Coexistence of competitors: competition-colonization tradeoffs

Can dispersal and colonization promote coexistence among competitors? Many species in nature are somewhat “weedy”. Weeds typically are not strong competitors but they are very good dispersers that can rapidly colonize empty sites. They typify one end of the competition-colonization tradeoff, where some species specialize in efficient capture of resources (competition) while others specialize in efficient dispersal. How does increased dispersal ability allow the weaker competitor to persist in the presence of a stronger competitor? The key is that there must be spatial variation that allows the weaker competitor to persist (temporarily) in sites where the stronger competitor has not yet arrived. How does that work?

To focus on the effect of migration, we’ll use the basic metapopulation model that we saw in chapter 6. But now we are keeping track of two different species.

Assume that species 1 is the better competitor, which always drives species 2 extinct. Patches can be empty or they can be occupied by either species 1 or 2. But both species cannot be present at the same time because we assume that species 1 will always win the site. Like the other metapopulation model, we’ll assume that the dynamics of competition happen very quickly so we only need to keep track of the fraction of patches that are occupied by species 1, and the fraction of patches that are occupied by species 2.

First we’ll look at the dominant competitor. Species 1 can colonize empty patches, and can also take over patches where species 2 is present. Any patch that is not currently occupied by species 1 is a potential site for colonization.

Recall from chapter 6 the basic metapopulation model. This time we need to keep track of two species, so we need to add subscripts. But the equation for species 1 is exactly the same as before.

$$\frac{dP_1}{dt} = c_1 P_1 (1 - P_1) - e_1 P_1$$

We already know the general solution to this metapopulation model:

$$\hat{P}_1 = 1 - \frac{e_1}{c_1}$$

Clearly species 1 can persist as long as $e_1 < c_1$.

Now, can the weaker competitor (species 2) persist in a metapopulation along with species 1?
Species 2 (the weaker competitor) can colonize empty patches, but cannot colonize patches where species 1 is already present. It can only colonize sites where neither species is present. The fraction of patches without either species is the product \((1 - P_2)(1 - P_1)\) so the equation for species 2 becomes

\[
\frac{dP_2}{dt} = c_2 P_2 (1 - P_2) (1 - P_1) - e_2 P_2
\]

As always, the equilibrium for species 2 will be when colonizations and extinctions balance so

\[
c_2 P_2 (1 - P_2) (1 - P_1) = e_2 P_2
\]

And at the joint equilibrium for both species we can substitute \(\hat{P}_1\) for \(P_1\)

\[
c_2 P_2 (1 - P_2) (1 - (1 - \frac{c_1}{c_2})) = e_2 P_2
\]

Now we start simplifying

\[
c_2 P_2 (1 - P_2) (1 - 1 + \frac{e_1}{c_1}) = e_2 P_2
\]

\[
c_2 (1 - P_2) \left(\frac{e_1}{c_1}\right) = e_2
\]

\[
(1 - P_2) = \frac{e_2 c_1}{c_2 e_1}
\]

and finally

\[
\hat{P}_2 = 1 - \frac{e_2 c_1}{c_2 e_1}
\]

To understand this equation, let’s first consider a simple case where the extinction rates are equal. If \(e_2 = e_1\), then those terms cancel so \(\hat{P}_2 = 1 - \frac{c_1}{c_2}\). That will be positive if \(c_2 > c_1\). That is an interesting result and shows the lesson of this whole exercise: the only thing that is required to maintain the weaker competitor in the metapopulation is that its colonization rate is higher than the colonization rate of species 1. Looking at competition alone the two species can never coexist. But if they occur in a metapopulation then differences in colonization ability can allow the weaker competitor to persist.

In general, the equilibrium patch occupancy for species 2 will be positive as long as

\[
\frac{e_2 c_1}{c_2 e_1} < 1.
\]

That can be rearranged as \(\frac{c_2}{c_1} > \frac{e_2}{e_1}\). So the general result is that the weaker competitor can persist in a metapopulation as long as its colonization:extinction ratio is greater than that of species 1.