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COMPETITION AND REGIONAL COEXISTENCE¹

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Abstract. A model of the competition between two species is developed which is based on the work of Cohen (1970) and Levins and Culver (1971) and which considers the effect of competition on the colonization and extinction rates of the two species. The results are that in some cases it is possible for one species to exclude another species from a geographic region, but there is no possibility of a "priority effect" where the first species in the region can always exclude the other. Thus the equilibrium level of each species is determined by the parameters of the system and not by the initial conditions. Also, it is possible for two similar species to coexist in a region. A predator can increase the extinction rate of each species and, in some cases, permit coexistence where it would otherwise not be possible.

Key words: *Colonization; competition; extinction; geographic structure; mathematical model; predator; prey; regional coexistence.*

INTRODUCTION

Two different approaches to the modeling of competition between species have been used. First, models introduced by Volterra (1926) and Gause (1934) and developed extensively by later authors are based on the assumption that the number of individuals of a species in a community is influenced by the numbers of all other species present in the same community. A formal description of this competition has been made in terms of the "community matrix" defined by Levins (1968).

The second type of model was introduced by Cohen (1970) and Levins and Culver (1971). In these models, the relevant variables are not the numbers of individuals of each species within a community but the numbers of habitats in a region which are colonized by each species. In a geographic region, there is assumed to be a large number of habitats that can be colonized by all the species under consideration. The habitats are assumed to be isolated enough from each other that there is no interaction between the populations in different habitats. The effect of competition is to change the probability of colonization or extinction within a single habitat. The number of individuals of each species in each of the habitats is not considered. The second type of model has become important with the realization that extinction and colonization within individual communities is a far more common occurrence than previously supposed (MacArthur and Wilson 1967, Ehrlich et al. 1972).

The difference between these two types of models is not one of mechanism but of scale. Within each of the habitats, the species could be described by the Lotka-Volterra or some more general set of equations. The predictions of these equations could

be related to the extinction and colonization probabilities. For example, in the unstable Lotka-Volterra system, the outcome of competition depends on the initial conditions. Therefore, the probability of a successful colonization of a habitat already occupied by one species would depend on the size of the propagule. Only if the propagule is large enough would colonization be possible. The rate of decrease of one population in the presence of another could determine the extinction rate. Consequently, given the size distribution of the propagules, the parameters of the Lotka-Volterra model can be related to those of the colonization-extinction model. Whether one or the other type of model is appropriate depends on the particular questions to be answered and the particular data available.

Cohen's (1970) model assumes that the probability of extinction in a habitat is increased and the probability of colonization is decreased in the presence of a second species. The model also assumes that the probability of colonization of a single habitat in a given time period is constant and does not depend on how many other habitats are occupied. The latter assumption is valid when the potential colonists come from an outside source, as would be the case for an island system colonized from a mainland or individuals colonized (infected) from a reservoir of parasites (for example, the resident mosquito population). However, when the principal sources of colonists are the other habitats that have been colonized, as would be the case in many geographic regions or in the epidemic spread of diseases, that assumption would not be valid. In order to analyze these cases, Cohen's model must be modified to include the assumption that the rate of colonization of a habitat by a species is a function of the number of habitats already colonized by that species. An important point in Cohen's model is that, for one habitat type and two species, there are three

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independent variables (P_1 , the fraction of the total number of habitats which is occupied by species 1 alone; P_2 , the fraction of the habitats which is occupied by species 2 alone; and P_3 , the fraction of the habitats which is occupied by both species).

Levins and Culver (1971) develop a model similar to Cohen's, but with two important differences. First, they assume that the rate of colonization of a habitat is proportional to the number of habitats already colonized by the species. Second, they assume that the fraction of habitats occupied by both species is equal to the product of the fractions of habitats occupied by each of the species. In other words, the two species are independently distributed. Following Cohen's notation, we define $Y_1 = P_1 + P_3$, the total fraction of habitats occupied by species 1, and $Y_2 = P_2 + P_3$, the total fraction occupied by species 2. Levins and Culver assume that $P_3 = Y_1 \cdot Y_2$. Once this assumption is made, the number of independent variables is reduced from three (P_1 , P_2 and P_3) to two (Y_1 , Y_2) and the resulting mathematical model becomes tractable. In fact, the equations that Levins and Culver derive in this way are formally the same as the Lotka-Volterra competition equations, and the criteria for coexistence and exclusion can be written down directly.

The difficulty with the Levins and Culver model is that it can lead to some conclusions that do not agree with one's biological intuition. An example given in their paper is of the effect of a species which is rare in a region but which increases the extinction rate of the other species by a large amount. They show that if the increase in the extinction rate is large enough, the rare species can exclude the other, even though the other species could be abundant in the region in the absence of the rare species. To be specific, let us suppose that the rare species occupies 1% of the available habitats and increases the extinction rate of the other species by a large amount in those habitats where the two species both occur. Species 1 effectively excludes species 2 from all the habitats species 1 occupies. If we assume that species 2 can invade the region in the absence of species 1, then the Levins and Culver model predicts that a decrease in the number of available habitats by 1% is sufficient to prevent species 2 from invading. Furthermore, the conclusion does not depend on the fraction of habitats which species 2 would occupy at equilibrium in the absence of species 1.

The reason that Levins and Culver reach this conclusion is their assumption that the two species are independently distributed. In the above example, since species 1 excludes species 2 from a habitat, $P_3 = 0$. However, using the assumption of independence, $P_3 = Y_1 \cdot Y_2$ and is not 0. Therefore, the term describing the effect of competition between the two species is necessarily greater than it should

be because the number of habitats in which the species occur together is overestimated. In our example the only effect of competition should be on the propagules of either species which invade habitats where the other species is already present.

The problem with the Levins and Culver model is that the assumption that the presence or absence of a species in a habitat affects the colonization and extinction rates of the other species in the habitat is not consistent with the assumption that the species are independently distributed. Conclusions derived from a model that uses both of these assumptions must be carefully considered. Horn and MacArthur (1972) follow the Levins and Culver approach to analyze the case of two species in a region with two different habitat types. Because of the complexity of their system, it is not clear what effect incorporating the above considerations would have.

THE MODEL

We consider only the simplest case of two species and habitats of only one type. We let P_0 , P_1 , P_2 , and P_3 be the fractions of the habitats which are occupied by neither of the species, species 1 alone, species 2 alone, and both species together. For each habitat we assume that the rate of extinction of species 1 (which is a probability per unit time) is e_1 in the absence of species 2 and $e_1 + \epsilon_1$ in the presence of species 2, we define e_2 and ϵ_2 similarly. So far there is no change from Cohen's model. Next, the rate of colonization of an empty habitat by species 1 is proportional to $Y_1 = P_1 + P_3$, the total fraction of habitats occupied by species 1. We let m_1 be the constant of proportionality. Similarly, the rate of colonization of a habitat occupied by species 2 is proportional to Y_2 with a constant of proportionality $m_2 - \mu_2$. m_2 and μ_2 are defined in the same way. We are assuming that the propagules are equally likely to come from any occupied habitat. The effect of the spatial arrangement of the habitats is ignored and would have to be considered when the dispersal distance of the species is much smaller than the size of the region.

The ϵ 's and the μ 's measure the effect of each species on the other. Positive values for the ϵ 's and μ 's represent competition. I am assuming that the production of propagules is not changed when the two species co-occur. If competition between the two species reduces the number of propagules, then, for example, the rates of colonization by species 1 would be proportional to $P_1 + (1 - \gamma_1)P_3$ where γ_1 is the measure of the effect of species 2 on the production of propagules by species 1. We will not consider this possibility here. Frost (1972) has analyzed the problem in certain cases.

We can derive the deterministic equations for this

system using the above assumptions. We ignore the stochastic fluctuations in the P 's.

$$\frac{dP_0}{dt} = -(m_1 Y_1 + m_2 Y_2)P_0 + e_1 P_1 + e_2 P_2 \quad (1)$$

$$\begin{aligned} \frac{dP_1}{dt} = & m_1 Y_1 P_0 - [e_1 + (m_2 - \mu_2) Y_2] P_1 \\ & + (e_2 + \epsilon_2) P_3 \end{aligned} \quad (2)$$

$$\begin{aligned} \frac{dP_2}{dt} = & m_2 Y_2 P_0 - [e_2 + (m_1 - \mu_1) Y_1] P_2 \\ & + (e_1 + \epsilon_1) P_3 \end{aligned} \quad (3)$$

$$\begin{aligned} \frac{dP_3}{dt} = & (m_1 - \mu_1) Y_1 P_2 + (m_2 - \mu_2) Y_2 P_1 \\ & - (e_1 + \epsilon_1 + e_2 + \epsilon_2) P_3 \end{aligned} \quad (4)$$

where $Y_1 = P_1 + P_3$ and $Y_2 = P_2 + P_3$. We assume that the rates of double transitions, from state 0 to state 3 and from state 1 to state 2 and the reverse are 0. Only three of the equations are independent since $P_0 + P_1 + P_2 + P_3 = 1$.

Two questions can be answered with the system of equations (1)–(4). First, at equilibrium, can the two species coexist in the region? Second, when one species is at equilibrium in the region in the absence of the other, can the other species invade the region? In order to answer the first question, it is necessary to find all the equilibrium points of (1)–(4) which have acceptable values for the P_i ($P_i > 0$ and $\sum P_i = 1$) and to test the stability for each of the equilibrium points. If we can find at least one stable equilibrium point, then we could conclude that coexistence is possible. Unfortunately, I could not find an analytic solution for all of the equilibrium points and therefore had to proceed indirectly by first answering the second question and using that answer to give some indication to the answer to the first. The conclusions reached by means of this procedure were checked by a direct numerical iteration of the difference equations derived from (1)–(4) by approximating $\frac{dP_i}{dt}$

as $\frac{P_i(t + \Delta t) - P_i(t)}{\Delta t}$.

If we set $dP_i/dt = 0$ in (1)–(4), there are always at least two solutions to the resulting algebraic equations:

$$\begin{aligned} \text{(i)} \quad & P_0 = e_1/m_1 & \text{(ii)} \quad & P_0 = e_2/m_2 \\ & P_1 = 1 - e_1/m_1 & & P_2 = 1 - e_2/m_2 \\ & P_2 = P_3 = 0 & & P_1 = P_3 = 0. \end{aligned} \quad (5)$$

The first we interpret as species 1 being present in the region alone and the second as species 2 present in the region alone. We assume that each of the species can in fact inhabit the region in the absence of the other, so $e_1 < m_1$ and $e_2 < m_2$. We consider the stability of each of these two equilibrium points and argue that if either is a stable point, then the

species which is present can prevent the other species from invading the region. Conversely, if either point is unstable, then the other species can invade.

There are four possible outcomes of the stability analysis of the two boundary points:

- (a) (i) and (ii) are both unstable
- (b) (i) is stable and (ii) is unstable
- (c) (i) is unstable and (ii) is stable
- (d) (i) and (ii) are both stable.

In case (a) each species can invade when the other is present and we would predict that coexistence would be possible. In principle, there could be more than one stable internal equilibrium point or even a stable limit cycle, but the simplicity of the system of equations (1)–(4) makes it unlikely for there to be more than a single stable internal equilibrium point. That intuition about the properties of the model is correct and is verified by the direct numerical calculations.

In case (b) we would expect that species 1 could always eliminate species 2 from the region, so there would be no stable internal equilibrium point. Similarly in case (c) we would predict that species 2 could always exclude species 1 from the region. In case (d) we would expect the outcome of competition to depend on the initial fractions of the habitats occupied by each of the species. The first species to occupy the region could exclude the other. In other words, there would be a "priority effect" of the same kind as for the unstable Lotka-Volterra model of competition between two species.

We chose one of the equilibrium points arbitrarily (species 2 present and species 1 absent) to consider in detail. We define $\hat{P}_2 = 1 - e_2/m_2$ and $\hat{P}_0 = e_2/m_2$ and let

$$\begin{aligned} P_0 &= \hat{P}_0 + P'_0 \\ P_1 &= P'_1 \\ P_2 &= \hat{P}_2 + P'_2 \\ P_3 &= P'_3. \end{aligned} \quad (6)$$

Linearizing the resulting equations for the primed variables gives

$$\begin{aligned} \frac{dP'_0}{dt} = & -m_2 \hat{P}_2 P'_0 - (m_1 \hat{P}_0 - e_1) P'_0 \\ & - (m_1 + m_2) \hat{P}_0 P'_3 \end{aligned} \quad (7a)$$

$$\begin{aligned} \frac{dP'_1}{dt} = & [m_1 \hat{P}_0 - e_1 - (m_2 \mu_2) \hat{P}_2] P'_1 \\ & + (m_1 \hat{P}_0 + e_2 + \epsilon_2) P'_3 \end{aligned} \quad (7b)$$

$$\begin{aligned} \frac{dP'_2}{dt} = & m_2 \hat{P}_2 P'_0 - (m_1 - \mu_1) \hat{P}_2 P'_1 \\ & + [m_2 \hat{P}_0 - (m_1 - \mu_1) \hat{P}_2 + e_1 + \epsilon_1] P'_3 \end{aligned} \quad (7c)$$

$$\frac{dP'_3}{dt} = [(m_1 - \mu_1) \hat{P}_2 + (m_2 - \mu_2) \hat{P}_2] P'_1$$

$$+ [(m_1 - \mu_1)\hat{P}_2 - e_1 - \epsilon_1 - e_2 - \epsilon_2]P'_3 \quad (7d)$$

where the fact that $m_2\hat{P}_0 - e_2 = 0$ has been used. We can reduce the number of independent variables to three by noting

$$P'_0 + P'_1 + P'_2 + P'_3 = 0 \quad (8)$$

to obtain the system of linear differential equations

$$\frac{d}{dt} \begin{pmatrix} P'_1 \\ P'_2 \\ P'_3 \end{pmatrix} = \mathbf{A} \begin{pmatrix} P'_1 \\ P'_2 \\ P'_3 \end{pmatrix} \quad (9)$$

where the matrix \mathbf{A} has the coefficients.

$$\begin{aligned} a_{11} &= m_1\hat{P}_0 - e_1 - (m_2 - \mu_2)\hat{P}_2 \\ a_{12} &= 0 \\ a_{13} &= m_1\hat{P}_0 + e_2 + \epsilon_2 \\ a_{21} &= -(m_1 - \mu_1) - m_2\hat{P}_2 \\ a_{22} &= -m_2\hat{P}_2 \\ a_{23} &= -m_2\hat{P}_2 + m_2\hat{P}_0 - (m_1 - \mu_1)\hat{P}_2 + e_1 + \epsilon_1 \\ a_{31} &= (m_1 - \mu_1 + m_2 - \mu_2)\hat{P}_2 \\ a_{32} &= 0 \\ a_{33} &= (m_1 - \mu_1)\hat{P}_2 - e_1 - \epsilon_1 - e_2 - \epsilon_2. \end{aligned} \quad (10)$$

The stability of the equilibrium point is determined by the eigenvalues of \mathbf{A} . Since \mathbf{A} has two conveniently placed zeros, the equation for the eigenvalues is

$$(\lambda - a_{22})[a_{31}a_{13} - (a_{11} - \lambda)(a_{33} - \lambda)] = 0. \quad (11)$$

In specifying the model, we want all of the extinction and colonization rates to be positive, so $e_1, m_1, e_2, m_2 > 0$ and $m_1 > \mu_1$ and $m_2 > \mu_2$.

Since $a_{22} < 0$, one of the eigenvalues is always negative and real. The other two are obtained from the quadratic formula

$$\lambda = \frac{1}{2}(a_{11} + a_{33}) \pm \sqrt{(a_{11} + a_{33})^2 - 4(a_{11}a_{33} - a_{31}a_{13})} \quad (12)$$

The discriminant is $(a_{11} - a_{33})^2 + 4a_{31}a_{13}$ which is always positive, so the eigenvalues are real. For both of the solutions to (12) to be negative the following three conditions must be satisfied:

$$\begin{aligned} a_{11} &< 0 & (a) \\ a_{33} &< 0 & (b) \\ a_{13}a_{31} &< a_{11}a_{33}. & (c) \end{aligned} \quad (13)$$

If any of these are not satisfied, the point is unstable and species 1 can invade the region occupied by species 2. If all three are satisfied, then the point is stable and species 2 can prevent species 1 from invading.

The conditions in (13) are still sufficiently complicated that the criteria for the invasibility of a region are not very enlightening in their general form,

even though they can be written down directly (on a large enough sheet of paper). Instead of doing this, I will consider special cases which seem to be of the most biological interest: (1) like species ($m_1 = m_2, e_1 = e_2, \epsilon_1 = \epsilon_2, \mu_1 = \mu_2$), (2) migration competition ($\epsilon_1 = \epsilon_2 = 0$), (3) extinction competition ($\mu_1 = \mu_2 = 0$).

(1) Like species. If we are considering species that are alike or nearly alike in the values for their parameters, then we can set $m_1 = m_2 = m, \mu_1 = \mu_2 = \mu, e_1 = e$, and $\epsilon_1 = \epsilon_2 = \epsilon$. In this case condition (13c) reduces to

$$2(2e + \epsilon) < 2e + 2\epsilon - (m - \mu)\hat{P}_2. \quad (14)$$

Condition (14) with $\hat{P}_2 = 1 - e/m$ cannot be satisfied for any acceptable values m, e, ϵ , and μ . Therefore, we would predict that one species could always invade a region occupied by a similar species, regardless of how large the effect each species had on the colonization and extinction rates of the other. Of course each species could greatly reduce the abundance of the other species. Based on this conclusion, we would expect that the two species would be able to coexist in the region and that at least one stable equilibrium point would exist. As mentioned, it is possible that there could be more than one stable equilibrium point or a stable limit cycle. To test these possibilities I wrote a computer program to numerically iterate equations (1)–(4) for arbitrary initial conditions. I tested the stability of the numerical technique by halving the time step to see whether the results obtained were the same. Because of the simplicity of the system, there were no difficulties with the numerical solution. In all cases, a single equilibrium point was reached, and, although the more complicated results are theoretically possible, there is no evidence that they occur in this system.

(2) Migration competition. Levins and Culver (1971) introduced the term "migration competition" to describe the situation in which the only effect one species has on the other is to reduce the ability of the other's propagules to establish colonies in those habitats where the first species is present. There is no increase in the extinction rates when both species are present in a habitat. In terms of this model $\epsilon_1 = \epsilon_2 = 0$. The conditions (13) for stability of the boundary point reduce to

$$\begin{aligned} m_1\hat{P}_0 - e_1 &< (m_2 - \mu_2)\hat{P}_2 & (a) \\ (m_1 - \mu_1)\hat{P}_2 &< e_1 + e_2 & (b) \\ \left(1 - \frac{e_1}{m_1}\right) &< \frac{\mu_1}{m_1}\hat{P}_2. & (c) \end{aligned} \quad (15)$$

To understand these results, we assume that the values of e_1, e_2, m_1, m_2 are fixed and we consider whether the point is stable for different values of μ_1 and μ_2 . We can show that condition (15b) is always

satisfied when (15c) is. If we introduce the variable $\hat{P}_1 = 1 - e_1/m_1$, which is the fraction of habitats species 1 would occupy in the absence of species 2, then we can rewrite (15a) and (15c) to get the two conditions

$$\begin{aligned} \mu_2/m_2 &< 1 - (m_1/m_2)(\hat{P}_1/\hat{P}_2 - 1) & (a) \\ \mu_1/m_1 &> \hat{P}_1/\hat{P}_2. & (b) \end{aligned} \quad (16)$$

There are only two possibilities. If $\hat{P}_1 > \hat{P}_2$, then (16b) cannot be satisfied for any $\mu_1 < m_1$ and the boundary point is unstable (species 1 can invade). If $\hat{P}_1 < \hat{P}_2$, then (16a) is always satisfied and the boundary point is stable when (16b) is satisfied. Therefore, if $\hat{P}_1 < \hat{P}_2$ and μ_1 is large enough, species 2 can prevent species 1 from invading. In other words, if species 2 has a higher potential abundance than species 1, then species 2 can exclude species 1 from the region if it reduces the colonization rate of species 1 by a large enough amount.

By reversing the subscripts in (16), we can see that either both boundary points are unstable, in which case we would predict that coexistence of the two species is possible, or one of the points is unstable and the other stable, in which case we would predict that one species would always eliminate the other from the region. For the case on migration competition, then, it is not possible to have both of the boundary points stable, so there can be no "priority effect" where the first species in the region can exclude the other. These predictions were also verified by direct numerical calculations.

(3) Extinction competition. Levins and Culver (1971) introduced the term "extinction competition" to describe the situation in which the only effect of the competition between the two species is the increase of the extinction rates of both species when they are present in the same habitat. Each species is assumed to have no effect of the propagules of the other species. In terms of the present model, $\mu_1 = \mu_2 = 0$ and we consider whether the boundary points are stable for different values of ϵ_1 and ϵ_2 . The conditions (13) reduce to

$$\begin{aligned} m_1\hat{P}_0 - e_1 &< m_2\hat{P}_2 & (a) \\ m_1\hat{P}_2 - (e_1 + e_2) &< \epsilon_1 + \epsilon_2 & (b) \\ \frac{m_1\hat{P}_0 - e_1 - m_2\hat{P}_2}{(m_1 + m_2)\hat{P}_2} &> m_1\hat{P}_0 + e_2 + \epsilon_2 & (c) \end{aligned} \quad (17)$$

Condition (17a) does not depend on ϵ_1 or ϵ_2 . It states that \hat{P}_2 must be sufficiently large for exclusion to be possible, regardless of the degree of competition between the two species. It must be satisfied for the particular parameters being considered or the

boundary point is always unstable. The other two conditions can be written in the form

$$\begin{aligned} \epsilon_1 &> c_1 - \epsilon_2 & (a) \\ \epsilon_1 &> c_2 + c_3\epsilon_2 & (b) \end{aligned} \quad (18)$$

where

$$c_1 = m_1\hat{P}_2 - (e_1 + e_2) \quad (a)$$

$$c_2 = m_1\hat{P}_2 - (e_1 + e_2) - \frac{(m_1\hat{P}_0 + e_2)(m_1 + m_2)P_2}{m_1\hat{P}_0 - e_1 - m_2\hat{P}_2} \quad (b) \quad (19)$$

$$c_3 = 1 - \frac{(m_1 + m_2)\hat{P}_2}{m_1\hat{P}_0 - e_1 - m_2\hat{P}_2}. \quad (c)$$

Since $c_2 > c_1$ and $c_3 > -1$, (18a) is satisfied whenever (18b) is. Therefore (18b) is the only condition which we must consider. We can conclude that as long as (17a) is satisfied, there are large enough values for ϵ_1 that the boundary point is stable. We can interpret this result more easily by rewriting (17a) to get

$$(\hat{P}_1/\hat{P}_2 - 1) < m_2/m_1 \quad (20)$$

If $\hat{P}_1 < \hat{P}_2$ (20) is always satisfied and species 2 can exclude species 1 if it has a large enough effect on species 1 (ϵ_1 large enough). How large ϵ_1 must be depends on the exact values for the coefficients and on ϵ_2 . If $\hat{P}_1 > \hat{P}_2$ then species 2 can exclude species 1 only if m_2/m_1 is greater than one and if ϵ_1 is large enough. By reversing the subscripts we can show that the two boundary points cannot both be stable. Consequently there can also be no priority effect in the case of extinction competition.

DISCUSSION

We can summarize the results for the stability calculations of the boundary point, $P_2 = 1 - e_2/m_2$, $P_0 = e_2/m_2$, $P_1 = P_3 = 0$ as follows:

(1) Like species. The boundary point is always unstable and one species can invade when the other is present alone in the region.

(2) Migration competition. If $\hat{P}_1 > \hat{P}_2$, then species 1 can always invade, whereas if $\hat{P}_1 < \hat{P}_2$, then species 2 can exclude species 1 if $\mu_1/m_1 > \hat{P}_1/\hat{P}_2$.

(3) Extinction competition. If

$$(\hat{P}_1/\hat{P}_2 - 1) > m_2/m_1 \quad (21)$$

is satisfied, then species 1 can invade. If not, species 2 can exclude species 1 if

$$\epsilon_1 > c_2 + c_3\epsilon_2 \quad (22)$$

where c_2 and c_3 are given by (19).

The first result, that like species cannot exclude each other from a region by means of migration and extinction competition, is different from what one

might predict on the basis of intuition. It could be argued that similar species that have the same patterns of dispersal and the same food requirements would be most likely to exclude each other from a geographic region. That would be in agreement with Gause's principle (Gause 1934). However, we have found the opposite to be the case. Similar species can occupy the same geographic region even though they exclude each other from a single habitat. Since insects would be expected to have relatively large extinction rates and small habitat sizes, it seems likely that insect species that occupy the same ecological niche could be found in the same region, apparently in violation of Gause's principle.

We have found that competitive exclusion of species 2 by species 1 is most likely to occur when species 2 has the potential to be more abundant than species 1 ($\hat{P}_2 > \hat{P}_1$). Otherwise species 2 must have a very large effect on the extinction rate of species 1. In either case, the conditions for the exclusion of species 1 are such that species 1 cannot also exclude species 2, so there is no possibility of the priority effect in this model. From the analysis of the model, a common species in the region does not have much competitive advantage over a rare species simply because it is common. That is because the rate of colonization of new habitats is only proportional to the number of habitats already occupied. If the colonization rate increased more rapidly than a linear function of habitats occupied (for example with the square of the fraction of the habitats occupied) then the common species would have a greater advantage and the priority effect might be possible.

We have found that in two important ways—the coexistence of similar species and the lack of a priority effect—the predictions of this model differ from those based on the results of the theory of competition in a single community. The model can also be used to examine other problems of biological interest.

We reconsider the question that Levins and Culver raise of whether or not a rare species can exclude a species that could be relatively abundant in the region. If we assume that \hat{P}_2 is small, then with migration competition, a rare species cannot exclude a species which would be more abundant than itself at equilibrium alone (i.e., when $\hat{P}_1 > \hat{P}_2$). Under extinction competition, condition (21) cannot be satisfied if \hat{P}_2 is small and \hat{P}_1 is significantly greater than \hat{P}_2 unless $m_2 \gg m_1$. In this case, if ϵ_1 is large enough to satisfy (22), then species 2 can exclude species 1. Therefore, Levins and Culver's conclusion is correct, provided the rare species is sufficiently mobile (large m_2). Even though the rare species occupies only a small fraction of the habitats at any one time, it will affect a comparatively large number

of habitats during the time it takes for a relatively poor colonizer (small m_1) to establish itself. However, there must be extreme differences between the species for this situation to arise.

A second question we can ask is what the effect would be of a predator or some other external agent which had a detrimental effect on each of the species equally. We could imagine a situation where the two competing species occupy a collection of habitats that constitute some or all of the feeding range of some predators. We would assume that the foraging range of the predator is much larger than the habitat size of the prey. For example, a single population of birds could patrol a number of small islands or fields. The effect of the predator would be to increase the extinction rates of all of the prey species in its range. An herbicide or insecticide could have the same effect. Paine (1966) has proposed that predation in a single community can permit the coexistence of species which could otherwise not coexist.

In terms of this model, we can consider the question of whether an increase in the two extinction rates, e_1 and e_2 by the same amount can change a stable boundary point (exclusion of one species by the other) to an unstable point (coexistence of the two species). For the case of migration competition, exclusion of species 1 by species 2 can occur when $\hat{P}_1 < \hat{P}_2$ and

$$\mu_1/m_1 > \hat{P}_1/\hat{P}_2. \quad (23)$$

We let $e_1 = e_1 + k$ and $e_2 = e_2 + k$ where k is the increase in the extinction rates caused by the predator. If $m_2 - e_2 < m_1 - e_1$, then \hat{P}_1/\hat{P}_2 increases with positive values of k . Therefore, if k is large enough, then (23) will not be satisfied and coexistence will be possible. It has already been shown that the potential abundances of the two species (\hat{P}_1 and \hat{P}_2) are the most important quantities in determining the outcome of competition. In this example, even though the predator increases the extinction rate of each of the species by the same amount, its effect on \hat{P}_1 and \hat{P}_2 is not the same. The introduction of a predator can lead to coexistence when \hat{P}_2 is decreased by more than \hat{P}_1 . The same result is found for the case of extinction competition.

It would be possible, although complicated, to extend this type of model to more than two species competing for a single habitat type or for more than one habitat type. I think that the most important problems to be considered are the geographic aspect of the system, where the colonization probabilities depend on the distances of a habitat from the sources of colonists; and the effect of random fluctuations which have been ignored in this deterministic formulation. Skellam (1951) has analyzed the problem of the extension of the geographic range of a species

in the absence of competition. Frost (1972) has examined certain aspects of the stochastic problem.

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