A Calculating the coevolved dispersal distances

The calculations for the baseline model (monoculture evolution in the presence of moderate environmental variation) were presented in Snyder (2006). Here I show how to calculate the coevolved dispersal distances.

To find the coevolved dispersal distances, we find the evolutionarily stable (ESS) annual dispersal distance as a function of the perennial dispersal distance, then find the ESS perennial dispersal distance as a function of the annual dispersal distance. At the intersection of these two curves, neither species will be driven to adjust its dispersal strategy in response to the other's strategy, for each species is on its evolutionarily stable curve: this point is an evolutionarily stable coalition. Finally, we need to verify that evolutionary dynamics cause the system to converge to this point: i.e., that the intersection is not only evolutionarily stable but convergently stable, in the sense of Geritz et al. (1998).

To find, e.g., the ESS annual dispersal distance as a function of the perennial dispersal distance, consider an annual invader in the presence of annual and perennial residents. The invader is a mutant with dispersal distance a little larger or smaller that of the annual resident. If the invader has a positive long-run growth rate, it will replace the former resident and become subject to invasion attempts by new mutants. The process stops when the best strategy the annual invader could adopt is that of the annual resident — i.e., invader growth is maximized when the invader dispersal distance equals the resident dispersal distance. Signifying the invader long run growth rate by $\overline{r}_i(d_a, d_p, d_i)$, where d_a is the resident annual distance, d_p is the resident perennial distance, and d_i is the invader distance, the ESS annual dispersal distance d_a^* is given by the condition

$$\left.\frac{\partial \overline{r}_i(d_a, d_p, d_i)}{\partial d_i}\right|_{d_i = d_a = d_a^*} = 0. \tag{1}$$

Note that d_a^* depends on d_p, the perennial distance.

We see that finding the ESS dispersal distance requires us to find an expression for the long-run invader growth rate $\overline{r}_i$. Invader growth is affected by competition from the residents, which will in turn be determined by the spatiotemporal distribution of the resident populations. Let us first find an expression for $\overline{r}_i$ in terms of the resident populations and then find expressions for the population distributions.

Before dispersal, the local population of species j at time $t + 1$ is equal to the local growth rate $\lambda_j(x, t)$ times the local population at time t: $n_j(x, t + 1) = \lambda_j(x, t)n_j(x, t)$. To characterize the regional dynamics, we take the spatial average of both sides: $\langle n_j \rangle_x(t + 1) = \langle \lambda_j n_j \rangle_x(t)$, where $\langle \cdot \rangle_x$ denotes a spatial average. Expressing the dynamics in this form is not very useful because the righthand side is not a function of $\langle n_j \rangle_x$. However, we can rewrite the average of λ_j times n_j as the product of their averages plus their covariance, allowing us to factor out $\langle n_j \rangle_x$. Thus,

$$\langle n_j \rangle_x(t + 1) = \langle \lambda_j \rangle_x(t) \langle n_j \rangle_x(t) + \mathrm{Cov}(\lambda_j, n_j)_x(t)$$
$$= [\langle \lambda_j \rangle_x + \mathrm{Cov}(\lambda_j, n_j/\langle n_j \rangle_x)_x] \langle n_j \rangle_x(t). \tag{2}$$

The quantity in square brackets is the regional growth rate — the factor by which the spatially averaged population grows or shrinks in a year. We denote the regional growth

rate by $\widetilde{\lambda}_j$ and rewrite it as $\langle\lambda_j\rangle_x + \mathrm{Cov}(\lambda_j, \nu_j)_x$, where $\nu_j(x,t) = n_j(x,t)/\langle n_j\rangle_x$ is referred to as the relative population density (Chesson, 2000).

The regional growth rate fluctuates in time, and so the long-run growth of the population is given by the time average of the logarithm of the regional growth rate: $\overline{r}_j = \langle\ln\widetilde{\lambda}_j\rangle_t$ (Lewontin and Cohen, 1969). If we assume that fluctuations in fecundity and population are small $(O(\sigma)^*)$ relative to their means, then $\mathrm{Cov}(\lambda_j, \nu_j)_x$ is $O(\sigma^2)$ and we can Taylor expand the logarithm to $O(\sigma^2)$ to obtain

$$\overline{r}_j \approx \left\langle \ln\lambda_j^{(0)} + \frac{1}{\lambda_j^{(0)}}\left(\langle\lambda_j\rangle_x - \lambda_j^{(0)} + \mathrm{Cov}(\lambda_j, \nu_j)_x\right) - \frac{1}{2\lambda_j^{(0)2}}\left(\langle\lambda_j\rangle_x - \lambda_j^{(0)}\right)^2 \right\rangle_t, \quad (3)$$

where $\lambda_j^{(0)}$ is the growth rate of species j in the absence of spatial or temporal variation.

Happily, we need only deal with a single term of this expression. Our ESS condition, eq. 1, is a function of the invader long-run growth rate, $\overline{r}_i$. The invader is presumed to be of such low density that it does not contribute to competition, and thus λ_i does not depend on the invader population distribution or dispersal distance. (This assumption can be violated if the invader rapidly forms clusters in areas far from other sources of competition. Here, however, the invader will cluster in the same locations as the same-species resident, whose contribution to competition will dwarf that of the invader's.) The only term that depends on invader dispersal is $\frac{1}{\lambda_i^{(0)}}\langle\mathrm{Cov}(\lambda_i, \nu_i)_x\rangle_t$. Thus, the ESS dispersal condition reduces to

$$\left.\frac{\partial\langle\mathrm{Cov}(\lambda_i, \nu_i)_x\rangle_t(d_i, d_a, d_p)}{\partial d_i}\right|_{d_i=d_a=d_a^*} = 0. \quad (4)$$

We now need an approximate expression for $\langle\mathrm{Cov}(\lambda_i, \nu_i)_x\rangle_t$, valid when fluctuations in fecundity and population density are small. Let us write

$$F_j(x,t) = \langle F_j\rangle_x(t)(1 + \epsilon_j(x,t)), \quad (5)$$

where $\epsilon_j(x,t)$ is $O(\sigma)$ and has spatial mean zero. Furthermore, assume that there is no spatially synchronized component to the variation in fecundity: $\langle F_j\rangle_x$ does not vary with time and is equal to $\langle F_j\rangle_{x,t}$, the spatiotemporal average. Thus,

$$F_j(x,t) = \langle F_j\rangle_{x,t}(1 + \epsilon_j(x,t)). \quad (6)$$

By similar reasoning, let

$$n_j(x,t) = \langle n_j\rangle_x(t)(1 + u_j(x,t)) = \langle n_j\rangle_{x,t}(1 + u_j(x,t)), \quad (7)$$

where $u_j(x,t)$ is $O(\sigma)$ and has zero spatial and temporal mean. We want an $O(\sigma^2)$ expression for $\mathrm{Cov}(\lambda_i, \nu_i)$ (recall that our original expansion of $\overline{r}_i$ was $O(\sigma^2)$), which requires us to find $O(\sigma)$ expressions for $\nu_i(x,t)$ and $\lambda_i(x,t)$.

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*The technical definition of $O(\sigma^n)$ is that if $g(x)$ is $O(\sigma^n)$, then $g(x)$ decreases with σ and $\left|\frac{g(x)}{\sigma^n}\right|$ can be made less than or equal to some positive constant K for σ small enough. On a more practical note, σ is some measure of smallness that we use for bookkeeping purposes.

The relative population density $\nu_i(x,t)$ is simply $1+u_i(x,t)$, which is already $O(\sigma)$. What about $\lambda_i(x,t)$? Assuming an annual invader, the local invader growth rate is given by

$$\lambda_i(x,t) = \frac{g_i F_i(x,t)}{\gamma_{i1}(U_{i1} * g_1 n_1)(x,t) + \gamma_{i2}(U_{i2} * n_2)(x,t)} + s_i(1 - g_i), \tag{8}$$

where the notation $f * g$ denotes a convolution: $\int_{-\infty}^{\infty} f(x-y)g(y)\,dy$. Substituting our expressions for F_j and n_j into the expression for λ_i and Taylor expanding to $O(\sigma)$, we find that

$$\lambda_i(x,t) \approx \frac{g_i \langle F_i \rangle_{x,t}}{\gamma_{i1} g_1 \langle n_1 \rangle_{x,t} + \gamma_{i2} \langle n_2 \rangle_{x,t}} \left(1 + \epsilon_i(x,t) - D_{i1}(U_{i1} * u_1)(x,t) - D_{i2}(U_{i2} * u_2)(x,t)\right) \tag{9}$$

where

$$D_{i1} = \frac{\gamma_{i1} g_1 \langle n_1 \rangle_{x,t}}{\gamma_{i1} g_1 \langle n_1 \rangle_{x,t} + \gamma_{i2} \langle n_2 \rangle_{x,t}}, \qquad D_{i2} = \frac{\gamma_{i2} \langle n_2 \rangle_{x,t}}{\gamma_{i1} g_1 \langle n_1 \rangle_{x,t} + \gamma_{i2} \langle n_2 \rangle_{x,t}}. \tag{10}$$

Thus,

$$\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t = \frac{g_i \langle F_i \rangle_{x,t}}{\gamma_{i1} g_1 \langle n_1 \rangle_{x,t} + \gamma_{i2} \langle n_2 \rangle_{x,t}} \mathrm{Cov}\left(\epsilon_i(x,t) - D_{i1}(U_{i1} * u_1) - D_{i2}(U_{i2} * u_2), u_i\right)_{x,t}. \tag{11}$$

We can simplify both the covariance and the convolutions by taking the spatiotemporal Fourier transform of this expression. The Wiener-Khinchin theorem states that the Fourier transform of $\mathrm{Cov}(f,g)_{x,t}$ is given by

$$\mathscr{F}[\mathrm{Cov}(f,g)_{x,t}] = \lim_{N \to \infty} \frac{\widetilde{f}^{*(N)}(q,\omega) \widetilde{g}^{(N)}(q,\omega)}{N^2}, \tag{12}$$

where superscript * denotes the complex conjugate and $\widetilde{g}^{(N)}(q,\omega)$ equals the Fourier transform of $g(x,t)$ in the limit as N approaches infinity: $\widetilde{g}^{(N)}(q,\omega) = \sum_{x,t=-N/2}^{N/2} g(x,t) \exp(-i(qx + \omega t))$. Furthermore, the Fourier transform of a convolution is the product of the transforms of the factors: $\mathscr{F}[f * g] = \widetilde{f}\widetilde{g}$. Thus, the Fourier transform of eq. 11 is given by

$$\mathscr{F}\left[\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t\right] = \mathscr{F}\left[\mathrm{Cov}(\lambda_i, \nu_i)_{x,t}\right] = \lim_{N \to \infty} \frac{1}{N^2} \frac{g_i \langle F_i \rangle_{x,t}}{\gamma_{i1} g_1 \langle n_1 \rangle_{x,t} + \gamma_{i2} \langle n_2 \rangle_{x,t}}$$
$$\times \left[\widetilde{\epsilon}_i^{*(N)}(q,\omega) - D_{i1}\widetilde{U}_{i1}(q)\widetilde{u}_1^{*(N)}(q,\omega) - D_{i2}\widetilde{U}_{i2}(q)\widetilde{u}_2^{*(N)}(q,\omega)\right] \widetilde{u}_i^{(N)}(q,\omega). \tag{13}$$

(Honestly, this is an improvement.)

When we come to evaluate our ESS condition, eq. 4, we will find $\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t$ by taking the inverse Fourier transform of eq. 13, numerically integrating

$$\frac{1}{(2\pi)^2} \int_{-\infty}^{\infty} \mathscr{F}\left[\mathrm{Cov}(\lambda_i, \nu_i)_{x,t}\right] \, dq\, d\omega. \tag{14}$$

(There would normally be a factor of $\exp(i(qx + \omega t))$ in the integrand, where x and t are the spatial and temporal lags of the covariance, but we wish to find the covariance at zero lag, so the exponential equals 1.)

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We have now found an $O(\sigma^2)$ condition for the ESS (eq. 4), which depends on $\text{Cov}(\lambda_i, \nu_i)$, and we have found an $O(\sigma^2)$ expression for this covariance (eqs. 13 and 14). We aren't finished, because we ultimately need to express our ESS condition entirely in terms of environmental conditions, whereas $\text{Cov}(\lambda_i, \nu_i)$ depends on the Fourier transforms of the population densities: $\widetilde{u}_i(q, \omega)$, $\widetilde{u}_1(q, \omega)$, and $\widetilde{u}_2(q, \omega)$. Our next step is to express the population densities as functions of the environment.

We will begin with $\widetilde{u}_1(q, \omega)$. We can obtain an equation for the annual relative population density, $\nu_1(x, t)$, by dividing both sides of the dynamical equation for n_1 (eq. 3) by $\langle n_1 \rangle_x(t+1)$ and substituting $\widetilde{\lambda}_1(t)\langle n_1 \rangle_x(t)$ for $\langle n_1 \rangle_x(t+1)$ on the righthand side:

$$\nu_1(x, t+1) = \frac{1}{\widetilde{\lambda}_1(t)} \int_{-\infty}^{\infty} k_1(x - y) \frac{g_1 F_1(y, t)\nu_1(y, t)}{C_1(y, t)} \, dy + \frac{1}{\widetilde{\lambda}_1(t)} s_1(1 - g_1)\nu_1(x, t). \quad (15)$$

To $O(\sigma)$, however, $\widetilde{\lambda}_1(t)$ can be replaced by $\lambda_1^{(0)}$, which equals 1. (The annual resident is at equilibrium in the absence of environmental variation.) Substituting eqs. 6 and 7 for F and n, we Taylor expand to $O(\sigma)$ to find

$$u_1(x, t+1) = \frac{g_1 \langle F_1 \rangle_{x,t}}{\gamma_{11} g_1 \langle n_1 \rangle_{x,t} + \gamma_{12} \langle n_2 \rangle_{x,t}}$$
$$\times \left(k_1 * [\epsilon_1 + u_1 - D_{11} U_{11} * u_1 - D_{12} U_{12} * u_2]\right)(x, t) + s_1(1 - g_1)u_1(x, t), \quad (16)$$

where
$$D_{11} = \frac{\gamma_{11} g_1 \langle n_1 \rangle_{x,t}}{\gamma_{11} g_1 \langle n_1 \rangle_{x,t} + \gamma_{12} \langle n_2 \rangle_{x,t}}, \quad D_{12} = \frac{\gamma_{12} \langle n_2 \rangle_{x,t}}{\gamma_{11} g_1 \langle n_1 \rangle_{x,t} + \gamma_{12} \langle n_2 \rangle_{x,t}}. \quad (17)$$

Taking a spatial Fourier transform, we find

$$\widetilde{u}_1(q, t+1) = \frac{g_1 \langle F_1 \rangle_{x,t}}{\gamma_{11} g_1 \langle n_1 \rangle_{x,t} + \gamma_{12} \langle n_2 \rangle_{x,t}}$$
$$\times \widetilde{k}_1(q) \left[\widetilde{\epsilon}_1(q, t) + \widetilde{u}_1(q, t) - D_{11}\widetilde{U}_{11}(q)\widetilde{u}_1(q, t) - D_{12}\widetilde{U}_{12}(q)\widetilde{u}_2(q, t)\right] + s_1(1 - g_1)\widetilde{u}_1(q, t),$$
$$= A_{u_{11}}(q)\widetilde{u}_1(q, t) + A_{u_{12}}(q)\widetilde{u}_2(q, t) + A_{\epsilon_{11}}(q)\widetilde{\epsilon}_1(q, t) + A_{\epsilon_{12}}(q)\widetilde{\epsilon}_2(q, t), \quad (18)$$

where

$$A_{u_{11}}(q) = c_1 \widetilde{k}_1(q)\left(1 - D_{11}\widetilde{U}_{11}(q)\right) + s_1(1 - g_1) \qquad A_{u_{12}}(q) = -c_1 \widetilde{k}_1(q)D_{12}\widetilde{U}_{12}(q) \quad (19)$$

$$A_{\epsilon_{11}}(q) = c_1 \widetilde{k}_1(q) \qquad\qquad\qquad\qquad\qquad A_{\epsilon_{12}}(q) = 0 \quad (20)$$

and

$$c_1 = \frac{g_1 \langle F_1 \rangle_{x,t}}{\gamma_{11} g_1 \langle n_1 \rangle_{x,t} + \gamma_{12} \langle n_2 \rangle_{x,t}} = 1 - s_1(1 - g_1). \quad (21)$$

By the same process, we find

$$\widetilde{u}_2(q, t+1) = A_{u_{21}}(q)\widetilde{u}_1(q, t) + A_{u_{22}}(q)\widetilde{u}_2(q, t) + A_{\epsilon_{21}}(q)\widetilde{\epsilon}_1(q, t) + A_{\epsilon_{22}}(q)\widetilde{\epsilon}_2(q, t), \quad (22)$$

where

$$A_{u_{21}}(q) = -(1 - s_2)\widetilde{k}_2(q)D_{21}\widetilde{U}_{21}(q) \quad A_{u_{22}}(q) = (1 - s_2)\widetilde{k}_2(q)\left(1 - D_{22}\widetilde{U}_{22}(q)\right) + s_2 \quad (23)$$

$$A_{\epsilon_{21}}(q) = 0 \qquad\qquad\qquad A_{\epsilon_{22}}(q) = (1 - s_2)\widetilde{k}_2(q). \qquad (24)$$

Creating a vector of population fluctuations $\widetilde{\mathbf{u}}(q,t) = (\widetilde{u}_1, \widetilde{u}_2)^T(q,t)$ and a vector of environmental fluctuations $\widetilde{\boldsymbol{\epsilon}}(q,t) = (\widetilde{\epsilon}_1, \widetilde{\epsilon}_2)^T(q,t)$, we can express the dynamics in compact form:

$$\widetilde{\mathbf{u}}(q, t + 1) = \mathbf{A}_u(q)\widetilde{\mathbf{u}}(q,t) + \mathbf{A}_\epsilon(q)\widetilde{\boldsymbol{\epsilon}}(q,t). \qquad (25)$$

We can write $\widetilde{\mathbf{u}}(q,t)$ in terms of a series of past environmental conditions:

$$\widetilde{\mathbf{u}}(q,t) = \sum_{j=0}^{t-1} \mathbf{A}_u^{t-1-j}(q)\mathbf{A}_\epsilon(q)\widetilde{\boldsymbol{\epsilon}}(q,j) = \sum_{j=0}^{\infty} \mathbf{M}(q, t - j)\widetilde{\boldsymbol{\epsilon}}(q,j), \qquad (26)$$

where

$$\mathbf{M}(q, n) = \begin{cases} \mathbf{A}_u^{n-1}(q)\mathbf{A}_\epsilon(q) & n > 0 \\ 0 & n \leq 0 \end{cases}. \qquad (27)$$

The second expression for $\widetilde{\mathbf{u}}(q,t)$ is a time convolution of $\mathbf{M}(q, t - j)$ with $\widetilde{\boldsymbol{\epsilon}}(q,t)$. By taking the temporal Fourier transform, we can turn this convolution into a product: $\widetilde{\mathbf{u}}(q,\omega) = \widetilde{\mathbf{M}}(q,\omega)\widetilde{\boldsymbol{\epsilon}}(q,\omega)$, where $\widetilde{\mathbf{u}}(q,\omega)$ and $\widetilde{\boldsymbol{\epsilon}}(q,\omega)$ are the spatiotemporal Fourier transforms of $\mathbf{u}(x,t)$ and $\boldsymbol{\epsilon}(x,t)$ and $\widetilde{\mathbf{M}}$ is the temporal Fourier transform of $\mathbf{M}(q,t)$:

$$\widetilde{\mathbf{M}}(q,\omega) = \sum_{t=-\infty}^{\infty} \mathbf{M}(q,t)e^{-i\omega t} = \sum_{t=1}^{\infty} \mathbf{A}_u^{t-1}(q)\mathbf{A}_\epsilon(q)e^{-i\omega t}. \qquad (28)$$

For any matrix $\mathbf{A}$ whose eigenvalues have modulus less than 1, $\sum_{j=0}^{\infty} \mathbf{A}^j = (\mathbf{I} - \mathbf{A})^{-1}$, where $\mathbf{I}$ is the identity matrix. We only consider fluctuations about stable population equilibria, so the eigenvalues of $\mathbf{A}_u(q)$ all have moduli less than 1, and the series converges. Performing the sum and multiplying through by $\exp(i\omega)$, we get

$$\widetilde{\mathbf{u}}(q,\omega) = \left(e^{i\omega}\mathbf{I} - \mathbf{A}_u(q)\right)^{-1}\mathbf{A}_\epsilon(q)\widetilde{\boldsymbol{\epsilon}}(q,\omega). \qquad (29)$$

The transfer function $\left(e^{i\omega}\mathbf{I} - \mathbf{A}_u(q)\right)^{-1}\mathbf{A}_\epsilon(q)$ is a 2×2 matrix. We can write the ijth component in polar form as $R_{ij}(q,\omega)\exp(i\phi_{ij}(q,\omega))$, so that, for example,

$$\widetilde{u}_1(q,\omega) = R_{11}(q,\omega)e^{i\phi_{11}(q,\omega)}\widetilde{\epsilon}_1(q,\omega) + R_{12}(q,\omega)e^{i\phi_{12}(q,\omega)}\widetilde{\epsilon}_2(q,\omega), \qquad (30)$$

where $R_{ij}(q,\omega)$ equals the squareroot of the square of the real part of $\left[\left(e^{i\omega}\mathbf{I} - \mathbf{A}_u(q)\right)^{-1}\mathbf{A}_\epsilon(q)\right]_{ij}$ plus the square of the imaginary part, while $\phi_{ij}(q,\omega)$ equals the inverse tangent of the imaginary part divided by the real part.

We have our ESS condition (eq. 4). We have expressed the ESS condition in terms of the resident and invader population distributions (eq. 13, with eq. 14). We have expressions for the resident population distributions (eq. 29). All that remains is to find an expression

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for the invader population distribution. We follow the same procedure as for the residents, writing

$$\nu_i(x, t+1) = \frac{1}{\widetilde{\lambda}_i(t)} \int_{-\infty}^{\infty} k_i(x-y) \frac{g_i F_i(y,t)\nu_i(y,t)}{C_i(y,t)} \, dy + \frac{1}{\widetilde{\lambda}_i(t)} s_i(1-g_i)\nu_i(x,t). \tag{31}$$

We again substitute the growth rate in the absence of variation, $\lambda_i^{(0)}$, for $\widetilde{\lambda}_i$; however because the invader is not at equilibrium, $\lambda_i^{(0)}$ does not equal 1. Except for this change, the analysis remains the same. We substitute eqs. 6 and 7 for F and n, Taylor expand to $O(\sigma)$, and take the spatial Fourier transform to find

$$\widetilde{u}_i(q, t+1) = b_{u_i}(q)\widetilde{u}_i(q,t) + b_{u_1}(q)\widetilde{u}_1(q,t) + b_{u_2}(q)\widetilde{u}_2(q,t) + b_{\epsilon_i}\widetilde{\epsilon}_i(q,t), \tag{32}$$

where

$$b_{u_i}(q) = c_1\widetilde{k}_i(q) - c_2 \qquad\qquad b_{\epsilon_i}(q) = c_1\widetilde{k}_i(q) \tag{33}$$

$$b_{u_1}(q) = -D_{i1}\widetilde{U}_{i1}(q)b_{\epsilon_i}(q) \qquad\qquad b_{u_2}(q) = -D_{i2}\widetilde{U}_{i2}(q)b_{\epsilon_i}(q), \tag{34}$$

$$c_1 = \frac{1}{\lambda_i^{(0)}} \frac{g_i\langle F_i\rangle_{x,t}}{\gamma_{i1}g_1\langle n_1\rangle_{x,t} + \gamma_{i2}\langle n_2\rangle_{x,t}} \qquad\qquad c_2 = \frac{1}{\lambda_i^{(0)}} s_i(1-g_i) \tag{35}$$

$$\lambda_i^{(0)} = \frac{g_i\langle F_i\rangle_{x,t}}{\gamma_{i1}g_1\langle n_1\rangle_{x,t} + \gamma_{i2}\langle n_2\rangle_{x,t}} + s_i(1-g_i), \tag{36}$$

and

$$D_{i1} = \frac{\gamma_{i1}g_1\langle n_1\rangle_{x,t}}{\gamma_{i1}g_1\langle n_1\rangle_{x,t} + \gamma_{i2}\langle n_2\rangle_{x,t}} \qquad D_{i2} = \frac{\gamma_{i2}\langle n_2\rangle_{x,t}}{\gamma_{i1}g_1\langle n_1\rangle_{x,t} + \gamma_{i2}\langle n_2\rangle_{x,t}}. \tag{37}$$

In parallel with the development for the resident dynamics, we can now write

$$\widetilde{u}_i(q,t) = \sum_{j=0}^{t-1} b_{u_i}^{t-1-j}(q)b_{\epsilon_i}(q)\left[\widetilde{\epsilon}_i(q,t) - D_{i1}\widetilde{U}_{i1}(q)\widetilde{u}_1(q,t) - D_{i2}\widetilde{U}_{i2}(q)\widetilde{u}_2(q,t)\right]. \tag{38}$$

Again in parallel with the resident dynamics, we rewrite each term as a convolution, take the temporal Fourier transform, and find

$$\widetilde{u}_i(q,\omega) = G(q,\omega)e^{i\psi(q,\omega)}\left[\widetilde{\epsilon}_i(q,\omega) - D_{i1}\widetilde{U}_{i1}(q)\widetilde{u}_1(q,\omega) - D_{i2}\widetilde{U}_{i2}(q)\widetilde{u}_2(q,\omega)\right], \tag{39}$$

where

$$G(q,\omega) = \frac{b_{\epsilon_i}(q)}{1 + b_{u_i}^2(q) - 2b_{u_i}(q)\cos(\omega)} \tag{40}$$

$$\psi(q,\omega) = \tan^{-1}\left(\frac{-\sin(\omega)}{\cos(\omega) - b_{u_i}(q)}\right), \tag{41}$$

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and $\tan^{-1}$ has a range of $-\pi$ to π. Using eq. 30 and the equivalent for species 2 to substitute for $\widetilde{u}_1(q,\omega)$ and $\widetilde{u}_2(q,\omega)$, we can express the invader distribution solely in terms of the environments experienced by the two residents and the invader:

$$\widetilde{u}_i(q,\omega) = G(q,\omega)e^{i\psi(q,\omega)}\Big[\widetilde{\epsilon}_i(q,\omega) -$$
$$\Big(D_{i1}\widetilde{U}_{i1}(q)R_{11}(q,\omega)e^{i\phi_{11}(q,\omega)} + D_{i2}\widetilde{U}_{i2}(q)R_{21}(q,\omega)e^{i\phi_{21}(q,\omega)}\Big)\widetilde{\epsilon}_1(q,\omega)$$
$$-\Big(D_{i1}\widetilde{U}_{i1}(q)R_{12}(q,\omega)e^{i\phi_{12}(q,\omega)} + D_{i2}\widetilde{U}_{i2}(q)R_{22}(q,\omega)e^{i\phi_{22}(q,\omega)}\Big)\widetilde{\epsilon}_2(q,\omega)\Big]. \quad (42)$$

We now have $O(\sigma)$ expressions for the Fourier transforms of the resident and invader populations in terms of their environments. Substituting these into our expression for the Fourier transform of $\mathrm{Cov}(\lambda_i, \nu_i)$ (eq. 13), we can at last express $\mathrm{Cov}(\lambda_i, \nu_i)_{x,t}$ entirely in terms of the environments experienced by the residents and the invader:

$$\mathscr{F}\left[\mathrm{Cov}(\lambda_i,\nu_i)_{x,t}\right] = \lim_{N\to\infty} \frac{1}{N^2}\frac{g_i\langle F_i\rangle_{x,t}}{\gamma_{i1}g_1\langle n_1\rangle_{x,t} + \gamma_{i2}\langle n_2\rangle_{x,t}}\Big[\widetilde{\epsilon}_i^{*(N)}(q,\omega)$$
$$\Big(D_{i1}\widetilde{U}_{i1}(q)R_{11}(q,\omega)e^{i\phi_{11}(q,\omega)} + D_{i2}\widetilde{U}_{i2}(q)R_{21}(q,\omega)e^{i\phi_{21}(q,\omega)}\Big)\widetilde{\epsilon}_1^{*(N)}(q,\omega)$$
$$-\Big(D_{i1}\widetilde{U}_{i1}(q)R_{12}(q,\omega)e^{i\phi_{12}(q,\omega)} + D_{i2}\widetilde{U}_{i2}(q)R_{22}(q,\omega)e^{i\phi_{22}(q,\omega)}\Big)\widetilde{\epsilon}_2^{*(N)}(q,\omega)\Big]$$
$$\times G(q,\omega)e^{i\psi(q,\omega)}\Big[\widetilde{\epsilon}_i^{(N)}(q,\omega) -$$
$$\Big(D_{i1}\widetilde{U}_{i1}(q)R_{11}(q,\omega)e^{i\phi_{11}(q,\omega)} + D_{i2}\widetilde{U}_{i2}(q)R_{21}(q,\omega)e^{i\phi_{21}(q,\omega)}\Big)\widetilde{\epsilon}_1^{(N)}(q,\omega)$$
$$-\Big(D_{i1}\widetilde{U}_{i1}(q)R_{12}(q,\omega)e^{i\phi_{12}(q,\omega)} + D_{i2}\widetilde{U}_{i2}(q)R_{22}(q,\omega)e^{i\phi_{22}(q,\omega)}\Big)\widetilde{\epsilon}_2^{(N)}(q,\omega)\Big] \quad (43)$$

As it stands, we would need to know precisely how the environment varied in space and time in order to calculate the $\widetilde{\epsilon}^{*(N)}$s and evaluate this expression. With a bit of cleverness, however, we can write the above in terms of the autocovariance of the environment: we don't care precisely how the environment varies, just how it is correlated in space and time. Eq. 43 contains many terms of the form $[\text{stuff}] \times \lim_{N\to\infty}\widetilde{\epsilon}_j^{*(N)}\widetilde{\epsilon}_k^{(N)}/N^2$. We obtain $\lim_{N\to\infty}\widetilde{\epsilon}_j^{*(N)}\widetilde{\epsilon}_k^{(N)}/N^2$ from the Fourier transform of the covariance of ϵ_j and ϵ_k, which is proportional to the covariance of fecundities F_j and F_k: $\mathrm{Cov}(\epsilon_j, \epsilon_k)_{x,t}(x',t') = \mathrm{Cov}(F_j, F_k)_{x,t}(x',t')/(\langle F_j\rangle_{x,t}\langle F_k\rangle_{x,t}) = \cos(\theta)V\exp(-|x'|/\xi)\exp(-|t'|/\tau)$ (from eq. 1). Thus,

$$\lim_{N\to\infty}\widetilde{\epsilon}_j^{*(N)}\widetilde{\epsilon}_k^{(N)}/N^2 = \mathscr{F}[\mathrm{Cov}(\epsilon_j,\epsilon_k)_{x,t}] = \cos(\theta)V\sum_{x=-\infty}^{\infty}\sum_{t=-\infty}^{\infty}e^{-|x|/\xi}e^{-|t|/\tau}e^{i(qx+\omega t)}$$
$$= \cos(\theta)V\left(\frac{1 - e^{-2/\tau}}{1 - 2e^{-1/\tau}\cos(\omega) + e^{-2/\tau}}\right)\left(\frac{1 - e^{-2/\xi}}{1 - 2e^{-1/\xi}\cos(q) + e^{-2/\xi}}\right). \quad (44)$$

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