Next-Generation Tools for Evolutionary Invasion Analyses

Amy Hurford       Daniel Cownden       Troy Day

In this electronic supplementary material we provide proofs of two results from the main article. In our discussion of the next-generation theorem (Section 2) we use the fact that \( \vec{I}_k(t) \to 0 \) in the limit \( t \to \infty \) to relate next-generation tools to the traditional approach. This is proved in Appendix A. In Section 3.3 we mention that for evolutionary invasion analysis we are often interested in mutant and resident traits that are similar. This leads to the useful approximation (3.24). The derivation of this formula is provided in Appendix B.

Appendix A

Proof. We wish to show that \( \lim_{t \to \infty} \vec{I}_k(t) = 0 \). It suffices to prove that,

\[
|\vec{I}_k(t)| \leq e^{-|V|t} |F|^k |\vec{x}_0| \frac{t^k}{k!},
\]

(A.1)

since the righthand side of expression (A.1) goes to 0 in the limit \( t \to \infty \) because the \( e^{-|V|t} \) factor decays exponentially whereas the \( t^k \) factor of the expression only grows polynomially. If the norm of the vector \( \vec{I}_k(t) \) goes to zero, then we know that the vector itself must go to zero also. The norms in (A.1) are vector norms (\( |\vec{I}_k(t)| \) and \( |\vec{x}_0| \)) and norms for bounded linear operators (\( |F| \) and \( |V| \)). Here bold face \( e^{-Vt} \) denotes the matrix exponential and \( e^{-|V|t} \) is the usual exponential function with scalar argument.
We use induction. As a base case consider \( \vec{I}_0(t) \). From equation (2.4) we have
\[
\dot{\vec{I}}_0(t) = -\mathbf{V}\vec{I}_0(t),
\]
solving this differential equation, with initial condition \( \vec{I}_0(0) = \vec{x}_0 \), we have that
\[
\vec{I}_0(t) = e^{-\mathbf{V}t}\vec{x}_0.
\]
Then,
\[
|\vec{I}_0| = |e^{-\mathbf{V}t}\vec{x}_0| \leq |e^{-\mathbf{V}t}||\vec{x}_0|.
\] (A.2)

Here, \( e^{-\mathbf{V}t} \) is a bounded linear operator that maps vectors to vectors. Since \( \mathbf{V} \) is a finite dimensional matrix, we know that \( |\mathbf{V}| \) is bounded. The above inequality is a property of a norm acting on the space of bounded linear operators (Rudin 1966, Definition 5.3). Next,
\[
|e^{-\mathbf{V}t}||\vec{x}_0| \leq |e^{|\mathbf{V}|t}||\vec{x}_0| \\
\leq e^{-|\mathbf{V}|t}||\vec{x}_0| \\
= e^{-|\mathbf{V}|t}\left|0 \rightarrow 0\right| \left|\vec{x}_0\right|.
\] (A.3)

where the inequalities are due to the properties of the norms and the triangle inequality. This completes the proof of the base case.

Now consider \( |\vec{I}_k(t)| \) and assume \( |\vec{I}_{k-1}(t)| \leq e^{-t|\mathbf{V}|}|\mathbf{F}|^{k-1}|\vec{x}_0| \frac{k-1}{(k-1)!} \). From equation (2.4) we have the differential equation
\[
\dot{\vec{I}}_k(t) = \mathbf{F}\vec{I}_{k-1}(t) - \mathbf{V}\vec{I}_k(t)
\]
with initial condition \( \vec{I}_k(0) = 0 \) for all \( k \neq 0 \). Using an integrating factor and separation of variables we can solve this equation as follows,
\[ \begin{align*}
\dot{I}_k(t) &= F\tilde{I}_{k-1}(t) - V I_k(t) \\
e^{Vt}\dot{I}_k(t) + e^{Vt}VI_k(t) &= e^{Vt}F\tilde{I}_{k-1}(t) \\
\frac{d}{dt}\left(e^{Vt}\dot{I}_k(t)\right) &= e^{Vt}F\tilde{I}_{k-1}(t) \\
\frac{d}{dt}\int_0^t e^{V\tau}I_k(\tau)d\tau &= \int_0^t e^{V\tau}F\tilde{I}_{k-1}(\tau)d\tau \\
\tilde{I}_k(t) &= e^{-Vt}\int_0^t e^{V\tau}F\tilde{I}_{k-1}(\tau)d\tau, 
\end{align*} \]

for \( k > 0 \). Note that the order of integration and differentiation and switched due to the continuity of \( \tilde{I}_k(t) \) and \( \dot{I}_k(t) \). Then since our induction hypothesis is about the norm of \( \tilde{I}_k(t) \),

\[ |\tilde{I}_k(t)| = \left| e^{-Vt}\int_0^t e^{V\tau}F\tilde{I}_{k-1}(\tau)d\tau \right| \]

\[ \leq |e^{-Vt}| \left| \int_0^t e^{V\tau}F\tilde{I}_{k-1}(\tau)d\tau \right| \]

\[ \leq e^{-|V|t} \left| \int_0^t |e^{V\tau}F\tilde{I}_{k-1}(\tau)|d\tau \right| \]

\[ \leq e^{-|V|t} \int_0^t |e^{V\tau}||F||\tilde{I}_{k-1}(\tau)|d\tau. \]

Here the norm is moved inside the integral due to the triangle inequality for integration. This is justified provided \( \int_0^t e^{V\tau} F\tilde{I}_{k-1}(\tau) \, d\tau \) is Riemann integrable and this is certainly the case since \( \tilde{I}_{k-1}(\tau) \) is the solution to a differential equation and is therefore continuous. The justification for the other inequalities is the same as for the base case. Using our assumption on \( |\tilde{I}_{k-1}(t)| \),
\[
e^{-|V| t} \int_0^t |e^{V \tau}||F||\tilde{r}_{k-1}(\tau)| d\tau \leq e^{-|V| t} \int_0^t e^{V \tau}|F|e^{-V \tau}|F|^{k-1} |x_0| \frac{\tau^{k-1}}{(k-1)!} d\tau \\
\leq e^{-|V| t} \int_0^t |F|^k \frac{\tau^{k-1}}{(k-1)!} |x_0| d\tau \\
= e^{-|V| t} |F|^k |x_0| \frac{t^k}{k!}.
\]

(A.6)

\[
\square
\]

Appendix B

For evolutionary models we are interested in calculating invasion fitness where \( y_m \approx y \).
Performing a first-order Taylor series approximation of equation (3.22) around the
point \( y_m = y \) simplifies equation (3.22) to equation (3.24). From equation (3.22),

\[
\rho(FV^{-1}) = \tilde{v}^T F V^{-1} \tilde{u},
\]

where \( \tilde{v}^T \) and \( \tilde{u} \) are left and right eigenvectors of \( FV^{-1} \). The first-order Taylor series
approximation is,

\[
\rho(FV^{-1}) \approx \rho(FV^{-1})\big|_{y_m=y} + \frac{\partial(\rho(FV^{-1}))}{\partial y_m}\big|_{y_m=y} \\
\approx 1 + \frac{\partial(\rho(FV^{-1}))}{\partial y_m}\big|_{y_m=y},
\]

(B.2)

where as noted in Section 3.1, \( \rho(FV^{-1}) = 1 \) when the mutant and resident population
have the same trait value. In this approximation, \( \tilde{u} \) and \( \tilde{v}^T \) are the eigenvectors
associated with the eigenvalue 1. Differentiating \( \rho(FV^{-1}) \) with respect to \( y_m \) we have,
\[ \rho(FV^{-1}) \approx 1 + \left. \frac{\partial(v^T)}{\partial y_m} \right|_{y_m = y} FV^{-1} \bar{u} + \left. v^T \frac{\partial(FV^{-1})}{\partial y_m} \right|_{y_m = y} \bar{u} + v^T FV^{-1} \left. \frac{\partial \bar{u}}{\partial y_m} \right|_{y_m = y}, \quad (B.3) \]

noting that \( v^T FV^{-1} = \bar{v}^T \) and \( FV^{-1} \bar{u} = \bar{u} \), since these are eigenvectors for the matrix \( FV^{-1} \) for the eigenvalue 1. Finally,

\[ \rho(FV^{-1}) \approx 1 + v^T \frac{\partial FV^{-1}}{\partial y_m} \bar{u}, \quad (B.4) \]

since the eigenvectors do not depend on the mutant trait. This is equation (3.24) in the main text.