Online Resources

Online Resource 1. Mean dynamics

According to Eq. 3.5.14 of Gardiner (2004), the mean dynamics of a multivariate Markov process is a system of ordinary differential equations given by an approximation that ignores correlations

\[ \frac{dn_i}{dt} \sim A_i, \]  

(OR.1.1)

for each species \( i \). The

\[ n_i \equiv \sum_m mP\left( \tilde{N}_i = m \right) \]  

(OR.1.2)

are promoted from a discrete index to a continuous variable and

\[ A_i + O(\epsilon) = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \int_{|\tilde{m} - \tilde{n}| < \epsilon} d\tilde{m} \ (m_i - n_i)P\left( \tilde{N}(t + \Delta t) = \tilde{m} | \tilde{N}(t) = \tilde{n} \right), \]  

(OR.1.3)

are the first-order jump moments as defined by Eq. 3.4.2 of Gardiner (2004). For the transition probabilities of Eq. 7, we find

\[ P\left( \tilde{N}(t + \Delta t) = \tilde{m} | \tilde{N} = \tilde{n}(t) \right) = \sum_{j=1}^{S} \left( \delta((\tilde{m} + \tilde{e}_j) - \tilde{n})g_{j,\tilde{n}} + \delta((\tilde{m} - \tilde{e}_j) - \tilde{n})r_{j,\tilde{n}} \right) \Delta t + o(\Delta t), \]  

(OR.1.4)

so

\[ A_i = g_{i,\tilde{n}} - r_{i,\tilde{n}}, \]  

(OR.1.5)

and Eq. OR.1.1 yields Eq. 8. For the transition probabilities of Eq. 12, we find

\[ P\left( \tilde{N}(\tau + \Delta \tau) = \tilde{m} | \tilde{N} = \tilde{n}(\tau) \right) = \sum_{k=1}^{S} \sum_{j=1, j \neq k}^{S} \left( \delta((\tilde{m} - \tilde{e}_j + \tilde{e}_k) - \tilde{n})T_{j,k,\tilde{n}} \right. \]  

\[ + \left. \delta((\tilde{m} - \tilde{e}_k + \tilde{e}_j) - \tilde{n})T_{k,j,\tilde{n}} \right) \Delta \tau + o(\Delta \tau), \]  

(OR.1.6)
so

\[ A_i = \sum_{j=1,j\neq i} (T_{j,i,n} - T_{i,j,n}) \tag{OR.1.7} \]

and Eq. OR.1.1, with \( t \to \tau \), yields Eq. 13, given \( p_i \equiv n_i/J \) and the assumption of sufficiently weak competitive asymmetry such that \( w_{i,n} << \sum_{k=1}^{S} w_{k,n}n_k \) and \( a_{ij} << \sum_{k=1}^{S} a_{ik}n_k \) for every \( i \) and \( j \). A Kramers-Moyal expansion or Van Kampen system size expansion yields mean dynamics identical to the ones derived here (see, e.g., Gardiner (2004, p. 251)).

**Online Resource 2. Obtaining the Ricker model from the mean dynamics of a simple birth-death process**

Eq. 8 prescribes the single-species dynamics

\[ \frac{dn_1}{dt} = n_1(w_{1,0}e^{-a_{11}n_1/w_{1,0}} - d_1). \tag{OR.2.1} \]

Let \( \tau = d_1t \) and descritize the derivative to obtain

\[ n_{1\tau+1} = n_{1\tau} + n_{1\tau} \left( \frac{w_{1,0}}{d_1} e^{-a_{11}n_{1\tau}/w_{1,0}} - 1 \right), \]

\[ = n_{1\tau} e^{r(1-n_{1\tau}/K)}, \tag{OR.2.2} \]

where

\[ r = \log(w_{1,0}/d_1), \]

\[ K = \frac{w_{1,0}}{a_{11}} \log(w_{1,0}/d_1). \tag{OR.2.3} \]

Eq. OR.2.2 is the Ricker model.

**Online Resource 3. The mean dynamics of a Moran model retains the zero-sum rule**

Summing Eq. 13 over all species, we obtain

\[ \sum_{i=1}^{S} \frac{dp_i}{d\tau} = \sum_{i=1}^{S} c_i p_i \left( 1 - \sum_{j=1}^{S} p_j \right). \tag{OR.3.1} \]
If $\sum_{j=1}^S p_j(0) = 1$, then $\sum_{i=1}^S dp_i/d\tau|_{\tau=0} = 0$, which is sufficient to guarantee that $\sum_{j=1}^S p_i(\tau) = 1$ for all $\tau$.

**Online Resource 4. Dynamics of a simple Moran model**

In the $S = 2$ case of Eq. 11, the stochastic dynamics can be written, without approximation, as a univariate master equation for the marginal distribution of the first species

$$\frac{dP_{n_1}}{d\tau} = g_{n_1-1} \Theta(n_1 - 1) P_{n_1-1} + r_{n_1+1} \Theta(J - (n_1 + 1)) P_{n_1+1} - (g_{n_1} \Theta(J - (n_1 + 1)) + r_{n_1} \Theta(n_1 - 1)) P_{n_1}, \quad \text{(OR.4.1)}$$

with

$$g_{n_1} \equiv T_{2,1,(n_1,n_2)} = \frac{J - n_1}{J} \left( \frac{e^{-((B_1+B_2)n_1/J-B_2-a_{12}/w_{1,0}+a_{22}/w_{2,0})n_1}}{e^{-((B_1+B_2)n_1/J-B_2-a_{12}/w_{1,0}+a_{22}/w_{2,0})n_1 + J - n_1 - 1}} \right),$$

$$r_{n_1} \equiv T_{1,2,(n_1,n_2)} = \frac{n_1}{J} \left( \frac{J - n_1}{e^{-((B_1+B_2)n_1/J-B_2+a_{21}/w_{2,0}-a_{11}/w_{1,0})n_1 - 1} + J - n_1} \right). \quad \text{(OR.4.2)}$$

This master equation also governs marginal dynamics for the asymmetric species in a nearly neutral community where all other species, labelled 2 thru $S$, are symmetric (see Noble et al (2011)).

To calculate the temporal evolution of *conditional* abundance probability distributions, as plotted in Fig. 1, we start by discretizing the univariate birth-death
process of Eq. OR.4.1 to obtain
\[ P_{n_1, \tau + 1} = g_{n_1-1} \Theta(n_1 - 1) P_{n_1-1, \tau} + r_{n_1+1} \Theta(J - (n_1 + 1)) P_{n_1+1, \tau} \]
\[ + (1 - g_n \Theta(J - (n_1 + 1)) - r_n \Theta(n_1 - 1)) P_{n_1, \tau} \]
\[ = \sum_{m=0}^{J} P_{m, \tau} W_{mn_1}, \quad \text{(OR.4.3)} \]

where
\[ W = \begin{pmatrix} 1 - g_0 & g_0 & 0 & \cdots & 0 & 0 & 0 \\ r_1 & 1 - r_1 - g_1 & g_1 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 - r_{J-1} - g_{J-1} & g_{J-1} & 0 \\ 0 & 0 & 0 & \cdots & r_J & 1 - r_J & 0 \end{pmatrix}. \quad \text{(OR.4.4)} \]

The unconditioned abundance probability distribution at any integer time \( \tau \), denoted \( \tilde{P}_{\tau} \), is given by
\[ \tilde{P}_{\tau} = \tilde{P}_0 W^\tau. \quad \text{(OR.4.5)} \]

The abundance probability distribution conditioned against extinction and monodominance is
\[ P_{cn_1, \tau} \equiv \frac{P_{n_1, \tau}}{1 - P_{0, \tau} - P_{J, \tau}}, \quad \text{(OR.4.6)} \]
for \( n_1 = 1, \ldots, J - 1 \).

**Online Resource 5. Recovering non-zero-sum dynamics from zero-sum dynamics**

Our general approach is to treat empty space as the \((S + 1)\)th species in a community of \(S\) species. Let \( w_{(S+1), 0} \) be the rate at which death events generate empty space and set all the \( a_{ij} \) to zero for \( i, j = S + 1 \). Given this setup, we consider the dynamics of a large–\(J\) community as \( n_{S+1} \to J \).
Starting from the master equation for the Moran model in Eq. 11, we find

\[ T_{i,S+1,n} \sim \frac{n_i}{J}, \]

\[ T_{S+1,i,n} \sim \frac{w_{i,n}}{w_{(S+1),0} J}, \]  

(OR.5.1)

and all other transition probabilities are higher-order in \( n_i/J \) for \( i \neq S+1 \). Now let \( r \) be the overall transition rate. Rescaling \( w_{i,n} \rightarrow w_{(S+1),0} w_{i,n}/r \), setting \( \tau = r J t \), and identifying \( T_{S+1,i} \) and \( T_{i,S+1} \) with \( g_{i,n} \) and \( r_{i,n} \), respectively, we find that Eq. 11 reduces to Eq. 6 with \( d_i = r \).

Starting from the mean dynamics of the Moran model in Eq. 13, and using \( p_i = n_i/J \), we find

\[ \frac{dn_i}{d\tau} \sim \frac{w_{i,n}}{w_{(S+1),0} J} - \frac{n_i}{J}, \]  

(OR.5.2)

with all other terms being higher-order in \( n_i/J \) for \( i \neq S+1 \). The same rescalings as before yield Eq. 8 with \( d_i = r \).

**Online Resource 6. Corrections to stability criteria of the simple Moran model for low levels of speciation and migration**

In a nearly neutral metacommunity where only the first species is distinct in ecological function, parameters for the symmetric species are identical: \( w_{i,0} = w_{2,0} \) and \( a_{ij} = a_{2j} \) for all \( i > 1 \) and all \( j \). If the number of symmetric species, \( S - 1 \), is large such that terms of \( O(S) \) can be ignored in Eq. 18, then the mean dynamics for the asymmetric species can be written as

\[ \frac{dp_1}{d\tau} = \frac{1}{J_M} \left( (1 - \nu_1) e^{-((B_1+B_2)p_1-B_2)} - (1 - \nu_2) e^{-((B_1+B_2)p_1-B_2)} p_1 (1 - p_1) - \frac{\nu_2}{J_M} p_1 \right), \]  

(OR.6.1)

where \( B_1 \) and \( B_2 \) are given by Eq. 16 with the substitution \( J \rightarrow J_M \). The stable fixed point of the nearly neutral metacommunity can be calculated perturbatively in \( \nu_1 \) and
\( \nu_2 \). At leading order, we find

\[
\begin{align*}
\nu_1^* &= \frac{B_2 - C_{\nu_1} \nu_1 - C_{\nu_2} \nu_2}{B_1 + B_2} + O(\nu_1^2, \nu_2^2, \nu_1 \nu_2), \\
\nu_{i>1}^* &= \frac{1 - \nu_i^*}{S - 1},
\end{align*}
\]

where

\[
C_{\nu_1} = 1, \quad C_{\nu_2} = \frac{B_2}{B_1}. \tag{OR.6.3}
\]

Stability requirements can be found from the linearization

\[
\frac{dp_1}{d\tau} = -\frac{1}{J_M} \frac{(B_1 + D_{\nu_1} \nu_1)(B_2 + D_{\nu_2} \nu_2)}{B_1 + B_2} (p_1 - p_1^*) + O(\nu_1^2, \nu_2^2, \nu_1 \nu_2), \tag{OR.6.4}
\]

where

\[
D_{\nu_1} = \frac{B_2^2 - B_1^2 - B_1 B_2^2}{B_2(B_1 + B_2)}, \quad D_{\nu_2} = \frac{B_2^2}{B_1^2} \left(2 - \frac{B_1 B_2}{B_1 + B_2}\right). \tag{OR.6.5}
\]

For a nearly neutral local community, the dynamics of the asymmetric species, as prescribed by Eq. 21, can be written as

\[
\frac{dp_1}{d\tau} = \frac{1}{J_M} \frac{(1 - \nu_1) e^{-(B_1 + B_2) p_1 - B_2} - (1 - \nu_2) e^{-(B_1 + B_2) p_1 - B_2} p_1 + 1 - p_1}{1 - p_1} p_1 (1 - p_1) - \frac{\nu_2}{J_M} p_1. \tag{OR.6.6}
\]

where \( B_1 \) and \( B_2 \) are given by Eq. 16 with the substitution \( J \rightarrow J_L \). The stable fixed point of the nearly neutral local community can be calculated perturbatively in \( m_1 \) and \( m_2 \). At leading order, we find

\[
\begin{align*}
\nu_1^* &= \frac{B_2 - C_{m_1} m_1 - C_{m_2} m_2}{B_1 + B_2} + O(m_1^2, m_2^2, m_1 m_2), \\
\nu_{i>1}^* &= \frac{1 - \nu_i^*}{S - 1}, \tag{OR.6.7}
\end{align*}
\]
where

\[
C_{m1} = 1 - x_1 \frac{B_1 + B_2}{B_2},
\]

\[
C_{m2} = \frac{B_2}{B_1} - x_1 \frac{B_1 + B_2}{B_1}.
\]

(OR.6.8)

Stability requirements can be found from the linearization

\[
\frac{dp_1}{d\tau} = -\frac{1}{J_L} \frac{(B_1 + D_{m1}m_1)(B_2 + D_{m2}m_2)}{B_1 + B_2} (p_1 - p_1^*) + O(m_1^2, m_2^2, m_1m_2),
\]

(OR.6.9)

where

\[
D_{m1} = \frac{1}{B_2^2(B_1 + B_2)} \left( B_2^3(1 - x_1) + 2B_1^2B_2^2x_1(1 - x_1) \\
- B_1B_2(B_1 + B_2^2)(1 - x_1)^2 - 3B_1x_1(2 - B_2x_1) \right),
\]

\[
D_{m2} = \frac{1}{B_1^2(B_1 + B_2)} \left( 2B_2^3(1 - x_1) + 2B_1^2B_2^2x_1(1 - x_1) \\
+ B_1B_2^2(2 - B_2(1 - x_1)^2 - 3x_1) + B_1^3x_1(1 - B_2x_1) \right).
\]

(OR.6.10)

**Online Resource 7. Calculation of extinction times in a nearly neutral metacommunity**

If we assume a sufficiently large number of symmetric species such that \(O(1/S)\) terms in the master equation are negligible, marginal dynamics for the asymmetric species are governed by Eq. OR.4.1 with

\[
g_{n_1} = \frac{J_M - n_1}{J_M} \left( 1 - \nu_1 \right) \frac{e^{-(B_1 + B_2)n_1/J_M - B_2 - a_{12}/w_{1,0} + a_{22}/w_{2,0})n_1 + J_M - n_1 - 1}}{e^{-(B_1 + B_2)n_1/J_M - B_2 - a_{12}/w_{1,0} + a_{22}/w_{2,0})n_1} \left( 1 + \nu_2 \right),
\]

\[
r_{n_1} = \frac{n_1}{J_M} \left( 1 - \nu_2 \right) \frac{J_M - n_1}{e^{-(B_1 + B_2)n_1/J_M - B_2 + a_{21}/w_{2,0} - a_{11}/w_{1,0})n_1 - 1 + J_M - n_1 + \nu_2}},
\]

(OR.7.1)

where \(B_1\) and \(B_2\) are given by Eq. 16 with the substitution \(J \to J_M\). Hubbell’s univariate metacommunity dynamics (Hubbell 2001) are included as the fully
symmetric limit. For an initial abundance of \( n_{1,0} \), the mean times to extinction, \( \tau_E \), are calculated using (Gardiner, 2004, p. 260)

\[
\tau_E = \sum_{p=0}^{n_{1,0}-1} \phi_p^M \sum_{q=p+1}^{J_M-1} \frac{1}{g_q^M \phi_q^M},
\]

(OR.7.2)

where \( \phi_0^M = 1 \) and for \( p > 0 \)

\[
\phi_p^M = \prod_{m=1}^{p} \frac{r_m^M}{g_m^M}.
\]

(OR.7.3)

**Online Resource 8. Fluctuations in large local communities**

In Hubbell’s theory of local communities, the expected abundance of each species at equilibrium is

\[
\lim_{\tau \to \infty} \langle N_i(\tau) \rangle = x_i J_L.
\]

(OR.8.1)

Vallade and Houchmandzadeh (2003) first calculated the variance at equilibrium

\[
\lim_{\tau \to \infty} \langle (N_i(\tau) - \langle N_i(\tau) \rangle)^2 \rangle = x_i (1 - x_i) J_L \frac{J_L + I}{1 + I},
\]

(OR.8.2)

where \( I = (J_L - 1)m/(1 - m) \) is called the “fundamental dispersal number” (Etienne and Alonso, 2005). Then, for large \( J_L \), we obtain the approximation in Eq. 24.

**Online Resource 9. A stationary distribution for the asymmetric species in a nearly neutral local community with weak competitive interactions**

Marginal dynamics for the asymmetric species are governed by Eq. OR.4.1 with

\[
g_{n_1} = \frac{J_L - n_1}{J_L} \left( (1 - m_1) \frac{\rho_g(n_1) n_1}{\rho_g(n_1) n_1 + J_L - n_1} + m_1 \frac{\rho_g(n_1) x_1}{\rho_g(n_1) x_1 + 1 - x_1} \right),
\]

\[
r_{n_1} = \frac{n_1}{J_L} \left( (1 - m_2) \frac{J_L - n_1}{\rho_r(n_1) (n_1 - 1) + J_L - n_1} + m_2 \frac{1 - x_1}{\rho_r(n_1) x_1 + 1 - x_1} \right),
\]

(OR.9.1)
where
\[ \rho_g(n_1) = e^{-((B_1 + B_2)n_1/J_L - B_2 - a_{12}/w_{1,0} + a_{22}/w_{2,0})}, \]
\[ \rho_r(n_1) = e^{-((B_1 + B_2)n_1/J_L - B_2 - a_{21}/w_{2,0} - a_{11}/w_{1,0})}. \]  
(OR.9.2)

and \( B_1 \) and \( B_2 \) are given by Eq. 16 with the substitution \( J \to J_L \). We now assume
weak competitive interactions such that
\[ \rho_g(n_1) \sim 1 - ((B_1 + B_2)n_1/J_L - B_2 - a_{12}/w_{1,0} + a_{22}/w_{2,0}) \]
\[ \equiv c_g + d n_1, \]
\[ \rho_r(n_1) \sim 1 - ((B_1 + B_2)n_1/J_L - B_2 + a_{21}/w_{2,0} - a_{11}/w_{1,0}) \]
\[ \equiv c_r + d n_1, \]  
(OR.9.3)

where
\[ c_g = 1 + \log \frac{w_{1,0}}{w_{2,0}} + (J_L - 1) \frac{a_{22}w_{1,0} - a_{12}w_{2,0}}{w_{1,0}w_{2,0}}, \]
\[ c_r = 1 + \log \frac{w_{1,0}}{w_{2,0}} + J_L \frac{a_{22}w_{1,0} - a_{12}w_{2,0}}{w_{1,0}w_{2,0}} + \frac{a_{11}w_{2,0} - a_{21}w_{1,0}}{w_{1,0}w_{2,0}}, \]
\[ d = -\frac{w_{1,0}(a_{22} - a_{21}) + w_{2,0}(a_{11} - a_{12})}{w_{1,0}w_{2,0}}. \]  
(OR.9.4)

We specialize to the case where \( a_{11} = a_{22}, a_{12} = a_{21}, \) and \( w_{1,0} = w_{2,0}, \) so that
\( c_g = c_r \equiv c. \) The stationary distribution, \( P_{n_1}^* \equiv \lim_{\tau \to \infty} P_{n_1}(\tau), \) is given by a
well-known formula
\[ P_{n_1}^* = P_0 \prod_{i=0}^{n_1-1} \frac{g_i}{r_{i+1}}. \]  
(OR.9.5)

After some algebra, we obtain the closed form
\[ P_{n_1}^* = Z \left( \frac{J_L}{n_1} \right) \left( 1 + \frac{x(c + d n_1)}{1 - x} \right) \eta^{n_1} (c/d)_{n_1} \]
\[ \times \frac{B(\lambda_{a+} + n_1, \xi_{a+} - n_1)B(\lambda_{a-} + n_1, \xi_{a-} - n_1)}{B(\lambda_{a+}, \xi_{a+})B(\lambda_{a-}, \xi_{a-})} \]
\[ \times \frac{B(\lambda_{b+} + n_1, \xi_{b+} - n_1)B(\lambda_{b-} + n_1, \xi_{b-} - n_1)}{B(\lambda_{b+}, \xi_{b+})B(\lambda_{b-}, \xi_{b-})}, \]  
(OR.9.6)
where \((y)_z \equiv \Gamma(y + z)/\Gamma(y)\) is the Pochhammer symbol, \(B(y, z) = \Gamma(y + z)/\Gamma(y)\Gamma(z)\) is the Beta function, and

\[
Z^{-1} = \binom{6}{4}(-J_L, c/d, \lambda_{a+}, \lambda_{a-}, \lambda_{b+}, \lambda_{b-}; 1 - \xi_{a+}, 1 - \xi_{a-}, 1 - \xi_{b+}, 1 - \xi_{b-}; -\eta) \\
+ xc \binom{6}{4}(-J_L, c/d + 1, \lambda_{a+}, \lambda_{a-}, \lambda_{b+}, \lambda_{b-}; 1 - \xi_{a+}, 1 - \xi_{a-}, 1 - \xi_{b+}, 1 - \xi_{b-}; -\eta),
\]

(OR.9.7)

and

\[
\begin{align*}
\lambda_{a\pm} &= \frac{1}{2d} \left( c + d - 1 \pm \sqrt{(1 - c + d)^2 - 4d(J_L - 1)} \right), \\
\lambda_{b\pm} &= \frac{1}{2dx} \left( 1 - m - x + cx \pm \sqrt{(1 - m - x + cx)^2 - 4mdx^2(J_L - 1)} \right), \\
\xi_{a\pm} &= \frac{1}{2d} \left( 1 - c + 2d \pm \sqrt{(1 - c)^2 - 4d(J_L - 1)} \right), \\
\xi_{b\pm} &= \frac{1}{2d(m_2 - x)} \left( 1 + (d - c)m_2 - (d - c + 1)x - (1 - m_2)dx(J_L - 1) \right. \\
&\quad \pm \sqrt{(1 - (d + c)m_2 + (d + c - 1)x - (1 - m_2)dx(J_L - 1))^2} \cdot \\
&\quad \left. \cdots - 4(J_L - 1)d(m_2 - x)(x + x(c + d)(m_2 - 1) - 1) \right), \\
\eta &= \frac{dx}{m_2 - x}. 
\end{align*}
\]

(OR.9.8)

Eq. OR.9.6 is a generalized hypergeometric distribution (Kemp, 1968; Johnson et al., 1992).