



# Dying on the way: The influence of migrational mortality on neutral models of spatial variation



Thomas Nagylaki

Department of Ecology and Evolution, The University of Chicago, 1101 East 57th Street, Chicago, IL 60637, USA

## ARTICLE INFO

### Article history:

Received 18 August 2014

Available online 18 November 2014

### Keywords:

Geographical structure  
Population structure  
Subdivided populations

## ABSTRACT

Migrational mortality is introduced into the classical Malécot model for migration, mutation, and random genetic drift. To assess the influence of mortality, its effect on the backward migration rates and on the probabilities of identity in allelic state are studied. Perhaps surprisingly, some of the former may increase, but as is intuitive, their sum always decreases. As expected, in the island model, mortality does not change the migration pattern, but it decreases the migration rate. Furthermore, it decreases the expected heterozygosity, but increases the genetic diversity and differentiation. The circular habitat and the unbounded, linear stepping-stone model also illustrate the general results. Arbitrary migration is also analyzed. If migration is sufficiently weak, then mortality diminishes every migration rate; it decreases the expected heterozygosity and the genetic similarity between demes. In the strong-migration limit, mortality may raise or lower the probability of identity in state. Perhaps unexpectedly, under mild and reasonable biological assumptions, mortality *does not* alter the diffusion limit of the probabilities of identity.

© 2014 Elsevier Inc. All rights reserved.

## 1. Introduction

In many situations, migration must be associated with mortality. Animals crossing an unsuitable area may drown, starve, dehydrate, freeze, or overheat; they may be killed by a predator. If a species is territorial, migrants may be killed or fatally injured. Seeds may dry out or land where they cannot sprout. Migrational mortality also affects the results of release–recapture experiments. Nonetheless, this phenomenon appears to have received only one very brief treatment (Nagylaki, 1992, p. 152).

Since migration enters both neutral and selective models through the backward migration matrix  $M$ , we must investigate the influence of migrational mortality on  $M$  and on the probabilities of identity in allelic state. In this paper, we do this in Malécot's model for the probabilities of identity under migration, mutation, and random genetic drift (Malécot, 1951; Nagylaki, 1976, 1980, 1983; Sawyer, 1976). The extensive literature on this model can be traced from Nagylaki (1989, 2011), Ayati et al. (1999), Charlesworth et al. (2003), and Rousset (2004).

In Section 2, we formulate our problem and establish some general results. The island model, the circular habitat, and the unbounded, linear stepping-stone model are the subjects of

Sections 3–5, respectively. For an arbitrary arrangement of demes, in Sections 6 and 7 we examine weak and strong migration, respectively. For arbitrary migration in a linear habitat, in Section 8 we derive the diffusion limit. In Section 9, we summarize our results and discuss some open problems.

## 2. Formulation and general results

We assume that a monoecious, diploid population is subdivided into  $n$  ( $\geq 2$ ) individually panmictic colonies that exchange gametes in a fixed, genotype-independent pattern. Generations are discrete and nonoverlapping; the analysis is restricted to a single neutral locus; every allele mutates to new alleles at rate  $u$  ( $0 < u < 1$ ). We measure time,  $t$  ( $= 0, 1, 2, \dots$ ), in generations. Random drift acts through population regulation.

To begin the life cycle, every one of the  $N_i$  adults in deme  $i$  produces the same very large number of gametes, which then disperse within and between colonies. Complete random union of gametes within each colony follows. Therefore, a proportion  $1/N_i$  of the zygotes whose two gametes came from adults in deme  $i$  is produced by self-fertilization. Mutation is next, and finally population regulation returns the number of individuals in deme  $i$  to  $N_i$ . This simple way of introducing random drift agrees with biologically more realistic models (Nagylaki, 1995, 1997).

Let  $f_{ij}(t)$  denote the probability that two distinct genes chosen at random from adults just before gametogenesis in generation  $t$ ,

E-mail address: [nagylaki@uchicago.edu](mailto:nagylaki@uchicago.edu).

one from deme  $i$  and the other from deme  $j$ , are the same allele. The probability of allelic identity is a measurable function of our rather complicated Markov chain. Its complement,

$$h_{ij} = 1 - f_{ij}, \quad (2.1)$$

is an index of the amount and pattern of genetic variability in the population. In particular,  $f_{ii}$  and  $h_{ii}$  represent the expectations of the homozygosity and heterozygosity in deme  $i$ , respectively.

Let the constant  $m_{ij}$  designate the probability that a gamete in deme  $i$  after dispersion was produced in deme  $j$ . The  $n \times n$  backward migration matrix  $M = (m_{ij})$  is stochastic:  $m_{ij} \geq 0$  for every  $i, j \in \mathcal{J}$  and

$$\sum_{j \in \mathcal{J}} m_{ij} = 1 \quad (2.2)$$

for every  $i \in \mathcal{J}$ , where

$$\mathcal{J} = \{1, 2, \dots, n\} \quad (2.3)$$

signifies the set of demes. Since the gametes disperse independently, after one generation we have (Malécot, 1951; Sawyer, 1976; Nagylaki, 1980)

$$f'_{ij} = v \left[ \sum_{k, \ell} m_{ik} m_{j\ell} f_{k\ell} + \sum_k m_{ik} m_{jk} (2N_k)^{-1} (1 - f_{kk}) \right], \quad (2.4)$$

where

$$v = (1 - u)^2 \quad (2.5)$$

and the prime indicates the next generation.

We placed mutation after fertilization only for definiteness; actually, (2.4) holds if mutation occurs at any time between gametogenesis and population regulation. During this period, population regulation would have no effect if it were sufficiently weak to leave very large numbers of gametes and zygotes. Clearly, (2.4) applies also to a model with  $2N_i$  haploid individuals in deme  $i$ , as Sawyer (1976) has noted.

It is easy to see by induction from (2.4) that if  $0 \leq f_{ij}(0) \leq 1$  for every  $i, j \in \mathcal{J}$ , then  $0 \leq f_{ij}(t) \leq 1$  for every  $t$  and every  $i, j \in \mathcal{J}$ .

As  $t \rightarrow \infty$ ,  $f_{ij}(t) \rightarrow \hat{f}_{ij}$  for every  $i, j \in \mathcal{J}$ , the unique equilibrium of (2.4), at least as fast as  $(\text{const.})v^t$  (Nagylaki, 1980). Furthermore, there is some genetic variability at equilibrium: from (2.4) we infer by contradiction that  $\hat{f}_{ij} < 1$  for some  $i \in \mathcal{J}$  and some  $j \in \mathcal{J}$  (Nagylaki, 1986).

Now we are ready to introduce migrational mortality. Let the constant  $\tilde{m}_{ij}$  denote the probability that a randomly chosen gamete in deme  $i$  disperses to deme  $j$ , given that it survives to do so. The constant  $a_{ij}$  designates the probability that this gamete does survive dispersion. Thus, the  $n \times n$  forward migration matrix  $\tilde{M} = (\tilde{m}_{ij})$  is stochastic:  $\tilde{m}_{ij} \geq 0$  for every  $i, j \in \mathcal{J}$  and

$$\sum_{j \in \mathcal{J}} \tilde{m}_{ij} = 1 \quad (2.6)$$

for every  $i \in \mathcal{J}$ . We must have

$$0 \leq a_{ij} \leq 1 \quad \text{and} \quad a_{ii} = 1 \quad (2.7)$$

for every  $i, j \in \mathcal{J}$ , but we do not assume that  $a_{ij} = a_{ji}$ .

Let  $N_i^*$  represent the number of individuals in deme  $i$  after dispersion. We can write the number of gametes that disperse from deme  $i$  to deme  $j$  in terms of either  $M$  or  $\tilde{M}$ :

$$2N_i a_{ij} \tilde{m}_{ij} = 2N_j^* m_{ji}. \quad (2.8)$$

Summing (2.8) over  $i$  with aid of (2.2), we obtain

$$N_j^* = \sum_i N_i a_{ij} \tilde{m}_{ij}, \quad (2.9)$$

whence (2.8) yields

$$m_{ij} = \frac{N_j a_{ji} \tilde{m}_{ji}}{\sum_k N_k a_{ki} \tilde{m}_{ki}}. \quad (2.10)$$

From (2.4) we see that if  $M$  is given, migrational mortality need not be considered. However,  $M$  reflects spatial variation not only of the migration rates, but also of the subpopulation numbers. Since  $\tilde{M}$  depends only on the former, assumptions should be made on  $\tilde{M}$ ; then we can use (2.10) and (2.4) to study the effect of mortality on  $M$  and  $f_{ij}$ .

If there is no migrational mortality, i.e.,  $a_{ij} = 1$  for every  $i, j \in \mathcal{J}$ , then (2.10) reduces to the classical result (Malécot, 1948; Nagylaki, 1992, p. 133)

$$\check{m}_{ij} = \frac{N_j \tilde{m}_{ji}}{\sum_k N_k \tilde{m}_{ki}}. \quad (2.11)$$

We shall always use a “cup” to signify the absence of migrational mortality.

If migration is also conservative (Nagylaki, 1980), i.e.,  $N_i^* = N_i$  for every  $i \in \mathcal{J}$ , then (2.8) becomes (Nagylaki, 1992, p. 135)

$$N_i \check{m}_{ij} = N_j \tilde{m}_{ji}, \quad (2.12)$$

which simplifies to

$$\check{M} = (\check{m}_{ij}) = \tilde{M}^T \quad (2.13)$$

when  $N_i = N$  for some  $N$  and every  $i \in \mathcal{J}$ .

Conservative migration without mortality has two interesting special cases.

Migration is reciprocal if the number of gametes that disperse from deme  $i$  to deme  $j$  equals the number that disperse from deme  $j$  to deme  $i$ :

$$N_i \tilde{m}_{ij} = N_j \tilde{m}_{ji} \quad (2.14)$$

for every  $i, j \in \mathcal{J}$ . Then (2.9), (2.14), and (2.6) give  $N_j^* = N_j$  for every  $j \in \mathcal{J}$ ; therefore, migration is, indeed, conservative. Hence, (2.12) and (2.14) reveal that (Nagylaki, 1992, p. 136)

$$\check{M} = \tilde{M}. \quad (2.15)$$

The second special case is doubly stochastic  $\tilde{M}$ :

$$\sum_i \tilde{m}_{ij} = 1 \quad (2.16)$$

for every  $j \in \mathcal{J}$ . In the rest of this paragraph, we posit that  $N_i = N$  for every  $i \in \mathcal{J}$ . Then (2.9) and (2.16) immediately give  $N_j^* = N$  for every  $j \in \mathcal{J}$ ; thus, migration is again conservative. From (2.11) and (2.16) we infer (2.13), so  $\check{M}$  is also doubly stochastic. This situation arises in problems with a natural periodicity, such as demes in a circle. In this case, we assume that migration is homogeneous: with a slight abuse of notation,  $\tilde{m}_{ij} = \tilde{m}_{j-i}$  for every  $i$  and  $j$ , i.e.,  $\tilde{M}$  depends only on displacement, rather than on both initial and final positions. On account of (2.13), the backward migration pattern is also homogeneous:  $\check{m}_{ij} = \check{m}_{ji} = \check{m}_{i-j}$  for every  $i$  and  $j$ . If migration is symmetric, i.e.,  $\tilde{M} = \tilde{M}^T$ , then (2.14) shows that it is both reciprocal and doubly stochastic and (2.13) yields (2.15) (Nagylaki, 1992, p. 136).

Returning to the effect of migrational mortality, we establish that it decreases the total backward migration rate  $1 - m_{ii}$ .

**Proposition 2.1.** For each  $i \in \mathcal{J}$ , if  $\tilde{m}_{ii} > 0$  and there exists  $j = j_i$  such that  $\tilde{m}_{ji} > 0$  and  $a_{ji} < 1$ , then  $m_{ii} > \check{m}_{ii}$ .

Download English Version:

<https://daneshyari.com/en/article/6372356>

Download Persian Version:

<https://daneshyari.com/article/6372356>

[Daneshyari.com](https://daneshyari.com)