

ONLINE APPENDIX A: Stability of the consumer-resource interaction

The consumer-resource model (Equation (1) in the main text) yields three equilibria: the trivial equilibrium ($R^* = 0, C^* = 0$), a boundary equilibrium ($R^* = 1/q, C^* = 0$), and an interior equilibrium:

$$\begin{aligned} R^* &= \frac{d}{a(f - dh)} \\ C^* &= \frac{rf(a(f - dh) - qd)}{a^2(f - dh)^2} \end{aligned} \quad (\text{A.1})$$

The Jacobian matrix of Equation (1) is given by:

$$J = \begin{bmatrix} -rqR^* + \frac{a^2hR^*C^*}{(1+ahR^*)^2} & -\frac{aR^*}{1+ahR^*} \\ \frac{faC^*}{(1+ahR^*)^2} & 0 \end{bmatrix}.$$

The interior (coexistence) equilibrium is stable if $Tr(J) < 0$ and $\det(J) > 0$. Note that $Tr(J) = J_{11}$ and $\det(J) = J_{12}J_{21}$ (because $J_{22} = 0$). Since $J_{12} < 0$, $\det(J) > 0$ always. Hence, stability of the coexistence equilibrium is determined by whether $J_{11} < 0$. The stability boundary at which the consumer-resource system undergoes a bifurcation from a stable focus to limit cycle oscillations is given by $J_{11} = 0$ (Murdoch et al., 2003):

$$\frac{rd(ah(-f + dh) + (f + dh)q)}{fa(f - dh)} = 0 \quad (\text{A.2})$$

Solving $J_{11} = 0$ for a and rearranging terms yields the stability boundary:

$$\frac{ah}{q} = \frac{f + dh}{f - dh}. \quad (\text{A.3})$$

From Equation (A.1) we see that positivity of the resource equilibrium requires that $e > dh$, i.e., the consumer's conversion efficiency should exceed the fraction of its lifetime spent handling resources. This means that the right hand side of Equation (A.3) is positive, and unlikely to exceed unity by a large amount unless the consumer spends a large fraction ($> 25\%$) of its lifetime handling prey. The important consequence is that the stability of the coexistence equilibrium is driven mainly by the

ratio $\frac{ah}{q}$ ($q > 0$) which scales the negative and positive feedback effects on species' per capita growth rates).

The consumer-resource model (Equation (1) in the main text) yields a resource isocline that is a quadratic (Fig. 1a), the maximum of which is the critical resource abundance (R_c) at which the interaction moves from a stable point equilibrium (focus) to limit cycle oscillations (Rosenzweig, 1971). This is derived using the following steps.

Note that the resource isocline depicts the resource species' per capita growth rate:

$$\frac{1}{R} \frac{dR}{dt} = r(1 - qR) - \frac{aC}{1 + ahR}. \quad (\text{A.4})$$

At equilibrium, the resource species' per capita growth is zero. We solve $\frac{1}{R} \frac{dR}{dt} = 0$ for consumer abundance C , which yields:

$$C = \frac{r(1 - qR)(1 + ahR)}{a}. \quad (\text{A.5})$$

Now we take the derivative of C with respect to R , which gives us the rate at which consumer abundance changes relative to resource abundance:

$$\frac{\partial C}{\partial R} = r\left(h - \frac{q}{a} - 2hqR\right). \quad (\text{A.6})$$

The last step is to set the derivative to zero and solve for R , which gives us the critical resource density at which the consumer-resource interaction undergoes a transition from a stable equilibrium to limit cycle oscillations:

$$R_c = \frac{\frac{ah}{q} - 1}{2ah}. \quad (\text{A.7})$$

As can be seen, the critical resource density is determined entirely by the relative magnitudes of ah and q , which scale the positive and negative feedback effects on the resource per capita growth rate. Of note, although it is the product ah that determines strength of positive feedback, it is the handling time that generates such feedback. The attack rate only serves to mediate the strength of positive feedback.

ONLINE APPENDIX B: Taylor series approximation of mean fitness

When the attack rate is evolving with the handling time as a constraint, the fitness of an individual consumer is given by its per capita growth rate $W_C(x, R)$:

$$W_C(x, R) = f \frac{a(x)R}{1 + a(x)hR} - d. \quad (\text{B.1})$$

The mean fitness is obtained by integrating the fitnesses of all consumer individuals over all values of x :

$$\bar{W}_C(\bar{x}, R) = \int_{-\infty}^{+\infty} W_C(x, R) p(x, \bar{x}) dx. \quad (\text{B.2})$$

This integral cannot be solved analytically. However, as it involves the expectation of a ratio, i.e.,

$$E[W_C(\bar{x}, R)] = E \left[\frac{a(x)R}{1 + a(x)hR} \right], \quad (\text{B.3})$$

we can use the Taylor series expansion of this ratio to approximate the integral (Heijmans, 1999). For notational simplicity, let $f = \frac{A}{B}$ where $A = a(x)R$ and $B = 1 + a(x)hR$ with means μ_A and μ_B . Then a Taylor series expansion about the point (μ_A, μ_B) to the first order is given by:

$$f(A, B) = f(\mu_A, \mu_B) + f'_A(\mu_A, \mu_B)(A - \mu_A) + f'_B(\mu_A, \mu_B)(B - \mu_B). \quad (\text{B.4})$$

Taking expectations of both sides, we get:

$$\begin{aligned} E[f(A, B)] &= E \left[f(\mu_A, \mu_B) + f'_A(\mu_A, \mu_B)(A - \mu_A) + f'_B(\mu_A, \mu_B)(B - \mu_B) \right] \\ &\approx E \left[f(\mu_A, \mu_B) \right] + E \left[f'_A(\mu_A, \mu_B)(A - \mu_A) \right] + E \left[f'_B(\mu_A, \mu_B)(B - \mu_B) \right] \\ &= E \left[f(\mu_A, \mu_B) \right] + f'_A(\mu_A, \mu_B) E \left[(A - \mu_A) \right] + f'_B(\mu_A, \mu_B) E \left[(B - \mu_B) \right]. \end{aligned} \quad (\text{B.5})$$

Given that $E[(A - \mu_A)] = 0$ and $E[(B - \mu_B)] = 0$, and that $\mu_A = E[A]$ and $\mu_B = E[B]$, we have:

$$E[f(A, B)] \approx E[f(\mu_A, \mu_B)] = \frac{E[A]}{E[B]}. \quad (\text{B.6})$$

Applying this to the expression for mean fitness (Equation (B.3)), we get:

$$\begin{aligned} E[W_C(\bar{x}, R)] &= \frac{E[a(x)R]}{E[1 + a(x)hR]} \\ &= \frac{E[a(x)]R}{1 + E[a(x)]hR} \end{aligned} \quad (\text{B.7})$$

where

$$E[a(x)] = \int_{-\infty}^{+\infty} a(x)p(x, \bar{x})dx = \bar{a}(\bar{x}) \quad (\text{B.8})$$

is given by:

$$\bar{a}(\bar{x}) = \frac{\alpha\tau_a}{\sqrt{\sigma_a^2 + \tau_a^2}} e^{-\frac{(x-\theta_a)^2}{2(\sigma_a^2 + \tau_a^2)}}. \quad (\text{B.9})$$

Numerical analyses show that the approximation of mean fitness (Equation (B.2) using Equation (B.7) is valid in the limit of weak phenotypic variance and low to moderate stabilizing selection (Fig. B1). The approximation works well over the relevant ecological parameter space as well (Fig. B2). The consumer's death rate is the most sensitive parameter, with higher mortality rates causing greater deviation at higher values of the phenotypic variance (Fig. B2(c)).

ONLINE APPENDIX C: Sensitivity analysis

Ecological dynamics: propensity for extinction as a function of oscillatory tendency

High attack rates and long handling times increase the strength of positive feedback relative to negative feedback, and lead to large-amplitude oscillations that predispose consumer-resource interactions to deterministic collapse or stochastic extinction at low abundances. As can be seen from the stability boundary that delineates a stable point equilibrium from oscillatory dynamics Equation (A.3), higher values of the consumer's conversion efficiency (f) and death rate (d) can increase the oscillatory ten-

dency, while higher values of resource self-limitation (q) decrease it. Because the critical resource density at which the system undergoes a bifurcation from a stable equilibrium to limit cycle is determined by the quantity $\frac{ah}{q}$ (Equation (A.7)), resource self-limitation has the strongest effect on the oscillatory tendency of consumer-resource interactions (Fig. C1).

Eco-evolutionary dynamics: roles of heritability, phenotypic variation, and self-limitation strength on attack rate and handling time evolution

Higher heritabilities lead to faster evolutionary dynamics, a finding reported in previous studies of eco-evolutionary dynamics of species interactions (Schreiber et al., 2011; Vasseur et al., 2011), but do not alter the qualitative nature of the long-term evolutionary outcomes (Fig. C2). When the attack rate and handling time evolve jointly, with each trait under direct stabilizing selection, lower levels of phenotypic variation lead to the evolution of higher attack rates or longer handling times, but oscillation-induced extinction restricts attack rate - handling time combinations such that high attack rates are associated with short handling times and *vice versa* (Fig. C3). As with ecological dynamics resource self-limitation has a strong effect on the combination of attack rates and handling times that evolve, with stronger self-limitation allowing the evolution of higher attack rates and longer handling times (Figs. C2-C3).

Literature Cited

- Heijmans, R. 1999. When does the expectation of a ratio equal the ratio of expectations? Statistical Papers 40.
- Murdoch, W., C. J. Briggs, and N. R. M. 2003. Consumer resource dynamics. Princeton University Press, Princeton New Jersey.
- Rosenzweig, M. L. 1971. Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. Science 171:385–387.

Schreiber, S., D. Bolnick, and R. Burger. 2011. The community effects of phenotypic and genetic variation within a predator population. *Ecology* 93:1582–1593.

Vasseur, D. A., P. Amarasekare, V. Rudolf, and J. Levine. 2011. Eco-evolutionary dynamics of coexistence via neighbor dependent selection. *American Naturalist* 178:96–109.

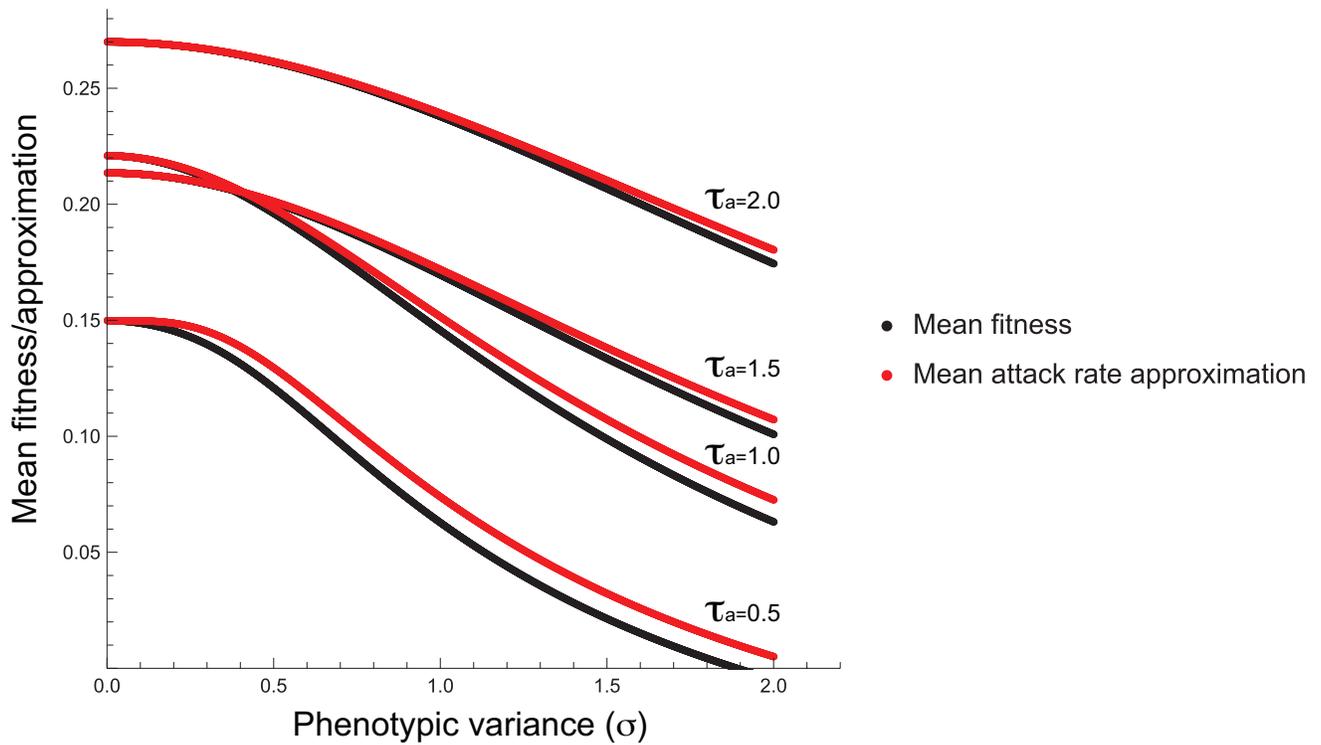


Figure B1. Numerical evaluations of mean fitness (Appendix B, Equation (B.2)) and its Taylor series approximation to the first order (Appendix B, Equation (B.7)) when the consumer's attack rate evolves with the handling time as a constraint. The black and red circles depict, respectively, the mean fitness and its Taylor approximation as a function of phenotypic variance (σ_a) for varying levels of stabilizing selection strength (τ_a). Parameter values are: $r = 5.0, q = 0.04, \theta_a = 1.0, \alpha = 2.0, h = 0.1, f = 0.2, d = 0.1$.

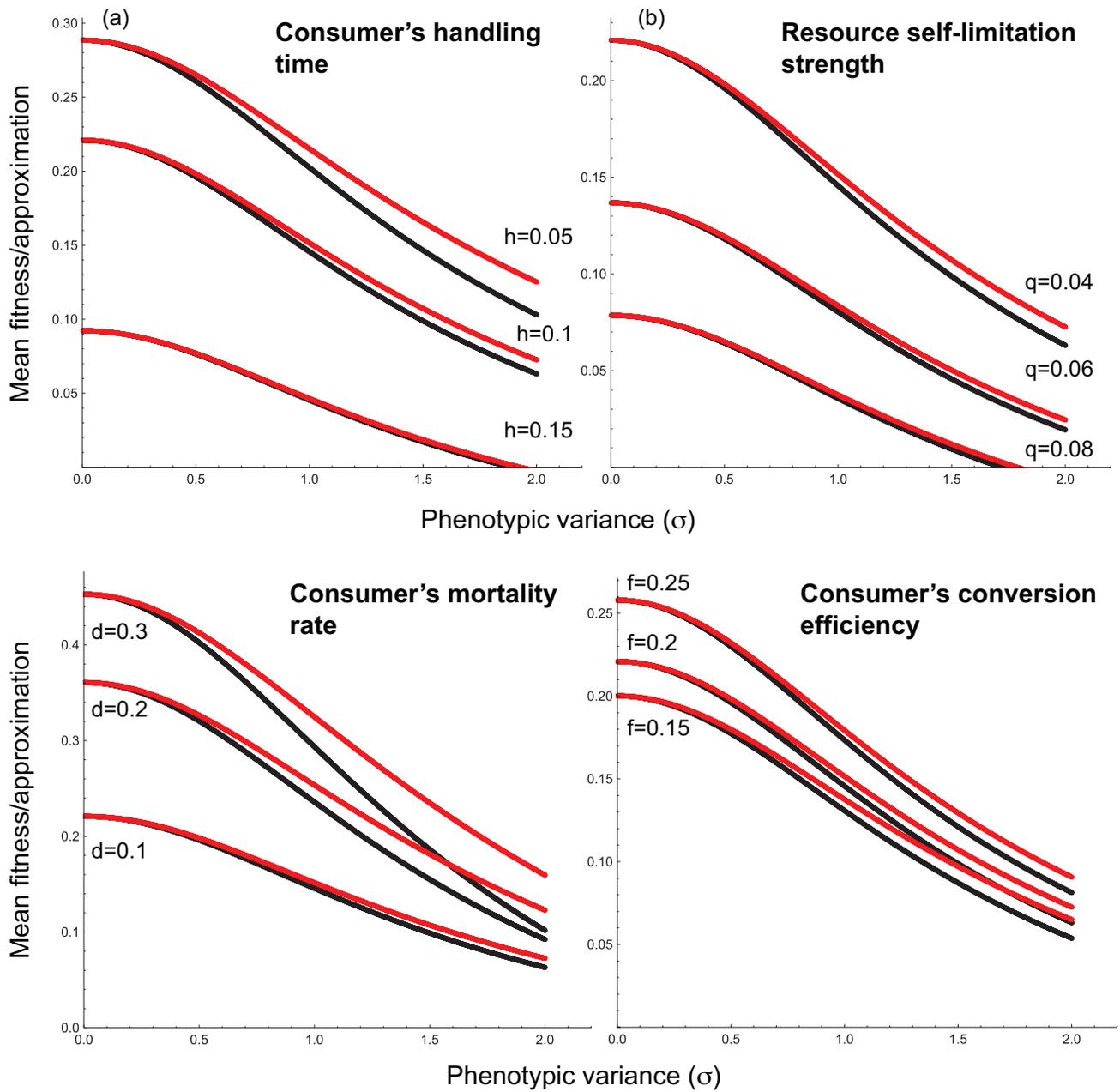


Figure B2. Numerical evaluations of mean fitness (Appendix B, Equation (B.2)) and its Taylor series approximation to the first order (Appendix B, Equation (B.7)) when the consumer's attack rate evolves with the handling time as a constraint. The black and red circles depict, respectively, the mean fitness and its Taylor approximation as a function of phenotypic variance (σ_n) for varying levels of the handling time (panel (a)), resource self-limitation (panel (b)), consumer's mortality rate (panel (c)) and conversion efficiency (panel (d)). Other parameter values are: $r = 5.0$, $\theta_n = 1.0$, $\alpha = 2.0$, $f = 0.2$.

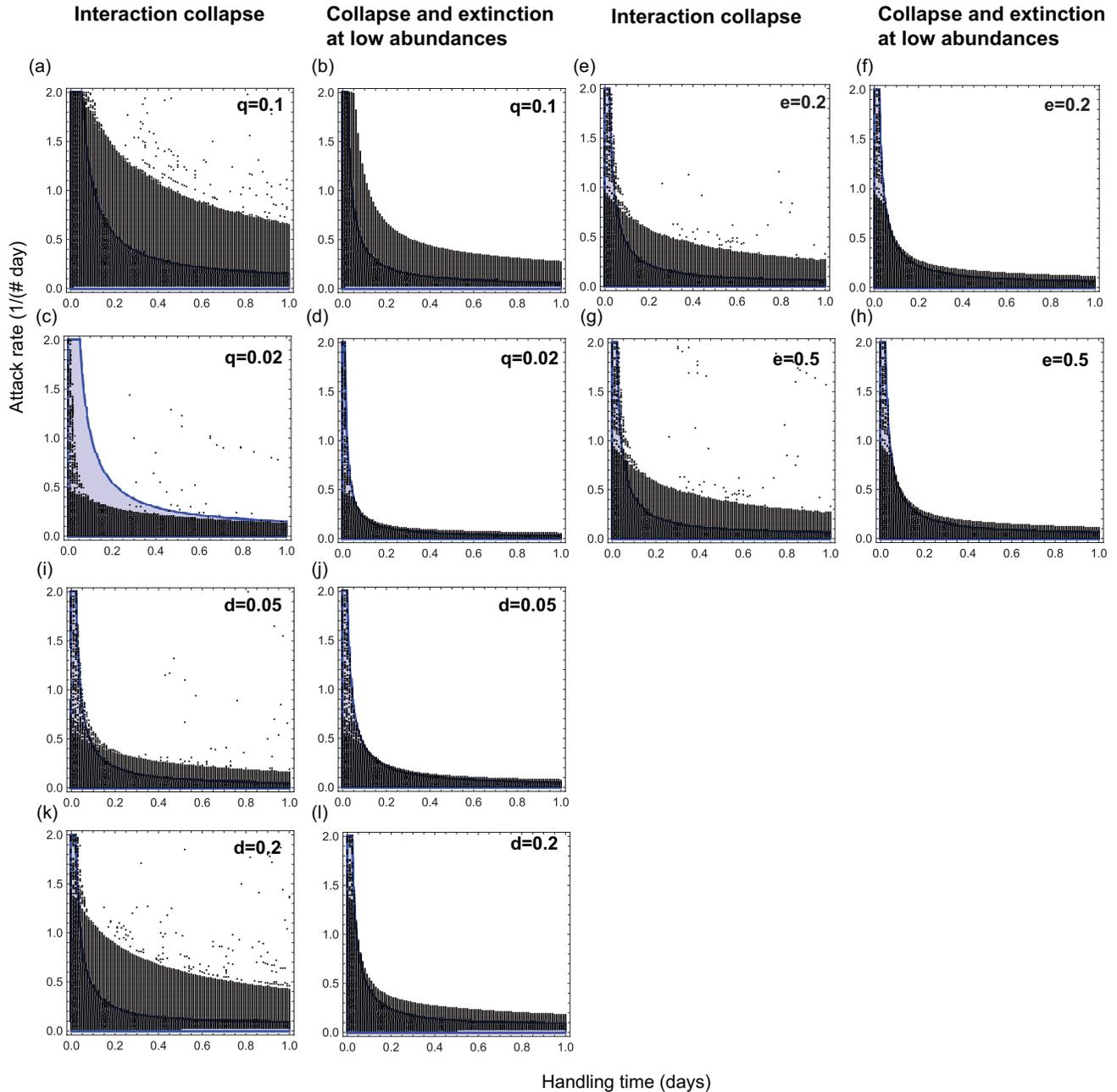


Figure C1. Attack rate - handling time combinations for persistent consumer-resource interactions superimposed on the stability region for the consumer-resource equilibrium. Panels on the left column depict the combinations that remain after deterministic collapse of interactions with high attack rates and long handling times, and panels on the right column, those that remain after deterministic collapse and stochastic extinction at low abundances. In all panels, the blue shaded region depicts the attack rate - handling time combinations that yield a stable equilibrium. Panels (a)-(d) depict the effects of strong ($q = 0.1$; panels (a) and (b)) and weak resource self-limitation ($q = 0.02$, panels (c) and (d)) with $r = 5, e = 0.5, d = 0.1$. Panels (e)-(h) depict the effects of lower ($e = 0.2$; panels (e) and (f)) and higher ($e = 0.5$; panels (g) and (h)) conversion efficiency with $r = 5, d = 0.1, q = 0.04$. Panels (i)-(l) depict the effects of lower ($d = 0.05$; panels (i) and (j)) and higher ($d = 0.2$; panels (k) and (l)) consumer mortality with $r = 5, e = 0.5, q = 0.04$.

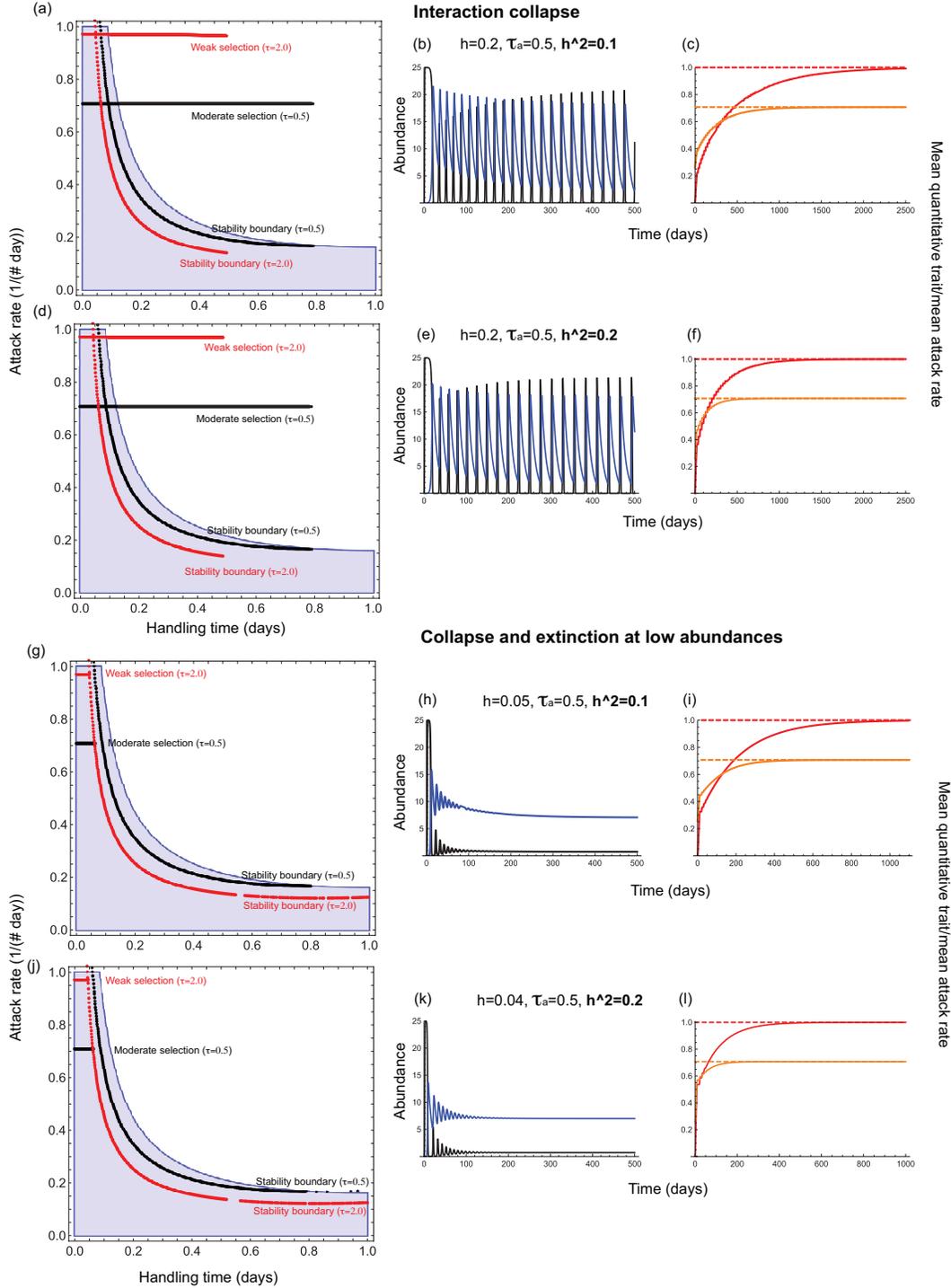


Figure C2. Effects of heritability on attack rate evolution under deterministic collapse of unstable interactions (panels (a)-(f)) and deterministic collapse combined with extinction at low abundances (panels (g)-(l)). Panels (a)-(c) and (g)-(i) depict evolutionary outcomes when heritability (h_a^2) is 0.1; panels (d)-(f) and (j)-(l) depict the outcomes when $h_a^2 = 0.2$. Increase in heritability has no qualitative effect on evolutionary outcomes (compare panel (a) with (d), and (g) with (j)). It does however lead to faster evolutionary rates (compare panel (c) with (f), and (i) with (l)). Parameter values are: $\theta_a = 1.0, \alpha = 1.0, \sigma_a^2 = 0.5, r = 5.0, d = 0.1, e = 0.2, q = 0.04$.

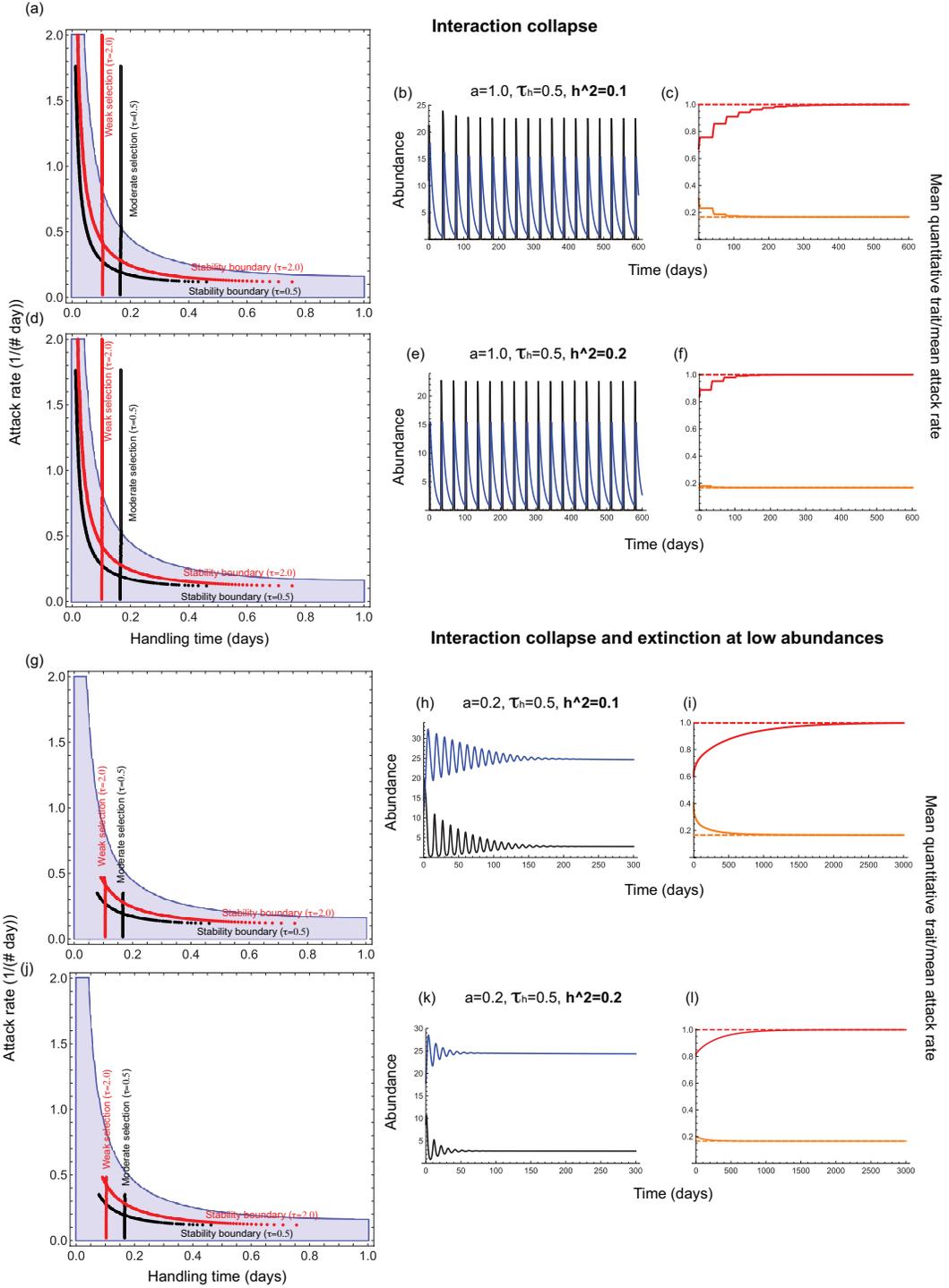


Figure C3. Effects of heritability on handling time evolution when the handling time is a consumer trait. Panels (a)-(f) depict evolutionary outcomes under deterministic collapse, and panels (g)-(l), deterministic collapse combined with extinction at low abundances. Panels (a)-(c) and (g)-(i) depict evolutionary outcomes when heritability (h_a^2) is 0.1; panels (d)-(f) and (j)-(l) depict the outcome when $h_a^2 = 0.2$. Increase in heritability has no qualitative effect on evolutionary outcomes (compare panel (a) with (d), and (g) with (k)). It does however lead to faster evolutionary rates (compare panel (c) with (f), and (i) with (l)). Parameter values are: $\theta_h = 1.0, \eta = 0.1, \sigma_h^2 = 0.5, r = 5.0, d = 0.1, e = 0.2, q = 0.04$.