently be processed into wood pulp. But in the southern United States, loblolly pine commercial stands composed of trees carrying certain transgenes could pose an ecological hazard to nearby natural pine forests because of the possibility of transgene transfer (see Williams [13]). Uncertainties abound about effects that will accrue from the spread of transgenes in natural forest environments and this heightens unease about the risks that could accompany use of this technology. As a result, there is interest in studying the possible fate of transgenes that have entered nontargeted populations.

§2. Model background

Density-dependent selection may be studied by considering a diploid population with two alleles, A and a, at a single autosomal locus. Here, a population of density x consists of individuals with one of three genotypes, AA, Aa, or aa. Let p denote the frequency of the A allele, where $0 \leq p \leq 1$, and hence $1-p$ is the frequency of the a allele. The effects of natural selection determine an average per capita replacement rate or *fitness* f_{ij} for the ij-genotype, where $i, j = A, a$, which measures fertility and viability of that genotype. Allele fitnesses f_A and f_a are linear combinations of genotype fitnesses weighted by allele frequency and are defined by $f_A \equiv pf_{AA} + (1-p)f_{Aa}$ and $f_a \equiv pf_{Aa} + (1-p)f_{aa}$. The population mean fitness f is given by $f \equiv pf_A + (1-p)f_a$. For this study we assume density-dependent selection, i.e., genotypic fitnesses $f_{ij}(x)$ depend on population density x and are independent of the allele frequency p.

When population density is small, each genotype does well but genotype fitness decreases as population density increases because of the detrimental effects of crowding. Such functions f_{ij} are referred to as *pioneer* fitness functions [8]. Exponential (see Ricker [4]), rational (see Hassell and Comins [2]), and linear (see Selgrade and Roberds [9, 10]) functions have been used as pioneer fitnesses in modeling populations. More specifically, we assume that each $f_{ij}(0) > 1$ and that $f_{ij}(x) \searrow 0$ as $x \to \infty$. This guarantees that for each fixed $p \in [0,1]$, there is a population density $x > 0$ such that the population equilibrates, i.e., $f(p,x) = 1$. Henceforth, for $i, j = A, a$ we assume:

(A1) $f'_{ij}(x) < 0$ **for all** $x > 0$, $f_{ij}(0) > 1$ **and** $f_{ij}(x) \to 0$ **as** $x \to \infty$.

To study the migration of a population of constant allele frequency into another population, we appeal to a one-island model discussed by Roberds and Selgrade, see [5] and [11]. Such a model might represent the migration into a natural population of a controlled population, e.g., a transgenic population. Let x and p denote the island population density and allele frequency, respectively. Following selection in each generation, assume gametes are contributed to the island population by immigration from a population with allele frequency the constant q with $0 \le q \le 1$. Random mating occurs following migration so that the number of additional zygotes in the next generation produced as a consequence of immigration is denoted by y. In [5] and [11], we derived the following system of difference equations that describes changes in allele frequency and population size between generations:

$$
\begin{aligned}
p_{n+1} &= \frac{p_n\, x_n\, f_A + q\, y}{x_n\, f + y} \\
x_{n+1} &= x_n\, f + y\,.
\end{aligned}
\tag{1}
$$

Here p_{n+1} and x_{n+1} represent allele frequency and population size in the next generation.

It is convenient both mathematically and biologically to introduce a per capita migration rate for $x > 0$ given by

$$h(x) \equiv \frac{y}{x}\,,$$

which measures the per capita migration per generation relative to the island population size x. It is biologically reasonable to assume that $h(x)$ is a nonincreasing function of population size, i.e., $h'(x) \le 0$. There are two standard examples of migration in this form. The simplest case occurs when the same amount of migration takes place each generation so that y is constant and $h'(x) = -y/x^2 < 0$. The second type occurs when the amount of migration increases linearly with x in each generation as discussed in Selgrade and Roberds [11], i.e., $y = mx$ where m is a constant. For this study, we consider migration of the former type, i.e., we assume that y is constant.

After replacing y by $xh(x)$ in (1), the transition equations become

$$\begin{aligned} p_{n+1} &= \frac{p_n f_A + q h}{f + h} \\ x_{n+1} &= x_n (f + h) . \end{aligned} \tag{2}$$

In (2), $f + h$ denotes the per capita transition function for the island population. For $x > 0$, systems (1) and (2) are equivalent so, henceforth, we study (2).

§3. Properties of equilibria

The phase space for system (2) is the slot in the (p, x)-plane designated by

$$\mathcal{S} \equiv \{(p, x) : 0 \le p \le 1, 0 < x\} .$$

When $y = 0$ (i.e., $h = 0$), the boundary lines of $\mathcal{S}$, $\{p = 0\}$ and $\{p = 1\}$, represent allele fixation and, therefore, are invariant. If $y > 0$ (i.e., $h > 0$) and $0 < q < 1$, points on the vertical boundaries of $\mathcal{S}$ are mapped into the interior of $\mathcal{S}$.

An equilibrium E is an allele frequency $\overline{p}$, $0 \le \overline{p} \le 1$, and a population density $\overline{x} > 0$ which remain constant across generations, i.e., $p_n = \overline{p}$ and $x_n = \overline{x}$ for all n. Such an E is said to be a *polymorphism* if $0 < \overline{p} < 1$. From (2), an equilibrium $E = (\overline{p}, \overline{x})$ satisfies the system:

$$\begin{aligned} p &= p f_A + q h \\ 1 &= f + h . \end{aligned} \tag{3}$$

Since the frequency of the allele a is $1 - p$ and is constant at equilibrium, the equation $1 - p_{n+1} = 1 - p_n$ implies that the following equation must also be satisfied at equilibrium

$$1 - p = (1 - p) f_a + (1 - q) h . \tag{4}$$

Hence, a polymorphism is a point of intersection of the three isocline curves:

$$\begin{aligned}
&\mathcal{C} \equiv \{(p,x) : f(p,x) + h(x) = 1\} \\
(5) \qquad &\mathcal{C}_A \equiv \{(p,x) : p\,[f_A(p,x) - 1] + q\,h(x) = 0\} \quad \text{and} \\
&\mathcal{C}_a \equiv \{(p,x) : (1-p)\,[f_a(p,x) - 1] + (1-q)\,h(x) = 0\}\,.
\end{aligned}$$

Any pair of equations in (5) will determine E.

Since genotype fitnesses are decreasing then $\partial f_A/\partial x < 0$, $\partial f_a/\partial x < 0$ and $\partial f/\partial x < 0$. With $h'(x) < 0$, it follows from the implicit function theorem that the curves defined in (5) may be considered as the graphs of x as functions of p, which will be denoted by $\tilde{x}(p)$, $\tilde{x}_A(p)$ and $\tilde{x}_a(p)$, respectively. Using the implicit function theorem and the fact that $\frac{\partial f}{\partial p} = 2\,(f_A - f_a)$, we compute that

$$\text{(6a)} \qquad \frac{d\tilde{x}}{dp} = \frac{-\,2\,(f_A - f_a)}{\frac{\partial f}{\partial x} + h'}\,,$$

$$\text{(6b)} \qquad \frac{d\tilde{x}_A}{dp} = \frac{1 - f_A - p\,\frac{\partial f_A}{\partial p}}{p\,\frac{\partial f_A}{\partial x} + q\,h'}\,,$$

$$\text{(6c)} \qquad \frac{d\tilde{x}_a}{dp} = \frac{f_a - 1 - (1-p)\,\frac{\partial f_a}{\partial p}}{(1-p)\,\frac{\partial f_a}{\partial x} + (1-q)\,h'}\,.$$

From (A1) and the fact that $h(x) \searrow 0$ as $x \to \infty$, it follows that for each value of $p \in [0,1]$, there is an x so that $f(p,x) + h(x) = 1$ and so the function $\tilde{x}(p)$ exists for all p and the curve $\mathcal{C}$ separates $\mathcal{S}$ into two subsets. Similar arguments show that the functions $\tilde{x}_A(p)$ and $\tilde{x}_a(p)$ exist for $0 < p < 1$. In addition, it follows that as $p \to 0$ the function $\tilde{x}_A(p)$ approaches infinity and that as $p \to 1$ the function $\tilde{x}_a(p)$ approaches infinity, see [5]. By rewriting the equation that defines $\mathcal{C}$ as

$$p\,[f_A(p,x) - 1] + q\,h(x) + (1-p)\,[f_a(p,x) - 1] + (1-q)\,h(x) = 0\,,$$

it follows that the graph of the function $\tilde{x}(p)$ is exactly between the graphs of $\tilde{x}_A(p)$ and $\tilde{x}_a(p)$. In fact, Roberds and Selgrade [5] showed that these isoclines must cross at least once and so there is at least one polymorphism.

Theorem 3.1. Existence of a polymorphism [5]. *Fix* $0 < q < 1$. *Assume that each genotype fitness* f_{ij} *satisfies (A1) and that* $h(x) = y/x$ *where* y *is a constant. Then (2) has at least one polymorphic equilibrium* $E = (\overline{p}, \overline{x})$, *i.e.,* $0 < \overline{p} < 1$ *and* $\overline{x} > 0$.

§4. Dominance assumptions

Here we introduce two classical notions of dominance from genetics that describe genotypic effects on fitness, e.g., see [1] or [6]. First we assume that the presence of the allele A confers maximal fitness on a genotype and consider the case where genotypic fitnesses exhibit *complete dominance* (CD). Thus, for all $x > 0$, we assume that

$$\text{(CD)} \qquad f_{AA}(x) = f_{Aa}(x) > f_{aa}(x)\,.$$

With complete dominance, the allele and mean fitnesses become

$$\begin{aligned} f_A &= f_{AA} \\ f_a &= p\, f_{AA} + (1-p)\, f_{aa} \qquad (7) \\ f &= p\,(2-p)\, f_{AA} + (1-p)^2\, f_{aa}\,. \end{aligned}$$

For the second case, we assume that the heterozygote fitness is the average of the homozygote fitnesses, i.e., for all $x > 0$

$$\text{(ND)} \qquad f_{Aa}(x) = (f_{AA}(x) + f_{aa}(x))/2\,.$$

In this case the fitnesses are said to be *additive* or to exhibit *no dominance* (ND). Allele and mean fitnesses then become

$$\begin{aligned} f_A &= p\,(f_{AA} - f_{aa})/2 + (f_{AA} + f_{aa})/2 \\ f_a &= (1-p)\,(f_{aa} - f_{AA})/2 + (f_{AA} + f_{aa})/2 \qquad (8) \\ f &= p\, f_{AA} + (1-p)\, f_{aa}\,. \end{aligned}$$

It follows that $f_A - f_a = (1-p)\,(f_{AA} - f_{aa})$ if (CD) holds and $f_A - f_a = 0.5\,(f_{AA} - f_{aa})$ if (ND) holds.

§5. Uniqueness of polymorphism

From Theorem 3.1, (2) always has at least one polymorphism. In the case of complete dominance (CD), we show here that this polymorphism is unique. Also, we obtain conditions for uniqueness if (ND) holds. To do this we study the geometry of the isoclines (5).

The curve $\mathcal{C}$ in $\mathcal{S}$ is the graph the function $\tilde{x}(p)$. So for each fixed $p \in [0, 1]$, the x-coordinate of a point on $\mathcal{C}$ is determined by the intersection of the two functions of x, i.e., $f(p, x)$ and $1 - y/x$. Since $f_{ii}(0) > 1$ and $f_{ii}(x) \searrow 0$ as $x \to \infty$ for $i = A, a$, $f_{AA}(x)$ crosses $1 - y/x$ at some $x_A > y$ and $f_{aa}(x)$ crosses $1 - y/x$ at some $x_a > y$, see Figure 1. If $x_A = x_a$ then for all $p \in [0, 1]$ it follows from (7) or (8) that

$$f(p, x_A) = f_{AA}(x_A) = 1 - \frac{y}{x_A}$$

and $\mathcal{C}$ is the horizontal line $\{(p, x) : x = x_A = x_a\}$. If $x_A \neq x_a$ then define $m = \min\{x_a, x_A\}$ and $M = \max\{x_a, x_A\}$. Clearly for all $x \in [m, M]$, one of the genotype fitnesses is larger than the other fitness (Figure 1) and, for each p, $f(p, x)$ is a decreasing function of x which lies in between the curves $f_{AA}(x)$ and $f_{aa}(x)$. Hence $f(p, x)$ crosses $1 - y/x$ uniquely at x-value given by $\tilde{x}(p) \in [m, M]$. If $m = x_a$ (which is the case for (CD)) then $f_{AA}(x) - f_{aa}(x) > 0$ for all $x \in [m, M]$ and (6a) implies that $\tilde{x}(p)$ is an increasing function of p. If $m = x_A$ then $f_{AA}(x) - f_{aa}(x) < 0$ for all $x \in [m, M]$ and (6a) implies that $\tilde{x}(p)$ is an decreasing function of p. We have established the following result:

Proposition 5.1. *Assume (A1) and (CD) or (ND) for all $x > 0$. Then one of the following three cases applies:*
(i) $\mathcal{C}$ is the graph of the increasing function $\tilde{x}(p)$ from $\tilde{x}(0) = x_a$ to $\tilde{x}(1) = x_A$ and $f_{AA}(x) - f_{aa}(x) > 0$ for all $x \in [m, M] = [x_a, x_A]$.
(ii) $\mathcal{C}$ is the graph of the decreasing function $\tilde{x}(p)$ from $\tilde{x}(0) = x_a$ to $\tilde{x}(1) = x_A$ and $f_{AA}(x) - f_{aa}(x) < 0$ for all $x \in [m, M] = [x_A, x_a]$.
(iii) $\mathcal{C}$ is the horizontal line $\{(p, x) : x = x_A = x_a\}$ and $f_{AA}(x) - f_{aa}(x) = 0$ for all $x \in [m, M]$.

If $E = (\overline{p}, \overline{x})$ is a polymorphism then multiplying the second equation in (3) by $\overline{p}$ and subtracting from the first equation in (3) gives

$$h(\overline{x})\,(\overline{p} - q) = \begin{cases} p\,(1-p)^2\,(f_{AA}(\overline{x}) - f_{aa}(\overline{x})) & \text{if (CD) holds} \quad (9a) \\ 0.5\,p\,(1-p)\,(f_{AA}(\overline{x}) - f_{aa}(\overline{x})) & \text{if (ND) holds} \quad (9b) \end{cases}$$

Hence, the terms $(f_{AA}(\overline{x}) - f_{aa}(\overline{x}))$ and $(\overline{p} - q)$ have the same sign. If case (iii) of Prop. 5.1 holds then $\overline{x} = x_A = x_a$. From (9), It follows that $\overline{p} = q$ and so the polymorphism $E = (q, x_A)$ is unique. If (CD) holds then case (i) of Prop. 5.1 applies and $\tilde{x}(p)$ is an increasing function of

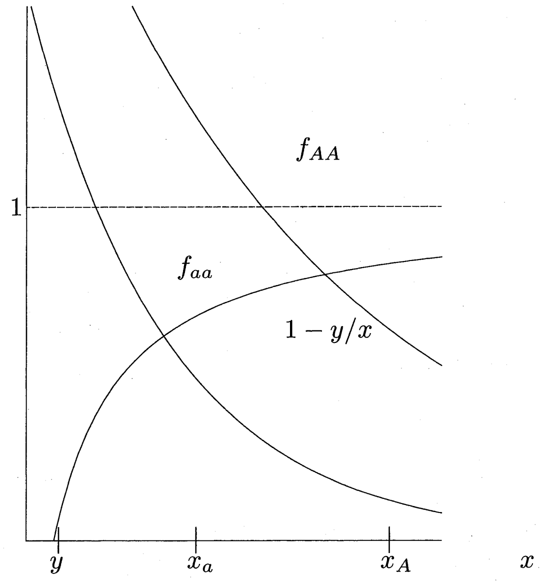

Fig. 1. Graphs of $f_{AA}(x)$, $f_{aa}(x)$ and $1-y/x$ when $x_a < x_A$.

p. Using (7), the numerator of (6b) is

$$1 - f_A - p\frac{\partial f_A}{\partial p} = 1 - f_{AA}(x).$$

which is positive along $\mathcal{C}_A$. Hence, $\tilde{x}_A(p)$ is a decreasing function of p and may intersect $\tilde{x}(p)$ at most once. With Theorem 3.1 and (9a), we have the result:

Theorem 5.2. Uniqueness of polymorphism for (CD). *Assume that each genotype fitness f_{ij} satisfies (A1) and (CD) for all $x > 0$. If $0 < q < 1$ then there exist a unique polymorphic equilibrium $E = (\overline{p}, \overline{x})$ where $\overline{x} > 0$ and $q < \overline{p} < 1$.*

The situation is more difficult when (ND) holds because $\tilde{x}_A(p)$ and $\tilde{x}_a(p)$ may not be monotone functions. This problem is avoided by assuming that both homozygote fitnesses $f_{ii}(x)$ decrease faster than $h(x) = y/x$ for $i = A, a$. Many biologically reasonable fitnesses behave this way. Linear fitnesses may not but are not typically used in discrete models because population sizes may become negative. The precise assumption we make for $i = A, a$ is:

(A2) $f'_{ii}(x) < h'(x) = -y/x^2$ **for all** $x \in [m, M]$**.**

We proceed by considering cases (i) and (ii) of Prop. 5.1 where (ND) holds.

For $E = (\overline{p}, \overline{x})$ in case (i), we have $x_a \le \overline{x} \le x_A$ and $f_{AA}(x) - f_{aa}(x) > 0$ for all $x \in [x_a, x_A]$. From (9b) it follows that $\overline{p} > q$. We use the equations for $\mathcal{C}$ and $\mathcal{C}_A$ in (5) to find two functions for p in terms of x whose intersections determine $E = (\overline{p}, \overline{x})$. Then we show that these curves intersect only once if $q \ge 0.5$.

Multiply the equation for $\mathcal{C}$ by p and combine the result with the equation for $\mathcal{C}_A$ to eliminate the quadratic term in p. The resulting equation may be solved for p in terms of x giving

$$(10) \qquad p = \frac{2\,q\,h(x)}{1 + h(x) - f_{AA}(x)} \equiv F(x)\,.$$

Let the right side of (10) define the function $F(x)$ for $x \in [x_a, x_A]$ where the denominator is not zero. Because of (A2), the denominator is increasing on $[x_a, x_A]$ and positive at any equilibrium $\overline{x}$ value. Hence, $F(x)$ is defined on a subinterval of $[x_a, x_A]$ containing all the x-coordinates of equilibria. Also $\mathcal{C}$ determines p in terms of x by solving $f(p, x) = 1 - h(x)$ to define the function $p = G(x)$ as

$$(11) \qquad p = \frac{1 - h(x) - f_{aa}(x)}{f_{AA}(x) - f_{aa}(x)} \equiv G(x)\,.$$

The points (p, x) of intersection of the F and G curves are the equilibria for $0 < p < 1$ and $x \in [x_a, x_A]$. Setting $F(x) = G(x)$ yields the condition

$$(12) \qquad 0 < \frac{2\,q\,h(x)}{1 + h(x) - f_{AA}(x)} = \frac{1 - h(x) - f_{aa}(x)}{f_{AA}(x) - f_{aa}(x)} < 1\,.$$

For $E = (\overline{p}, \overline{x})$ the first ratio in (12) implies that

$$0 < 2\,q\,h(\overline{x}) < 1 + h(\overline{x}) - f_{AA}(\overline{x})$$

or

$$(13) \qquad (2\,q - 1)\,h(\overline{x}) < 1 - f_{AA}(\overline{x})\,.$$

Hence, if $q \ge 0.5$ then $0 < 1 - f_{AA}(\overline{x})$. Clearly

$$(14) \qquad F'(\overline{x}) = \frac{2\,q\,h'(\overline{x})\,[1 - f_{AA}(\overline{x})] + 2\,q\,h(\overline{x})\,f'_{AA}(\overline{x})}{[1 + h(\overline{x}) - f_{AA}(\overline{x})]^2}\,,$$

so $F'(\overline{x}) < 0$ if $q \geq 0.5$. Since $f_{AA}(\overline{x}) - f_{aa}(\overline{x}) > 0$ then the second ratio in (12) gives

$$0 < 1 - h(\overline{x}) - f_{aa}(\overline{x}) < f_{AA}(\overline{x}) - f_{aa}(\overline{x}) \,, \tag{15}$$

which implies that

$$1 - h(\overline{x}) - f_{AA}(\overline{x}) < 0 \,. \tag{16}$$

Computing

$$\begin{aligned} G'(\overline{x}) \;&=\; \frac{-h'(\overline{x})[f_{AA}(\overline{x}) - f_{aa}(\overline{x})] - f'_{AA}(\overline{x})[1 - h(\overline{x}) - f_{aa}(\overline{x})]}{[f_{AA}(\overline{x}) - f_{aa}(\overline{x})]^2} \\ &+\; \frac{f'_{aa}(\overline{x})[1 - h(\overline{x}) - f_{AA}(\overline{x})]}{[f_{AA}(\overline{x}) - f_{aa}(\overline{x})]^2} \end{aligned} \tag{17}$$

and using (15) and (16), we see that $G'(\overline{x}) > 0$. Hence, if $q \geq 0.5$, for each $\overline{x}$ where the F and G curves intersect we must have

$$F'(\overline{x}) < 0 \quad \text{and} \quad G'(\overline{x}) > 0 \,. \tag{18}$$

Since F and G are continuous on the subinterval of $[x_a, x_A]$ containing all $\overline{x}$, an application of the intermediate value theorem implies that (18) may hold at only one $\overline{x}$. Hence, the polymorphism $E = (\overline{p}, \overline{x})$ is unique.

Finally, for E in case (ii) of Prop. 5.1, we have $x_A \leq \overline{x} \leq x_a$ and $f_{AA}(x) - f_{aa}(x) < 0$ for all $x \in [x_A, x_a]$. From (9b) it follows that $\overline{p} < q$. We use the equations for $\mathcal{C}$ and $\mathcal{C}_a$ in (5) to find two functions for p in terms of x whose intersections determine $E = (\overline{p}, \overline{x})$. Then we show that these curves intersect only once if $q \leq 0.5$.

Multiply the equation for $\mathcal{C}$ by $1-p$ and combine the result with the equation for $\mathcal{C}_a$ to eliminate the term with factor $p(1-p)$. The resulting equation may be solved for $1 - p$ in terms of x giving

$$1 - p = \frac{2\,(1-q)\,h(x)}{1 + h(x) - f_{aa}(x)} \,. \tag{19}$$

Since $0 < 1 - p < 1$, from (19) we see that for $E = (\overline{p}, \overline{x})$

$$0 < 2\,(1-q)\,h(\overline{x}) < 1 + h(\overline{x}) - f_{aa}(\overline{x})$$

which implies that

$$(1 - 2\,q)\,h(\overline{x}) < 1 - f_{aa}(\overline{x}) \,. \tag{20}$$

Hence, if $q \leq 0.5$ then $0 < 1 - f_{aa}(\overline{x})$. Solve (19) for p in terms of x to obtain the function

$$H(x) \equiv 1 - \frac{2\,(1-q)\,h(x)}{1 + h(x) - f_{aa}(x)}\,. \tag{21}$$

As with $F(x)$ using (A2), we see that the denominator in (21) is increasing on $[x_A, x_a]$ and positive at any equilibrium $\overline{x}$ value. Hence, $H(x)$ is defined on a subinterval of $[x_A, x_a]$ containing all the x-coordinates of equilibria. Compute

$$H'(\overline{x}) = \frac{-2\,(1-q)\ [h'(\overline{x})\,(1 - f_{aa}(\overline{x})) + h(\overline{x})\,f'_{aa}(\overline{x})]}{[1 + h(\overline{x}) - f_{aa}(\overline{x})]^2} \tag{22}$$

and notice that $H'(\overline{x}) > 0$ if $q \leq 0.5$. Recall $\mathcal{C}$ determines $G(x)$ defined in (11) and the points (p, x) of intersection of the H and G curves are the equilibria for $0 < p < 1$ and $x \in [x_A, x_a]$. Since $f_{AA}(x) - f_{aa}(x) < 0$ and $0 < G(\overline{x}) < 1$, from (11) we conclude that

$$f_{AA}(x) - f_{aa}(x) < 1 - h(\overline{x}) - f_{aa}(\overline{x}) < 0$$

and so

$$0 < 1 - h(\overline{x}) - f_{AA}(\overline{x})\,.$$

With these inequalities, it is clear that each term in the numerator in (17) is negative and hence $G'(\overline{x}) < 0$. Hence, if $q \leq 0.5$, for each $\overline{x}$ where the G and H curves intersect we must have

$$G'(\overline{x}) < 0 \quad \text{and} \quad H'(\overline{x}) > 0\,, \tag{23}$$

which may occur at most once on a closed interval.

Thus we have established the following result where the three cases correspond to those in Proposition 5.1.

Theorem 5.3. Uniqueness of polymorphism for (ND). *Assume (A1), (A2) and no dominance (ND) for all $x > 0$. Suppose that $E = (\overline{p}, \overline{x})$ is a polymorphism, i.e., $0 < \overline{p} < 1$. Then one of the following three statements holds:*
(i) $x_a < \overline{x} < x_A$ and $q < \overline{p}$. In addition, if $q \geq 0.5$ then E is unique.
(ii) $x_A < \overline{x} < x_a$ and $\overline{p} < q$. In addition, if $q \leq 0.5$ then E is unique.
(iii) $x_a = \overline{x} = x_A$ and $E = (q, x_A)$.

§6. Conclusion

Selgrade and Roberds [12] present an example of transgenic immigration with exponential fitnesses satisfying (CD). If $q = 0.9$, the unique polymorphism $E = (0.906, 1.80)$ appears globally attracting. In fact, if the A allele is absent in the island population, numerical results indicate that within five generations of immigration the island population evolves so that p is at least 0.9.

In general, the stability of the unique polymorphism is not known. In [5] where immigration depends on the population size x, examples of saddle point equilibria are presented for (CD). We conjecture similar behavior for the case of constant immigration studied here and this will be a topic of future investigation. Also, whether or not the bound on q in Theorem 5.3 is necessary for equilibrium uniqueness needs to be determined.

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