Metapopulations II — Interacting Species

Competing species

Assumptions and notation

The model presented here (from Case) is very simplified, with numerous assumptions:

- Species 1 is totally competitively superior:
  - If species 1 invades a patch occupied by species 2, it immediately extirpates species 2 and takes over that patch.
  - Species 1 cannot invade a patch occupied by species 2.
- The species have colonization rates of \( c_1 \) and \( c_2 \) respectively; these are per available patch per occupied patch per unit time.
- The species have extinction rates of \( e_1 \) and \( e_2 \) respectively; these are per occupied patch per unit time.
- Within-patch dynamics are ignored (implicitly assuming that local populations reach a stable carrying capacity very rapidly relative to the rates of colonization and extinction.

From this last assumption, the variables describing the state of the system are simply the fractions of patches occupied by species 1, denoted \( J_1 \), or by species 2, denoted \( J_2 \). The fraction of patches which are empty, \( J_0 \), is simply \( 1 - J_1 - J_2 \).

Model

The rate of change in the fraction of patches occupied by the superior competitor, species 1, is exactly as in the single-species Levins metapopulation model (since species 2 has no effect on species 1):

\[
\frac{d}{dt} J_1 = c_1 (1 - J_1) J_1 - e_1 J_1 \\
= [c_1 (1 - J_1) - e_1] J_1
\]

(eqn. 1)

The rate of change in the fraction of patches occupied by the inferior competitor, species 2, is the difference between the rate of colonization of empty patches, and the rates of extinction of species-2 patches both naturally and by invasion by species 1:

\[
\frac{d}{dt} J_2 = c_2 (1 - J_1 - J_2) J_2 - e_2 J_2 - c_1 J_2 J_1 \\
= [c_2 (1 - J_1 - J_2) - e_2 - c_1 J_1] J_2
\]

(eqn. 2)
Equilibria

Because of its absolute competitive superiority, the dynamics of species 1 are exactly as in the Levins model. It therefore will have a stable equilibrium at

\[
J_1^* = 1 - \frac{e_1}{c_1}
\]  

(eqn. 3)

if \(c_1 > e_1\), and will not persist otherwise.

Species 2 will be at equilibrium when \(\frac{d}{dt} J_2 = 0\) which occurs when \(J_2 = 0\) or when

\[
J_2^* = \left(1 - \frac{e_2}{c_2}\right) - J_1^* \left(1 + \frac{c_1}{c_2}\right)
\]  

(eqn. 4)

Substituting in the expression for \(J_1^*\) gives

\[
J_2^* = \frac{c_2 - e_2}{c_2} - \left(1 + \frac{c_1}{c_2}\right) \left(\frac{c_2 + c_1}{c_2}\right)
\]  

(eqn. 5)

From this is, the condition required for \(J_2^*\) to be positive — for species 2 to persist — can be found to be
One conclusion, so obvious it is almost trivial, arises directly from this result: Since the colonization rate of species 2, i.e., \(c_2\), must be finite, persistence of species 2 requires that the extinction rate of species 1, i.e., \(e_1\), is greater than 0. If there were no extinctions of species-1 patches, species 1 would eventually occupy all the patches (\(J_1^* = 1\)), leaving no patches for species 2.

If extinction rates are equal

If we assume the two extinctions rates are equal, \(e_1 = e_2 = e\), the equilibria become:

\[
c_2 > \frac{c_1(c_1 + e_2 - e_1)}{e_1}
\]  

(eqn. 6)
and the condition in eqn. 6 simplifies considerably, to

\[
J_2^* = \left(1 - \frac{e}{c_2}\right) - J_1^* \left(\frac{c_2 + c_1}{c_2}\right)
\]

and the condition in eqn. 6 simplifies considerably, to

\[
c_2 > \frac{c_1 c_1}{e} \quad \text{or} \quad \frac{c_2}{c_1} > \frac{c_1}{e}
\]

Since persistence of species 1 requires that \(c_1 > e\), the preceding condition implies that coexistence of the two species requires that

\[
\frac{c_2}{c_1} > 1 \quad \text{or} \quad c_2 > c_1
\]

In other words, if the species’ extinction rates are equal, species 2’s colonization rate must be greater than that of species 1. (Note that since actually \(c_1 > e\), the ratio \(c_2 / c_1\) must exceed 1; the true requirement is more stringent than given by eqn. 9, which thus is a necessary but not sufficient condition.)

Any extinction rates

More generally, from the condition in eqn. 6 we see that for any values of \(c_1, e_1,\) and \(e_2\) (so long as \(e_1 > 0\)), there will be some value of \(c_2\) large enough to satisfy the condition: the inferior species can coexist so long as its colonization rate is great enough to offset its competitive disadvantage. How high this colonization rate must be, relative to that of the superior species, depends on their relative extinction rates: if the extinction rate of species 2 is enough smaller than that of species 1, coexistence will be possible even with species 2 having a lower colonization rate than species 1, while if the extinction rates are similar or species 2 has the higher extinction rate, species 2 will have to have the higher colonization rate.
**Predator and prey**

**Assumptions and notation**

The model presented here also is very simplified, with numerous assumptions:

- Predators cannot exist in a patch without prey.
- Empty patches are colonized by prey at a rate which is proportional to the fraction of empty patches available for colonization and to the fraction of patches occupied by only prey. This colonization rate (per empty patch per prey-only patch per unit time) will be denoted by \( c \).
  (Other versions of the model have prey colonists also coming from patches with both prey and predators. Omitting this, as I do here, implies that colonization of a patch by predators quickly reduces the prey population to a level at which emigration is negligible compared to that from prey-only patches.)
- Prey-only patches remain in that state until colonized by predators; there is no prey extinction other than due to predation.
- Prey-only patches are colonized by predators at a rate proportional to how many such patches there are, and to the fraction of patches occupied by predators (thus the supply of possible predators for colonization); the rate (per prey-only patch, per prey-and-predators patch, per unit time) will be denoted by \( p \).
- Prey-and-predators patches go extinct at a rate proportional to how many such patches there are, with the rate (per prey-and-predator patch, per unit time) denoted by \( e \).
- Within-patch dynamics are ignored (implicitly assuming that local populations reach a stable carrying capacity very rapidly relative to the rates of colonization and extinction.

From this last assumption, patches can be described as being in any of three states: empty, occupied only by prey, or occupied by both prey and predators. The dynamic variables in the model are the fractions of patches in each of these states, denoted by \( J_0 \), \( J_V \), and \( J_P \) respectively; these of course must sum to 1 so only two of them need actually be modeled. The parameters of the model then are the rates of the possible transitions among the three patch states.

**Model**

The rate of change of prey-only patches will equal the rate of colonization of empty patches minus the sum of the rate of extinction of prey-only patches and the rate of colonization of such patches by predators:

\[
\frac{d}{dt} J_V = c J_0 J_V - p J_V J_P = [c(1 - J_V - J_P) - p J_P] J_V
\]

(eqn. 10)
The rate of change of prey-and-predator patches will equal the rate of colonization of prey-only patches by predators minus the rate of extinction of prey-and-predator patches:

$$\frac{d}{dt} J_p = p J_V J_p - e J_p$$  \hspace{1cm} (eqn. 11)

$$= (p J_V - e) J_p$$

**Analysis**

**Equilibria**

From equation 11, we see that equilibrium ($dJ_p/dt = 0$) requires either that there are no such patches — no predators — or that

$$0 = p J_V^* - e$$

$$J_V^* = \frac{e}{p}$$  \hspace{1cm} (eqn. 12)

In other words, there must be exactly enough prey-only patches for the rate of colonization of these patches by predators to balance the rate of extinction of predator patches.

From eqn. 10, the rate of change of the fraction of prey-only patches will be 0 if there are no prey-only patches ($J_V = 0$), or if there are no predators and all patches are occupied by prey ($J_P = 0$ and $J_V = 1$), or if $c(1 - J_V - J_P) - p J_P = 0$. Rearranging the latter expression gives the equation for the prey-only 0-growth isocline:

$$c(1 - J_V - J_P) - p J_P = 0$$

$$c(1 - J_V - J_P) = p J_P$$

$$c(1 - J_V) = (c + p) J_P$$  \hspace{1cm} (eqn. 13)

$$\frac{c(1 - J_V)}{c + p} = J_P$$

Substituting the result above for into this equation gives the equilibrium fraction of prey-and-predator patches:

$$J_P^* = \frac{c(1 - J_V^*)}{c + p}$$

$$= \frac{c}{c + p} \left( 1 - \frac{e}{p} \right)$$  \hspace{1cm} (eqn. 14)

One condition for coexistence is apparent from these equilibria: $e$ (the rate of extinction of prey-and-predator patches) must be smaller than $p$ (the rate of invasion of prey-only patches by
predators). If this condition is met, and there is some extinction of predator patches \((e > 0)\), there is an equilibrium with both species present \((J_V^* \text{ and } J_P^* \text{ both positive})\).

**Stability**

The stability of the equilibrium can be analyzed easily by examining the 0-growth isoclines. From eqn. 12 the isocline for prey-and-predator patches (labelled the predator isocline in the figure to the right) is a vertical line. There is no density-dependence (on \(J_P\)) of the “per capita” rates of colonization or extinction; the latter is a constant and the former depends only on the density of prey-only patches available for colonization.

From eqn. 13, the isocline for prey-only patches is a straight line with negative slope. This reflects the density dependence of colonization: the more occupied patches there are, the lower the rate of colonization (per prey-only patch). Therefore when \(J_V\) is large, a lower rate of invasion by predators is sufficient to balance the rate of colonization of empty patches.

These isoclines show that the equilibrium is stable; the Jacobian matrix would have the form

\[
\begin{bmatrix}
- & - \\
+ & 0
\end{bmatrix}.
\]