Fixation probability of an allele in a subdivided population with asymmetric migration

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Summary

The question of loss of genetic diversity in spatially structured populations has been considered by many authors, who have either assumed symmetric migration between subpopulations or restricted the analysis to two subpopulations and allowed asymmetric migration. In this paper we briefly discuss the two-subpopulation case that has been dealt with by other authors and then find a general formula for fixation probabilities for a population divided into three and four subpopulations. The number of individuals in the subpopulations can be different, but the size of each subpopulation is constant over time. Migration between the subpopulations may be asymmetric, that is the number of migrants moving from subpopulation *i* to subpopulation *j* is not the same as the number of migrants moving from subpopulation *j* to subpopulation *i*. When migration is symmetric, the results of previous authors are confirmed. The result for asymmetric migration shows that the influence a subpopulation has on the fixation probability for the whole population is determined by its size and the net amount of gene flow out of the subpopulation, directly and indirectly, to the whole population. The position of a subpopulation relative to the other subpopulations (that is, edge versus centre) is only important in that it can determine the amount of net gene flow from a subpopulation. Some examples are given of how this result can be applied, and of applications to conservation genetics. We conclude that when considering a management plan with the intention of maintaining genetic diversity, the relative strength and direction of migration must be considered.

1. Introduction

The probability of fixation of an allele is a fundamental question in the study of evolution. It was one of the first questions addressed in theoretical population genetics (Fisher, 1922; Wright, 1931). It is also a fundamental question in the study of conservation biology. One of the questions that arises regarding fixation probability is 'How does population structure affect fixation probability?' This paper aims to answer that question for a neutral allele in a subdivided population with asymmetric migration.

The probability of fixation of an allele in a subdivided population has been considered by many authors. The problem was first considered by Pollak (1966), who used branching processes to show that when migration is symmetric, the probability of fixation is the same as for an unsubdivided population. Maruyama (1970, 1974, 1977) used a Moran model and a diffusion model to show that when migration is symmetric a similar result holds. Tachida & Iizuka (1991) considered a population divided into two subpopulations in which selection is strong and migration is asymmetric.

The question of asymmetric migration between more than two subpopulations has been considered using deterministic models to look at other problems. For example, Hill (1974) uses a deterministic model with overlapping generations to examine the effect of artificial selection on improving populations (such as herds of farm animals). In Hill's model there are multiple age groups and asymmetric 'migration' between the age groups. In finding the return from improvement it is necessary to invert the migration matrix in much the same way that the migration

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matrix is inverted in this paper. Despite the apparent similarities between the models, there are fundamental differences in the underlying mathematics between a deterministic and stochastic model, and in the assumptions that go along with them. The most significant of these is an implied assumption in the deterministic model that genetic stochasticity has a relatively minor effect on the genetic make-up of the population, that is, that the population is large. Deterministic models can be used to find the equilibrium distribution of alleles for a large population but a stochastic model must be used to find the fixation probability – a quantity of greater relevance for the small populations that we consider here (indeed an equilibrium distribution cannot exist in a small population where genetic stochasticity has a relatively large effect on the population).

This paper extends the results of these previous authors to the more general case of three and four populations where there is no selection and migration is asymmetric and stochastic using a discrete time, discrete state-space model. The results of previous authors are confirmed in the case of symmetric, stochastic migration.

An interpretation of the results is given using a graph theory. Examples are given that demonstrate the role of population structure in determining the fixation probability. The implications of this result for conservation genetics are also discussed.

2. Discussion of the two-subpopulation case

The two-subpopulation case will not be examined in detail here as it does not show some of the more interesting results that appear in the three- and four-subpopulation cases. The fixation probability for an allele is a weighted average of the initial frequency in each subpopulation, where the weights are $\mu_{ij} N_i$ and μ_{ij} is the average number of successful migrants from subpopulation i to subpopulation j in a given generation and N_i is the population size of subpopulation i. That is, the influence that a subpopulation has on the fixation probability for the overall population is dependent on its size and the amount of direct gene flow out of the subpopulation. This means that if a subpopulation is 'upstream' from another subpopulation then it will have a greater bearing on the fixation probability for the whole population than the 'downstream' subpopulation.

3. Description of model for three subpopulations

The mathematical model used in this section involves three subpopulations and is based on the Wright–Fisher model, that is, it is a stochastic, discrete time,
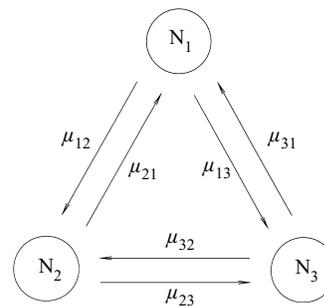
Fig. 1. Diagrammatic representation of the three-subpopulation migration model. N_1, N_2 and N_3 are the population sizes of the three subpopulations and the μ values are the migration rates.

discrete state-space Markov chain. This assumes that generations are non-overlapping and there is no selection. One haploid locus is considered and at this locus there are two alternative alleles, A_1 and A_2. The three subpopulations are of constant size N_1, N_2 and N_3. Migration is allowed between the three subpopulations. The population structure is represented in Fig. 1. The probability of a successful migrant from subpopulation i to subpopulation j in a given generation is μ_{ij}. (The mean number of successful migrants is also μ_{ij}). There is a maximum of one successful migrant from any subpopulation, i, to any other subpopulation, j, in a given generation. The variable of interest is the number of alleles of type A_1 present in each subpopulation at a given time, t, where X_t is the number present in subpopulation 1, Y_t is the number present in subpopulation 2 and Z_t is the number present in subpopulation 3.

We assume that migration occurs by juveniles moving from one subpopulation to another in proportion to the migration rates. Individuals are then recruited, approximately binomially, to the breeding population from a very large pool of juveniles. Migration is small compared with the size of the subpopulations, which implies that the genotype of a leaving individual does not affect the distribution of gene frequencies of the remaining individuals. This is equivalent to assuming that $X_{t+1} | (x_t, y_t, z_t)$, $Y_{t+1} | (x_t, y_t, z_t)$ and $Z_{t+1} | (x_t, y_t, z_t)$ are independent. This assumption will be approximately correct unless the number of juveniles per adult is very low and almost all juveniles recruit to the breeding stock.

The model also applies to plant species, where 'migration' occurs by either seed dispersal or pollen dispersal.

(i) *Transition probabilities*

The transition probability for a given subpopulation can be found by considering the way in which that subpopulation can have x_{t+1} individuals with the A_1

allele at time $t+1$. The number of migrants from subpopulation i to subpopulation j in a given generation is a random variable with the probability of a migrant equal to μ_{ij}. The distribution of the number of migrants from subpopulation i to subpopulation j in generation t is denoted by $M_{ij}(t)$ and the distribution of the number of these which have the A_1 allele is denoted by the variable $M'_{ij}(t)$. The number of migrants that occur in generation t is $m_{ij}(t)$ and of these $m'_{ij}(t)$ have the A_1 allele. The transition probability for subpopulation 1 is:

$$
\begin{aligned}
P(X_{t+1} &= x_{t+1} \,|\, X_t = x_t, Y_t = y_t, Z_t = z_t) \\
&= \sum_{m'_{31}(t)} \sum_{m'_{21}(t)} P(m'_{21}(t+1)A_1 \text{ alleles from pop 2,} \\
&\quad m'_{31}(t+1)A_1 \text{ alleles from pop 3,} \\
&\quad x_{t+1} - m'_{21}(t+1) - m'_{31}(t+1)A_1 \text{ alleles from} \\
&\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad \text{pop 1}), \quad (1)
\end{aligned}
$$

with similar formulae for subpopulations 2 and 3 (Y_{t+1} and Z_{t+1}).

Because of the assumed independence,

$$
\begin{aligned}
P(X_{t+1} &= x_{t+1}, Y_{t+1} = y_{t+1}, Z_{t+1} = z_{t+1} \,|\, X_t = x_t, Y_t = y_t, \\
Z_t &= z_t) \\
&= P(X_{t+1} = x_{t+1} \,|\, X_t = x_t, Y_t = y_t, Z_t = z_t) \\
&\quad \times P(Y_{t+1} = y_{t+1} \,|\, X_t = x_t, Y_t = y_t, Z_t = z_t) \\
&\quad \times P(Z_{t+1} = z_{t+1} \,|\, X_t = x_t, Y_t = y_t, Z_t = z_t).
\end{aligned}
$$

4. Fixation probability

Theorem. *The probability of fixation of an allele, when the initial number of individuals possessing the allele present is x_0 in subpopulation 1, y_0 in subpopulation 2 and z_0 in subpopulation 3, is*

$$
\alpha(x_0, y_0, z_0) = \frac{\gamma_1 x_0 + \gamma_2 y_0 + \gamma_3 z_0}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3}, \quad (2)
$$

where

$$
\begin{aligned}
\gamma_1 &= \mu_{13}\mu_{32} + \mu_{13}\mu_{12} + \mu_{12}\mu_{23}, \\
\gamma_2 &= \mu_{21}\mu_{13} + \mu_{23}\mu_{21} + \mu_{23}\mu_{31}, \\
\gamma_3 &= \mu_{32}\mu_{21} + \mu_{32}\mu_{31} + \mu_{31}\mu_{12}. \quad (3)
\end{aligned}
$$

The proof of this theorem is given in the Appendix.

The coefficient γ_1 is the sum of three terms. Each term is the product of the probabilities associated with the transitions in Fig. 2. Each of the diagrams in Fig.
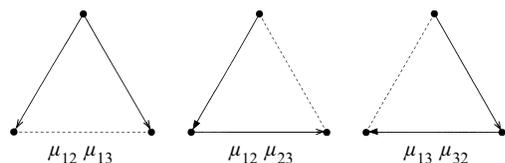
Fig. 2. The terms that make up the coefficient γ_1 in the expression for the fixation probability correspond to these three graphs. There are corresponding graphs for γ_2 and γ_3.
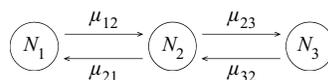
Fig. 3. The three-subpopulation model with the minimal number of connections between subpopulations and asymmetric migration between subpopulations. N_1, N_2 and N_3 are the population sizes of the three subpopulations and the μ values are the migration rates.

Fig. 4. The coefficient γ_1 consists of only one term, corresponding to the above graph, when there is the minimal number of connections between the subpopulations.

2 can be thought of as representing a *path* consisting of two transitions that lead from the point of interest to each other point, either directly or indirectly, exactly once. A term for all the possible paths of this type is included in the sum which makes γ_1. So γ_1 is 'the amount of total population covering migration out of subpopulation 1'. Thinking of γ_1 in this way can be useful in calculating the coefficients when the population structure is altered, such as when one of the links joining two subpopulations is removed.

As an example of the application of (2) to calculate the coefficients, γ_1, γ_2 and γ_3, consider the case where the three subpopulations are arranged with two subpopulations not directly connected, as in Fig. 3, and there is no direct migration from subpopulation 1 to subpopulation 3. Now to calculate γ_1 the only path that goes from subpopulation 1 to each other subpopulation under the modified structure is the path to subpopulation 2 and then from subpopulation 2 to subpopulation 3. Thus the coefficient for subpopulation 1 is $\gamma_1 = \mu_{12}\mu_{23}$ as shown in Fig. 4. By looking at the paths for the other two subpopulations it can be seen that the coefficients are $\gamma_2 = \mu_{21}\mu_{23}$ and $\gamma_3 = \mu_{32}\mu_{21}$.

(i) *Interpreting the coefficients*

Taking the formula in (2) and defining $f_1 = x_0/N_1$, $f_2 = y_0/N_2$ and $f_3 = z_0/N_3$, the probability of fixation is

$$
\alpha(x_0, y_0, z_0) = \frac{\gamma_1 f_1 N_1 + \gamma_2 f_2 N_2 + \gamma_3 f_3 N_3}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3}. \quad (4)
$$

Equation (4) shows that the fixation probability is in fact the weighted average of the initial frequencies of allele A_1 in each of the subpopulations, weighted by the quantity $\gamma_i N_i$. Thus, all other things being equal,
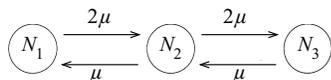
Fig. 5. Diagrammatic representation of directional flow in the case where there is the minimum number of connections between subpopulations. In this case there is twice as much flow from the left to the right as there is from the right to the left.

a subpopulation with a larger γ has a greater influence on the fixation probability than a subpopulation with a smaller γ.

5. Examples of the three-population case

(i) *Example 1: Symmetric migration between subpopulations with all subpopulations directly connected*

In this example we will show that even when the migration is symmetric but not equal, that is $\mu_{ij} = \mu_{ji}$ $\forall i,j$, the fixation probability of the A_1 allele is still equal to the initial frequency of the allele in the whole population.

Let $\mu_{ij} = \mu_{ji}$ $\forall i,j$, then γ_1 can be rearranged using $\mu_{ji} = \mu_{ij}$ and we can show that $\gamma_1 = \gamma_2 = \gamma_3$:

$$\gamma_1 = \mu_{13}\mu_{32} + \mu_{13}\mu_{12} + \mu_{12}\mu_{23}$$
$$= \mu_{21}\mu_{13} + \mu_{23}\mu_{21} + \mu_{23}\mu_{31} = \gamma_2$$
$$= \mu_{32}\mu_{21} + \mu_{32}\mu_{31} + \mu_{31}\mu_{12} = \gamma_3$$

so,

$$\alpha(x_0, y_0, z_0) = \frac{x_0 + y_0 + z_0}{N_1 + N_2 + N_3}.$$

Once again all the coefficients are equal and the fixation probability is equal to the initial frequency in the whole population. This is also true for the case where two of the subpopulations are not directly connected and migration is symmetric, as $\mu_{13} = \mu_{31} = 0$ is just a special case of the formula considered above.

(ii) *Example 2: Directional flow in the model where two of the subpopulations are not directly connected*

Suppose now that two of the subpopulations are not directly connected with a constant directional flow. For example, this could be thought of as a current or a prevailing wind carrying twice as many seeds in one direction as the other. In the example illustrated in Fig. 5, the transition probabilities are $\mu_{13} = \mu_{31} = 0$, $\mu_{32} = \mu_{21} = \mu$ and $\mu_{12} = \mu_{23} = 2\mu$. Upon substituting these transition probabilities into the equations for the coefficients, we get $\gamma_1 = 4\mu^2$, $\gamma_2 = 2\mu^2$ and $\gamma_3 = \mu^2$. Thus,

$$\alpha(x_0, y_0, z_0) = \frac{4x_0 + 2y_0 + z_0}{4N_1 + 2N_2 + N_3}.$$
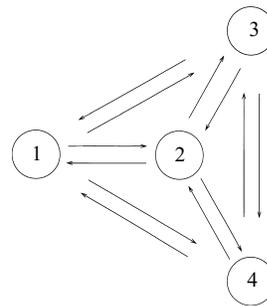
Fig. 6. Diagrammatic representation of the four-subpopulation migration model. The subpopulation sizes are N_1, N_2, N_3 and N_4 and the migration rates are μ_{ij}.

This is fairly intuitive as it suggests that if the flow is from left to right in Fig. 5, then the further left a subpopulation is, the further 'upstream' it is and hence the more important its initial allele frequency is in determining the fixation probability.

6. Four subpopulations

(i) *Description of the model*

In this section we extend the three-subpopulation model to the case of four subpopulations. The assumptions are essentially unchanged and are as follows. The mathematical model used is a discrete time, discrete state-space Markov chain model. This assumes that generations are non-overlapping and there is no selection. One haploid locus is considered and at this locus there are two alleles: A_1 and A_2. There are four subpopulations of constant sizes: N_1, N_2, N_3 and N_4. Migration is allowed between the four populations. The population structure is represented in Fig. 6. The probability that there will be a migrant from subpopulation i to subpopulation j in a given generation is μ_{ij}. The variable of interest is the number of alleles of type A_1 present in each subpopulation at a given time, t. The mathematics of the model will not be written out in full for the case of four subpopulations as it is analogous to the case of the three subpopulations. As in the case of three subpopulations, it will also be assumed that the genotype of a leaving individual does not affect the gene frequencies of the remaining individuals. Clearly in practice this will not be exactly true, but in most situations it will be approximately correct.

(ii) *Fixation probabilities*

The fixation probabilities are given by the formula

$$\alpha(w_0, x_0, y_0, z_0) = \frac{\gamma_1 w_0 + \gamma_2 x_0 + \gamma_3 y_0 + \gamma_4 z_0}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3 + \gamma_4 N_4},$$

where w_0, x_0, y_0 and z_0 are the initial numbers of individuals with the A_1 allele in populations 1, 2, 3 and 4 respectively.
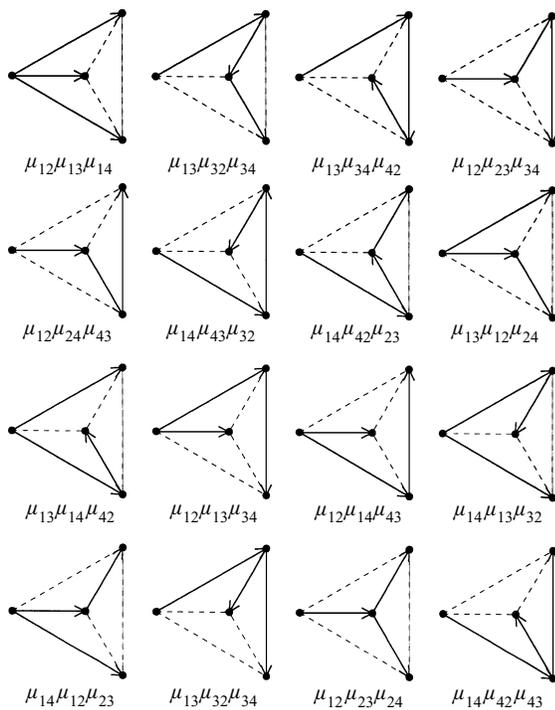
Fig. 7. The 16 terms that make up the coefficient γ_1 in the expression for the fixation probability for the four-subpopulation model.
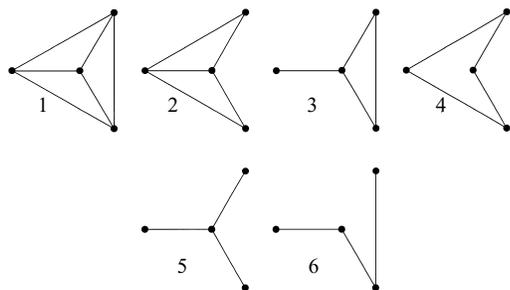
Fig. 8. The different population structures possible with four subpopulations. These are the only ways in which four subpopulations can be linked.

Where there are four subpopulations the arithmetic involved becomes far more complicated although the physical interpretation of the coefficients is essentially the same. Each coefficient can be thought of as being the sum of a term corresponding to each 'path', consisting of three transitions, which starts at the point of interest and goes through each other point exactly once. As an example, the paths that represent the terms of γ_1 are shown in Fig. 7. The number of terms involved in each coefficient is 16.

(iii) *Different population structures*

There are six different ways in which four subpopulations can be connected if the magnitude of migration between subpopulations is not considered. These are represented in Fig. 8. The lines represent links between two subpopulations. The actual physical distance between two subpopulations in the diagram does not represent the magnitude of migration between the two subpopulations. The method discussed earlier of calculating the coefficients under different population structures by adding a term for each of the paths from a subpopulation is a useful way of finding the coefficients quickly. If the population does not have a link between each pair of subpopulations then the coefficients are simplified.

(iv) *Fixation probabilities under equal migration*

In each of the following cases a link exists between subpopulations i and j. The numbers refer to the diagram numbers in Fig. 8.

Structure 1: This is the fully connected model where each coefficient consists of the full 16 terms. Each term contributes μ_3 to the coefficient so $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4 = 16\mu^3$. The fixation probability is therefore equal to the initial frequency in the population as a whole.

Structure 2: In this model two of the subpopulations are connected to each of the other subpopulations and two of the subpopulations are connected only to two of the other subpopulations. For each subpopulation there are eight paths connecting it to each of the other subpopulations, each contributing μ^3, so $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4 = 8\mu^3$. Thus the fixation probability is equal to the initial frequency in the population as a whole.

Structure 3: In this model three of the subpopulations are connected with each other and the fourth subpopulation is connected with one of these subpopulations only. Intuitively it would seem that the subpopulation which is connected with only one other should have less influence on the fixation probability than the other subpopulations which are all connected with each other. However, there are three paths from each subpopulation so each coefficient has three terms giving $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4 = 3\mu^3$.

Structure 4: This model is equivalent to having four subpopulations equally spaced on the corners of a square. Intuitively it would seem that each subpopulation should have the same effect on the fixation probability as the system is symmetric. There are four paths from each subpopulation to the other populations, so $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4 = \mu^3$.

Structure 5: One subpopulation is central and is connected to each of the other subpopulations. Each of the other subpopulations is connected only to the central subpopulation. Once again it would seem

that the central subpopulation would have the most important effect on the fixation probabilities, but for each subpopulation there is only one path connecting it to all of the other subpopulations, so $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4 = \mu^3$.

Structure 6: The minimally connected model. The subpopulations are arranged linearly and are only connected to their neighbours. Once again, for each subpopulation there is only one path connecting it to all of the other subpopulations, so $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4 = \mu^3$.

Thus for each of the population structures, $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4$. This means that in each case, the fixation probability is just equal to the initial frequency in the population as a whole when one-step migration between connected subpopulations is equal.

(v) *Unequal migration between subpopulations*

There are endless possible combinations of migration probabilities that could be considered, but only three will be considered here: the minimally connected model with directional flow; the case for structure number 5 where the central subpopulation is most productive; and the case where two 'clusters' of subpopulations are connected by a weaker, directional link. These examples will be compared with the three-subpopulation case.

(vi) *Example 1: Constant flow of individuals in one direction*

It is assumed that gene flow is twice as likely in one direction as in the other. Thus

$$\mu_{12} = \mu_{23} = \mu_{34} = 2\mu,$$

$$\mu_{21} = \mu_{32} = \mu_{43} = \mu,$$

Each point has just one path to the other three points, so there is only one term in each coefficient. The coefficients are:

$$\gamma_1 = 8\mu^3, \gamma_2 = 4\mu^3, \gamma_3 = 2\mu^3, \gamma_4 = \mu^3.$$

Therefore as in the case of three subpopulations, when the flow is from left to right, the populations on the left are the most important in determining the fixation probability. That is, subpopulations which are 'upstream' in terms of the migration have the greatest impact on fixation probability.

(vii) *Example 2: One central patch, three peripheral patches, the central subpopulation is most productive*

Consider a population structured as in diagram 5 in Fig. 8 with the central subpopulation labelled popu-

lation 2. Once again there is only one path from each of the subpopulations, so each coefficient has only one term. The migration probabilities are:

$$\mu_{21} = \mu_{23} = \mu_{24} = 2\mu,$$

$$\mu_{12} = \mu_{32} = \mu_{42} = \mu.$$

Thus,

$$\gamma_1 = 4\mu^3, \gamma_2 = 8\mu^3, \gamma_3 = 4\mu^3, \gamma_4 = 4\mu^3,$$

showing once again that the subpopulation which produces the most migrants is the most important subpopulation in determining the fixation probability.

(viii) *Example 3: Two pairs of subpopulations that are weakly linked to each other*

Suppose that we have a population structure like structure 6 but with minimally connected subpopulations 1 and 2 close together. Each of these is distant from subpopulations 3 and 4, which are also close together. Let the migration probabilities be

$$\mu_{12} = \mu_{21} = \mu_{34} = \mu_{43} = \mu, \mu_{23} = \mu_a, \mu_{32} = \mu_b,$$

where $\mu \gg \mu_a > \mu_b$. Then $\gamma_1 = \gamma_2 = \mu^2\mu_a$ and $\gamma_3 = \gamma_4 = \mu^2\mu_b$. This means that the subpopulations within each pair have the same influence on the fixation probability. The pair that on average sends migrants to the other pair has a greater influence on fixation probability than the other pair. This again demonstrates that the subpopulations which produce the most migrants have the greatest influence on fixation probability. Note also here that two subpopulations within a pair which are symmetrically linked to each other have the same influence on fixation probability.

7. Discussion

A formula has been found for the fixation probability of a neutral allele, A_1, for a population divided into three or four subpopulations where migration is asymmetric. This is a significant advance over the existing theory for more than two subpopulations (Pollak, 1966; Maruyama, 1977), which assumes symmetric migration, and allows a wider range of population structures to be considered with greater variety in direction and strength of migration. This paper also extends the results of Tachida & Iizuka (1991) who considered the case where there is asymmetric migration for a two-population model. The conclusions relating to the fixation probability in the case of symmetric migration support the conclusions of other authors who have considered the problem using other models.

The fixation probability found here for the stochastic model is equal to the equilibrium allele frequency found for very large populations using an equivalent

population structure with a deterministic model. This result would not hold if selection were introduced into the model as the equilibrium distribution is fixation of the selected allele, but in a stochastic model there is a chance that the selected allele will become extinct.

We draw two new conclusions from this work. First, the position of a subpopulation within the population is not important in determining its impact on the fixation probability of the whole population. That is, an edge and a centre subpopulation have an equal impact on the fixation probability of the whole population if they are each producing the same net number of migrants.

Second, when migration is asymmetric then, in general, the subpopulations that produce the greatest surplus of migrants are the most important subpopulations in determining the fixation probability. That is, those subpopulations that send out a lot more migrants than they receive are the most important subpopulations in determining the fixation probability of the whole population, provided the migrants are

going to subpopulations of equal importance. If one of these subpopulations tends to send migrants to a subpopulation that in turn has a large surplus of migrants, whereas the other subpopulation tends to send migrants to a subpopulation that does not have a net surplus of migrants, then the first of these subpopulations will have a greater impact on the fixation probability of the population as a whole. This is because the first of these subpopulations is indirectly having its alleles spread more widely than the second subpopulation.

This model would be difficult to parameterize in practice but provides some useful insights into fixation probabilities in subdivided populations, which have implications for conservation genetics. It is clear that when considering a management plan with the intention of maintaining genetic diversity, the relative strength of migration in different directions must be considered to give a clear picture of the genetic properties of the population and the likely genetic consequences of management actions.

Appendix. Proof of theorem

Using the backward Kolmogorov equations

$$\alpha(x_t, y_t, z_t) = \sum_{i=0}^{N_1} \sum_{j=0}^{N_2} \sum_{k=0}^{N_3} P(x_t, y_t, z_t; i, j, k)\, \alpha(i, j, k). \tag{A 1}$$

Using the independence of $X_{t+1}|x_t, y_t, z_t$, $Y_{t+1}|x_t, y_t, z_t$ and $Z_{t+1}|x_t, y_t, z_t$ this can be rewritten as

$$P(x_t, y_t, z_t; i, j, k) = P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, P(Y_{t+1} = j \,|\, x_t, y_t, z_t)\, P(Z_{t+1} = k \,|\, x_t, y_t, z_t), \tag{A 2}$$

so (A 1) can be written as

$$\alpha(x_t, y_t, z_t) = \sum_{i=0}^{N_1} \sum_{j=0}^{N_2} \sum_{k=0}^{N_3} P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, P(Y_{t+1} = j \,|\, x_t, y_t, z_t)\, P(Z_{t+1} = k \,|\, x_t, y_t, z_t)\, \alpha(i, j, k). \tag{A 3}$$

Substituting the solution into (A 3) gives

$$\text{l.h.s.} = \frac{\gamma_1 i + \gamma_2 j + \gamma_3 k}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3}, \tag{A 4}$$

$$\begin{aligned}
\text{r.h.s.} = {} & \sum_{i=0}^{N_1} \sum_{j=0}^{N_2} \sum_{k=0}^{N_3} P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, P(Y_{t+1} = j \,|\, x_t, y_t, z_t)\, P(Z_{t+1} = k \,|\, x_t, y_t, z_t)\, \frac{\gamma_1 i}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \\
& + \sum_{i=0}^{N_1} \sum_{j=0}^{N_2} \sum_{k=0}^{N_3} P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, P(Y_{t+1} = j \,|\, x_t, y_t, z_t)\, P(Z_{t+1} = k \,|\, x_t, y_t, z_t)\, \frac{\gamma_2 j}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \\
& + \sum_{i=0}^{N_1} \sum_{j=0}^{N_2} \sum_{k=0}^{N_3} P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, P(Y_{t+1} = j \,|\, x_t, y_t, z_t)\, P(Z_{t+1} = k \,|\, x_t, y_t, z_t)\, \frac{\gamma_3 j}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \\
= {} & \sum_{i=0}^{N_1} P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, \frac{\gamma_1 i}{\gamma_1 N_1 + \gamma_2 N_1 + \gamma_3 N_3} \sum_{j=0}^{N_2} \sum_{k=0}^{N_3} P(Y_{t+1} = j \,|\, x_t, y_t, z_t)\, P(Z_{t+1} = k \,|\, x_t, y_t, z_t) \\
& + \sum_{j=0}^{N_2} P(Y_{t+1} = j \,|\, x_t, y_t, z_t)\, \frac{\gamma_2 j}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \sum_{i=0}^{N_1} \sum_{k=0}^{N_3} P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, P(Z_{t+1} = k \,|\, x_t, y_t, z_t) \\
& + \sum_{k=0}^{N_3} P(Z_{t+1} = k \,|\, x_t, y_t, z_t)\, \frac{\gamma_3 k}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \sum_{i=0}^{N_1} \sum_{j=0}^{N_2} P(X_{t+1} = i \,|\, x_t, y_t, z_t)\, P(Y_{t+1} = j \,|\, x_t, y_t, z_t)
\end{aligned}$$

$$= \sum_{i=0}^{N_1} P(X_{t+1}=i \mid x_t, y_t, z_t) \frac{\gamma_1 i}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} + \sum_{j=0}^{N_2} P(Y_{t+1}=j \mid x_t, y_t, z_t) \frac{\gamma_2 j}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3}$$

$$+ \sum_{k=0}^{N_3} P(Z_{t+1}=k \mid x_t, y_t, z_t) \frac{\gamma_3 k}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3}$$

$$= E \left[\frac{\gamma_1 X_{t+1}}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \mid x_t, y_t, z_t \right] + E \left[\frac{\gamma_2 Y_{t+1}}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \mid x_t, y_t, z_t \right]$$

$$+ E \left[\frac{\gamma_3 Z_{t+1}}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3} \mid x_t, y_t, z_t \right]$$

$$= \frac{\gamma_1 E(X_{t+1} \mid x_t, y_t, z_t) + \gamma_2 E(Y_{t+1} \mid x_t, y_t, z_t) + \gamma_3 E(Z_{t+1} \mid x_t, y_t, z_t)}{\gamma_1 N_1 + \gamma_2 N_2 + \gamma_3 N_3}. \tag{A 5}$$

The expected value of X_{t+1} can easily be calculated using its conditional distribution. With probability $\mu_{21}\mu_{31}$ there will be a migrant from subpopulation 2 and subpopulation 3 to subpopulation 1. In this case X_{t+1} has conditional distribution

$$X_{t+1} \mid X_t = x_t\, Y_t = y_t, Z_t = z_t, \text{ migrant from pop 2 and 3}$$
$$\sim \text{Bin}(N_1 - 2, x_t/N_1) + \text{Bin}(1, y_t/N_2) + \text{Bin}(1, z_t/N_3) \tag{A 6}$$

which has expected value

$$\frac{x_t(N_1 - 2)}{N_1} + \frac{y_t}{N_2} + \frac{z_t}{N_3}. \tag{A 7}$$

With probability $\mu_{31}(1-\mu_{21})$ there will be a migrant from subpopulation 3 but no migrant from subpopulation 2 to subpopulation 1, giving conditional distribution

$$X_{t+1} \mid X_t = x_t, Y_t = y_t, Z_t = z_t, \text{ migrant from pop 3}$$
$$\sim \text{Bin}(N_1 - 1, x_t/N_1) + \text{Bin}(1, z_t/N_3), \tag{A 8}$$

which has expected value

$$\frac{x_t(N_1 - 1)}{N_1} + \frac{z_t}{N_3}. \tag{A 9}$$

With probability $(1-\mu_{31})\mu_{21}$ there will be a migrant from subpopulation 2 but no migrant from subpopulation 3 to subpopulation 1, giving conditional distribution

$$X_{t+1} \mid X_t = x_t, Y_t = y_t, Z_t = z_t, \text{ migrant from pop 2} \sim \text{Bin}(N_1 - 1, x_t/N_1) + \text{Bin}(1, y_t/N_2), \tag{A 10}$$

which has expected value

$$\frac{x_t(N_1 - 1)}{N_1} + \frac{y_t}{N_2}. \tag{A 11}$$

With probability $(1-\mu_{31})(1-\mu_{21})$ there will be no migrants from subpopulation 2 or 3 to subpopulation 1, giving conditional distribution

$$X_{t+1} \mid X_t = x_t, Y_t = y_t, Z_t = z_t, \text{ no migrants} \sim \text{Bin}(N_1, x_t/N_1), \tag{A 12}$$

which has expected value x_t.

Thus the expected value of X_{t+1}, unconditional on whether or not there is a migrant, is

$$E(X_{t+1}) = E(E(X_{t+1} \mid \text{whether or not there is a migrant}))$$

$$= \mu_{21}\mu_{31} \left[\frac{x_t(N_1 - 2)}{N_1} + \frac{y_t}{N_2} + \frac{z_t}{N_3} \right] + \mu_{21}(1-\mu_{31}) \left[\frac{x_t(N_1 - 1)}{N_1} + \frac{y_t}{N_2} \right]$$

$$+ (1-\mu_{21})\mu_{31} \left[\frac{x_t(N_1 - 1)}{N_1} + \frac{z_t}{N_3} \right] + (1-\mu_{21})(1-\mu_{31}) x_t$$

$$= \left[1 - \frac{\mu_{21} + \mu_{31}}{N_1} \right] x_t + \frac{\mu_{21}}{N_2} y_t + \frac{\mu_{31}}{N_3} z_t. \tag{A 13}$$

Now substituting this back in to (A5) gives

$$\text{r.h.s.} = \frac{\gamma_1\left[\left(1-\dfrac{\mu_{21}+\mu_{31}}{N_1}\right)x_t+\dfrac{\mu_{21}}{N_2}y_t+\dfrac{\mu_{31}}{N_3}z_t\right]+\gamma_2\left[\left(1-\dfrac{\mu_{12}+\mu_{32}}{N_2}\right)y_t+\dfrac{\mu_{12}}{N_1}x_t+\dfrac{\mu_{32}}{N_3}z_t\right]+\gamma_3\left[\left(1-\dfrac{\mu_{13}+\mu_{23}}{N_3}\right)z_t+\dfrac{\mu_{13}}{N_1}x_t+\dfrac{\mu_{23}}{N_2}y_t\right]}{\gamma_1 N_1+\gamma_2 N_2+\gamma_3 N_3} \tag{A 14}$$

after substituting for γ's and rearranging

$$\text{r.h.s.} = \frac{\gamma_1 x_t+\gamma_2 y_t+\gamma_3 z_t}{\gamma_1 N_1+\gamma_2 N_2+\gamma_3 N_3} \tag{A 15}$$

as required.

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