Appendix from O. Leimar, "The Evolution of Phenotypic Polymorphism: Randomized Strategies versus Evolutionary Branching"

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Convergence Stability and Phenotypic Polymorphism

This appendix contains derivations for several results and examples in the main text. Equations in the main text are referred to using their numbers.

Multidimensional Convergence Stability

Consider an equilibrium point $\hat{x}$, where the selection gradient (3) is 0 in an n-dimensional trait space. From equations (4) and (5), we can write the canonical equation linearized around $\hat{x}$ as

$$\frac{d}{dt}(x_i - \hat{x}_i) = \sum_{jk} \mathbf{K}_{ij}\mathbf{J}_{jk}(x_k - \hat{x}_k),$$

where $\mathbf{K}_{ij} = m(\hat{x})\mathbf{C}_{ij}(\hat{x})$. Since $m(\hat{x}) > 0$ and $\mathbf{C}(\hat{x})$ is a covariance matrix, the $n \times n$ matrix $\mathbf{K}$ is symmetric and positive definite (or, possibly, positive semidefinite). It is of interest to characterize the set of Jacobian matrices $\mathbf{J}$ having the property that the eigenvalues of the matrix product $\mathbf{KJ}$ have negative real parts for any symmetric, positive definite matrix $\mathbf{K}$.

We then have the following result: For $\mathbf{J}$ negative definite (i.e., the symmetric part of $\mathbf{J}$ negative definite) and $\mathbf{K}$ symmetric and positive definite, all eigenvalues of $\mathbf{KJ}$ have negative real parts, whereas if $\mathbf{J}$ is not negative semidefinite, there is some symmetric, positive definite $\mathbf{K}$ such that some eigenvalue of $\mathbf{KJ}$ has a positive real part.

This matrix algebra result was demonstrated by Hines (1980) and Cressman and Hines (1984), and it was used by them to study evolutionary stability for matrix games. For our purposes here, the result means that if the Jacobian matrix of the selection gradient is negative definite at an equilibrium point $\hat{x}$, then this point will be an asymptotically stable equilibrium of the canonical equation for any (smoothly varying) covariance matrix $\mathbf{C}(x)$. This is called strong convergence stability. The result also means that if the Jacobian is indefinite or positive definite, then we can find some covariance matrix making $\hat{x}$ an unstable equilibrium of the canonical equation. For a positive definite Jacobian matrix, a variant of the result would state that all eigenvalues of $\mathbf{KJ}$ have positive real parts, meaning that $\hat{x}$ is an unstable equilibrium for any positive definite covariance matrix, whereas for an indefinite Jacobian matrix, some covariance matrices may make $\hat{x}$ a stable equilibrium of the canonical equation, but others would make it an unstable equilibrium.

Criteria for the Evolution of Polymorphism

The aim is to derive expressions for the Jacobian and Hessian matrices for a point corresponding to a pure strategy equilibrium with primary trait $\hat{z}$ in an extended trait space of randomized strategies $x = (z_1, z_2; q_1, q_2)$. The matrices then yield criteria for branching and the evolution of a randomized strategy. The primary traits z are N-dimensional vectors with component traits z_m. The extended trait space has $2N + 1$ dimensions, corresponding to z_1, z_2, and q_1 (because $q_2 = 1 - q_1$). Notations like $z_{\mu m}$, where $\mu = 1, 2$ and $m = 1, \ldots, N$, will be used for the mth component of the primary trait z_μ of a mixture.

We are then faced with the problem of computing various first- and second-order partial derivatives of a general (smooth) invasion fitness $F(x', x)$, with respect to mutant and resident trait components. A possible form for invasion fitness would be

$$F(x', x) = G\left[\sum_\mu q'_\mu g(z'_\mu, x), x\right], \tag{A1}$$

where the G and g are smooth functions and each dependence on x is through some form of averaging using the distribution given by x. Many simple models lead to invasion fitness of this type, where the function G is increasing in its first argument, which can represent, for instance, expected reproductive success or survival of mutant individuals when interacting with residents. A more general form of invasion fitness would be

$$F(x', x) = H\left[\sum_\mu q'_\mu h_1(z'_\mu, x),\ \sum_{\mu\nu} q'_\mu q'_\nu h_2(z'_\mu, z'_\nu, x),\ \dots, x\right], \tag{A2}$$

where the ellipsis indicates any number of additional joint averages over functions of mutant trait combinations (singles, pairs, triplets, etc.) and where each dependence on x is of a similar averaging kind. Such an invasion fitness can, for instance, come about when relatives interact, implying that mutant individuals may interact with each other. The expressions below apply to any such invasion fitness (in fact, using functional analysis, one can show that they apply to any smooth real-valued function of mutant and resident extended traits, regarded as distributions, but I will refrain from going into the mathematical details). From the above kinds of expressions for invasion fitness, one readily verifies that we can write

$$\left.\frac{\partial F(x', x)}{\partial z'_{\mu m}}\right|_{z'_1 = z'_2 = z_1 = z_2 = z} = q'_\mu s_m(z), \tag{A3}$$

where $s_m(z)$ is a function of the primary trait z. At an equilibrium $\hat{x} = (\hat{z}, \hat{z}, \hat{q}_1, \hat{q}_2)$, all first-order mutant derivatives should be 0. Assuming $0 < \hat{q}_1 < 1$, we then have the condition for equilibrium

$$s_m(\hat{z}) = 0, \tag{A4}$$

because it is evident that the partial derivative of F with respect to q'_1 is 0 when $z'_1 = z'_2$. Going on to second-order derivatives, we get from equation (A2) that

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_{\mu m} \partial z'_{\nu n}}\right|_{z'_1 = z'_2 = z_1 = z_2 = z} = q'_\mu \delta_{\mu\nu} \mathbf{B}_{mn}(z) + q'_\mu q'_\nu \mathbf{C}_{mn}(z), \tag{A5}$$

where $\mathbf{B}_{mn}(z)$ and $\mathbf{C}_{mn}(z)$ are functions of z and $\delta_{\mu\nu}$ is the Kronecker delta ($\delta_{11} = \delta_{22} = 1$, $\delta_{12} = \delta_{21} = 0$). However, when invasion fitness has the simple form (A1), with G increasing in its first argument, the second term in equation (A5) will be 0, at least at an equilibrium $\hat{z}$, so that

$$\mathbf{C}_{mn}(\hat{z}) = 0 \tag{A6}$$

for such a special case. For equation (A1) to hold, there should be no interaction between relatives and the mutant trait should enter as a single average in invasion fitness. For the mutant-resident mixed second derivative of a general fitness function, we get

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_{\mu m} \partial z_{\nu n}}\right|_{z'_1 = z'_2 = z_1 = z_2 = z} = q'_\mu q_\nu \mathbf{D}_{mn}(z), \tag{A7}$$

where $\mathbf{D}_{mn}(z)$ is a function of z. There are also expressions for second-order derivatives involving q'_1 and q_1, but these will not be needed.

We can write an extended trait as $x = (\zeta, \eta, \rho)$, where ζ and η are given by equation (10), applied to vectorial primary traits, and ρ is also given by equation (10). The inverse transformation is

$$\begin{aligned} z_1 &= \zeta - (1+\rho)\eta, \\ z_2 &= \zeta + (1-\rho)\eta, \\ q_1 &= \frac{1}{2}(1-\rho). \end{aligned} \tag{A8}$$

To compute partial derivatives with respect to the components of ζ and η, we can introduce the differential operators

$$\begin{aligned} \frac{\partial}{\partial \zeta'_m} &= \frac{\partial}{\partial z'_{1m}} + \frac{\partial}{\partial z'_{2m}}, \\ \frac{\partial}{\partial \eta'_m} &= -2q'_2 \frac{\partial}{\partial z'_{1m}} + 2q'_1 \frac{\partial}{\partial z'_{2m}}. \end{aligned}$$

Using equation (A3), we then get

$$\left. \frac{\partial F(x', x)}{\partial \zeta'_m} \right|_{\eta'=\eta=0,\, \zeta'=\zeta=z} = s_m(z) \tag{A9}$$

and

$$\left. \frac{\partial F(x', x)}{\partial \eta'_m} \right|_{\eta'=\eta=0,\, \zeta'=\zeta=z} = 0. \tag{A10}$$

Since it is obvious that

$$\left. \frac{\partial F(x', x)}{\partial \rho'} \right|_{\eta'=\eta=0,\, \zeta'=\zeta=z} = 0, \tag{A11}$$

we thus have all first-order mutant derivatives, corresponding to the components S_{ζ_m}, S_{η_m}, and S_ρ of the selection gradient in the extended trait space. For the second-order mutant derivatives, we can use equation (A5) to get

$$\left. \frac{\partial^2 F(x', x)}{\partial \zeta'_m \partial \zeta'_n} \right|_{\eta'=\eta=0,\, \zeta'=\zeta=z} = \mathbf{B}_{mn}(z) + \mathbf{C}_{mn}(z) \tag{A12}$$

and

$$\left. \frac{\partial^2 F(x', x)}{\partial \eta'_m \partial \eta'_n} \right|_{\eta'=\eta=0,\, \zeta'=\zeta=z} = 4q'_1 q'_2 \mathbf{B}_{mn}(z), \tag{A13}$$

whereas the mixed second derivative with respect to ζ'_m and η'_n is 0. Because $F(x', x)$ does not depend on ρ' when $\eta' = 0$, it follows that the mutant second derivatives involving ρ' are all 0. For convenience, we can introduce the notation

$$\mathbf{A}_{mn}(z) = \mathbf{B}_{mn}(z) + \mathbf{C}_{mn}(z) \tag{A14}$$

for the right-hand side of equation (A12). Next, using equation (A7), we get the mutant-resident second derivative

$$\left.\frac{\partial^2 F(x',x)}{\partial \zeta'_m \partial \zeta_n}\right|_{\eta'=\eta=0,\,\zeta'=\zeta=z} = \mathbf{D}_{mn}(z), \tag{A15}$$

whereas all other mutant-resident second derivatives are readily found to be 0.

In order to connect to invasion fitness $f(z',z)$ in the primary trait space, we can use the identity

$$F(x',x)\Big|_{\eta'=\eta=0,\,\zeta'=z',\,\zeta=z} = f(z',z). \tag{A16}$$

From this we obtain

$$\left.\frac{\partial F(x',x)}{\partial \zeta'_m}\right|_{\eta'=\eta=0,\,\zeta'=\zeta=z} = \left.\frac{\partial f(z',z)}{\partial z'_m}\right|_{z'=z} = s_m(z), \tag{A17}$$

so that $s_m(z)$ is the selection gradient in the primary trait space, and

$$\left.\frac{\partial^2 F(x',x)}{\partial \zeta'_m \partial \zeta'_n}\right|_{\eta'=\eta=0,\,\zeta'=\zeta=z} = \left.\frac{\partial^2 f(z',z)}{\partial z'_m \partial z'_n}\right|_{z'=z} = \mathbf{A}_{mn}(z), \tag{A18}$$

$$\left.\frac{\partial^2 F(x',x)}{\partial \zeta'_m \partial \zeta_n}\right|_{\eta'=\eta=0,\,\zeta'=\zeta=z} = \left.\frac{\partial^2 f(z',z)}{\partial z'_m \partial z_n}\right|_{z'=z} = \mathbf{D}_{mn}(z), \tag{A19}$$

showing that $\mathbf{A}_{mn}(z)$ and $\mathbf{D}_{mn}(z)$ are second derivatives of invasion fitness in the primary trait space. Thus, out of the nonzero derivatives we computed, only the one in equation (A13) goes beyond the quantities we can compute from invasion fitness in the primary trait space. For a one-dimensional primary trait space, equations (A17), (A18), (A19), and (A13) correspond to equations (11), (12), (13), and (14) in the text.

We now have all the derivatives we need for the Jacobian and Hessian matrices at an equilibrium $\hat{x} = (\hat{z}, \hat{z};\ \hat{q}_1, \hat{q}_2) = (\hat{z}, 0, \hat{\rho})$ in the extended trait space. Since an extended trait $x = (\zeta, \eta, \rho)$ has $2N + 1$ components, namely $\zeta_1, \ldots, \zeta_N, \eta_1, \ldots, \eta_N$, and ρ, which correspond to the x_j in equations (5) and (6), the matrices can conveniently be partitioned into blocks. For the Jacobian matrix (5), only two of the blocks are nonzero:

$$(\mathbf{J}_{\zeta\zeta})_{mn} = \mathbf{A}_{mn}(\hat{z}) + \mathbf{D}_{mn}(\hat{z}), \tag{A20}$$

$$(\mathbf{J}_{\eta\eta})_{mn} = 4\hat{q}_1\hat{q}_2\mathbf{B}_{mn}(\hat{z}), \tag{A21}$$

where a notation like $(\mathbf{J}_{\zeta\zeta})$ was used for an $N \times N$ matrix block. Similarly, for the Hessian matrix (6), only two of the blocks are nonzero:

$$(\mathbf{H}_{\zeta\zeta})_{mn} = \mathbf{A}_{mn}(\hat{z}), \tag{A22}$$

$$(\mathbf{H}_{\eta\eta})_{mn} = 4\hat{q}_1\hat{q}_2\mathbf{B}_{mn}(\hat{z}). \tag{A23}$$

From equations (A18) and (A19) we can note that equation (A20) is in fact the Jacobian and equation (A22) the Hessian in the primary trait space.

Stability Criteria

We can conclude that the equilibrium $\hat{x}$ is strongly convergence stable in the extended trait space when the matrices $\mathbf{A}(\hat{z}) + \mathbf{D}(\hat{z})$ and $\mathbf{B}(\hat{z})$ are both negative definite and that $\hat{x}$ is uninvadable when the matrices $\mathbf{A}(\hat{z})$ and $\mathbf{B}(\hat{z})$ are both negative definite (note that there will only be neutral stability with respect to $\hat{\rho}$; we assume $-1 < \hat{\rho} < 1$). If we assume that $\mathbf{A}(\hat{z}) + \mathbf{D}(\hat{z})$ is negative definite, so that $\hat{z}$ is strongly convergence stable in the primary trait space, there may be branching in the primary trait space when $\mathbf{A}(\hat{z})$ is indefinite or positive definite, whereas

$\hat{x}$ lacks strong convergence stability when $\mathbf{B}(\hat{z})$ is indefinite or positive definite, in which case a randomized strategy may evolve from $\hat{x}$. In the simple situations where equation (A6) holds, branching and the evolution of a randomized strategy will be equally possible. However, if the matrix $\mathbf{C}(\hat{z})$ is positive definite, there is stronger selection for a genetic polymorphism than for the evolution of a randomized strategy, and the opposite holds when $\mathbf{C}(\hat{z})$ is negative definite. For an indefinite matrix $\mathbf{C}(\hat{z})$, the situation is more complicated, with branching being favored for certain primary trait combinations and randomization for other combinations.

This latter situation is not possible for the one-dimensional primary trait space dealt with in the text and in figure 1, where the matrices **A**, **B**, and **D** are just real numbers, referred to as A, B, and D. For both A and B negative, $\hat{x}$ is uninvadable and is a continuously stable strategy in the extended space, although there is only neutral stability along the ρ direction; the Jacobian and Hessian matrices are both negative semidefinite. For A positive, there is branching along the ζ direction ($\mathbf{J}_{\zeta\zeta}$ is negative and $\mathbf{H}_{\zeta\zeta}$ positive), and for B positive, there is no longer convergence stability of $\hat{x}$ but instead divergence along the η direction ($\mathbf{J}_{\eta\eta}$ is positive), corresponding to the evolution of a strategy with nonzero η that randomizes between two primary traits. In such a case, there is also disruptive selection on η because $\mathbf{H}_{\eta\eta}$ is positive, but one should expect η to move away from 0 rather than branching taking place along this direction. Thus, for A positive, there can be evolutionary branching and, for B positive, a nonzero η can evolve. If both A and B are positive, both outcomes are possible, with relative likelihoods that depend on the magnitudes of A and B and on details of genetic variation.

Example: Spatially Varying Environments

For a rare mutant with trait x' in a resident population with x, the population projection matrix for mutant population densities in the two patches can be written

$$\mathbf{M}(x', x) = \begin{pmatrix} (1-m)\dfrac{\beta_1(x')}{\beta_1(x)} & m\dfrac{\beta_2(x')}{\beta_2(x)} \\ m\dfrac{\beta_1(x')}{\beta_1(x)} & (1-m)\dfrac{\beta_2(x')}{\beta_2(x)} \end{pmatrix},$$

where m is the probability of migration and β is from equation (2). The leading eigenvalue of this matrix is

$$\lambda(u_1, u_2) = (1-m)\frac{u_1+u_2}{2} + \sqrt{\frac{1}{4}(1-m)^2(u_1-u_2)^2 + m^2u_1u_2},$$

with $u_i = \beta_i(x')/\beta_i(x)$. Note that for random dispersal ($m = 0.5$), the leading eigenvalue is a linear function of u_1 and u_2, in that $\lambda = (u_1 + u_2)/2$. Invasion fitness is given by

$$F(x', x) = \log\lambda\left[\frac{\beta_1(x')}{\beta_1(x)}, \frac{\beta_2(x')}{\beta_2(x)}\right].$$

It is now straightforward but somewhat tedious to compute derivatives of invasion fitness. Using equations (1) and (2), we get

$$\left.\frac{\partial F(x', x)}{\partial z'_\mu}\right|_{z'_1=z'_2=z_1=z_2=z} = q'_\mu \frac{1}{2}\left[\frac{\alpha'_1(z)}{\alpha_1(z)} + \frac{\alpha'_2(z)}{\alpha_2(z)}\right] = q'_\mu \frac{z_0 - z}{\sigma^2}$$

for the first-order mutant derivative at a pure strategy point in the extended trait space. Comparing with equation (A3), we see that the selection gradient is given by $s(z) = (z_0 - z)/\sigma^2$, implying that $\hat{z} = z_0$ is the only pure strategy equilibrium. For the second-order derivatives at this equilibrium, we get

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_\mu \partial z'_\nu}\right|_{z'_1=z'_2=z_1=z_2=z_0} = q'_\mu \delta_{\mu\nu}\left(\frac{\delta^2}{\sigma^4} - \frac{1}{\sigma^2}\right) + q'_\mu q'_\nu \frac{1-2m}{m}\frac{\delta^2}{\sigma^4}$$

for the mutant-mutant derivatives and

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_\mu \partial z_\nu}\right|_{z'_1=z'_2=z_1=z_2=z_0} = q'_\mu q_\nu \frac{m-1}{m}\frac{\delta^2}{\sigma^4}$$

for the mutant-resident derivatives. Comparing with equations (A5), (A7), and (A14), we thus obtain equation (17) in the text.

Example: Temporally Varying Environments

For the simple lottery model described in the text, the stochastic dynamics of a rare mutant population, having size N'_t in season t, that uses strategy x' in a resident population using strategy x is

$$N'_{t+1} = N'_t\left[1 - b + b\frac{\beta_i(x')}{\beta_i(x)}\right].$$

In this equation, the environmental condition i is 1 or 2 with equal probability, b is the proportion recruited each season, and β_i is from equation (2). Invasion fitness is given by the logarithm of the geometric mean mutant success, so that

$$F(x', x) = \frac{1}{2}\log\left[1 - b + b\frac{\beta_1(x')}{\beta_1(x)}\right] + \frac{1}{2}\log\left[1 - b + b\frac{\beta_2(x')}{\beta_2(x)}\right].$$

Computing the first-order mutant derivative at a pure strategy, we get

$$\left.\frac{\partial F(x', x)}{\partial z'_\mu}\right|_{z'_1=z'_2=z_1=z_2=z} = q'_\mu \frac{1}{2} b\left[\frac{\alpha'_1(z)}{\alpha_1(z)} + \frac{\alpha'_2(z)}{\alpha_2(z)}\right] = q'_\mu b\frac{z_0 - z}{\sigma^2},$$

so that $\hat{z} = z_0$ is the only equilibrium. For the second-order derivatives at this equilibrium, we get

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_\mu \partial z'_\nu}\right|_{z'_1=z'_2=z_1=z_2=z_0} = q'_\mu \delta_{\mu\nu} b\left(\frac{\delta^2}{\sigma^4} - \frac{1}{\sigma^2}\right) - q'_\mu q'_\nu b^2\frac{\delta^2}{\sigma^4}$$

for the mutant-mutant derivatives and

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_\mu \partial z_\nu}\right|_{z'_1=z'_2=z_1=z_2=z_0} = -q'_\mu q_\nu b(1-b)\frac{\delta^2}{\sigma^4}$$

for the mutant-resident derivatives. Comparing with equations (A5), (A7), and (A14), we thus obtain equation (18) in the text.

Example: Competition between Relatives

For the model described in the text, let p be the probability that a deme persists for another nondispersing generation and $1 - p$ the probability that it is in its final generation, with its two inhabitants producing dispersing offspring. The total duration of a deme is then geometrically distributed, so that the probability that the deme ends and produces dispersing offspring in generation t of its existence (with $t = 0$ indicating production of dispersing offspring of the founding individuals) is

$$u_t = (1-p)p^t.$$

We now focus on the situation where one founder has a mutant genotype and the other founder a resident genotype. Let P_{nt} be the probability that the deme has n mutant individuals (where n is 0, 1, or 2) in generation t. It is easy to see that

$$P_{1t} = \frac{1}{2^t},$$

$$P_{2t} = P_{0t} = \frac{1}{2} - \frac{1}{2^{t+1}}.$$

Letting P_n denote the expectation of P_{nt}, we have

$$P_1 = \sum_{t=0}^{\infty} P_{1t} u_t = 2\frac{1-p}{2-p},$$

$$P_2 = P_0 = \frac{1}{2} - \frac{1}{2}P_1 = \frac{1}{2}\frac{p}{2-p}.$$

When we introduce $r = p/(2-p)$, it is easy to see that, for small mutant frequency in the pool of dispersers, we can interpret r as the probability that a randomly selected mutant individual at the time of production of dispersing offspring has a mutant deme partner. Thus, r can be viewed as a coefficient of relatedness.

For an individual with randomized trait x' sharing the patch with an individual with trait x, the expected fecundity is

$$\beta(x', x) = q_1' q_1 \alpha(z_1', z_1) + q_1' q_2 \alpha(z_1', z_2) + q_2' q_1 \alpha(z_2', z_1) + q_2' q_2 \alpha(z_2', z_2),$$

where $\alpha(z', z)$ is defined in equation (19). Consider a situation with resident trait x and a small proportion of individuals using a mutant strategy x'. Because a new deme is founded by a random pair of dispersers, those demes containing mutant strategies will predominantly be founded by one mutant and one resident type. It is now straightforward to see that, at the time when dispersing offspring are produced, a proportion $1 - r$ of the mutant individuals will share the patch with a resident individual and a proportion r will share it with a mutant individual (this follows because $r = 2P_2$).

We only consider primary traits satisfying $|z - z_0| < \sqrt{2/\gamma}$ because traits outside this range are not viable according to equations (19) and (20). If we then introduce the ratio of the expected reproductive successes of a random mutant and a random resident individual as

$$w(x', x) = \frac{(1-r)\beta(x', x) + r\beta(x', x')}{\beta(x, x)},$$

invasion fitness is given by

$$F(x', x) = \log w(x', x) = \log[(1-r)\beta(x', x) + r\beta(x', x')] - \log\beta(x, x).$$

Computing the first-order mutant derivative at a pure strategy, we get

$$\left.\frac{\partial F(x', x)}{\partial z'_\mu}\right|_{z_1'=z_2'=z_1=z_2=z} = q_\mu' \frac{\gamma(z_0 - z)}{g(z)},$$

so that $\hat{z} = z_0$ is the only equilibrium. For the second-order derivatives at this equilibrium, we get

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_\mu \partial z'_\nu}\right|_{z_1'=z_2'=z_1=z_2=z_0} = q_\mu' \delta_{\mu\nu}\left[-\gamma + (1+r)\frac{1}{2\sigma^2}\right] - q_\mu' q_\nu' r \frac{1}{\sigma^2}$$

for the mutant-mutant derivatives and

$$\left.\frac{\partial^2 F(x', x)}{\partial z'_\mu \partial z_\nu}\right|_{z'_1 = z'_2 = z_1 = z_2 = z_0} = -q'_\mu q_\nu (1 - r) \frac{1}{2\sigma^2}$$

for the mutant-resident derivatives. Comparing with equations (A5), (A7), and (A14), we thus obtain equation (22) in the text.