Ecological Archives **E090-010-A3**

Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. ***Ecology*** **90:170–182.**

Appendix C. Invasibility criteria

Throughout this paper, we focus on stable coexistence of competitors defined by the invasibility (Turelli 1978, Chesson and Ellner 1989, Ellner 1989). In an invasion analysis, one species ('the invader') is removed from the system and reintroduced at low density (effectively zero) when the densities of $n - 1$ other species ('the residents') have converged to a joint stationary distribution. The success of invasion is measured by the invader's long-term growth rate ($\overline{r_i}$), as defined below. If the long-term growth rate of the invader is positive, we conclude that its population increases in long run, and the invasion is successful. If the long-term growth rate of each species as invader is positive, we say the species coexist.

We define the growth rate of any species for the time interval t to $t + 1$ as the change in ln population size, i.e.

(C.1) $$r(t) = \ln N(t+1) - \ln N(t),$$

which is the same as ln $\lambda(t)$ where

(C.2) $$\lambda(t) = N(t+1)/N(t)$$

is the finite rate of increase. Note that the finite rate of increase is defined even when $N(t) = 0$, although the right hand side of (C.2) would not apply. It is average individual fitness more generally, and this concept has a well-defined value in models. In our models, the finite rate of increase of a prey species is

(C.3) $$\lambda(t) = s(1-G(t)) + G(t)Ye^{-C(t)-aP(t)} ,$$

which remains meaningful when $N(t) = 0$. The growth rate is

(C.4) $$r(t) = \ln\left(s(1-G) + GYe^{-C(t)-aP(t)}\right).$$

The long-term population growth rate for residents is defined as

(C.5) $$\bar{r} = \lim_{T\to\infty} \frac{\sum_{t=0}^{T-1} r(t)}{T} = \lim_{T\to\infty} \frac{\sum_{t=0}^{T-1} \ln N(t+1) - \ln N(t)}{T} = \lim_{T\to\infty} \frac{\ln N(T) - \ln N(0)}{T} .$$

For the residents, population densities will normally converge on a stationary stochastic process (Chesson and Ellner 1989, Ellner 1989) . Residents persist when the stationary probability distribution for the population density of each species is on the positive real numbers. For this stationary distribution, the expected value of $r(t)$ is zero because $E[\ln N(t+1)]$ must equal $E[\ln N(t)]$. The law of large numbers for stationary processes (Breiman 1968) now guarantees that $\bar{r} = 0$. For an invader species i, $r_i(t)$ is evaluated for $N_i(0) = 0$ using equation (C.4). This quantity, $\bar{r}_i$, can be regarded as the limit as $N_i(0) \to 0$ of the quantity on the right in (C.5) (taking this limit before letting $T \to \infty$), or simply as the time average of $r_i(t)$, as defined above with $N_i(0) = 0$. The long-term growth rate, $\bar{r}_i$, can be regarded as the long-term growth trend while the invader remains at low density. Invader growth rates can be positive, negative or zero. As mentioned above, for coexistence we seek conditions that lead to positive invader growth rates ($\bar{r}_i > 0$) .

Literature Cited

Breiman, L. 1968. Probability. Addison-Wesley, Menlo Park, California.

Chesson, P. L., and S. Ellner. 1989. Invasibility and Stochastic Boundedness in Monotonic Competition Models. Journal of Mathematical Biology **27**:117-138.

Ellner, S. 1989. Convergence to Stationary Distributions in 2-Species Stochastic Competition Models. Journal of Mathematical Biology **27**:451-462.

Turelli, M. 1978. Re-Examination of Stability in Randomly Varying Versus Deterministic Environments with Comments on Stochastic Theory of Limiting Similarity. Theoretical

Population Biology **13**:244-267.