Ecological Archives **E090-115-A2**

Abhyudai Singh, William W. Murdoch, and Roger M. Nisbet. 2009. Skewed attacks, stability, and host suppression. *Ecology* 90:1679–1686.

Appendix B: Stability analysis for host-parasitoid models

Consider the general class of discrete-time models

$$H_{t+1} = RH_t f(r(H_t)P_t) \tag{B.1}$$

$$P_{t+1} = k(RH_t - H_{t+1}) \tag{B.2}$$

where the monotonically decreasing function $f(r(H_t)P_t)$ represents the fraction of host that escape parasitism and $f(0) = 1$. The function $r(H_t)$ takes non-negative values for $H_t \geq 0$ and is assumed to be such such that $r(H_t)H_t$ is an increasing function of H_t while $r(H_t)/H_t$ is a decreasing function of H_t, i.e.,

$$\frac{d(H_t r(H_t))}{dH_t} > 0, \quad \frac{d(r(H_t)/H_t)}{dH_t} < 0, \text{ for all } H_t > 0. \tag{B.3}$$

Discrete-time model

$$H_{t+1} = RH_t \int_{x=0}^{\infty} p(x) \exp(-xP_t) dx \tag{B.4}$$

$$P_{t+1} = k(RH_t - H_{t+1}) \tag{B.5}$$

is a special case of (B.1)-(B.2) with $r(H_t) = 1$ and

$$f(P_t) = \int_{x=0}^{\infty} p(x) \exp(-xP_t) dx. \tag{B.6}$$

Phenomenological models that incorporate both variability in risk and a parasitoid Type II or Type III functional responses are given by

$$H_{t+1} = RH_t \int_{x=0}^{\infty} p(x) \exp\left(-\frac{xH_t^{n-1}P_t}{\bar{H}^n + H_t^n}\right) dx \tag{B.7}$$

$$P_{t+1} = k(RH_t - H_{t+1}) \tag{B.8}$$

where $\bar{H}$ is a positive constant and n can take values one (corresponds to a Type II functional response) and two (corresponds to a Type III functional response). The model (B.7)-(B.8) also corresponds to the general class of discrete-time models (B.1)-(B.2) with

$$r(H_t) = \frac{H_t^{n-1}}{\bar{H}^n + H_t^n}, \;\; n = 1,2 \tag{B.9}$$

$$f(r(H_t)P_t) = \int_{x=0}^{\infty} p(x) \exp\left(-\frac{xH_t^{n-1}P_t}{\bar{H}^n + H_t^n}\right) dx. \tag{B.10}$$

We now perform a stability analysis of the general class of discrete-time models (B.1)-(B.2).

We assume there exists a non-trivial equilibrium for the discrete-time model (B.1)-(B.2) which is given as the solution of

$$\frac{1}{R} \;=\; f(r(H^*)P^*), \;\; P^* = k(R-1)H^*, \tag{B.11}$$

where H^* and P^* denote the adult host and parasitoid equilibrium, respectively. Denoting small fluctuation around the equilibrium H^* and P^* by $h_t := H_t - H^*$ and $p_t := P_t - P^*$, respectively, one obtains using linearization the following linear discrete system

$$\begin{bmatrix} h_{t+1} \\ p_{t+1} \end{bmatrix} = A \begin{bmatrix} h_t \\ p_t \end{bmatrix}, \tag{B.12}$$

with

$$A = \begin{bmatrix} 1 + RH^* f'(r(H^*)P^*) r'(H^*)P^* & RH^* f'(r(H^*)P^*) r(H^*) \\ k(R - 1 - RH^* f'(r(H^*)P^*) r'(H^*)P^*) & -kRH^* f'(r(H^*)P^*) r(H^*) \end{bmatrix} \tag{B.13}$$

where

$$f'(r(H^*)P^*) = \frac{df(x)}{dx}\Big|_{x=r(H^*)P^*}, \;\; r'(H^*) = \frac{dr(H_t)}{dH_t}\Big|_{H_t=H^*}. \tag{B.14}$$

The above equilibrium is stable, if and only if, the following three Jury conditions (Elaydi 1996) hold

$$1 - tr(A) + det(A) \;>\; 0 \tag{B.15}$$

$$1 + tr(A) + det(A) \;>\; 0 \tag{B.16}$$

$$1 - det(A) \;>\; 0, \tag{B.17}$$

which implies

$$-kR(R-1)H^* f'(r(H^*)P^*)\tfrac{d(H_t r(H_t))}{dH_t}|_{H_t=H^*} > 0 \tag{B.18}$$

$$2 - kRH^* f'(r(H^*)P^*)\left(\tfrac{d(H_t r(H_t))}{dH_t}|_{H_t=H^*} - RH^{*2}\tfrac{d(r(H_t)/H_t)}{dH_t}|_{H_t=H^*}\right) > 0 \tag{B.19}$$

$$1 + kR^2 H^* r(H^*) f'(r(H^*)P^*) > 0. \tag{B.20}$$

Using (B.3), $R > 1$ and the fact that $f'(r(H^*)P^*) < 0$ (f is a monotonically decreasing function), inequalities (B.18)-(B.19) always hold and the stability condition is given by inequality (B.20), which using $P^* = k(R-1)H^*$ becomes

$$-P^* r(H^*) f'(r(H^*)P^*) < \tfrac{1}{R} - \tfrac{1}{R^2}. \tag{B.21}$$

For the discrete-time model (B.4)-(B.5) we have $r(H_t) = 1$, and hence from the above equation, the host-parasitoid equilibrium of (B.4)-(B.5) is stable, if and only if,

$$-P^* f'(P^*) < \tfrac{1}{R} - \tfrac{1}{R^2}. \tag{B.22}$$

Differentiating the first equation in (B.11) with respect to R we have

$$\frac{1}{R^2} = -f'(r(H^*)P^*)\left(r'(H^*)P^*\frac{dH^*}{dR} + r(H^*)\frac{dP^*}{dR}\right). \tag{B.23}$$

From $P^* = k(R-1)H^*$ we have

$$\frac{1}{P^*}\frac{dP^*}{dR} = \left(\frac{1}{R-1} + \frac{1}{H^*}\frac{dH^*}{dR}\right). \tag{B.24}$$

Substituting (B.24) in (B.23) and using $P^* = k(R-1)H^*$ gives us

$$\frac{1}{R} - \frac{1}{R^2} = -P^* r(H^*) f'(r(H^*)P^*)\left(1 + (R-1)\frac{1}{r(H^*)H^*}\frac{dH^*}{dR}\frac{d(H_t r(H_t))}{dH_t}|_{H_t=H^*}\right). \tag{B.25}$$

Substituting (B.25) in the stability condition (B.21) and using the (B.3) we have that the stability condition is

$$\frac{dH^*}{dR} > 0. \tag{B.26}$$

From (B.24), the stability condition in terms of the parasitoid equilibrium is

$$\frac{1}{P^*}\frac{dP^*}{dR} > \frac{1}{R-1}. \tag{B.27}$$

REFERENCES

Elaydi, S., 1996. An Introduction to Difference Equations. New York.