

This is an appendix to the paper by Gandon and Rousset 1999 Evolution of stepping-stone dispersal rates. *Proc. R. Soc. Lond. B* **266**, 2507–2513.

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## Appendix

Notations not defined here are defined in the main text of the paper.

### a. Genetic models of isolation by distance

This section summarizes without derivation some formulae used for computing the probabilities of identity in the lattice models first formulated by Malécot (1950, 1951). The required mathematics may also be found in later accounts, e.g. Malécot (1975) or Nagylaki (1976), and in textbooks on characteristic functions and Fourier transforms.

The life cycle of Malécot’s lattice model is exactly the one described in the text, with ideally infinite fecundity. When there may be a cost of dispersal, one must distinguish forward and backward dispersal rates: the former rate measures the probability that an offspring leaves its natal patch, the latter rate measures the probability that an adult had its parent in a given deme (i.e. after the cost of dispersal is paid and after competition). Let  $\gamma \equiv (1 - u)^2$ , and let  $m_{\mathbf{r}}$  be the (backward) probability of dispersal at distance  $\mathbf{r} \equiv (r_x, r_y)$ . A basic recursion of the model is

$$Q_{\mathbf{r}}^{(t+1)} = \gamma \sum_{\mathbf{r}_1} \sum_{\mathbf{r}_2} m_{\mathbf{r}_1} m_{\mathbf{r}_2} Q_{\mathbf{r}+\mathbf{r}_2-\mathbf{r}_1}^{(t)} + \gamma \sum_{\mathbf{r}_1} m_{\mathbf{r}_1} m_{\mathbf{r}_1-\mathbf{r}} \frac{1 - Q_{\mathbf{0}}^{(t)}}{N}. \quad (\text{A.1})$$

(Malécot, 1975, equation 2, and Malécot, 1951), here written for probabilities of identity among offspring after dispersal but before competition, so that it is also valid for  $N = 1$ .

We consider the characteristic function (Fourier transform) of the distribution of backward dispersal distance,  $\psi(\mathbf{z}) \equiv \sum_{\mathbf{r}} m_{\mathbf{r}} e^{i\mathbf{r}\cdot\mathbf{z}}$  where  $i \equiv \sqrt{-1}$ . Likewise we consider  $\mathcal{Q}(\mathbf{z})$ , the Fourier transform of the  $Q$ ’s:  $\mathcal{Q}(\mathbf{z}) \equiv \sum_{\mathbf{r}} Q_{\mathbf{r}} e^{i\mathbf{r}\cdot\mathbf{z}}$ . From Malécot (1975, equation 14) we have at equilibrium

$$\frac{\mathcal{Q}(\mathbf{z})}{1 - Q_{\mathbf{0}}} = \frac{1}{N} \frac{\gamma \psi(\mathbf{z}) \psi(-\mathbf{z})}{1 - \gamma \psi(\mathbf{z}) \psi(-\mathbf{z})} \quad (\text{A.2})$$

so that inverse transformation yields  $Q_{\mathbf{r}} = L_{\mathbf{r}}(1 - Q_{\mathbf{0}})/N$  where

$$L_{\mathbf{r}} \equiv \mathcal{L}_{\mathbf{r}} \left( \frac{\gamma \psi(\mathbf{z}) \psi(-\mathbf{z})}{1 - \gamma \psi(\mathbf{z}) \psi(-\mathbf{z})} \right) \quad (\text{A.3})$$

where  $\mathcal{L}_{\mathbf{r}}$  is the inverse transform defined for some function  $\mathcal{Q}$  as

$$\mathcal{L}_{\mathbf{r}}(\mathcal{Q}) \equiv \frac{1}{n_x} \frac{1}{n_y} \sum_{q_x=0}^{n_x-1} \sum_{q_y=0}^{n_y-1} \mathcal{Q}(2\pi q_x/n_x, 2\pi q_y/n_y) e^{-i2\pi q_x r_x/n_x} e^{-i2\pi q_y r_y/n_y}. \quad (\text{A.4})$$

If the dispersal distribution is axially symmetric,  $\psi(-\mathbf{z}) = \psi(\mathbf{z})$ , and it follows that

$$L_{\mathbf{r}} = \frac{NQ_{\mathbf{r}}}{1 - Q_0} = \mathcal{L}_{\mathbf{r}} \left( \frac{\gamma\psi^2(\mathbf{z})}{1 - \gamma\psi^2(\mathbf{z})} \right) \quad (\text{A.5})$$

is independent of  $N$ , and for all  $\mathbf{r}_1, \mathbf{r}_2$ ,  $L_{\mathbf{r}_1} - L_{\mathbf{r}_2}$  has a finite limit as  $\gamma \rightarrow 1$  ( $u \rightarrow 0$ ). The differences  $(L_0 - L_{\mathbf{r}})/N$  qualify as relatedness coefficients in a narrow sense (see Rousset and Billiard (submitted) for discussion) and their properties are discussed in Rousset (1997) where they are described as  $F_{\text{STR}}/(1 - F_{\text{STR}})$ .

When  $n_x \rightarrow \infty$  and  $n_y = 1$  in the one dimensional model, the inverse transform converges to an integral:

$$L_j \rightarrow \frac{1}{\pi} \int_0^\pi \frac{\gamma\psi^2(x)}{1 - \gamma\psi^2(x)} \cos(jx) dx. \quad (\text{A.6})$$

(Malécot, 1950; Nagylaki, 1976; Sawyer, 1977). Likewise when  $n_x$  and  $n_y \rightarrow \infty$  in the two dimensional model,

$$L_{\mathbf{r}} \rightarrow \frac{1}{\pi^2} \int_0^\pi \int_0^\pi \frac{\gamma\psi^2(\mathbf{z})}{1 - \gamma\psi^2(\mathbf{z})} \cos(r_x x) \cos(r_y y) dx dy, \quad (\text{A.7})$$

with  $\mathbf{z} \equiv (x, y)$ .

*Analysis of equation (5) of the main text.* Here we simplify equation (5) and obtain an approximate solution common to all dispersal models. In all models considered here, using vector indices for the more general two dimensional model,  $g_0(z) = 1 - z$ , and for  $\mathbf{k} \neq \mathbf{0}$ ,  $g_{\mathbf{k}} = (1 - c)z d_{\mathbf{k}}$  where  $d_{\mathbf{k}}$  is the fraction of offspring that disperse by  $\mathbf{k}$  steps on the lattice among those who disperse, and is determined by the fixed distribution of forward dispersal distances. Hence  $\partial g_{\mathbf{i}}/\partial z = (g_{\mathbf{i}} - \delta_{\mathbf{i}\mathbf{0}})/z$  where  $\delta_{\mathbf{i}\mathbf{0}}$  is 1 if  $\mathbf{i} = \mathbf{0}$  and 0 otherwise, and at the ESS

$$0 = \lim_{u \rightarrow 0} \frac{S}{1 - Q_0} = \sum_{\mathbf{i}} \lim_{u \rightarrow 0} \frac{Q_{\mathbf{i}}' - 1}{1 - Q_0} \sum_{\mathbf{k}} \frac{g_{\mathbf{k}}(z)(g_{\mathbf{k}-\mathbf{i}}(z) - \delta_{\mathbf{k}\mathbf{i}})/z}{\left(\sum_{\mathbf{j}} g_{\mathbf{k}-\mathbf{j}}(z_j)\right)^2} \quad (\text{A.8})$$

$$\Rightarrow 0 = \lim_{u \rightarrow 0} \sum_{\mathbf{i}} \frac{Q_{\mathbf{i}}' - 1}{1 - Q_0} \sum_{\mathbf{k}} m_{\mathbf{k}}(1 - cz)(m_{\mathbf{k}-\mathbf{i}}(1 - cz) - \delta_{\mathbf{k}\mathbf{i}}) \quad (\text{A.9})$$

in terms of backward dispersal rates, where  $1 - cz$  appears as the value of  $\sum_{\mathbf{j}} g_{\mathbf{k}-\mathbf{j}}(z)$  for any  $\mathbf{k}$ . From equation (A.1),  $Q_0 = \gamma \sum_{\mathbf{k}} \sum_{\mathbf{l}} m_{\mathbf{k}} m_{\mathbf{k}-\mathbf{l}} Q'_1$  so that the numerator of the above expression simplifies to  $(Q_0/\gamma - 1)(1 - cz) - \sum_{\mathbf{l}} m_{\mathbf{l}}(Q'_1 - 1)$ . Hence the ESS condition is

$$0 = \lim_{u \rightarrow 0} \left( \frac{1 - Q_0 + \gamma - 1}{\gamma(1 - Q_0)} (1 - cz) - \frac{1 - Q'_0}{1 - Q_0} m_0 - \sum_{\mathbf{l}} m_{\mathbf{l}} \frac{1 - Q_1}{1 - Q_0} \right) \quad (\text{A.10})$$

$$\propto \left( 1 - \frac{1}{Nn} \right) (1 - cz) - \left( 1 - \frac{1}{N} \right) m_0 - \sum_{\mathbf{l}} m_{\mathbf{l}} \left( 1 + \lim_{u \rightarrow 0} \frac{Q_0 - Q_1}{1 - Q_0} \right) \quad (\text{A.11})$$

$$\propto \left( 1 - \frac{1}{Nn} \right) (1 - cz) + \frac{m_0}{N} - 1 - \lim_{u \rightarrow 0} \sum_{\mathbf{l}} m_{\mathbf{l}} \frac{Q_0 - Q_1}{1 - Q_0}. \quad (\text{A.12})$$

The last sum is  $\lim_{u \rightarrow 0} \sum_{\mathbf{l}} m_{\mathbf{l}}(L_0 - L_1)/N$  and can be evaluated as follows. We express this sum of inverse transforms as a sum on  $(q_x, q_y)$  as in equation (A.4). For each value of  $(q_x, q_y)$ , there appears a factor  $\sum_{\mathbf{r} \neq \mathbf{0}} m_{\mathbf{r}} (1 - \cos(2\pi q_x/n_x r_x) \cos(2\pi q_y/n_y r_y)) = 1 - \psi(2\pi q_x/n_x, 2\pi q_y/n_y)$  and therefore, using equation (A.4), we can evaluate some terms of equation A.12 as

$$\begin{aligned} \frac{m_0}{N} - \lim_{u \rightarrow 0} \sum_{\mathbf{l}} m_{\mathbf{l}} \frac{L_0 - L_1}{N} &= \frac{\mathcal{L}_0(\psi)}{N} - \frac{1}{N n_x n_y} \sum_{q_x=0}^{n_x-1} \sum_{q_y=0}^{n_y-1} \frac{\psi^2(1 - \psi)}{1 - \psi^2} \\ &= \frac{1}{N} \mathcal{L}_0 \left( \frac{\psi}{1 + \psi} \right). \end{aligned} \quad (\text{A.13})$$

Thus, although we can evaluate the ESS by expressing it as function of several differences  $L_i - L_j$  and evaluating them, it is more direct to simplify eq. A.12 using eq. A.13 and to evaluate the resulting expression. In particular, neglecting the  $(1 - 1/(Nn))$  factor in equation (A.12), if  $c > 0$  the ESS obeys

$$z = \frac{1}{cN} \mathcal{L}_0 \left( \frac{\psi}{1 + \psi} \right), \quad (\text{A.14})$$

We will deduce a low backward migration approximation to this expression. When high cost of migration implies low backward migration rate, this will also be an approximation for high cost of dispersal. To that aim we write  $m_{\mathbf{i}}$  ( $\mathbf{i} \neq \mathbf{0}$ ) as  $m\mu_{\mathbf{i}}$  and let the total backward dispersal rate  $m \rightarrow 0$  for a fixed distribution of dispersal distance (i.e.  $\mu_{\mathbf{j}}/\mu_{\mathbf{i}}$  constant for all  $\mathbf{i}, \mathbf{j} \neq \mathbf{0}$ ). We note that  $\psi/(1 + \psi) = 1/2 - (1 - \psi)/4 + O(m^2)$  so that its  $\mathcal{L}_0$  transform is  $(1/2 - m/4 + O(m^2))/N$ . Neglecting the  $O(m^2)$  term, in an infinite population the ESS satisfies

$$d \approx \frac{1}{cN} \left( \frac{1}{2} - \frac{m}{4} \right). \quad (\text{A.15})$$

The relevant root of this equation is given by equation (7) in the main text.

*Generating functions for the different dispersal models.* In the one-dimensional stepping stone model, the generating function of dispersal distance is

$$\psi(x) = 1 - m + \frac{m}{2}(e^{ix} + e^{-ix}) = 1 - m + m \cos(x). \quad (\text{A.16})$$

In the four neighbors model,  $\psi(\mathbf{z})$  is

$$1 - m + \frac{m}{4}(e^{ix} + e^{-ix} + e^{iy} + e^{-iy}) = 1 - m + \frac{m}{2}(\cos(x) + \cos(y)). \quad (\text{A.17})$$

Finally, in the eight neighbors model,  $\psi(\mathbf{z})$  is

$$\begin{aligned} 1 - m + \frac{m}{8}(e^{ix} + e^{i(x+y)} + e^{iy} + e^{i(y-x)} + e^{-ix} + e^{-i(x+y)} + e^{-iy} + e^{i(x-y)}) \\ = 1 - \frac{9m}{8} + \frac{m}{8}(1 + 2 \cos(x))(1 + 2 \cos(y)). \end{aligned} \quad (\text{A.18})$$

## b. References

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