

## Appendix from A. Best et al., “The Evolution of Host-Parasite Range” (Am. Nat., vol. 176, no. 1, p. 000)

### Methods

#### Derivation of Invasion Fitnesses

We assume an evolutionary trade-off between  $a$  and  $u$  in the host and one between  $\beta_0$  and  $v$  in the parasite. Given these trade-offs and the transmission rate of equation (2), we can rewrite the dynamics of equation (1) as

$$\frac{dX}{dt} = a(u)X - qX(X + Y) - bX - \beta_0(v)\left[1 - \left(1 + e^{-2(u-v)}\right)^{-1}\right]XY, \quad (\text{A1})$$

$$\frac{dY}{dt} = \beta_0(v)\left[1 - \left(1 + e^{-2(u-v)}\right)^{-1}\right]XY - (\alpha + b)Y, \quad (\text{A2})$$

where

$$a(u) = a_{\max} - (a_{\max} - a_{\min})\frac{1 - [(u - u_{\max})/(u_{\min} - u_{\max})]}{1 + p_a[(u - u_{\max})/(u_{\min} - u_{\max})]}, \quad (\text{A3})$$

and similarly for  $\beta_0(v)$ . Note that we have not included the recovery term here. Including recovery from infection in our model complicates our analysis considerably because it leads to a structured host population. For tractability, we therefore do not include recovery in our analysis here. However, the results from our numerical simulations indicate that our analytic predictions are qualitatively robust to the inclusion of recovery.

To calculate the invasion fitness, we must consider the dynamics of rare mutant types,  $\bar{X}$  and  $\bar{Y}$ , arising in a resident population that is at an equilibrium ( $X^*$ ,  $Y^*$ ). In the parasite, we can simply express the dynamics of the rare mutant as  $d\bar{Y}/dt = r(\bar{v}, u, v)\bar{Y}$ , where

$$r(\bar{v}, u, v) = \beta_0(\bar{v})\left[1 - \left(1 + e^{-2(u-\bar{v})}\right)^{-1}\right]X^* - (\alpha + b) \quad (\text{A4})$$

is by definition the invasion fitness of the mutant parasite. Similarly, so long as we do not include the recovery term, we can obtain the mutant host fitness by considering  $d\bar{X}/dt = s(\bar{u}, u, v)\bar{X}$ , where

$$s(\bar{u}, u, v) = a(\bar{u}) - q(X^* + Y^*) - b - \beta_0(v)\left[1 - \left(1 + e^{-2(\bar{u}-v)}\right)^{-1}\right]Y^*. \quad (\text{A5})$$

#### Details of the Analysis

We use the methods of adaptive dynamics to analyze the evolutionary behavior of the host-parasite interaction (Dieckmann and Law 1996; Marrow et al. 1996; Geritz et al. 1998). The host, with resistance range  $u$ , and the parasite, with infection range  $v$ , will coevolve in the direction of their respective local fitness gradients until a singular point is reached:

$$\begin{aligned}\frac{\partial s}{\partial \bar{u}} \Big|_{\bar{u}=u} &= 0, \\ \frac{\partial r}{\partial \bar{v}} \Big|_{\bar{v}=v} &= 0,\end{aligned}\tag{A6}$$

where  $s$  and  $r$  are the invasion fitnesses of equations (A3) and (A5), respectively. The behavior at the singularity depends on the second-order terms, evolutionary stability and convergence stability. Each species is evolutionarily stable, provided that

$$\begin{aligned}E_H &= \frac{\partial^2 s}{\partial \bar{u}^2} \Big|_{\bar{u}=u} < 0, \\ E_P &= \frac{\partial^2 r}{\partial \bar{v}^2} \Big|_{\bar{v}=v} < 0.\end{aligned}\tag{A7}$$

Assuming equal mutation speeds, the convergence stability is governed by the  $2 \times 2$  Jacobian,

$$\begin{bmatrix} X^*(E_H + M_H) & X^*A_H \\ Y^*A_P & Y^*(E_P + M_P) \end{bmatrix} = \begin{bmatrix} X^* \left( \frac{\partial^2 s}{\partial \bar{u}^2} + \frac{\partial^2 s}{\partial \bar{u} \partial u} \right) & X^* \frac{\partial^2 s}{\partial \bar{u} \partial v} \\ Y^* \frac{\partial^2 r}{\partial \bar{v} \partial u} & Y^* \left( \frac{\partial^2 r}{\partial \bar{v}^2} + \frac{\partial^2 r}{\partial \bar{v} \partial v} \right) \end{bmatrix}.\tag{A8}$$

Again, note that for the analytic results we must assume that there is no recovery from infection. However, numerical analysis (e.g., the simulations of fig. 2) suggests that the general results will hold when  $\gamma > 0$ .

Using the parameters and trade-offs given in figure 2 (except  $\gamma = 0$ ), we find a singular point at ( $u^* = 8$ ,  $v^* = 8.5$ ). We can evaluate the evolutionary stability conditions at this point as  $E_H = 0.42$ ,  $E_P = -2.05$ . Therefore, the singularity is evolutionarily unstable in the host but evolutionarily stable in the parasite. The eigenvalues of the Jacobian are  $\lambda = -0.76 \pm 0.91i$ , and so the singular point is convergence stable. To ensure branching, we must also insist that  $\partial^2 s / \partial \bar{u} \partial u = M_H < 0$  for two host strains to be able to coexist around the singular point (Geritz et al. 1998). We find that  $M_H = -0.15$ , and so the host will indeed branch, while the parasite will (temporarily) remain at the singular point.

## Proof That a Fast-Evolving Parasite Can Always Branch with Two Hosts

Let us assume that the host population has branched, giving two susceptible classes,  $X_1$  and  $X_2$ , with strategies  $u_1$  and  $u_2$ , and one infected class,  $Y$ , with strategy  $v$ . We choose some strategy set  $(\hat{u}_1, \hat{u}_2, \hat{v})$  and positive population densities  $(X_1^*, X_2^*, Y^*)$ . From the population dynamics equation (1), we can then derive  $a(\hat{u}_1)$ ,  $a(\hat{u}_2)$ , and  $\beta_0(\hat{v})$ .

We now assume that the parasite mutates rapidly relative to the host, such that for any  $(u_1, u_2)$  pair the parasite will be at a singular point  $v^*(u_1, u_2)$ . Using critical-function analysis (e.g., Kisdi 2006) for the evolving parasite, we can then find  $\beta'_0(\hat{v})$ , such that  $\hat{v} = v^*(\hat{u}_1, \hat{u}_2)$  is singular. Furthermore, we can calculate  $M_P$  when  $\beta'_0(\hat{v})$  is known: we find that  $M_P < 0$  and that therefore evolutionary branching is possible for the parasite.

However, for evolutionary branching to occur, we must insist that the two host populations will converge to  $(\hat{u}_1, \hat{u}_2)$ . We therefore calculate their fitness gradients, given that the parasite is at  $v^*(u_1, u_2)$ . Assuming that the strategy pair is singular, we can again use critical-function analysis to find  $a'(\hat{u}_1)$  and  $a'(\hat{u}_2)$ . The coevolutionary convergence of the two-host system depends on the two-dimensional Jacobian with  $a''(\hat{u}_1)$  and  $a''(\hat{u}_2)$  appearing in the respective diagonal entries. By diagonal dominance, we can insist that, provided that  $a''(\hat{u}_1)$  and  $a''(\hat{u}_2) \ll 0$ , the two-host system will converge to  $(\hat{u}_1, \hat{u}_2)$ .

Our final task, then, is to choose a trade-off curvature in the parasite,  $\beta''_0(\hat{v})$ , such that it lacks evolutionary stability ( $E_P > 0$ ) but is convergent ( $E_P + M_P < 0$ ); given  $M_P < 0$ , we can always find one. Therefore, one can choose the local properties of the trade-off functions such that the chosen strategy set  $(\hat{u}_1, \hat{u}_2, \hat{v})$  is singular and

locally convergence stable and that the parasite will branch at this singularity. Note also that the host strategies cannot branch at  $(\hat{u}_1, \hat{u}_2, \hat{v})$  because there cannot be more host residents than the number of parasite residents plus 1.

## Construction of Classification Diagrams

We now keep the general trade-off forms  $a(u)$  and  $\beta_0(v)$  in the host and parasite, respectively, and do not specify them explicitly. We use an analysis similar to critical-function analysis (Kisdi 2006; Best et al. 2009; Svennungsen and Kisdi 2009) by assuming equal mutation rates, which allows us to fully predict all possible coevolutionary outcomes for any pair of trade-off shapes  $a''(u)$  and  $\beta''(v)$ .

Choosing values of some singular point  $(u^*, v^*)$ , we derive conditions on the first derivatives of the trade-offs:  $a'(u)$ ,  $\beta'_0(v)$ . The curvatures of the trade-offs affect the evolutionary stability terms  $E_H = E_H(a''(u))$  and  $E_P = E_P(\beta''_0(v))$  (Kisdi 2006). As shown in figure 3, these produce the (left-hand) vertical lines for the host and the horizontal lines for the parasite that partition the trade-off shapes into evolutionarily stable and unstable regions in a simple linear manner. We also consider the single-species evolution convergence stability terms  $E_H + M_H$  and  $E_P + M_P$ . We find that  $M_P = 0$  (hence there is one horizontal line in fig. 3, marking both evolutionary stability and single-species convergence stability in the parasite) and  $M_H < 0$  (giving the right-hand vertical line in fig. 3, which bounds the dark, single-species branching region in the host).

For coevolutionary convergence stability, we consider the Jacobian of equation (A8). This produces two conditions for convergence stability: the trace and the determinant of that Jacobian. The trace condition produces the diagonal line in figure 3, whereas the determinant condition produces the hyperbolae. We can therefore construct the plots of figure 3 with  $a''(u)$  on the  $X$ -axis and  $\beta''_0(v)$  on the  $Y$ -axis. By plotting the boundaries for evolutionary stability and convergence stability as functions of the trade-off curvatures, we can ascertain the coevolutionary behavior at the singular point for any pair of trade-off shapes.

## Numerical Simulations

We carried out simulations of the mutation-selection process to confirm our analytic results. An array of host and parasite strains are established, subject to their trade-offs. Initially, the density of all but one each of these strains (one host, one parasite) is set to 0. We then numerically solve the ordinary differential equations (ODEs) of equation (1) for enough time that they will approach equilibrium. We then introduce a host/parasite strain (which neighbors a current resident type and is chosen on the basis of the relative population density of each type) at a low density, and the ODEs are solved again with these updated conditions. At the end of each run of the ODEs, any types below a (low) threshold density are assumed to be extinct. Note that this means that our simulations are not strictly mutation limited, because mutants enter the population before the dynamics have reached equilibrium, and therefore more than one strain can exist at any one time (the shorter the time between mutations, the wider each branch in fig. 2 becomes, consisting of several coexisting neighboring strains). This does not affect our results, which are robust, provided that there is sufficient time between mutation events and that mutations are sufficiently small (see Meszena et al. 2005). We control  $\phi$  by controlling the respective mutation rates of the host and the parasite.

## Literature Cited Only in the Appendix

Meszena, G., M. Gyllenberg, F. J. Jacobs, and J. A. J. Metz. 2005. Link between population dynamics and dynamics of Darwinian evolution. *Physical Review Letters* 95:078105.