

Regional Coexistence of Species and Competition between Rare Species

(mathematical model/habitable patches)

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ABSTRACT A model is developed for the coexistence and exclusion of species over a region of similar habitable patches. Since the balance of local extinction and colonization would leave some patches unoccupied even without competitors, species may coexist even when all the patches are the same. Regional competition coefficients are found when species affect the local extinction or migration rates of each other. Rare species can regulate each other and even exclude other species completely.

Many environments have a patchy, island-like pattern of occurrence. It is generally assumed that species that occur on a small fraction of the available patches will have little effect on each other because their co-occurrence would be an exceedingly rare event. However, we have recently obtained evidence of competition between rare species. A group of predaceous ants recorded by Gregg (1) in Colorado, all of which are rare, showed a lower than expected microhabitat overlap. MacArthur and Pianka (2) predicted reduced microhabitat overlap for 'searching' predators competing for the same prey; our data seemed to confirm MacArthur and Pianka's optimization model. The problem is not why the ants reduced competition by the optimization proposed by MacArthur and Pianka, but rather, how there could be any significant competition to reduce. We will use an immigration-extinction model developed by Levins (3, 4) for predicting the number of islands, or island-like habitats, occupied by a species, and we will allow competition to affect either the migration or extinction rate. In contrast to traditional competition theory, the focus of our attention will be on changes in the number of populations of a species, rather than on the sizes of the local populations.

We will first present the migration-extinction model for a species in the absence of competitors, then the possibility of significant competitive effects on a rare species by other species, conditions for coexistence of two species, the effect of environment on coexistence, and mechanisms for the avoidance of competition. Finally, we will discuss situations where the model might be applicable.

Let N be the number of local populations, T the total number of sites, x the extinction rate per population, and m' the rate of migration from one given site to another given site. Then

$$\frac{dN}{dt} = m'N(T - N) - xN. \quad (1)$$

This formulation assumes that the migration rate from one patch to any other patch is the same. Letting $p = N/T$ and $m = m'T$ makes the equation more manageable:

$$\frac{dp}{dt} = mp(1 - p) - xp. \quad (2)$$

At equilibrium:

$$\hat{p} = 1 - x/m, \quad (3)$$

which is the proportion of sites occupied in the absence of competitors. For a rare species, a ten-fold change in p from 0.01 to 0.1 requires only about a 10% change in x/m , from 0.99 to 0.90. Finally, \hat{p} is more sensitive to differences in the parameters x and m if these are separately small:

$$\frac{\partial \hat{p}}{\partial m} = \frac{x}{m^2} = \frac{1 - \hat{p}}{m} \quad (4)$$

$$\frac{\partial \hat{p}}{\partial x} = \frac{-(1 - \hat{p})}{x}. \quad (5)$$

Thus, small differences in m and x can make one species common and a species with a similar biology rare. A standard explanation is that species are rare because suitable habitats are rare. While this may be true for many situations, the arguments above indicate that this is not necessarily the case, and we are justified in looking for competition between initially rare species.

COMPETITION AFFECTING EXTINCTION RATE

The simplest model for the effect of competition on extinction rate is to let the extinction rate be x_1 when the second species is present and x_0 when the second species is absent. Then

$$\frac{dp}{dt} = mp(1 - p) - p[x, q + x_0(1 - q)], \quad (6)$$

where q is the proportion of sites occupied by the second species. Rearrangement yields an equation of the familiar form

$$\frac{dN_1}{dt} = r_1 N_1 (K_1 - N_1 - d_{12} N_2):$$

$$\frac{dp}{dt} = mp \left[1 - \frac{x_0}{m} - p - \left(\frac{x_1 - x_0}{m} \right) q \right]. \quad (7)$$

At equilibrium:

$$\hat{p} = 1 - \frac{x_0}{m} - \left(\frac{x_1 - x_0}{m} \right) q. \quad (8)$$

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Thus, $1 - \frac{x_0}{m}$ is the K of the logistic form and $\frac{x_1 - x_0}{m}$ is α .

We prefer to define $\alpha_{i\theta}$ in the community matrix (5) as $\frac{-\partial \hat{p}}{\partial q}$,

which is a more general definition than is usually assigned to α . For the model we are considering

$$\frac{-\partial}{\partial q \hat{p}} = \frac{x_1 - x_0}{m}. \tag{9}$$

Let us now consider under what conditions one species can exclude another from a region. From Eq. (8), we see that for $\hat{p} = 0$

$$q \geq \frac{m - x_0}{x_1 - x_0} \text{ or } x_1 \geq \frac{m + x_0}{q} - x_0. \tag{10}$$

For example, if the resident species (q) occurs in 0.01 of the available patches, and the invading species (p) would occur in 0.01 of the available patches if q were absent, x_1 must be approximately 2.01 for invasion by p to be impossible. Thus, one rare species can exclude another rare species from a region. The usual explanation for allopatry, particularly of rare species, is that there has not been sufficient time for the species to reinvade the area where the other closely related species occurs. However, the above arguments indicate that competitive exclusion may be important.

Two species can coexist when the product $\alpha_{12}\alpha_{21}$ is less than one. In the symmetric case ($\hat{p} = \hat{q}$), this reduces to:

$$m > x_1 - x_0, \tag{11}$$

For rare species, $m \approx x_0$, and so x_1 cannot be more than two times x_0 .

Migration rate depends primarily on the distance between patches (3), whereas the extinction rate depends upon local conditions. Therefore, we are justified in looking at the effect on coexistence of increasing extinction rates while the migration rate is held constant, and of decreasing migration rate while the extinction rates are held constant. If x_0 is increased, then the most reasonable form is that x_1 also increases by the same amount. Let this increase be a . Then

$$\alpha = \frac{x_1 + a - (x_0 + a)}{m} = \frac{x_1 - x_0}{m}. \tag{12}$$

If the increase is multiplicative

$$\alpha = \frac{a(x_1 - x_0)}{m} > \frac{x_1 - x_0}{m}, \tag{13}$$

which decreases the likelihood of cooccurrence. Reduction in migration rate, i.e., increase of patch distance, also increases α . Since increase of environmental severity probably acts in an additive way, changes in distance between patches probably affect α , and thus the alternatives of allopatry and sympatry, more strongly.

Two possible evolutionary responses by a species faced with competition acting on extinction rate are to avoid patches where the second species is present or to reduce x_1 . Let θ be the probability that species p avoids a patch where species q is present. Then Eq. (6) becomes

$$\frac{dp}{dt} = mp(1 - p) - p[x_1(q - \theta q) + x_0(1 - q + \theta q)]. \tag{14}$$

At equilibrium:

$$\hat{p} = 1 - \frac{x_0}{m} - \left(\frac{x_1 - x_0}{m}\right)(q - \theta q). \tag{15}$$

The sensitivity of p to changes in θ is

$$\frac{\partial \hat{p}}{\partial \theta} = q \left(\frac{x_1 - x_0}{m}\right). \tag{16}$$

By comparison, the sensitivity of p to reduction in x_1 is

$$\frac{-\partial \hat{p}}{\partial x_1} = \frac{q}{m}. \tag{17}$$

If $x_1 - x_0$ is less than 1.0, reduction in x_1 will be more effective than increasing θ . Of course, a species may not be able to reduce x_1 , and increasing θ may be the only possible strategy.

We can relate the rate of extinction (x_1 or x_0) at any particular site to stability of the local community matrix at least in a qualitative way. The rate of return to equilibrium of the community matrix depends upon the separate eigenvalues of the matrix, but the rate of return in a fluctuating environment depends on the product of the eigenvalues; the faster the rate of return, the more stable to community. On the other hand, the higher the extinction rate, the more unstable is the community. Since the determinant is equal to the product of the eigenvalues, a large determinant should indicate low extinction rates for the species involved and vice versa.

COMPETITION AFFECTING MIGRATION RATE

By an analogous procedure for competition affecting extinction rate, we let the migration rate be m_1 when the second species is present, and m_0 when the second species is absent. The most reasonable interpretation of m_1 and m_0 is that they are the rate of 'successful' migration. Of course, 'successful' migration is difficult to define (5), but the essential point is that the model allows for the effect of residence on a site by another species. One possible definition of successful migration is one where the propagules reproduce at least once. The rate of change of p is

$$\frac{dp}{dt} = p(1 - p)[m_1q + m_0(1 - q)] - xp. \tag{18}$$

At equilibrium:

$$\hat{p} = 1 - \frac{x}{qm_1 + m_0(1 - q)}. \tag{19}$$

and α is

$$\frac{-\partial \hat{p}}{\partial q} = \frac{(m_0 - m_1)x}{[q(m_1 - m_0) + m_0]^2}. \tag{20}$$

Note that α is not a constant, but depends on the value of q .

Let us now consider under what conditions one species can exclude another species from a region. From Eq. (19), we see that for $\hat{p} = 0$

$$q \geq \frac{m_0 - x}{m_0 - m_1}. \tag{21}$$

If the resident species (q) occurs in 0.01 of the available patches, and the invading species (p) would occur in 0.01 of the available patches if q were absent, m_1 must be 0.0 for

invasion by p to be impossible. Thus, migration competition is not as effective as extinction competition for exclusion of one rare species by another rare species.

The competition coefficient, α , can be written in the following way:

$$\alpha = \frac{m_0 - m_1}{(m_1 - m_0)q + m_0} (1 - \hat{p}). \quad (22)$$

In the symmetric case ($\hat{p} = \hat{q}$), α must be less than one, and Eq. (22) reduces to

$$\frac{m_0}{m_0 - m_1} > 1 \quad (23)$$

in the stable case. If $m_1 \neq 0$, Eq. (23) always holds. When $m_1 = 0$, α equals one even for asymmetric cases. Eq. (22) becomes

$$\alpha_{pq} = (1 - \hat{p}) \left[\frac{1}{(1 - q)} \right], \quad (24)$$

so the product $\alpha_{pq}\alpha_{qp} = 1$. Thus, exclusion occurs only when $m_1 = 0$, and sympatry is possible in all other cases. An increase in local extinction rate decreases p and increases α , but not enough to prevent sympatry. Reduction in m_1 has a similar effect.

In a similar manner to the analysis of extinction competition, a species can avoid patches where q is present, or evolve to reduce m_1 . By analogy to (14):

$$\frac{dp}{dt} = p(1 - p)[m_1(q - \theta q) + m_0(1 - q + \theta q)] - xp. \quad (25)$$

The sensitivity of \hat{p} to changes in θ is

$$\frac{\partial \hat{p}}{\partial \theta} = \frac{x(m_0 - m_1)q}{[(q - \theta q)(m_1 - m_0) + m_0]^2}. \quad (26)$$

Similarly, the sensitivity of \hat{p} to reduction in m_1 is

$$\frac{\partial \hat{p}}{\partial m_1} = \frac{qx}{[q(m_1 - m_0) + m_0]^2}. \quad (27)$$

In general, for low values of θ , a reduction in m_1 would be more effective in reducing competition.

Although we have discussed the model mainly in the context of competition between rare species in relatively large areas, we believe that the model applies, at least potentially, to many situations. The model may apply to two kinds of patchy environments: ones in which any patch contains a small fraction of the species able to live in the patch, and ones in which a species occupies a small fraction of the habitable patches. An example of the first case is aquatic insect nymphs living in various microhabitats of freshwater streams. An example of the second case is a group of parasites utilizing the same vertebrate species as host.

Additional theoretical developments are also necessary. We have not discussed the n -species case, because this would require specifying the extinction rates X_k for communities with K species present and calculating the frequencies of local communities with K species. A general treatment is formidable mathematically, yet we do not now have a reasonable basis for the addition of simplifying assumptions.

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