Appendix A
The Conditional and Marginal of a Multivariate Gaussian Distribution

A multivariate Gaussian distribution for the random m-dimensional vector $\boldsymbol{x}$ takes the form

$$f(\boldsymbol{x}) = \frac{1}{\sqrt{(2\pi)^m |\Sigma|}} \exp\left[-\frac{1}{2}(\boldsymbol{x}-\boldsymbol{\mu})^T \Sigma^{-1} (\boldsymbol{x}-\boldsymbol{\mu})\right] \tag{A.1}$$

where $\boldsymbol{\mu}$ is the mean value of $\boldsymbol{x}$, Σ is the covariance matrix and $|\Sigma|$ its determinant. We wish to calculate the conditional distribution for this process, given some subset of $\boldsymbol{x}$ is fixed, and also the marginal distribution given that we integrate out a subset of the $\boldsymbol{x}$ variables. We begin by partitioning the vectors $\boldsymbol{x}$ and $\boldsymbol{\mu}$ and the matrices Σ;

$$\boldsymbol{x} = \begin{pmatrix} \boldsymbol{x}_1 \\ \boldsymbol{x}_2 \end{pmatrix}, \quad \boldsymbol{\mu} = \begin{pmatrix} \boldsymbol{\mu}_1 \\ \boldsymbol{\mu}_2 \end{pmatrix}, \quad \Sigma = \begin{pmatrix} \Sigma_{11} & \Sigma_{12} \\ \Sigma_{21} & \Sigma_{22} \end{pmatrix}, \tag{A.2}$$

where we note that $\Sigma_{21} = \Sigma_{12}^T$, and Σ_{11} and Σ_{22} are symmetric. Further, let the elements of the partitioned inverse of Σ be denoted with upper indices, so that

$$\Sigma^{-1} = \begin{pmatrix} \Sigma^{11} & \Sigma^{12} \\ \Sigma^{21} & \Sigma^{22} \end{pmatrix}. \tag{A.3}$$

Since Σ is symmetric, so is Σ^{-1}, so that $\Sigma^{12} = [\Sigma^{21}]^T$. Now, the partitioned elements of Σ and Σ^{-1} can be related by noting that

$$\Sigma\Sigma^{-1} = \begin{pmatrix} \Sigma_{11} & \Sigma_{12} \\ \Sigma_{21} & \Sigma_{22} \end{pmatrix} \begin{pmatrix} \Sigma^{11} & \Sigma^{12} \\ \Sigma^{21} & \Sigma^{22} \end{pmatrix} \tag{A.4}$$

$$= \begin{pmatrix} \Sigma_{11}\Sigma^{11} + \Sigma_{12}\Sigma^{21} & \Sigma_{11}\Sigma^{12} + \Sigma_{12}\Sigma^{22} \\ \Sigma_{21}\Sigma^{11} + \Sigma_{22}\Sigma^{21} & \Sigma_{21}\Sigma^{12} + \Sigma_{22}\Sigma^{22} \end{pmatrix} \tag{A.5}$$

$$= \begin{pmatrix} I & 0 \\ 0 & I \end{pmatrix}. \tag{A.6}$$

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Springer Theses, DOI 10.1007/978-3-319-21218-0

This allows us to express the inverted quantities Σ^{ij} more naturally in terms of the elements of the covariance matrix Σ_{kl}. Solving for Σ^{11} using the first column of (A.5) and for Σ^{22} using the second column, we obtain

$$\Sigma^{11} = \left(\Sigma_{11} - \Sigma_{12}\Sigma_{22}^{-1}\Sigma_{12}^{T}\right)^{-1}, \tag{A.7}$$

$$\Sigma^{22} = \left(\Sigma_{22} - \Sigma_{12}^{T}\Sigma_{11}^{-1}\Sigma_{12}\right)^{-1}, \tag{A.8}$$

and similarly for $\Sigma^{12} = [\Sigma^{21}]^T$,

$$\Sigma^{12} = -\Sigma_{11}^{-1}\Sigma_{12}\Sigma^{22}. \tag{A.9}$$

For our purposes, a more convenient form for Eq. (A.7) can be obtained. From the first element of Eq. (A.5) we have

$$\Sigma^{11} = \Sigma_{11}^{-1} - \Sigma_{11}^{-1}\Sigma_{12}\Sigma^{21}. \tag{A.10}$$

From the first entry in the second column of Eq. (A.5) we obtain

$$\Sigma^{12} = -\Sigma_{11}^{-1}\Sigma_{12}\Sigma^{22}, \quad \text{or equivalently} \quad \Sigma^{21} = -\Sigma^{22}\Sigma_{12}^{\mathrm{T}}\Sigma_{11}^{-1}. \tag{A.11}$$

Combining these gives an alternative form for Σ^{11},

$$\Sigma^{11} = \Sigma_{11}^{-1} + \Sigma_{11}^{-1}\Sigma_{12}\Sigma^{22}\Sigma_{12}^{T}\Sigma_{11}^{-1}. \tag{A.12}$$

With these partitioned quantities in hand, we may now proceed to consider an alternate form of the Gaussian distribution.

The Gaussian distribution (A.1) may be rewritten

$$f(\boldsymbol{x}) = \frac{1}{\sqrt{(2\pi)^m|\Sigma|}} \exp\left[-\frac{1}{2}Q(\boldsymbol{x_1}, \boldsymbol{x_2})\right] \tag{A.13}$$

where $Q(\boldsymbol{x_1}, \boldsymbol{x_2})$ is given by

$$Q(\boldsymbol{x_1}, \boldsymbol{x_2}) = ((\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T, (\boldsymbol{x}_2 - \boldsymbol{\mu}_2)^T) \begin{pmatrix} \Sigma^{11} & \Sigma^{12} \\ \Sigma^{21} & \Sigma^{22} \end{pmatrix} \begin{pmatrix} \boldsymbol{x}_1 - \boldsymbol{\mu}_1 \\ \boldsymbol{x}_2 - \boldsymbol{\mu}_2 \end{pmatrix}. \tag{A.14}$$

Expanding out the various partitioned elements, we arrive at

$$\begin{aligned} Q(\boldsymbol{x_1}, \boldsymbol{x_2}) &= (\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T\Sigma^{11}(\boldsymbol{x}_1 - \boldsymbol{\mu}_1) \\ &\quad + 2(\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T\Sigma^{12}(\boldsymbol{x}_2 - \boldsymbol{\mu}_2) + (\boldsymbol{x}_2 - \boldsymbol{\mu}_2)^T\Sigma^{22}(\boldsymbol{x}_2 - \boldsymbol{\mu}_2). \end{aligned}$$

Substituting expressions (A.9) and (A.12) into this leads to

$$\begin{aligned} Q(\boldsymbol{x_1}, \boldsymbol{x_2}) &= (\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1) \\ &+ \left[(\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T \Sigma_{11}^{-1} \Sigma_{12} \right] \Sigma^{22} \left[\Sigma_{12}^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1) \right] \\ &- 2 \left[(\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T \Sigma_{11}^{-1} \Sigma_{12} \right] \Sigma^{22} (\boldsymbol{x}_2 - \boldsymbol{\mu}_2) \\ &+ (\boldsymbol{x}_2 - \boldsymbol{\mu}_2)^T \Sigma^{22} (\boldsymbol{x}_2 - \boldsymbol{\mu}_2) \end{aligned} \tag{A.15}$$

or, by further simplifying, as

$$\begin{aligned} Q(\boldsymbol{x_1}, \boldsymbol{x_2}) = & (\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1) \\ & + \left\{ (\boldsymbol{x}_2 - \boldsymbol{\mu}_2)^T - \left[\Sigma_{12}^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1) \right]^T \right\} \\ & \times \Sigma^{22} \left\{ (\boldsymbol{x}_2 - \boldsymbol{\mu}_2) - \left[\Sigma_{12}^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1) \right] \right\}. \end{aligned}$$

To make this expression a little more compact, the vector function $\tilde{\boldsymbol{\mu}}_2(\boldsymbol{x}_1)$ is introduced,

$$\tilde{\boldsymbol{\mu}}_2(\boldsymbol{x}_1) = \boldsymbol{\mu}_2 + \Sigma_{12}^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1), \tag{A.16}$$

so that Eq. (A.15) can be rewritten in terms of the functions $Q_1(\boldsymbol{x}_1)$ and $Q_2(\boldsymbol{x}_1, \boldsymbol{x}_2)$

$$Q_1(\boldsymbol{x}_1) = (\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1), \tag{A.17}$$

$$Q_2(\boldsymbol{x}_1, \boldsymbol{x}_2) = \left[\boldsymbol{x}_2 - \tilde{\boldsymbol{\mu}}_2(\boldsymbol{x}_1) \right]^T \Sigma^{22} \left[\boldsymbol{x}_2 - \tilde{\boldsymbol{\mu}}_2(\boldsymbol{x}_1) \right], \tag{A.18}$$

as

$$Q(\boldsymbol{x}_1, \boldsymbol{x}_2) = Q_1(\boldsymbol{x}_1) + Q_2(\boldsymbol{x}_1, \boldsymbol{x}_2). \tag{A.19}$$

We have thus far separated the full Gaussian distribution for $\boldsymbol{x}$ into the product of two functions involving $Q_1(\boldsymbol{x}_1)$ and $Q_2(\boldsymbol{x}_1, \boldsymbol{x}_2)$ respectively. The first of these functions has the same functional form as a Gaussian distribution for only $\boldsymbol{x}_1$ with covariance matrix Σ_{11}. We would like to separate this distribution out entirely. To do this we must address the $|\Sigma|$ term in denominator of Eq. (A.1).

We wish to factorise the component of $|\Sigma|$ arising from Σ_{11}. To do this we note that Σ may be decomposed as

$$\begin{pmatrix} \Sigma_{11} & \Sigma_{12} \\ \Sigma_{21} & \Sigma_{22} \end{pmatrix} = \begin{pmatrix} \Sigma_{11} & 0 \\ \Sigma_{12}^T & I \end{pmatrix} \begin{pmatrix} I & \Sigma_{11}^{-1} \Sigma_{12} \\ 0 & \Sigma_{22} - \Sigma_{12}^T \Sigma_{11}^{-1} \Sigma_{12} \end{pmatrix}. \tag{A.20}$$

Since the determinant of the product of two matrices in the product of the determinant of each matrix, $|AB| = |A||B|$, we can write

$$
\begin{aligned}
|\Sigma| &= |\Sigma_{11}||\Sigma_{22} - \Sigma_{12}^T \Sigma_{11}^{-1} \Sigma_{12}| \\
&= |\Sigma_{11}|| \left[\Sigma^{22} \right]^{-1} |.
\end{aligned}
\tag{A.21}
$$

Substituting Eqs. (A.19) and (A.21) into (A.1),

$$
\begin{aligned}
f(\boldsymbol{x}) = &\frac{1}{\sqrt{(2\pi)^r |\Sigma_{11}|}} \exp\left[-\frac{1}{2}(\boldsymbol{x}_1 - \boldsymbol{\mu}_1)^T \Sigma_{11}^{-1} (\boldsymbol{x}_1 - \boldsymbol{\mu}_1) \right] \times \\
&\frac{1}{\sqrt{(2\pi)^{m-r} | \left[\Sigma^{22} \right]^{-1} |}} \exp\left[-\frac{1}{2}(\boldsymbol{x}_2 - \tilde{\boldsymbol{\mu}}_2(x_1))^T \Sigma^{22} (\boldsymbol{x}_2 - \tilde{\boldsymbol{\mu}}_2(x_1)) \right]
\end{aligned}
\tag{A.22}
$$

where we set $\boldsymbol{x}_1$ to be a vector of length r and $\boldsymbol{x}_2$ to be a vector of length $m - r$. This can of course be expressed as the product of two normal distributions;

$$
f(\boldsymbol{x}_1, \boldsymbol{x}_2) = \mathcal{N}_{(r)}(\boldsymbol{\mu}_1, \Sigma_{11}) \mathcal{N}_{(m-r)} \left(\tilde{\boldsymbol{\mu}}_2(x_1), \left[\Sigma^{22} \right]^{-1} \right),
\tag{A.23}
$$

where $\mathcal{N}_{(r)}$ is a distribution for the r $\boldsymbol{x}_1$ variables and $\mathcal{N}_{(m-r)}$ is a distribution for the $m - r$ $\boldsymbol{x}_2$ variables. From this the marginal distribution for $\boldsymbol{x}_1$ can be simply calculated by integrating over $\boldsymbol{x}_2$

$$
f(\boldsymbol{x}_1) = \int f(\boldsymbol{x}_1, \boldsymbol{x}_2) d\boldsymbol{x}_2 = \mathcal{N}_{(r)}(\boldsymbol{\mu}_1, \Sigma_{11}) .
\tag{A.24}
$$

The conditional distribution $f(\boldsymbol{x}_2|\boldsymbol{x}_1)$ can in turn be calculated from Bayes' theorem, Eq. (2.2);

$$
\begin{aligned}
f(\boldsymbol{x}_2|\boldsymbol{x}_1) &= \frac{f(\boldsymbol{x}_1, \boldsymbol{x}_2)}{f(\boldsymbol{x}_1)} \\
&= \mathcal{N}_{(m-r)} \left(\tilde{\boldsymbol{\mu}}_2(x_1), \left[\Sigma^{22} \right]^{-1} \right).
\end{aligned}
\tag{A.25}
$$

Following an analogous proof, the distribution $f(\boldsymbol{x}_1, \boldsymbol{x}_2)$ conditioned on $\boldsymbol{x}_2$ taking a particular value is given by

$$
f(\boldsymbol{x}_1|\boldsymbol{x}_2) = \mathcal{N}_{(r)} \left(\tilde{\boldsymbol{\mu}}_1(x_2), \left[\Sigma^{11} \right]^{-1} \right).
\tag{A.26}
$$

where Σ^{11} is given by Eq. (A.7), and $\tilde{\boldsymbol{\mu}}_1(x_2)$ is given by

$$\tilde{\boldsymbol{\mu}}_2(x_1) = \boldsymbol{\mu}_1 + \Sigma_{12}\Sigma_{22}^{-1}(\boldsymbol{x}_2 - \boldsymbol{\mu}_2). \tag{A.27}$$

In the case where the mean of the distribution is zero and the conditional variable is zero, $\boldsymbol{x}_2 = 0$, the distribution further simplifies to

$$f(\boldsymbol{x}_1|0) = \mathcal{N}_{(r)}\left(0, \left[\Sigma^{11}\right]^{-1}\right). \tag{A.28}$$

This is the type of conditioning applied to the zero-mean Gaussian noise term $\boldsymbol{\kappa}(t) = (\boldsymbol{\kappa}_z, \boldsymbol{\kappa}_w)$ in Chap. 3.

Appendix B
Floquet Theory

The analogue of a linear stability analysis for systems with periodic components is known as Floquet theory [6]. It can also play an important role in the analysis of stochastic fluctuations about a deterministic trajectory [2, 7]. In this appendix the general formulation of Floquet theory is discussed before the more detailed application to linear stochastic systems is given.

Floquet theory gives the solutions to sets of linear differential equations in the form of Eq. (3.42), where $J(t)$ is periodic with a period T. The general solution can be shown to be

$$\boldsymbol{\xi}(t) = \sum_{i=1}^{m} c_i \boldsymbol{q}^{(i)}(t) e^{\sigma^{(i)} t}, \tag{B.1}$$

where $\boldsymbol{q}^{(i)}(t)$ is a periodic vector and $\sigma^{(i)}$ are termed the Floquet exponents of the system. Meanwhile the quantities $\rho^{(i)} = e^{\sigma^{(i)} T}$ are called the Floquet multipliers of the system.

In particular one can work in a canonical form for calculational ease, with canonical quantities denoted with a further superscript 0. The canonical form is constructed from m decomposed solutions to Eq. (3.42) such that $\boldsymbol{\xi}^{(0,i)}(t) = \boldsymbol{q}^{(0,i)}(t) e^{\sigma^{(i)} t}$. A fundamental matrix of these solutions may then be introduced along with matrices $Y^{(0)}$ and $Q^{(0)}$. For the case $m = 3$ these may be expressed as

$$X^{(0)} = [\boldsymbol{\xi}^{(0,1)}(t), \boldsymbol{\xi}^{(0,2)}(t), \boldsymbol{\xi}^{(0,3)}(t)], \tag{B.2}$$

$$X^{(0)} = Q^{(0)} Y^{(0)}, \tag{B.3}$$

$$Q^{(0)} = [\boldsymbol{q}^{(0,1)}(t), \boldsymbol{q}^{(0,2)}(t), \boldsymbol{q}^{(0,3)}(t)], \tag{B.4}$$

$$Y^{(0)} = Diag[e^{\mu^{(i)} t}]. \tag{B.5}$$

A method for obtaining the Floquet multipliers $\mu^{(i)}$ along with the canonical form of the solutions is now required. Obtaining both is dependent on the determination of a matrix known as the monodromy matrix, which we shall now discuss.

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Springer Theses, DOI 10.1007/978-3-319-21218-0

The monodromy matrix, D, is defined such that $X(t+T) = X(t)D$, for any fundamental matrix $X(t)$ constructed from linearly independent solutions to Eq. (3.42). It can be shown that while the monodromy matrix is dependent on the fundamental matrix chosen, its eigenvalues are not [6]. The eigenvalues of D are $\rho^{(i)}$, the Floquet multipliers of the system. Further, if a matrix W is constructed from the eigenvectors of D, the canonical fundamental matrix $X^{(0)}(t)$ is related to a general fundamental matrix $X(t)$ via $X^{(0)}(t) = X(t)W$. Therefore, the monodromy matrix allows the canonical fundamental matrix $X^{(0)}(t)$ to be determined from a general fundamental matrix $X(t)$, along with the matrix $Y^{(0)}$. From these the periodic matrix $Q^{(0)}(t)$ can also be deduced.

In general, once the fundamental matrix is obtained it will have to be transformed into canonical form by a numerical determination of the monodromy matrix, $D = X^{-1}(t)X(t+T)$. For a system with initial conditions $t = 0$, $X(0) = I$, this simplifies to $D = X(T)$.

Now the stochastic system can be considered;

$$\frac{d\boldsymbol{\xi}}{dt} = J(t)\boldsymbol{\xi} + \boldsymbol{\eta}(t), \tag{B.6}$$

where $\boldsymbol{\eta}(t)$ is a vector of Gaussian white noise terms defined as in Eq. (2.67), except that now the noise covariance matrix depends explicitly on time through the varying parameter $\beta(t)$; $\langle \eta_i(t)\eta_j(t')\rangle = \varepsilon B_{ij}(t)\delta(t-t')$. The solution may be constructed as a sum of the general solution to Eq. (3.42) along with a particular solution, so that

$$\boldsymbol{\xi}(t) = X^{(0)}(t)\boldsymbol{\xi}^{(0)} + X^{(0)}(t)\int_{t_0}^{t}\left[X^{(0)}(s)\right]^{-1}\boldsymbol{\eta}(s)ds, \tag{B.7}$$

or, setting the initial conditions in the infinite past and making a change of integration variable $s \to s' = t - s$

$$\boldsymbol{\xi}(t) = Q^{(0)}(t)\int_{t_0}^{t} Y^{(0)}(s')\left[Q^{(0)}(t-s')\right]^{-1}\boldsymbol{\eta}(t-s')ds'. \tag{B.8}$$

In the course of the analysis conducted in Sect. 3.4, $\boldsymbol{\xi}(t)$ represents some stochastic fluctuation around limit cycle behaviour. An obvious quantity of relevance is the power spectrum of such fluctuations. To obtain the power spectrum, one first calculates the two-time correlation function $C(t+\tau, t) = \langle \boldsymbol{\xi}(t+\tau)\boldsymbol{\xi}^T(t)\rangle$; substituting Eq. (B.8) one obtains

$$C_{ij}(t+\tau, t) = Q^{(0)}(t+\tau)Y^{(0)}(\tau)\Lambda(t)\left[Q^{(0)}(t)\right]^T, \tag{B.9}$$

with

$$\Lambda(t) = \int_{t_0}^{\infty} Y^{(0)}(s)\Gamma(t-s)Y^{(0)}(s)ds \tag{B.10}$$

and

$$\Gamma(s) = \left[Q^{(0)}(s)\right]^{-1} B(s) \left[\left[Q^{(0)}(s)\right]^{-1}\right]^{T}. \tag{B.11}$$

The correlation function, $\mathcal{C}(\tau)$ is then simply related to the two-time correlation function by

$$\mathcal{C}(\tau) = \frac{1}{T}\int_0^T C(t+\tau, t)dt. \tag{B.12}$$

In turn, the Wiener-Khinchin theorem tells us that the power spectrum, $P(\omega)$, is simply the Fourier transform of the correlation function, and so

$$P_i(\omega) = \int \mathcal{C}_{ii}(\tau)e^{i\omega\tau}d\tau. \tag{B.13}$$

The intermediate steps are left to the reader, but full details are found in [3]. A key point to note is that Eqs. (B.7)–(B.11) hold *only* for the canonical matrices $X^{(0)}$, $Q^{(0)}$ and $Y^{(0)}$.

Appendix C
Derivation of the Fokker-Planck Equation for the Metapopulation Moran Model

In this appendix, the details of the master equation expansion (described in Sect. 2.4) are given for the metapopulation Moran model, introduced in Sect. 4.3. For generality, the expansion is described for the model with selection which is defined by the transition rates (4.11) with master Eq. (2.18). The neutral case can be recovered by setting $\boldsymbol{w}_A = \boldsymbol{w}_B = \mathbf{1}$.

As in the one-island case described in Sect. 2.9.1, expressions (4.11) are simplified by setting $[\boldsymbol{w}_B]_i = 1$ and $[\boldsymbol{w}_A]_i = 1 + s\alpha_i$ for each island. The parameter s is an indicative selection strength, while the elements of $\boldsymbol{\alpha}$ will be assumed to be of order 1 and will primarily be used to signify the direction of selection. If $\alpha_i > 0$ then $[\boldsymbol{w}_A]_i > [\boldsymbol{w}_B]_i$ and allele A is advantageous on island i, while if $\alpha_i < 0$, allele A will be deleterious on that island. Finally, if we assume that the selection strength s is small, we can express the above transition rates as a Taylor series in s. Suppressing the dependence of $T(\boldsymbol{n}|\boldsymbol{n}')$ on states that do not vary in a particular transition, we obtain

$$\begin{aligned}
T(n_i+1|n_i) = &\sum_{j=1}^{\mathcal{D}} \frac{(\beta_i N - n_i)}{\beta_i N - \delta_{ij}} G_{ij} \times \\
&\left(\frac{n_j}{\beta_j N} + s\alpha_j \frac{n_j(\beta_j N - n_j)}{(\beta_j N)^2} - s^2\alpha_j^2 \frac{n_j^2(\beta_j N - n_j)}{(\beta_j N)^3} + \mathcal{O}(s^3) \right), \\
T(n_i-1|n_i) = &\sum_{j=1}^{\mathcal{D}} \frac{n_i}{\beta_i N - \delta_{ij}} G_{ij} \times \\
&\left(1 - \frac{n_j}{\beta_j N} - s\alpha_j \frac{n_j(\beta_j N - n_j)}{(\beta_j N)^2} + s^2\alpha_j^2 \frac{n_j^2(\beta_j N - n_j)}{(\beta_j N)^3} + \mathcal{O}(s^3) \right).
\end{aligned}$$

The dynamics can be seen to be that of a one-step process; any one transition can only move the system from an initial state $\boldsymbol{n}' = (n_1, \ldots n_i, \ldots n_{\mathcal{D}})$ to the adjacent states $\boldsymbol{n} = (n_1, \ldots n_i \pm 1, \ldots n_{\mathcal{D}})$. We can exploit this fact notationally; introducing

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new state variables $\boldsymbol{x}$ such that $x_i = n_i/\beta_i N$, we can write $f_i^+(x_i)$ and $f_i^-(x_i)$ as shorthand for the transition rates (in terms of the new variables) for moving up to state $x_i + 1/\beta_i N$ or down in state $x_i - 1/\beta_i N$ from initial state $\boldsymbol{x}'$. This gives

$$\begin{aligned}
f_i^+(x_i) &= \frac{G_{ii}(1-x_i)}{1-(\beta_i N)^{-1}}\left[x_i + s\alpha_i x_i(1-x_i) - s^2\alpha_i^2 x_i^2(1-x_i)\right] \\
&\quad + (1-x_i)\sum_{j\neq i}^{\mathcal{D}} G_{ij}\left[x_j + s\alpha_j x_j(1-x_j) - s^2\alpha_j^2 x_j^2(1-x_j)\right] + \mathcal{O}(s^3), \\
f_i^-(x_i) &= \frac{G_{ii}x_i}{1-(\beta_i N)^{-1}}\left[(1-x_i) - s\alpha_i x_i(1-x_i) + s^2\alpha_i^2 x_i^2(1-x_i)\right] \\
&\quad + x_i\sum_{j\neq i}^{\mathcal{D}} G_{ij}\left[(1-x_j) - s\alpha_j x_j(1-x_j) + s^2\alpha_j^2 x_j^2(1-x_j)\right] + \mathcal{O}(s^3).
\end{aligned} \tag{C.1}$$

For now let us leave the specific form of these transition rate functions alone, pausing only to note that the typical deme size, N, now only appears in the first term of $f_i^+(x_i)$ and $f_i^-(x_i)$.

We now re-express the master equation in terms of the transition rates $f_i^+(x_i)$ and $f_i^-(x_i)$:

$$\begin{aligned}
\frac{dp}{dt} &= \sum_{i=1}^{\mathcal{D}}\left[f_i^+\left(x_i - \frac{1}{\beta_i N}\right)p\left(x_i - \frac{1}{\beta_i N}, t\right) - f_i^+(x_i)p(x_i, t)\right] \\
&\quad + \sum_{i=1}^{\mathcal{D}}\left[f^-\left(x_i + \frac{1}{\beta_i N}\right)p\left(x_i + \frac{1}{\beta_i N}, t\right) - f_i^-(x_i)p(x_i, t)\right].
\end{aligned} \tag{C.2}$$

This is equivalent to Eq. (2.29), albeit with a modified notation. Assuming the typical deme population N to be large, we can carry out a Taylor expansion in N^{-1} as described in Sect. 2.4. The right-hand side of the master Eq. (C.2) becomes

$$\begin{aligned}
&-\sum_{i=1}^{\mathcal{D}}\left\{\left(\frac{1}{\beta_i N}\right)\frac{\partial}{\partial x_i}\left[f_i^+(x_i)p(x_i,t)\right]\right\} + \frac{1}{2!}\sum_{i=1}^{\mathcal{D}}\left\{\left(\frac{1}{\beta_i N}\right)^2\frac{\partial^2}{\partial x_i^2}\left[f_i^+(x_i)p(x_i,t)\right]\right\} \\
&+\sum_{i=1}^{\mathcal{D}}\left\{\left(\frac{1}{\beta_i N}\right)\frac{\partial}{\partial x_i}\left[f_i^-(x_i)p(x_i,t)\right]\right\} + \frac{1}{2!}\sum_{i=1}^{\mathcal{D}}\left\{\left(\frac{1}{\beta_i N}\right)^2\frac{\partial^2}{\partial x_i^2}\left[f_i^-(x_i)p(x_i,t)\right]\right\},
\end{aligned}$$

plus terms in N^{-3} and higher.

We now return to the terms in f_i^+ and f_i^- which involve N. They are identical to lowest order in s, and equal

$$\frac{G_{ii}(1-x_i)x_i}{1-(\beta_i N)^{-1}}. \tag{C.3}$$

Now in the master equation f_i^+ and f_i^- appear with different signs in the terms involving the first derivative, and so they cancel. Although their contributions add in the terms involving the second derivative, if we expand the expression (C.3) in powers of N^{-1} we see that these give $\mathcal{O}(N^{-3})$ contributions in the expansion, which we are discarding. By the same argument, the terms in f_i^+ and f_i^- which involve N and powers of s will also give $\mathcal{O}(N^{-3})$ contributions when multiplying the second derivative, and so can also be discarded. Finally, when these s-dependent terms multiply the first derivative, they will give contributions s/N^2 and s^2/N^2, but we will not include such terms in the diffusion matrix B (see below), and so we do not include them in this context either. So, in summary, the N dependence which appears in f_i^+ and f_i^- in Eq. (C.1) may be omitted to the order we are working, and the only N dependence is that shown explicitly in the FPE.

We now define

$$A_i(\boldsymbol{x}) = \frac{1}{\beta_i}\left[f_i^+(\boldsymbol{x}) - f_i^-(\boldsymbol{x})\right], \qquad B_{ii}(\boldsymbol{x}) = \frac{1}{\beta_i^2}\left[f_i^+(\boldsymbol{x}) + f_i^-(\boldsymbol{x})\right]. \tag{C.4}$$

With these definitions the expansion of the master equation in inverse powers of N takes the form

$$\frac{\partial p(\boldsymbol{x},t)}{\partial t} = -\frac{1}{N}\sum_{i=1}^{\mathcal{D}}\frac{\partial}{\partial x_i}\left[A_i(\boldsymbol{x})p(\boldsymbol{x},t)\right] + \frac{1}{2N^2}\sum_{i=1}^{\mathcal{D}}\frac{\partial^2}{\partial x_i^2}\left[B_{ii}(\boldsymbol{x})p(\boldsymbol{x},t)\right]. \tag{C.5}$$

Substituting the explicit forms for $f_i^{\pm}$ given by Eq. (C.1) into Eq. (C.4) gives the elements of the vector $\boldsymbol{A}(\boldsymbol{x})$ as

$$A_i(\boldsymbol{x}) = \frac{1}{\beta_i}\left\{\sum_{j\neq i}^{\mathcal{D}} G_{ij}(x_j - x_i) + s\sum_{j=1}^{\mathcal{D}} G_{ij}\alpha_j x_j(1-x_j) \right.$$
$$\left. - s^2\sum_{j=1}^{\mathcal{D}} G_{ij}\alpha_j^2 x_j^2(1-x_j)\right\} + \mathcal{O}(s^3),$$

and a diagonal diffusion matrix with elements given by

$$B_{ii}(\boldsymbol{x}) = \frac{1}{\beta_i^2}\left\{x_i\sum_{j=1}^{\mathcal{D}} G_{ij} + \sum_{j=1}^{\mathcal{D}} G_{ij}x_j - 2x_i\sum_{j=1}^{\mathcal{D}} G_{ij}x_j\right\} + \mathcal{O}(s). \tag{C.6}$$

The truncation of the series in s, should be chosen to be consistent with the truncation in the expansion in terms of N. This will clearly depend on the assumed size of s. If one sets $s = 0$, the above model reduces to that stated for the neutral case, Eqs. (4.9) and (4.10).

Appendix D
Specification of Parameters Used in Figures

In order to aid the reproducibility of the results in this thesis, this appendix gives sets parameters omitted for brevity from Chaps. 5 and 6.

In Fig. 5.1, results from three different neutral metapopulation Moran systems are given. The results given in red/triangles are obtained from a system with the following parameters;

$$\boldsymbol{\beta} = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}, \qquad m = \begin{pmatrix} 0.892 & 0.082 & 0.253 \\ 0.068 & 0.896 & 0.137 \\ 0.040 & 0.022 & 0.610 \end{pmatrix}. \tag{D.1}$$

The results in blue/circles are obtained from a system with both a symmetric migration matrix and a symmetric H matrix;

$$\boldsymbol{\beta} = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}, \qquad m = \begin{pmatrix} 0.88 & 0.06 & 0.06 \\ 0.06 & 0.88 & 0.06 \\ 0.06 & 0.06 & 0.88 \end{pmatrix}. \tag{D.2}$$

The results in green/squares are obtained from an unusual system in which the probability of remaining on the first island is smaller than the probability that it migrates. The parameters for this system are

$$\boldsymbol{\beta} = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}, \qquad m = \begin{pmatrix} 0.014 & 0.029 & 0.006 \\ 0.847 & 0.932 & 0.077 \\ 0.139 & 0.039 & 0.917 \end{pmatrix}. \tag{D.3}$$

In the right panel of Fig. 5.2, the parameters for the plots are taken from some of the randomly generated systems which yield the r_N values in the histogram in the left panel. In the main plots, the results given in blue/circles correspond to a system with a small r_N value. The parameters used for this system are

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Springer Theses, DOI 10.1007/978-3-319-21218-0

$$\boldsymbol{\beta} = \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix}, \qquad m = \begin{pmatrix} 0.854 & 0.151 & 0.038 & 0.202 \\ 0.016 & 0.606 & 0.049 & 0.001 \\ 0.096 & 0.094 & 0.903 & 0.103 \\ 0.034 & 0.149 & 0.010 & 0.694 \end{pmatrix}. \tag{D.4}$$

The results in green/squares meanwhile are obtained from a system with a symmetric migration matrix, which yields $r_N = 1$. The parameters are

$$\boldsymbol{\beta} = \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix}, \qquad m = \begin{pmatrix} 0.9 & 0.03\ldots & 0.03\ldots & 0.03\ldots \\ 0.03\ldots & 0.9 & 0.03\ldots & 0.03\ldots \\ 0.03\ldots & 0.03\ldots & 0.9 & 0.03\ldots \\ 0.03\ldots & 0.03\ldots & 0.03\ldots & 0.9 \end{pmatrix}. \tag{D.5}$$

The results in the right-inset plots are related the distribution on the left-inset. Once again those in blue/circles correspond to a system with a small r_N value, with the parameters given by

$$\boldsymbol{\beta} = \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix}, \qquad m = \begin{pmatrix} 0.557 & 0.023 & 0.029 & 0.041 \\ 0.002 & 0.956 & 0.088 & 0.177 \\ 0.185 & 0.014 & 0.838 & 0.033 \\ 0.256 & 0.007 & 0.045 & 0.749 \end{pmatrix}. \tag{D.6}$$

The results in the inset plot in green/squares are again given by a symmetric migration matrix with islands all of the same size, and the parameters given by Eq. (D.5). The plots in red/triangles correspond to large r_N values in the left-inset histogram, with the following parameters used;

$$\boldsymbol{\beta} = \begin{pmatrix} 1 \\ 1 \\ 5 \\ 1 \end{pmatrix}, \qquad m = \begin{pmatrix} 0.803 & 0.079 & 0.128 & 0.033 \\ 0.027 & 0.802 & 0.159 & 0.012 \\ 0.083 & 0.042 & 0.556 & 0.025 \\ 0.087 & 0.077 & 0.157 & 0.930 \end{pmatrix}. \tag{D.7}$$

In Fig. 5.3 the migration matrix for each of the systems analysed is the same. This is

$$m = \begin{pmatrix} 0.513 & 0.056 & 0.208 \\ 0.231 & 0.833 & 0.208 \\ 0.256 & 0.111 & 0.584 \end{pmatrix}. \tag{D.8}$$

All the other parameters of the various systems are given in the caption to this figure.

In Fig. 5.4 the migration matrix for the system under consideration is

$$m = \begin{pmatrix} 0.714 & 0.050 & 0.143 & 0.077 \\ 0.036 & 0.750 & 0.190 & 0.077 \\ 0.071 & 0.050 & 0.619 & 0.077 \\ 0.179 & 0.150 & 0.048 & 0.769 \end{pmatrix}. \tag{D.9}$$

In Fig. 5.5 two sets of data related to two separate systems are compared. Data from the first system is given in blue/circles and relates to a two-deme system with the migration matrix

$$m = \begin{pmatrix} 0.856 & 0.167 \\ 0.154 & 0.833 \end{pmatrix}. \tag{D.10}$$

The second system, with results plotted in red/triangles, is one comprised of four demes with the migration matrix

$$m = \begin{pmatrix} 0.714 & 0.050 & 0.143 & 0.077 \\ 0.036 & 0.750 & 0.190 & 0.077 \\ 0.071 & 0.050 & 0.619 & 0.077 \\ 0.179 & 0.150 & 0.048 & 0.769 \end{pmatrix}. \tag{D.11}$$

All other parameters for these systems are listed in the caption of Fig. 5.5.

In Fig. 5.9 all the parameters for the main plots are given. The migration matrix relating to the inset plots was omitted in the main text however. It is

$$m = \begin{pmatrix} 0.800 & 0.050 & 0.025 & 0.100 & 0.025 \\ 0.050 & 0.800 & 0.025 & 0.025 & 0.100 \\ 0.025 & 0.025 & 0.800 & 0.000 & 0.150 \\ 0.100 & 0.025 & 0.000 & 0.800 & 0.075 \\ 0.025 & 0.100 & 0.150 & 0.075 & 0.650 \end{pmatrix}. \tag{D.12}$$

Finally, in Fig. 6.4, all the parameters relating to the plots have been omitted. The system yielding the stationary distribution in the left panel has parameters

$$\begin{matrix} \mathcal{D} = 3 \\ N = 150 \\ b = 0.5 \end{matrix}, \quad \boldsymbol{\beta} = \begin{pmatrix} 2 \\ 1 \\ 1.5 \end{pmatrix}, \quad \boldsymbol{\omega}_1 = \begin{pmatrix} 5 \times 10^{-3} \\ 6 \times 10^{-4} \\ 9 \times 10^{-4} \end{pmatrix}, \quad \boldsymbol{\omega}_2 = \begin{pmatrix} 1 \times 10^{-3} \\ 5 \times 10^{-3} \\ 4 \times 10^{-4} \end{pmatrix} \tag{D.13}$$

and

$$m = \begin{pmatrix} 0.900 & 0.050 & 0.030 \\ 0.100 & 0.900 & 0.070 \\ 0.000 & 0.050 & 0.900 \end{pmatrix}. \tag{D.14}$$

The system yielding the stationary distribution in the right panel meanwhile has parameters

$$\begin{array}{r}\mathcal{D} = 5\\ N = 120\,,\\ b = 0.5\end{array} \quad \boldsymbol{\beta} = \begin{pmatrix} 2 \\ 1 \\ 1.5 \\ 1 \\ 3 \end{pmatrix}, \quad \boldsymbol{\omega}_1 = \begin{pmatrix} 1 \times 10^{-4} \\ 5 \times 10^{-4} \\ 4 \times 10^{-4} \\ 2 \times 10^{-3} \\ 9 \times 10^{-5} \end{pmatrix}, \quad \boldsymbol{\omega}_2 = \begin{pmatrix} 5 \times 10^{-3} \\ 6 \times 10^{-4} \\ 9 \times 10^{-4} \\ 7 \times 10^{-3} \\ 1 \times 10^{-3} \end{pmatrix} \tag{D.15}$$

and the migration matrix

$$m = \begin{pmatrix} 0.900 & 0.050 & 0.020 & 0.010 & 0.020 \\ 0.020 & 0.850 & 0.030 & 0.020 & 0.020 \\ 0.020 & 0.050 & 0.920 & 0.010 & 0.030 \\ 0.020 & 0.090 & 0.010 & 0.960 & 0.020 \\ 0.040 & 0.020 & 0.020 & 0.000 & 0.910 \end{pmatrix}. \tag{D.16}$$

Appendix E
Moran Model with Selection: Fixation Time

The mean time to fixation in the reduced metapopulation system, $T(z_0)$, is found from the backward FPE, in exactly the same way as described in Sect. 2.5.2. Therefore, analogous to Eq. (2.52), the equation reads

$$\frac{\bar{A}(z_0)}{N}\frac{dT}{dz_0} + \frac{\bar{B}(z_0)}{2N^2}\frac{d^2T}{dz_0^2} = -1, \tag{E.1}$$

where z_0 is the initial starting point on the centre manifold (or slow subspace). The boundary conditions are as for the single island case, that is, $T(0) = 0$ and $T(1) = 0$. In this appendix we discuss the analytic solution of Eq. (E.1) when $\bar{A}(z_0)$ and $\bar{B}(z_0)$ are given by Eqs. (4.35) and (4.25).

The result for the neutral case is well known [5]. Setting $s = 0$ in Eq. (4.35) gives $\bar{A}(z_0) = 0$, and direct integration of Eq. (E.1) gives Eq. (2.54), albeit divided by a factor of b_1 and with x_0 replaced by z_0. At order s, $\bar{A}(z) = sa_1z(1-z)$, and so the equation for $T(z_0)$ becomes

$$\frac{\sigma z_0(1-z_0)}{M}\frac{dT}{dz_0} + \frac{z_0(1-z_0)}{M^2}\frac{d^2T}{dz_0^2} = -1, \tag{E.2}$$

where we have defined new parameters $M = N/\sqrt{b_1}$ and $\sigma = a_1s/\sqrt{b_1}$. The reason for introducing these new parameters, other than on grounds of simplicity, is that Eq. (E.2) is exactly the equation found in the single island case with selection.

To solve it we introduce $\phi(z_0) = dT/dz_0$, so that the equation now reads

$$\frac{d\phi}{dz_0} + M\sigma\phi = -\frac{M^2}{z_0(1-z_0)}. \tag{E.3}$$

This equation is difficult to deal with analytically and numerically because of the singularities on the right-hand side at precisely the values of z_0 where we need to impose the boundary conditions. One can avoid this problem by writing $\phi = \phi_0 + \phi_s$,

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and choosing ϕ_0 so that the term $d\phi_0/dz_0$ cancels the right-hand side of Eq. (E.3). This choice means that ϕ_0 is simply the $s = 0$ solution, and the equation for ϕ_s is then

$$\frac{d\phi_s}{dz_0} + M\sigma\phi_s = -M\sigma\phi_0 = M^3\sigma\left[\ln z_0 - \ln(1 - z_0)\right], \tag{E.4}$$

which on the left-hand side is exactly the same as the equation for ϕ, but with a right-hand side which is less divergent as $z_0 \to 0$ or $z_0 \to 1$. Although this right-hand side is still divergent, its integral is not, which is all that we need. If we do require a convergent expression we can repeat the process, and write $\phi_s = \phi_1 + \phi_2$, choosing ϕ_1 so that the term $d\phi_1/dz_0$ cancels the right-hand side of Eq. (E.4).

We can now multiply Eq. (E.4) by $e^{M\sigma z_0}$ to find

$$\frac{d}{dz_0}\left[e^{M\sigma z_0}\phi_s\right] = M^3\sigma\left[\ln z_0 - \ln(1 - z_0)\right] e^{M\sigma z_0}, \tag{E.5}$$

which allows the integration to be straightforwardly carried out. One finds

$$\begin{aligned} T_s(z_0) &= c_1 e^{-M\sigma z_0} + c_2 \\ &+ M^3\sigma \int_0^{z_0} dy\, e^{-M\sigma y} \int_0^{y} dx\, e^{M\sigma x}\, \left[\ln x - \ln(1 - x)\right], \end{aligned} \tag{E.6}$$

where T_s is such that $dT_s/dz_0 = \phi_s$ and c_1 and c_2 are integration constants. Before imposing the boundary conditions, we can simplify the double integral by differentiating the inner integral and integrating by parts. This gives

$$\begin{aligned} T_s(z_0) = c_1 e^{-M\sigma z_0} &+ c_2 \\ &- M^2 e^{-M\sigma z_0} \int_0^{z_0} dx\, e^{M\sigma x}\, \left[\ln x - \ln(1 - x)\right] \\ &+ M^2 \int_0^{z_0} dy\, \left[\ln y - \ln(1 - y)\right]. \end{aligned} \tag{E.7}$$

The last term in Eq. (E.7) is simply the $s = 0$ mean time to fixation, and so applying the boundary conditions one obtains the Eqs. (5.12) and (5.13) given in the main text.

The calculation of $T(z_0)$ when $\bar{A}(z_0)$ is taken to order s^2 can be carried out in a similar way, but the results are more complicated and an integration by parts cannot straightforwardly simplify the double integral down to a single integral. The analogous equation to (E.3) is

$$\frac{d\phi}{dz_0} + M\sigma\left(1 - s\kappa z_0\right)\phi = -\frac{M^2}{z_0(1 - z_0)}, \tag{E.8}$$

where $\kappa = k_2/k_1$ and σ is now given by $\sigma = k_1 s/\sqrt{b_1}$. This is just as singular as Eq. (E.3), and so we perform the same manoeuvre and write $\phi = \phi_0 + \phi_s$, choosing ϕ_0 so that the term $d\phi_0/dz_0$ cancels the right-hand side of Eq. (E.8). The equation for ϕ_s then reads

$$\frac{d\phi_s}{dz_0} + M\sigma\,(1 - s\kappa z_0)\,\phi_s = M^3\sigma\,(1 - s\kappa z_0)\;[\ln z_0 - \ln(1 - z_0)]\,. \tag{E.9}$$

The right-hand side is now less divergent, and one can proceed as before to multiply this equation by $e^{M\sigma(z_0 - s\kappa z_0^2/2)}$ and integrate twice. We find

$$\begin{aligned} &T(z_0) = -M^2\,[z_0\ln(z_0) + (1 - z_0)\ln(1 - z_0)] \\ &+ M^3\sigma \int_0^{z_0} dy\, e^{-M\sigma y(1 - s\kappa y/2)} \left\{ \int_0^y dx(1 - s\kappa x)\,\times \right. \\ &\left. e^{M\sigma x(1 - s\kappa x/2)} \int_0^y [\ln x - \ln(1 - x)] - c_3 \right\}, \end{aligned} \tag{E.10}$$

where the constant c_3 is given by

$$\begin{aligned} c_3 = &\left(\int_0^1 dy e^{-M\sigma y(1 - s\kappa y/2)}\right)^{-1} \int_0^1 dy\, e^{-M\sigma y(1 - s\kappa y/2)} \\ &\times \int_0^y dx\,(1 - s\kappa x)\, e^{M\sigma x(1 - s\kappa x/2)}\,[\ln x - \ln(1 - x)]\,. \end{aligned}$$

Appendix F
Calculation of the Metapopulation Moran Model Dynamics on the Slow Subspace

In this appendix some of the more technical aspects of finding the slow subspace and calculating the dynamics of the reduced system will be set out. So far we have only specified the natural variable which we use in the reduced system, that is $z = \sum_{i=1}^{\mathcal{D}} u_i^{(1)} x_i$.

More generally, we can define a linear transformation to the coordinate z and $\mathcal{D} - 1$ coordinates $\boldsymbol{w}$ such that

$$\begin{pmatrix} z \\ \boldsymbol{w} \end{pmatrix} = T^{-1}\boldsymbol{x}, \quad \boldsymbol{x} = T\begin{pmatrix} z \\ \boldsymbol{w} \end{pmatrix}. \tag{F.1}$$

A convenient choice for x_i is

$$x_i = z + \sum_{a=1}^{\mathcal{D}-1} Q_{ia} w_a. \tag{F.2}$$

Since, from Eq. (4.22), $x_i = z$ on the centre manifold in the neutral case, we ask that the w_a are of order s on the slow subspace in the case with selection. This will simplify our calculation because, as we will see, this means that we will only have to calculate the w_a as functions of z to leading order in s.

In terms of the transformation matrix T, the choices made so far mean that

$$T^{-1} = \begin{pmatrix} [\boldsymbol{u}^{(1)}]^T \\ R \end{pmatrix}, \quad T = (\mathbf{1} \quad Q)\,, \tag{F.3}$$

where R is a $\mathcal{D} - 1$ by $\mathcal{D}$ matrix and Q is a $\mathcal{D}$ by $\mathcal{D} - 1$ matrix. The form of the matrices R and Q is restricted through the conditions $TT^{-1} = T^{-1}T = I$, the

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identity matrix. The condition relevant if we are trying to express $\boldsymbol{x}$ in terms of z and $\boldsymbol{w}$, is

$$\sum_{i=1}^{\mathcal{D}} u_i^{(1)} Q_{ia} = 0, \quad a = 1, \ldots, \mathcal{D} - 1. \tag{F.4}$$

We will need to check that any choice we make for Q_{ia} satisfies this condition.

We now substitute the transformation (F.2) into Eq. (4.34) for the drift vector in terms of $\boldsymbol{x}$:

$$A_i(z, \boldsymbol{w}) = \sum_{j=1}^{\mathcal{D}} H_{ij} \left(z + \sum_{a=1}^{\mathcal{D}-1} Q_{ja} w_a \right) + sz(1-z) \sum_{j=1}^{\mathcal{D}} \frac{G_{ij}\alpha_j}{\beta_i}$$
$$+ s(1-2z) \sum_{j=1}^{\mathcal{D}} \frac{G_{ij}\alpha_j}{\beta_i} \sum_{a=1}^{\mathcal{D}-1} Q_{ja} w_a - s^2 z^2 (1-z) \sum_{j=1}^{\mathcal{D}} \frac{G_{ij}\alpha_j^2}{\beta_i} + \mathcal{O}(s^2 y, s^3). \tag{F.5}$$

Using (i) $\sum_{j=1}^{\mathcal{D}} H_{ij} z = z \sum_{j=1}^{\mathcal{D}} H_{ij} = 0$, from Eq. (4.16), and (ii) the slow subspace condition $\sum_{i=1}^{\mathcal{D}} u_i^{(a+1)} A_i = 0$, $a = 1, \ldots, \mathcal{D} - 1$ (see Eq. (4.21)), we find

$$0 = \sum_{i,j=1}^{\mathcal{D}} \sum_{a=1}^{\mathcal{D}-1} u_i^{(a+1)} H_{ij} Q_{ja} w_a + sz(1-z) \sum_{i,j=1}^{\mathcal{D}} \frac{u_i^{(a+1)} G_{ij}\alpha_j}{\beta_i}, \tag{F.6}$$

since the slow subspace condition must be satisfied order by order in s and $\boldsymbol{y}$ is assumed to be of order s. Choosing Q_{ja} to be the right-eigenvectors $v_j^{(a+1)}$, $a = 1, \ldots, \mathcal{D} - 1$, which is consistent with the conditions (F.4), we see that the first term on the right-hand side of Eq. (F.6) is simply $\lambda^{(a+1)} w_a$. Therefore

$$w_a(z) = -\frac{sz(1-z)}{\lambda^{(a+1)}} \sum_{i,j=1}^{\mathcal{D}} \frac{u_i^{(a+1)} G_{ij}\alpha_j}{\beta_i} + \mathcal{O}(s^2). \tag{F.7}$$

Substituting Eq. (F.7) into Eq. (F.5), the drift vector evaluated on the slow subspace is found to be

$$A_i(z) = -\, s q_i^{(0)} z(1-z) + s q_i^{(1)} z(1-z) - s^2 q_i^{(2)} z^2 (1-z)$$
$$- s^2 q_i^{(3)} z(1-z)(1-2z) + \mathcal{O}(s^3), \tag{F.8}$$

where the vectors $\boldsymbol{q}^0$, $\boldsymbol{q}^1$, $\boldsymbol{q}^2$ and $\boldsymbol{q}^3$ are the parameter combinations

$$
\begin{aligned}
q_i^{(0)} &= \sum_{a=1}^{\mathcal{D}-1} \sum_{j,k,l=1}^{\mathcal{D}} \frac{H_{ij} v_j^{(a+1)} u_k^{(a+1)} G_{kl} \alpha_l}{\beta_k \lambda^{(a+1)}}, \\
q_i^{(1)} &= \sum_{j=1}^{\mathcal{D}} \frac{G_{ij} \alpha_j}{\beta_i}, \quad q_i^{(2)} = \sum_{j=1}^{\mathcal{D}} \frac{G_{ij} \alpha_j^2}{\beta_i}, \\
q_i^{(3)} &= \sum_{a=1}^{\mathcal{D}-1} \sum_{j,k,l=1}^{\mathcal{D}} \frac{G_{ij} \alpha_j}{\beta_i} \frac{v_j^{(a+1)} u_k^{(a+1)}}{\lambda^{(a+1)}} \frac{G_{kl} \alpha_l}{\beta_k}.
\end{aligned} \tag{F.9}
$$

The elements of the diffusion matrix meanwhile, when evaluated on the slow subspace, have the form

$$
B_{ii}(z) = 2z(1-z) \sum_{j=1}^{\mathcal{D}} \frac{G_{ij}}{\beta_i^2} + \mathcal{O}(s). \tag{F.10}
$$

Since the matrix H is not in general symmetric, then the eigenvalues will not in general be real. However since the entries of H are real, the eigenvalues will occur in complex conjugate pairs, and the eigenvectors associated with an eigenvalue λ^* will be the complex conjugates of those associated with λ. Since the expressions for $q_i^{(0)}$ and $q_i^{(3)}$ in Eq. (F.9) take the form of sums over a, for each term which is not real there will be another term added to it which is its complex conjugate. Thus $q_i^{(0)}$ and $q_i^{(3)}$ are guaranteed to be real. Therefore, the procedure goes through whether the eigenvalues are real or not. Of course, if there are complex conjugate pairs, the corresponding y_a cannot be interpreted as coordinates. However this interpretation is not crucial to the method, and if one wishes, it is always possible to define real coordinates by working with the real and imaginary parts of the eigenvalues and eigenvectors.

Appendix G
The Probability of Fixation in the Metapopulation Moran Model with Selection

The probability of fixation in the reduced system, $Q(z_0)$, is found as the relevant solution to Eq. (2.59). In the notation for the reduced metapopulation this reads

$$\frac{\bar{A}(z_0)}{N}\frac{dQ}{dz_0} + \frac{\bar{B}(z_0)}{2N^2}\frac{d^2Q}{dz_0^2} = 0, \tag{G.1}$$

where z_0 is the initial starting point on the centre manifold (or slow subspace). The boundary conditions are as for the single island case, that is, $Q(0) = 0$ and $Q(1) = 1$. In this appendix we discuss the analytic solution of Eq. (G.1) when $\bar{A}(z_0)$ and $\bar{B}(z_0)$ are given by Eqs. (4.35) and (4.25).

The result for the neutral case and to linear order in s have the same form as in the one-island case, and are well known [5]. When $s = 0$, $\bar{A}(z_0) = 0$, and so the solution of Eq. (G.1) subject to the boundary conditions is simply $Q(z_0) = z_0$. At linear order in s, $\bar{A}(z) = sa_1z(1-z)$, and a straightforward integration of Eq. (G.1) gives Eq. (2.100), albeit with extra factors of a_1 and b_1 and with x_0 replaced by z_0 (see Eqs. (5.17) and (5.11)).

To second order in s, $\bar{A}(z)$ may be written in the form (5.14), while $\bar{B}(z)$ is still given by Eq. (4.25). The equation for the probability of fixation (G.1) now takes the form

$$\frac{s}{N}z_0(1-z_0)(k_1 - sk_2z_0)\frac{dQ}{dz_0} + \frac{1}{N^2}b_1z_0(1-z_0)\frac{d^2Q}{dz_0^2} = 0.$$

Integrating with respect to z_0 we arrive at the equation

$$\frac{dQ}{dz_0} = c_1 \exp\left[-\frac{Ns}{b_1}\left(k_1z_0 - \frac{sk_2}{2}z_0^2\right)\right],$$

where c_1 is a constant of integration yet to be determined and where we note from Eq. (4.26) that $b_1 > 0$.

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If $k_2 = 0$, the calculation is identical to that carried out to first order in s, Eq. (5.11), but with a_1 replaced by k_1. If $k_2 \neq 0$, we may complete the square in the exponent to find

$$\frac{dQ}{dz_0} = c_1 \exp\left[-\frac{Nk_1^2}{2b_1k_2}\right] \exp\left[\frac{N}{2b_1k_2}(sk_2z_0 - k_1)^2\right].$$

We now change variables from z_0 to l, where

$$l = \sqrt{\frac{N}{2b_1|k_2|}}(sk_2z_0 - k_1), \tag{G.2}$$

to obtain

$$\frac{dQ}{dl} = \begin{cases} -c_2 \exp(-l^2), & \text{if } k_2 < 0 \\ c_2 \exp(l^2), & \text{if } k_2 > 0, \end{cases} \tag{G.3}$$

where

$$c_2 = \frac{c_1}{s}\sqrt{\frac{2b_1}{|k_2|N}} \exp\left\{-\frac{Nk_1^2}{2b_1k_2}\right\}, \tag{G.4}$$

is another constant.

The integrals over the exponentials in Eq. (G.3) can be carried out in terms of functions related to the error function, namely the complementary error function [1]

$$\text{erfc}(y) = 1 - \text{erf}(y) = 1 - \frac{2}{\sqrt{\pi}}\int_0^y e^{-l^2}\,dl, \tag{G.5}$$

and the imaginary error function [4]

$$\text{erfi}(y) = \frac{2}{\sqrt{\pi}}\int_0^y e^{l^2}\,dl. \tag{G.6}$$

Implementing the boundary conditions $Q(l(z_0 = 0)) = 0$ and $Q(l(z_0 = 1)) = 1$, one finds

$$Q(z_0) = \frac{1 - \chi(z_0)}{1 - \chi(1)}, \tag{G.7}$$

where

$$\chi(z_0) = \frac{\text{erfc}(l(z_0))}{\text{erfc}(l(0))}, \quad \text{if } k_2 < 0, \tag{G.8}$$

and

$$\chi(z_0) = \frac{\text{erfi}(l(z_0))}{\text{erfi}(l(0))}, \quad \text{if } k_2 > 0. \tag{G.9}$$

If l is large, then asymptotic forms can be used to simplify both the complementary error function and the imaginary error function [1, 4]:

$$\mathrm{erfc}(l) = \frac{e^{-l^2}}{\sqrt{\pi} l}\left[1 + \mathcal{O}\left(\frac{1}{l^2}\right)\right], \tag{G.10}$$

and

$$\mathrm{erfi}(l) = \frac{e^{l^2}}{\sqrt{\pi} l}\left[1 + \mathcal{O}\left(\frac{1}{l^2}\right)\right]. \tag{G.11}$$

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About the Author

George William Albert Constable has a background in non-equilibrium statistical physics, and is especially interested in applying the ideas and techniques of stochastic theory to ecological and biological systems. His first degree was from the University of Glasgow and his Ph.D. was obtained from the University of Manchester. While there, his work was primarily concerned with the derivation of effective theories for microscopically defined individual based models. Currently, he is a postdoctoral researcher looking at the effects of spatial structure on population level dynamics in the Ecology and Evolutionary Biology Department at Princeton University.

G.W.A. Constable, *Fast Variables in Stochastic Population Dynamics*,
Springer Theses, DOI 10.1007/978-3-319-21218-0