# Stochastic population genetics: homework 6 To be returned on June 7 

June 2, 2017

## 1 Two-loci dynamics

In this problem we are interested in the dynamics of a large population of diploids (throughout the exercise we will always consider the limit of infinite population). We consider two loci in the genome: the first one has two possible alleles $A$ and $a$, and the second one has two possible alleles $B$ and $b$. The probabilities of the four types $\mathrm{AB}, \mathrm{Ab}, \mathrm{aB}, \mathrm{ab}$, are $x_{1}, x_{2}, x_{3}$ and $x_{4}$, respectively. We also define $p_{1}, q_{1}, p_{2}$ and $q_{2}$ respectively the probability of alleles $A, a, B$ and $b$. Finally, we define linkage disequilibrium as

$$
\begin{equation*}
D=x_{1}-p_{1} q_{1} \tag{1}
\end{equation*}
$$

a. Express $\left\{p_{i}\right\}$ and $\left\{q_{i}\right\}$ in terms of the $\left\{x_{i}\right\}$. Check that you can rewrite $D$ as $x_{1} x_{4}-x_{2} x_{3}$. If alleles are combined into gametes randomly and the system evolves over a long time, what should be the value of $D$ ?
b. We define the indicator random variable $l_{1}$ as 1 if the allele is $A$ and 0 if the allele is $a$. We define equivalently $l_{2}$ for alleles $B$ and $b$. Show that

$$
\begin{equation*}
D=\operatorname{cov}\left(l_{1}, l_{2}\right) \tag{2}
\end{equation*}
$$

Check that the $p$ and $q$ s are conserved.
c. We now introduce recombination: when alleles $W X / Y Z$ produce gametes, they will produce gametes $W X$ and $Y Z$ with probability $1-r$ (no recombination) and gametes $W Z$ and $Y X$ with probability $r$ (recombination). Show that

$$
\begin{equation*}
D_{t}=D_{0}(1-r)^{t} \tag{3}
\end{equation*}
$$

What is the typical time over which the system's linkage disequilibrium goes to 0 ?

We now introduce selection in the population: allele $i / j$ has fitness $w_{i, j}$ where $(i, j) \in \llbracket 1,4 \rrbracket^{2}$ and $i$ or $j$ equals $1,2,3,4$ correspond respectively to $\mathrm{AB}, \mathrm{Ab}, \mathrm{aB}$ and ab. Assuming symmetrical maternal and paternal influence on fitness and
that there is no cis-trans effect, i.e. $w_{i j}=w_{j i}$ and $w_{23}=w_{14}$, we can rewrite the fitness as a function of only nine coefficients.
d. Show that

$$
\begin{equation*}
x_{1}^{(t+1)}=\frac{x_{1}^{(t)}\left(\sum_{i} w_{1 i} x_{i}^{(t)}\right)-r w_{14} D_{t}}{\bar{w}^{(t)}} \tag{4}
\end{equation*}
$$

where $\bar{w}^{(t)}$ is the average fitness at time $t$. What is the equation for the other $x_{i}$ ?
e. Start from the equilibrium point where all the population if $A B / A B$. By introducing a small fraction of the population $\epsilon$ with a different genotype, determine the condition for the stability of the monomorphic type $A B / A B$.

