Chapter 5

Discrete-time population genetics model

In this chapter, the model of the previous chapter is extended to a 3-dimensional diffeomorphism. The dynamics are expected to be very similar, however, the analysis is more complicated. I am not aware of any papers that deal with this class of model. In Van Coller’s [23] thesis, there are two chapters that deal with the same kind of simple genetic variation in a single species: one chapter deals with pioneer type trees, and the other with climax trees. Again, the switch to the discrete-time system is in order to approximate discretely reproducing populations more accurately. I have found again that stable interior polymorphic equilibria or invariant circles can exist, and also that genetic variation is necessary for their existence by means of an example model. When one starts with only one of the two homozygotes, the competitive system excludes one of the two species, depending on the initial coordinates on the phase plane.

In the first section a simple linearization analysis is done to show that, again, local heterozygote superiority is a necessary condition for the occurrence of a Hopf bifurcation. In the second section, the same simplifying assumption, homozygote equality, is considered. Again, this allows us to reduce the dimension of the system using an invariant manifold. Finally in the last section, XPPAUT is used to demonstrate the possibility of a stable interior polymorphic invariant circle, and the consequences of fixation.
5.1 Model equations

As briefly described in the introduction, the dynamics for the gene frequency is slightly changed, and the system of maps becomes

\[ (p, M, N) \rightarrow (p^{\mu_A/\mu}, \mu M, \eta N) \quad (5.1) \]

where \( \mu, \mu_A, \mu_a \) are defined exactly the same as before, and \( \mu_{ij} \) are functions of \( M \) and \( N \) only. Equilibria are found when \( \mu = \eta = 1 \), so also \( \mu_A = \mu_a = 1 \). The last two conditions imply that the following must be satisfied:

\[
\begin{align*}
(p\mu_{AA} + (1-p)\mu_{Aa}) &= 1, \\
(p\mu_{Aa} + (1-p)\mu_{aa}) &= 1.
\end{align*}
\]

Unlike in the ODE case, this does not directly imply that homozygote superiority or inferiority is necessary. The identities of previous chapter, (4.7) and (4.8) still hold, and now the Jacobian at an internal equilibrium \( C \) becomes

\[
J(C) = I + \begin{pmatrix}
\frac{\partial}{\partial p} (\mu_A/\mu) & \frac{\partial}{\partial M} (\mu_A/\mu) & \frac{\partial}{\partial N} (\mu_A/\mu) \\
0 & M \frac{\partial \mu}{\partial M} & M \frac{\partial \mu}{\partial N} \\
0 & N \frac{\partial \mu}{\partial M} & N \frac{\partial \mu}{\partial N}
\end{pmatrix},
\]

where \( I \) is the three-dimensional identity matrix. The first eigenvalue of the Jacobian is just \( 1 + \frac{\partial}{\partial p} (\mu_A/\mu) \). Expanding the partial derivatives and employing the identities (4.7) and (4.8) leads to

\[
\lambda_1 = 1 + \mu_{AA} - \mu_{Aa}.
\]

For an interior equilibrium to be stable, all eigenvalues must lie inside the unit circle on the complex plane. Thus for stability we require

\[
|1 + \mu_{AA} - \mu_{Aa}| < 1 \\
\Rightarrow -2 < \mu_{AA} - \mu_{Aa} < 0,
\]

(5.6)
which is, again, the heterozygote superiority condition required at the equilibrium since the genotypes $AA$ and $aa$ are symmetric. The other two eigenvalues are from $I_2 + E(C)$ ($I_2$ is the $2 \times 2$ identity matrix), where again, $E$ is the lower right ecology submatrix.

If the total weighted population density variable is the same for each of the pioneer genotypes, that is if $\mu_{ij} = \mu_{ij}(Z)$, then there is a two-dimensional invariant manifold as in chapter 3. If $p \to p_0$, then the function $\mu(Z)$ in chapter 3 becomes

$$
\mu(Z) = p_0^2 \mu_{AA}(Z) + 2p_0(1 - p_0)\mu_{Aa}(Z) + (1 - p_0)^2 \mu_{aa}(Z).
$$

The same condition $\det C < 0$ must hold for Hopf bifurcation on the invariant manifold. Given that there exists a stable interior equilibrium or invariant circle on the 2-dimensional invariant manifold, they are locally exponentially stable if heterozygote is superior to both homozygotes in that neighborhood.

### 5.2 Homozygote equality

That $p \to p_0$ exponentially for some $p_0 > 0$ can be demonstrated, as before, if we assume a simplifying condition that the two homozygotes have identical fitness functions. Given that $\mu_{AA} = \mu_{aa}$ then

$$
\frac{\mu_A}{\mu} = \frac{p\mu_{AA} + (1 - p)\mu_{Aa}}{(2p^2 - 2p + 1)\mu_{AA} + 2p(1 - p)\mu_{Aa}},
$$

$$
\left| \frac{\mu_A}{\mu} \right|_{p=0.5} = 1,
$$

and one can show that again, $p \to 0.5$ as $t \to \infty$. A simple coordinate transformation $p = \frac{1}{2} + r$ takes the map for $p$ to

$$
r \quad \mapsto \quad \frac{\mu_A}{\mu} \left( r + \frac{1}{2} \right) - \frac{1}{2}
$$

$$
\mapsto \quad \frac{r(\mu_{AA} - \mu_{Aa}) + \frac{1}{2}(\mu_{AA} + \mu_{Aa})}{2r^2(\mu_{AA} - \mu_{Aa}) + \frac{1}{2}(\mu_{AA} + \mu_{Aa})}
$$

$$
\mapsto \quad \frac{2\mu_{AA}}{\mu_{AA} + \mu_{Aa}} r + \mathcal{O}(r^2)
$$
so that if \(\mu_{AA} - \varepsilon > \mu_{AA}\) for some \(\varepsilon > 0\), then the coefficient in front of \(r\) is strictly between 0 and 1, so the two-dimensional manifold \(r = 0\), or equivalently \(p = 0.5\), is exponentially stable. So again, the three dimensional system reduces to \(p = 0.5\) and

\[
(M, N) \mapsto ((\mu_{AA} + \mu_{Aa})M/2, \eta N).
\] (5.13)

As before, if both \(\mu_{AA}\) and \(\mu_{Aa}\) are functions of the same weighted total density \(Z\), then (5.13) is exactly the same system described and analyzed in chapter 4. Thus there would a be stable interior polymorphic equilibrium or an invariant circle given the same conditions given in that chapter. If the \(Z_{ij}\) are different, then for homozygote equality the analysis would be similar to the one given in chapter 4, but more complex. However, this case is not considered in this thesis. In the next section an exponential fitness function is analyzed using XPPAUT.

### 5.3 Numerical example

Consider the following exponential model:

\[
\mu_{ij}(Z) = e^{(a_{ij} - Z)},
\] (5.14)

\[
\eta(W) = We^{(b - W)}.
\] (5.15)

Figure 5.1 shows the trajectories before and after Hopf bifurcation at \(E_1\) for homozygote equality. Again, to show that the Hopf bifurcation is not restricted to homozygote equality, a two-parameter bifurcation is computed using XPPAUT. Figure 5.2 shows the two-parameter \((c_{11} \text{ and } a_{AA})\) bifurcation diagram for the Hopf bifurcation at \(E_1\), plotted against the equilibrium \(p\) in the \(z\)-axis. Note that heterozygote superiority is lost as \(a_{AA}\) increases past \(a_{Aa}\).

While it is not analytically obvious, it can again be demonstrated that in this model, genetic variation may be crucial in making a stable interior equilibrium possible. If there
Figure 5.1: Trajectories for discrete-time genetics model, before and after Hopf bifurcation. The parameters are $c_{22} = 1$, $a_{AA} = a_{Aa} = 0.2$, $a_{Aa} = 0.4$, $b = 1.2$, with $p(0) = 0.1$. The parameter $c_{11} = 0.5$ for the top diagrams, and $c_{11} = 4.3$ for the bottom diagrams. The diagrams on the right show the same trajectories projected onto the $Mp$-plane. Note that $p$ approaches 0.5 monotonically.
Figure 5.2: Two parameter continuation of Hopf bifurcation for the discrete-time model. The other constant parameter values are the same as in figure 5.1. The mark * indicates where the continuation was initiated, at homozygote equality \( a_{AA} = a_{aa} = 0.2 \). The vertical axis shows the equilibrium \( p \) value.

is only one of the homozygotes present initially, the system would exclude either species depending on the initial values, making stable coexistence impossible. Using the same model as above, consider trajectories starting with \( p = 0 \) or \( p = 1 \). As it can be seen from figure 5.3 below, in either case there is no longer a stable interior equilibrium, but the species exclude each other depending on the initial condition.

5.4 Summary

The results of this chapter are very similar to those of chapter 4. I have shown, through an analogous analysis to that of chapter 4, that there exists a stable interior polymorphic equilibrium or invariant circle, given the simplifying homozygote equality condition. I have also shown numerically that homozygote equality is not necessary for stable coexistence. Moreover, a numerical example showed a case where the genetic variation is
Figure 5.3: Trajectories under loss of genetic variation. The trajectories here for competition between climax and either of the homozygotes shows that the species exclude each other, depending on the initial condition. The parameter values are the same as those used in the top diagram of figure 5.1

a necessity in obtaining such an equilibrium: coexistence becomes impossible when the system initially starts with either of the homozygotes only.