

Competition and Coexistence in Regional Habitats

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ABSTRACT: Habitat heterogeneity plays a key role in the dynamics and structures of communities. In this article, a two-species meta-population model that includes local competitive dynamics is analyzed to study the population dynamics of two competing species in spatially structured habitats. When local stochastic extinction can be ignored, there are, as in Lotka-Volterra equations, four outcomes of interspecific competition in this model. The outcomes of competition depend on the competitive intensity between the competing pairs. An inferior competitor and a superior competitor, or two strongly competing species, can never stably coexist, whereas two weak competitors (even if they are very similar species) may coexist over the long term in such environments. Local stochastic extinction may greatly affect the outcomes of interspecific competition. Two competing species can or cannot stably coexist depending not only on the competitive intensity between the competing pairs but also on their precompetitive distributions. Two weak competitors that have similar precompetitive distributions can always regionally coexist. Two strongly competing species that competitively exclude each other in more stable habitats may be able to stably coexist in highly heterogeneous environments if they have similar precompetitive distributions. There is also a chance for an inferior competitor to coexist regionally or even to exclude a superior competitor when the superior competitor has a narrow precompetitive distribution and the inferior competitor has a wide precompetitive distribution.

Keywords: competition, exclusion, invasion, coexistence, habitat heterogeneity, local dynamics.

The competitive exclusion principle is a logical conclusion of Gause's experiments ([1934] 1964) and of Lotka-Volterra equations (Volterra [1926] 1931; Lotka 1932), which states that if two species occur together without niche differentiation, then one competing species will eliminate or exclude the other. Now, competitive exclusion has readily been accepted as an obvious principle and has gained an axiomatic status (Ekschmitt and Breckling 1994). However, the competitive exclusion principle immediately raises a paradox when applied to ecological communities (Hutchinson 1961). A generalized statement of competitive exclusion principle is that n species cannot coexist on fewer than n resources, or limiting factors (e.g., MacArthur and Levins 1964; Levins 1968; Tilman and Kareiva 1997). In contrast, a given habitat, such as a prairie or a lake, may contain hundreds of species, but the number of limiting resources—nutrients, light, space, and so forth—is relatively small, likely fewer than a dozen. This raises the question, when is the competitive exclusion principle valid and when is it not applicable? Since then, extensive hypotheses have been developed to explain the phenomena that many similar species persistently coexist in nature in spite of the validity of the exclusion principle.

Environmental fluctuations and unpredictable disturbances have been considered important factors affecting the properties of communities such as species composition, diversity, and niche overlap. It is argued that competition only structures communities at equilibrium, whereas environmental fluctuations and unpredictable disturbance would disrupt equilibria; prevent consistent effects of competition; and lead to ecological convergence, high niche overlap, and coexistence of many similar species (Hutchinson 1961; Wiens 1977; Hubbell 1979; Huston 1979; Connell 1980; Hubbell and Foster 1986; Ricklefs 1987). Ebenhoh (1994) showed in a model on phytoplankton communities that under conditions of pulsing limited resources, a large number of species may coexist and that the community is still open for invasions. According to this idea, there is no limit to the ecological similarity of coexisting species, as long as the species conform to a "trade-off condition" for growth parameters, which enables temporal organization of the competing species. However, after they reexamined the roles of harshness and

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environmental fluctuations, Chesson and Huntly (1997) proved that harshness alone does not lessen the importance of species interactions or limit their role in community structure, and fluctuations in environmental conditions only favor coexistence when fluctuations create spatial or temporal niche opportunities.

In recent years, metapopulation theories have been applied to interspecific competition, predicting that environmental heterogeneity may effectively support long-term coexistence of very similar species in model communities (Levins and Culver 1971; Slatkin 1974; Hanski 1983; Taneyhill 2000). Metapopulation dynamics is also by definition a stochastic process since the extinctions and recolonizations that form the two fundamental driving forces both involve chance events (Taneyhill 2000). The classic two-species metapopulation model (Slatkin 1974) assumes that local competitive exclusion rates in doubly occupied patches are constants, independent of their local density. So, it gives an unfair advantage to the species that happens to be regionally rarer. As Hanski (1999) pointed out, such models do not incorporate the usual situation in nature, where, if two species are really identical, the species to arrive first at a habitat patch should have a better chance of winning the patch than the later-arriving species because the first species will usually enter into local competition with a higher initial local abundance. Therefore, the regionally more common species should win more patches in local competition because it is more likely to arrive first at a given patch.

The goal of this article is to explore the competition dynamics of two competing species within regional habitats. The model we use is also based on the classic metapopulation model of two competing species (Slatkin 1974; Hanski 1983; Taneyhill 2000). We take the local competitive effects, expressed as functions of the two competing species' regional distributions, into consideration and examine the competitive dynamics in regional habitats. First, we consider a simple case that the local stochastic extinction can be ignored. The results show that the outcomes of competition in fragmented habitats depend on the competition intensity between the two competing pairs. Then, we analyze the competing dynamics within the true metapopulation model. The results show that local stochastic extinction may greatly affect the outcome of species competition. The analysis explains when two similar species exclude each other from regional habitats and when two completely competing species can stably coexist. The analysis also shows that the exclusion principle is not always valid in regional habitats.

The Model and Its Predictions

The model is based on the classic two-species metapopulation model constructed by Slatkin (1974). Let p_0 , p_1 , p_2 ,

and p_3 be the fractions of local patches that are occupied by neither of the species, species 1 alone, species 2 alone, and both species together. Let m_1 and μ_1 be the rates of colonization of species 1 to an empty habitat and a habitat occupied by species 2, respectively. We assume that the propagules are equally likely to come from any occupied habitat. Let ε_1 and e_1 be the extinction rates of species 1 caused by local stochastic extinction and by competitive effects of species 2, respectively. Colonization rates m_2 and μ_2 and extinction rates ε_2 and e_2 are defined in the same way.

The dynamics of the two competing species in a doubly occupied patch can be roughly described by Lotka-Volterra (Volterra [1926] 1931; Lotka 1932) equations or similar competition models (Taneyhill 2000). So, the competitive displacement rate in any one doubly occupied patch is correlated not only to the properties of the two competing species but also to their initial local density. For two species with comparable competition abilities, the one with higher initial local abundance will have a better chance to win the doubly occupied patch than its competitor. In other words, the competitive extinction rate of a species in a doubly occupied patch is negatively related with its local abundance and positively correlated with its competitor's local abundance. However, in fact, it is impossible for us to know the individual number of the two competitive species in any one doubly occupied patch. Instead, we use the assumption, which seems true in nature, that, because of emigration and colonization, species with wide distributions tend to be locally more abundant than species with narrow distributions (Hanski 1982, 1999; Brown 1984; Lawton 1993; Hanski and Gyllenberg 1997). Because of the positive relationship between a species' distribution and its local abundance and the positive relationship between the local abundance and its competitor's local competitive extinction rate, a positive relationship between a species' distribution and its competitor's average local competitive extinction rate also exists. In this case, the average local competitive extinction rate of a species in doubly occupied patches will be negatively correlated to the total proportions of the occupied patches by itself and positively correlated with the total proportions of the occupied patches of its competing species ($Y_i = p_i + p_3$). So, the average displacement rates of the two competing species in doubly occupied patches should be a function of $Y_1 = p_1 + p_3$ and $Y_2 = p_2 + p_3$, denoted as $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$. When the total fraction of the occupied patches by a species is small compared with that of the other species, the average local abundance of the former species in doubly occupied patches is relatively small and that species is prone to be excluded. When the total fraction of the occupied patches by a species is relatively large, the average local abundance of the species in doubly occupied

patches is large and its competitor is likely to be excluded rapidly.

Based on this argument, we get the deterministic equations for this system

$$\frac{dp_0}{dt} = -(m_1Y_1 + m_2Y_2)p_0 + \varepsilon_1p_1 + \varepsilon_2p_2, \quad (1a)$$

$$\begin{aligned} \frac{dp_1}{dt} &= m_1Y_1p_0 - \mu_2Y_2p_1 \\ &+ [e_2(Y_1, Y_2) + \varepsilon_2]p_3 - \varepsilon_1p_1, \end{aligned} \quad (1b)$$

$$\begin{aligned} \frac{dp_2}{dt} &= m_2Y_2p_0 - \mu_1Y_1p_2 \\ &+ [e_1(Y_1, Y_2) + \varepsilon_1]p_3 - \varepsilon_2p_2, \end{aligned} \quad (1c)$$

$$\begin{aligned} \frac{dp_3}{dt} &= \mu_1Y_1p_2 + \mu_2Y_2p_1 \\ &- [e_1(Y_1, Y_2) + e_2(Y_1, Y_2) + \varepsilon_1 + \varepsilon_2]p_3. \end{aligned} \quad (1d)$$

The equations have the similar form as the classic metapopulation model for interspecific competition (Slatkin 1974). The only difference is that we assume that the average local competitive displacement rates are the functions of the total fractions of the occupied patches of each competing species. To discuss the behavior of the model, we should write out the forms of $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$ explicitly. However, because there is no widely accepted model for the distribution–local abundance relationship (Hanski 1999) and the average time to local competitive exclusion for two species with different initial abundance is also very complicated, it is unlikely that there would be widely acceptable forms of $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$. In the following sections, we will consider two simple forms of $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$ to discuss the behavior of equations (1).

An Analytical Model

To begin our analysis, we first consider a simple case that the local stochastic extinction can be ignored ($\varepsilon_1 = \varepsilon_2 = 0$) as well as a simple form of $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$. Let e_1^0 be the extinction rate of species 1 and e_2^0 be the extinction rate of species 2 in a doubly occupied patch where the two competing species have the same initial local density. We assume that the average local extinction rate of a competing species is linearly correlated with its competitor’s distribution. Let $p_1^0, p_2^0,$ and p_3^0 be the specific values of $p_1, p_2,$ and $p_3,$ respectively, which will confirm that when $Y_1^0 = p_1^0 + p_3^0$ and $Y_2^0 = p_2^0 + p_3^0$ —the specific total fraction of habitats occupied by species 1 and 2—the two species have the same average abundance in

doubly occupied patches. In other words, when species 1 has the regional distribution Y_1^0 and species 2 has the regional distribution $Y_2^0,$ species 1 will have the average local competitive extinction rate e_1^0 and species 2 will have the average local competitive extinction rate e_2^0 in doubly occupied patches. When $Y_1 > Y_1^0$ and $Y_2 < Y_2^0,$ there are $e_1(Y_1, Y_2) < e_1^0$ and $e_2(Y_1, Y_2) > e_2^0.$ When $Y_1 < Y_1^0$ and $Y_2 > Y_2^0,$ there are $e_1(Y_1, Y_2) > e_1^0$ and $e_2(Y_1, Y_2) < e_2^0.$ In this case, $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$ can be written out as $e_1(Y_1, Y_2) = e_1^0Y_2/Y_2^0$ and $e_2(Y_1, Y_2) = e_2^0Y_1/Y_1^0.$ The system equations (1) can be written as

$$\frac{dp_0}{dt} = -(m_1Y_1 + m_2Y_2)p_0, \quad (2a)$$

$$\frac{dp_1}{dt} = m_1Y_1p_0 - \mu_2Y_2p_1 + \frac{e_2^0p_3Y_1}{Y_1^0}, \quad (2b)$$

$$\frac{dp_2}{dt} = m_2Y_2p_0 - \mu_1Y_1p_2 + \frac{e_1^0p_3Y_2}{Y_2^0}, \quad (2c)$$

$$\frac{dp_3}{dt} = \mu_1Y_1p_2 + \mu_2Y_2p_1 - \left(\frac{e_1^0Y_2}{Y_2^0} + \frac{e_2^0Y_1}{Y_1^0}\right)p_3. \quad (2d)$$

The best way to examine the properties of this model is to find all the equilibrium points of (2a)–(2d) that have acceptable values for the p_i ($p_i \geq 0$ and $\Sigma p_i = 1$) and to test the stability of each of the equilibrium points. Obviously, p_0 is a decreasing function of time, asymptotically approaching $p_0 = 0.$ Further, it is easy to find that there are three nontrivial equilibrium solutions of the system ($\hat{p}_0 = 0$):

$$\hat{p}_1 = 1, \hat{p}_2 = 0, \hat{p}_3 = 0; \quad (3a)$$

$$\hat{p}_1 = 0, \hat{p}_2 = 1, \hat{p}_3 = 0; \quad (3b)$$

$$\begin{aligned} \hat{p}_1 &= \frac{\frac{f_2}{\mu_2} \left(1 - \frac{f_1}{\mu_1}\right)^2}{1 - 3\frac{f_1}{\mu_1}\frac{f_2}{\mu_2} + \frac{f_1}{\mu_1}\left(\frac{f_2}{\mu_2}\right)^2 + \left(\frac{f_1}{\mu_1}\right)^2\frac{f_2}{\mu_2}}, \\ \hat{p}_2 &= \frac{\frac{f_1}{\mu_1} \left(1 - \frac{f_2}{\mu_2}\right)^2}{1 - 3\frac{f_1}{\mu_1}\frac{f_2}{\mu_2} + \frac{f_1}{\mu_1}\left(\frac{f_2}{\mu_2}\right)^2 + \left(\frac{f_1}{\mu_1}\right)^2\frac{f_2}{\mu_2}}, \\ \hat{p}_3 &= \frac{1 + \frac{f_1}{\mu_1}\frac{f_2}{\mu_2} - \frac{f_1}{\mu_1} - \frac{f_2}{\mu_2}}{1 - 3\frac{f_1}{\mu_1}\frac{f_2}{\mu_2} + \frac{f_1}{\mu_1}\left(\frac{f_2}{\mu_2}\right)^2 + \left(\frac{f_1}{\mu_1}\right)^2\frac{f_2}{\mu_2}}, \end{aligned} \quad (3c)$$

and where $f_1 = e_1^0/Y_2^0$ and $f_2 = e_2^0/Y_1^0.$ We interpret equations (3a) as species 1 being present in the region alone,

equations (3b) as species 2 being present in the region alone, and equations (3c) as the coexistence of the two species. The stability of the three equilibrium points can be found directly (table 1). The stable condition at the internal equilibrium point corresponds to the unstable conditions of two boundary equilibrium points.

When $e_1^0/\mu_1 < Y_2^0$ and $e_2^0/\mu_2 > Y_1^0$ or $e_1^0/\mu_1 > Y_2^0$ and $e_2^0/\mu_2 < Y_1^0$, there is no internal equilibrium point and only one boundary equilibrium point is stable. In these cases, one species invariably outcompetes the other in all the regional habitats. The first two inequalities indicate that species 1 will drive species 2 to extinction regionally and occupy all patches, while the last two inequalities indicate that species 2 will be the winner.

When $e_1^0/\mu_1 > Y_2^0$ and $e_2^0/\mu_2 > Y_1^0$, both of the boundary equilibria are stable and the internal equilibrium point is unstable. Which of these two outcomes, either species 1 or 2 alone, is actually attained is determined by the initial densities: the species that has the initial advantage will drive the other species to extinction. This case may occur in situations of two strongly interspecific competitors.

Finally, when $e_1^0/\mu_1 < Y_2^0$ and $e_2^0/\mu_2 < Y_1^0$, the interior equilibrium point is stable and the two boundary equilibria are unstable. In this case, two competing species can coexist stably in regional habitats. Obviously, the stability of the coexistence and the fraction of doubly occupied patches, if there is coexistence, are determined by the parameters of the system, not by initial conditions. Increasing colonization rate (μ_i) enlarges the stable region of interior equilibrium and the fraction of doubly occupied patches. On the contrary, increasing local competitive exclusion rate (e_i^0) reduces the fraction of doubly occupied patches and the stable region of interior equilibrium.

An Alternative Approach to Local Dynamics

Although the equilibrium points of the analytical model (eqq. [2]) can be solved directly, we had to introduce two new parameters, Y_1^0 and Y_2^0 . To avoid this disadvantage, we consider an alternative form of $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$. We still define e_1^0 as the extinction rate of species 1 and e_2^0 as the extinction rate of species 2 in a doubly occupied patch where the two competing species have the same initial local density. A further assumption is that the two competing species have the same reproduction and dispersal form. So, they have the same regional distribution–local abundance relationship. We show that $e_1(Y_1, Y_2) = 2e_1^0 Y_2 / (Y_1 + Y_2)$ and $e_2(Y_1, Y_2) = 2e_2^0 Y_1 / (Y_1 + Y_2)$. The meaning of the two forms is obvious. For example, for two competing species, when the two species have a similar distribution, they will have similar average local abundance. Then species 1 will have an average local competitive extinction rate e_1^0 and species 2 will have an

Table 1: Stability conditions of different equilibrium solutions

p_1	p_2	p_c
$\frac{e_2^0}{\mu_2} > Y_1^0$	$\frac{e_1^0}{\mu_1} > Y_2^0$	$\frac{e_1^0}{\mu_1} < Y_2^0; \frac{e_2^0}{\mu_2} < Y_1^0$

Note: Equilibrium solutions refer to equations (3a)–(3c); p_1 = boundary equilibrium point of species 1 present alone; p_2 = boundary equilibrium point of species 2 present alone; p_c = internal equilibria of the coexistence of two competing species.

average local competitive extinction rate e_2^0 in doubly occupied patches. When the two species have very different regional distributions, the species with the small distribution will have low local abundance and a higher local extinction rate, while its competitor will have a very low local extinction rate. Still, we ignore the local stochastic extinction, and the system of equations (1) can be written as

$$\frac{dp_0}{dt} = -(m_1 Y_1 + m_2 Y_2) p_0, \quad (4a)$$

$$\frac{dp_1}{dt} = m_1 Y_1 p_0 - \mu_2 Y_2 p_1 + \frac{2e_2^0 p_3 Y_1}{(Y_1 + Y_2)}, \quad (4b)$$

$$\frac{dp_2}{dt} = m_2 Y_2 p_0 - \mu_1 Y_1 p_2 + \frac{2e_1^0 p_3 Y_2}{(Y_1 + Y_2)}, \quad (4c)$$

$$\frac{dp_3}{dt} = \mu_1 Y_1 p_2 + \mu_2 Y_2 p_1 - \frac{2p_3(e_1^0 Y_2 + e_2^0 Y_1)}{(Y_1 + Y_2)}. \quad (4d)$$

As in the analytical model (eqq. [2]), the best way to discuss the behavior of the equations is to find all the equilibrium points. However, it is not practical to solve equations (4) for internal equilibria. Following Slatkin (1974), we can set one species at equilibrium in the region, in the absence of the other, and ask whether the second can invade.

As in the previous model, for all equilibria, $\hat{p}_0 = 0$. That is, at equilibrium, all patches will be occupied. Then, we have $\hat{p}_1 + \hat{p}_2 + \hat{p}_3 = 1$. So, only two of the three equilibria \hat{p}_1 , \hat{p}_2 , and \hat{p}_3 are independent of each other. It is easy to find that there are two boundary equilibrium points ($\hat{p}_0 = 0$):

$$\hat{p}_1 = 1, \hat{p}_2 = 0, \hat{p}_3 = 0; \quad (5a)$$

$$\hat{p}_1 = 0, \hat{p}_2 = 1, \hat{p}_3 = 0. \quad (5b)$$

We will discuss the stability of the two boundary equilibrium points and argue whether either is stable. If either boundary point is unstable, there is at least one stable internal equilibrium point. It is easy to prove that the

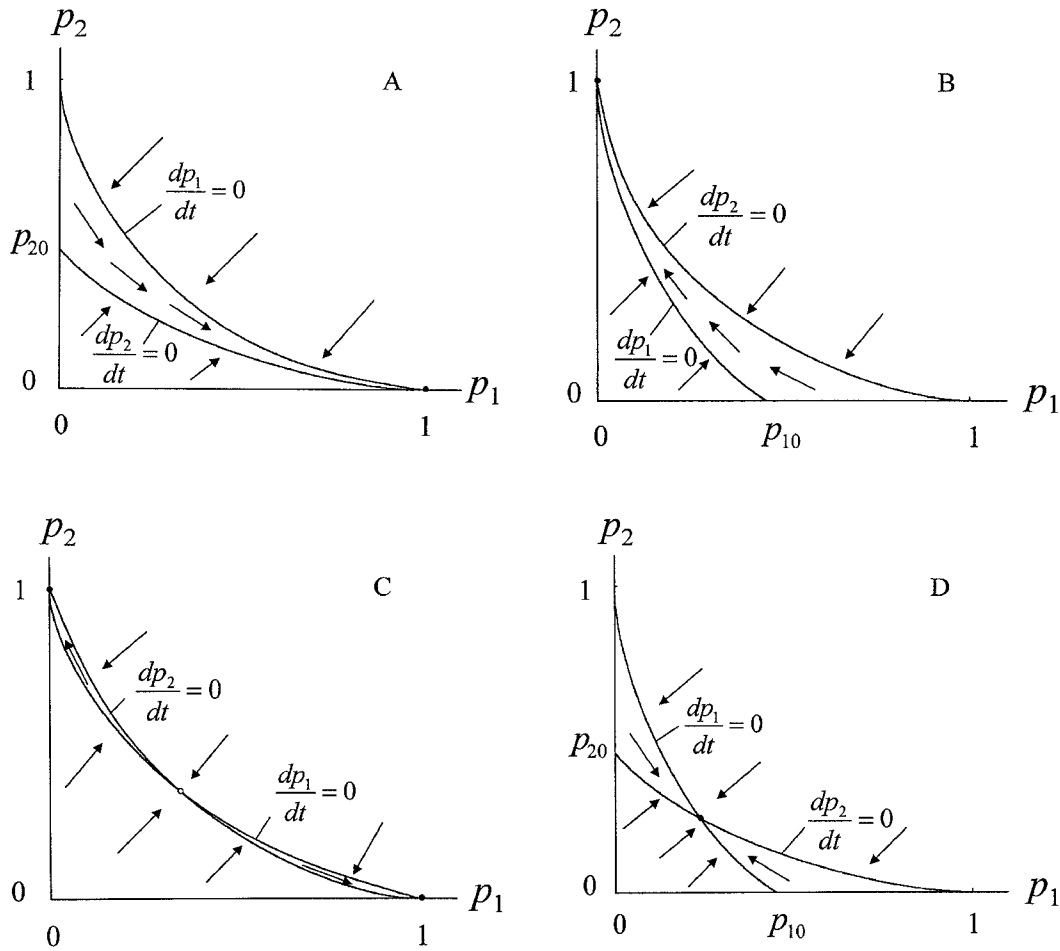


Figure 1: The outcomes of the competition generated by the two-species competition model (eqq. [4]). The vectors refer to the directions of competition, and the solid circles show stable equilibrium points, where $p_{10} = 1 - \sqrt{1 - (2e_2^0/\mu_2)}$ and $p_{20} = 1 - \sqrt{1 - (2e_1^0/\mu_1)}$.

stability condition of the boundary equilibrium point at which only species 1 is present (eq. [5a]) is

$$\frac{e_2^0}{\mu_2} > \frac{1}{2}. \tag{6a}$$

The boundary equilibrium point at which only species 2 is present (eq. [5b]) is

$$\frac{e_1^0}{\mu_1} > \frac{1}{2}. \tag{6b}$$

When neither of the two expressions of (6a) and (6b) can be satisfied, there is at least one stable internal equilibrium point, and the stability conditions of the internal equilibrium points are

$$\frac{e_1^0}{\mu_1} < \frac{1}{2}, \quad \frac{e_2^0}{\mu_2} < \frac{1}{2}. \tag{6c}$$

To further understand the behavior of the model, we use the zero isoclines to illustrate the above results (fig. 1). For simplification, we set $p_0 = 0$ in equations (4). Therefore, at equilibrium, there are only two independent equations of the four equations. As in the Lotka-Volterra model of interspecific competition (Begon et al. 1996), there are four different ways in which the two zero isoclines can be arranged relative to one another, and the outcomes of competition will be different in each case. The different cases can be defined and distinguished by the parameters of the system. We will discuss them respectively.

In figure 1A, $e_1^0/\mu_1 < 1/2$ and $e_2^0/\mu_2 > 1/2$. In this case, species 1 is a strong interspecific competitor, and species 2 is a weak interspecific competitor. The two species can

never stably coexist because species 1 will displace species 2 regionally and occupy all patches.

In figure 1B, $e_1^0/\mu_1 > 1/2$ and $e_2^0/\mu_2 < 1/2$. Under these conditions, the situation is reversed, and species 2 will exclude species 1 from all patches.

In figure 1C, $e_1^0/\mu_1 > 1/2$ and $e_2^0/\mu_2 > 1/2$. Both species are strong competitors. Though there is one internal equilibrium point, the internal equilibrium point is unstable. The outcomes of the competition that is actually attained are determined by the initial densities. The species that has the initial advantage will drive the other species to extinction regionally and occupy all the patches.

Finally, in figure 1D, $e_1^0/\mu_1 < 1/2$ and $e_2^0/\mu_2 < 1/2$. In this case, the interior equilibrium point is stable, and the two boundary equilibria are unstable. Each species has little competitive effect on the other species. Two competing species can stably coexist in regional habitats, in spite of their initial densities. These inequalities prove the general conditions for the stable coexistence of two competing species in spatially constructed but locally stable habitats.

The above two model approaches to local dynamics, equations (2) and equations (4), have similar behaviors. Both give out the conditions for regional coexistence of two competing species. However, the coexistence conditions in the second approach are stricter than those of the analytical model. For example, for two similar species, there are $Y_1^0 = Y_2^0 > 1/2$ (because $Y_1^0 = p_1^0 + p_3^0$, $Y_2^0 = p_2^0 + p_3^0$, and $p_1^0 + p_2^0 + p_3^0 = 1$). Two competitive species may coexist stably in the analytical model, but they may not be able to stably coexist in the general approach model.

The True Metapopulation Approach

To further our study and to make a comparison with original work (e.g., Slatkin 1974; Hanski 1983; Taneyhill 2000), we take the local stochastic extinction into consideration. We discuss one form of the above approaches to local competition dynamics. It is easy to prove that the other form have the same modeling behavior. Let $e_1(Y_1, Y_2) = 2e_1^0 Y_2 / (Y_1 + Y_2)$ and $e_2 = 2e_2^0 Y_1 / (Y_1 + Y_2)$ and the system equations (1) be written as

$$\frac{dp_0}{dt} = -(m_1 Y_1 + m_2 Y_2) p_0 + \varepsilon_1 p_1 + \varepsilon_2 p_2, \quad (7a)$$

$$\frac{dp_1}{dt} = m_1 Y_1 p_0 - \mu_2 Y_2 p_1 + \frac{2e_2^0 p_3 Y_1}{(Y_1 + Y_2)} - \varepsilon_1 p_1 + \varepsilon_2 p_3, \quad (7b)$$

$$\frac{dp_2}{dt} = m_2 Y_2 p_0 - \mu_1 Y_1 p_2 + \frac{2e_1^0 p_3 Y_2}{(Y_1 + Y_2)} - \varepsilon_2 p_2 + \varepsilon_1 p_3, \quad (7c)$$

$$\frac{dp_3}{dt} = \mu_1 Y_1 p_2 + \mu_2 Y_2 p_1 - \frac{2p_3(e_1^0 Y_2 + e_2^0 Y_1)}{(Y_1 + Y_2)} - (\varepsilon_1 + \varepsilon_2) p_3. \quad (7d)$$

As in the classic metapopulation model (Slatkin 1974), the internal equilibrium points cannot be solved analytically. Here, following the methods used by Slatkin (1974) and Hanski (1983), we discuss the stability of two boundary equilibrium points and find whether there are stable interior equilibrium points.

Since $p_0 + p_1 + p_2 + p_3 = 0$, only three equations are independent in the above system model. The boundary equilibrium point of species 2 can be written out directly:

$$\hat{p}_0 = \frac{\varepsilon_2}{m_2}, \hat{p}_1 = 0, \hat{p}_2 = 1 - \frac{\varepsilon_2}{m_2}, \hat{p}_3 = 0. \quad (8)$$

Following Hanski (1983), the system linear differential equations are

$$\frac{d}{dt} \begin{bmatrix} p_1' \\ p_2' \\ p_3' \end{bmatrix} = \mathbf{A} \begin{bmatrix} p_1' \\ p_2' \\ p_3' \end{bmatrix}, \quad (9)$$

where $p_i' = p_i - \hat{p}_i$ for $i = 0, 1, 2, 3$, and $p_0' + p_1' + p_2' + p_3' = 0$. The matrix \mathbf{A} has the coefficients

$$\begin{aligned} a_{11} &= m_1 \hat{p}_0 - \varepsilon_1 - \mu_2 \hat{p}_2, \\ a_{12} &= 0, \\ a_{13} &= m_1 \hat{p}_0 + \varepsilon_2, \\ a_{21} &= -(m_2 + \mu_1) \hat{p}_2, \\ a_{22} &= -m_2 \hat{p}_2, \\ a_{23} &= m_2 \hat{p}_0 - m_2 \hat{p}_2 - \mu_1 \hat{p}_2 + \varepsilon_1 + 2e_1^0, \\ a_{31} &= (\mu_1 + \mu_2) \hat{p}_2, \\ a_{32} &= 0, \\ a_{33} &= \mu_1 p_2 - \varepsilon_1 - \varepsilon_2 - 2e_1^0. \end{aligned}$$

The stability of the boundary equilibrium point of species 2 is determined by the eigenvalues of \mathbf{A} . Since $a_{12} = a_{32} = 0$ and $a_{22} = -m_2 \hat{p}_2$, one of the eigenvalues of \mathbf{A} is real and negative. Thus, the local stability of the boundary equilibrium point depends on two conditions:

$$a_{11} + a_{33} < 0, \quad (10a)$$

$$a_{13} a_{31} < a_{11} a_{33}. \quad (10b)$$

Because of the complex forms of equations (10), it is difficult to further the discussion on the criteria for the invasibility directly. Here, we consider two special cases:

two like species ($m_1 = m_2 = m$, $\mu_1 = \mu_2 = \mu$, $\varepsilon_1 = \varepsilon_2 = \varepsilon$, and $e_1^0 = e_2^0 = e^0$) and two species with the same colonization rate ($m_1 = m_2 = m$, $\mu_1 = \mu_2 = \mu$) but different local extinction rate.

It is easy to prove that, for each of the above two cases, it is always true that $a_{11} + a_{33} < 0$. That is, equation (10a) can always be satisfied. So, for the two cases below, we just need to discuss equation (10b). If (10b) is satisfied, the boundary is stable and species 2 can prevent species 1 from invading. If (10b) is not satisfied, the boundary point is unstable and species 1 can invade the region occupied by species 2.

Two Like Species. Equation (10b) reduces to

$$2e^0 - \mu > \varepsilon \left(2 - \frac{\mu}{m} \right). \quad (11)$$

When the local stochastic extinction rate is very low, much less than that of the local competitive displacement rate, equation (11) reduces to $2e^0 > \mu$. This is just the result in the “alternative approach model” for two like species. Whether a species can invade its competitor’s habitat depends on the intensity of interspecific competition only. When local stochastic extinction rate is larger than local competitive displacement rate ($\varepsilon > e^0$), equation (11) reduces to $e^0 - \mu > \varepsilon[1 - (\mu/m)]$. Because it is always true that $0 < \mu < m$ and $e^0 < \mu$, the equation can never be satisfied. In this case, a species can always invade the region occupied by its competitor, and the two competing species can stably coexist. If $0 < \varepsilon < e^0$, the outcome of competition is related not only to the interspecific competitive intensity of the competing pairs but to other parameters of the system (e.g., local stochastic extinction rate and the colonization ability). The stability region of boundary equilibrium point decreases with the increasing of local stochastic extinction rate. In other words, local stochastic extinction promotes regional coexistence of like species. In this case, two intrinsically rare like species are more likely to coexist than two intrinsically common like species. This is different from Hanski’s (1983) conclusion.

Two Species with the Same Colonization Rate. Equation (10b) reduces to

$$(\varepsilon_2 - \varepsilon_1 - \mu\hat{p}_2)(\mu\hat{p}_2 - \varepsilon_1 - \varepsilon_2 - 2e_1^0) - 4\mu\varepsilon_2\hat{p}_2 > 0. \quad (12)$$

To understand the effects of local stochastic extinction on the dynamics of regional competition, it is convenient to define a new variable φ :

$$\varphi = (\varepsilon_2 - \varepsilon_1 - \mu\hat{p}_2)(\mu\hat{p}_2 - \varepsilon_1 - \varepsilon_2 - 2e_1^0) - 4\mu\varepsilon_2\hat{p}_2.$$

It is easy to prove that φ is an increasing function of ε_1 [$\partial\varphi/\partial\varepsilon_1 = 2(\varepsilon_1 + e_1^0) > 0$] and a decreasing function of ε_2 ($\partial\varphi/\partial\varepsilon_2 < 0$ since $|\partial\varphi/\partial\varepsilon_2|_{\varepsilon_2=0} < 0$, $|\partial\varphi/\partial\varepsilon_2|_{\varepsilon_2=m} < 0$, and $\partial^2\varphi/\partial\varepsilon_2^2 < 0$). Because $0 \leq \varepsilon_1 \leq m$ and $0 \leq \varepsilon_2 \leq m$, it is necessary for us to discuss the value of φ at the following four points

$$\varphi(\varepsilon_1 = 0, \varepsilon_2 = 0) = \mu(-\mu + 2e_1^0), \quad (13a)$$

$$\varphi(\varepsilon_1 = m, \varepsilon_2 = 0) = (m + \mu)(m - \mu + 2e_1^0) > 0, \quad (13b)$$

$$\varphi(\varepsilon_1 = 0, \varepsilon_2 = m) = -m(m + 2e_1^0) < 0, \quad (13c)$$

$$\varphi(\varepsilon_1 = m, \varepsilon_2 = m) = 0. \quad (13d)$$

Equation (13a) is just the case of the above alternative approach model, and the necessary and sufficient condition for $\varphi(\varepsilon_1 = 0, \varepsilon_2 = 0) > 0$ is $\mu < 2e_1^0$. The four equations indicate that local stochastic extinction has an important influence on the outcomes of two-species competition. The invasibility of species 1 to a habitat occupied by species 2 decreases with increasing ε_1 and increases with increasing ε_2 . A species may be a competition winner if it has a low stochastic extinction rate but will be regionally excluded by its competitor if it has a high local stochastic extinction rate, while its competitor has a low local stochastic extinction rate. Because a species’ precompetitive distribution (\hat{p}_i ; $i = 1, 2$) decreases with increasing ε_i ($i = 1, 2$), it is difficult for a species with narrow distribution to invade the region occupied by a competing species with wide distribution. It is obvious that a criterion should exist to set the boundary between the stable and unstable region of the boundary equilibrium.

By reversing the subscripts in (12), we get the stability condition for the boundary point of species 1:

$$(\varepsilon_1 - \varepsilon_2 - \mu\hat{p}_1)(\mu\hat{p}_1 - \varepsilon_1 - \varepsilon_2 - 2e_2^0) - 4\mu\varepsilon_1\hat{p}_1 > 0. \quad (14)$$

By solving equations (12) and (14), we can get the criteria that the two species can stably coexist when they competitively exclude each other from regional habitat. However, it is difficult to get a simple form of the criteria. Instead, the ways equations (12) and (14) set the boundary between the boundary equilibrium point region and interior equilibrium region in the parameter space is illustrated in figure 2. Obviously, the competition intensity between the two competing pairs as well as their local stochastic extinction have important effects on the outcomes of regional competition. Two weak competitors ($\mu > 2e_1^0$ and $\mu > 2e_2^0$) can always regionally coexist if they

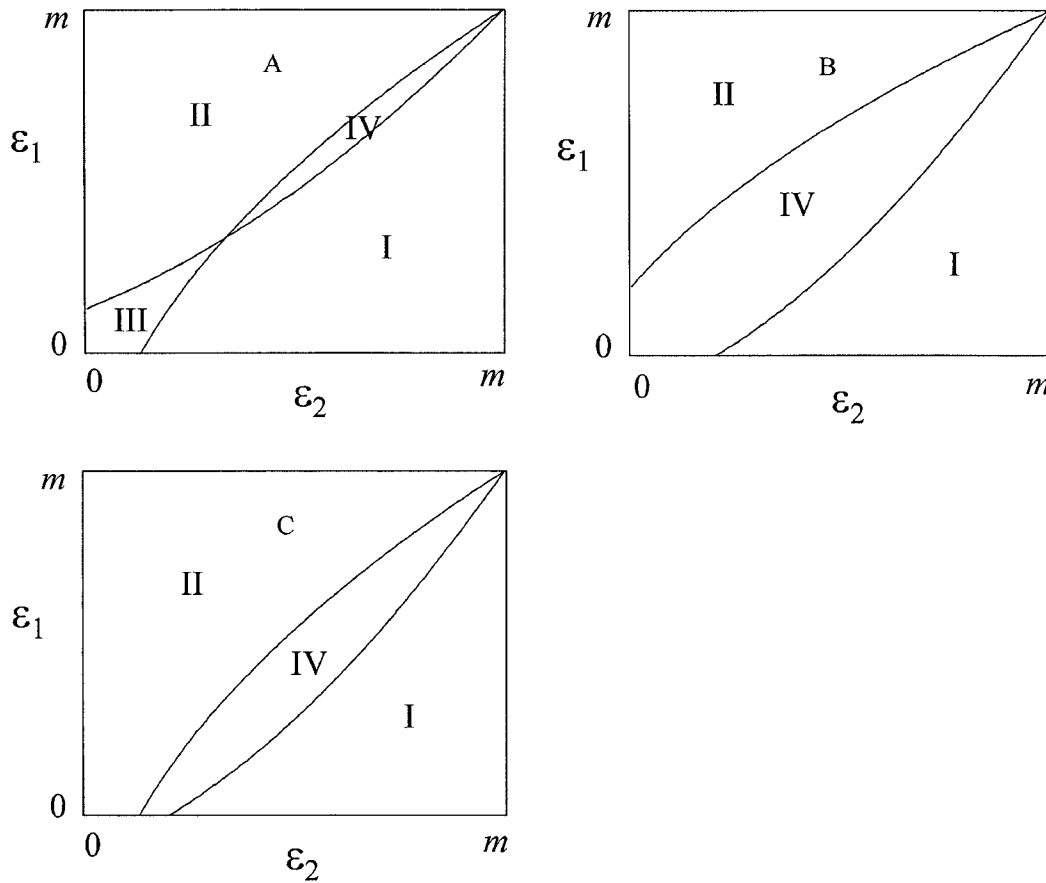


Figure 2: The stability of boundary equilibria generated by equations (12) and (14). A, Competition between two strongly competitive species, $\mu < 2e_1^0$ and $\mu < 2e_2^0$. B, Competition between two weak competitors, $\mu > 2e_1^0$ and $\mu > 2e_2^0$. C, Competition between an inferior competitor and a superior competitor, $\mu < 2e_1^0$ and $\mu > 2e_2^0$. In region I, the boundary equilibrium $p_1^* = 1 - (\epsilon_1/m)$ is stable, and in region II, the boundary equilibrium $p_2^* = 1 - (\epsilon_2/m)$ is stable. In region III, both equilibria are stable, and in region IV, both boundary equilibria are unstable (two-species regional coexistence).

have not much different local stochastic extinction. Two strongly competing species ($\mu < 2e_1^0$ and $\mu < 2e_2^0$) that competitively exclude each other in a stable environment may be able to stably coexist in highly heterogeneous habitats if they have similar local stochastic extinction rates. There is also a chance for an inferior competitor to regionally coexist or to exclude a superior competitor when the superior competitor has a high local stochastic extinction rate and the inferior competitor has a low local stochastic extinction rate.

Discussion

The classic two-species metapopulation model (Slatkin 1974) assumes that the local competitive exclusion rates of two competing species are constants. This gives unfair advantage to the species that happens to be regionally rarer

(Hanski 1999). To overcome this shortcoming, Hanski (1983) assumed that a species extinction probability decreases with the increasing of the species regional abundance. Hanski's (1983) rescue effect is more reasonable for local stochastic extinction events than for local competitive exclusion. In Taneyhill's (2000) article, for example, a distinct expression of rescue effects on local competitive exclusion is assumed. In that model, when p_2 is very little (approaching zero), the competitive exclusion rate of species 2 by species 1 is ϵ_{21} , and it should be at its maximum value. At the same time, species 1 still has a competitive extinction rate of $\epsilon_{12}(1 - \omega_1 p_1)$. It is difficult to imagine how a nearly extinct species can produce such large competitive effects.

The aim of this study was an attempt to take the local competition effects into the two-species metapopulation model. By assuming that a species' local density is posi-

tively related to its regional abundance, the local competitive displacements in doubly occupied patches are expressed by the system parameters. The difference between this model and Hanski's (1983) rescue effects is obvious. An important assumption in Hanski's (1983) model is that high migration rates from existing large populations may additionally "rescue" small populations from extinction (Hanski and Gyllenberg 1997). So, it is mainly about how a species' regional distribution influences its local extinction. In this model, it is assumed that a species' local competitive extinction both depends on the competitive intensity between the two competitors (as in classic models) and on their local densities (expressed by two-species regional abundance). So, the two modeling approaches have much different ecological meaning. In this model, we studied two cases: competition in spatially fragmented habitats (without local stochastic extinction) and a true metapopulation model.

In the cases where local stochastic extinction can be ignored, we first assumed that the average local extinction rate of a species is proportional to its competitor's distribution. The factors Y_1^0 and Y_2^0 can be determined in the following way. First, we should find out the average carrying capacity of the local patches. Then, by using the distribution-abundance relationship (e.g., Hanski and Gyllenberg's [1997] DA curve), we can find the values of Y_1^0 and Y_2^0 , which will confirm that there are, on average, equal abundance of the two species in doubly occupied patches. The advantage of the assumption is that all the equilibrium points of the model can be solved analytically. The disadvantage is that there is no widely accepted distribution-abundance relationship, which thus creates difficulty in determining the values of Y_1^0 and Y_2^0 . Then, to overcome the above disadvantage, we assumed another form of local competitive displacement rate of $e_1(Y_1, Y_2)$ and $e_2(Y_1, Y_2)$. Though the internal equilibrium point could not be solved directly, we still could analyze the behavior of the model by discussing the character of the boundary equilibrium points.

The two different models have similar behavior. There are, as in the Lotka-Volterra model, four outcomes of the competition of two competing species in the model. Two competing species can or cannot coexist in regional habitats depending on the intensity of competition. Two strongly competitive species (with high locally competitive displacement rates or low invasion rates or both) can never stably coexist, while two weakly competitive species (with low locally competitive displacement rates and high invasion rates) can coexist regionally over the long term. Increasing the invasion abilities of each species to its competitor's patches (μ_1 and μ_2) or decreasing the locally competitive displacement rates (e_1^0 and e_2^0) in doubly occupied patches will favor coexistence.

When local stochastic extinction cannot be ignored, we analyzed a true metapopulation model. Local stochastic extinction greatly influences the dynamics of two competing species. The competition outcomes of two similar species are related not only to their competitive intensity but also to their precompetitive distribution (expressed as a decreasing function of local stochastic extinction in this model). For two similar species, two weak competition pairs can always stably coexist, while two strong competition pairs can only regionally coexist in highly heterogeneous habitats (with a high local stochastic extinction rate). Habitat heterogeneity promotes coexistence of like species. In this case, two intrinsically rare similar species are more likely to coexist than two intrinsically common like species. This is different from the conclusions of Hanski's (1983) model.

A species' precompetitive distribution largely determines whether it will be successful in interspecific competition. The invasibility of a species to a habitat occupied by its competitor decreases with the increase of its local stochastic extinction rate. Competitive exclusion of species 1 by species 2 is more likely to occur when species 2 has the potential to be more abundant than species 1. In this case, a common species in the region has a competitive advantage over a rare species. This is in agreement with Hanski's (1983) result but is different from Slatkin's (1974) result. The difference comes from the fact that Slatkin's (1974) model assumed that local competitive exclusion rate of two competing species is independent of their local density. In this model, we assumed that the competitive exclusion of a species decreases with increases in its local density (expressed as an increasing function of its regional abundance and a decreasing function of its competitor's regional abundance). So, the regionally common species has a better chance of winning in local competition. There is also a chance for an inferior competitor to regionally coexist with or exclude a superior competitor when the superior competitor has a high local stochastic extinction rate and the inferior competitor has a low local stochastic extinction rate.

The prediction of the competitive exclusion of two strongly competing species in more stable habitats is consistent with competitive exclusion principle that species coexistence requires niche difference (Gause [1934] 1964; Hutchinson 1959; Hardin 1960; MacArthur and Levins 1967; Begon et al. 1996). Similar species have similar distributions due to shared habitat requirements. However, because of their highly competitive intensity, they are more likely to exclude each other from local patches and thus from regional habitat. This is different from the results of our previous model (Wang et al. 2000) and the metapopulation models (e.g., Slatkin 1974), in which two completely competing species can always coexist regionally.

However, two weakly competitive species can stably coexist in regional habitats. This situation may occur when the two competing species are sufficiently dissimilar or when the local competitive displacement rates of the two species are sufficiently low. For the second case, the coexistence of two competing species in regional habitats does not need a niche difference. These cases can always be seen in higher plants and some marine invertebrates. Although there is obviously competition among higher plants (Harper 1977), competitive displacement always takes a long time, even in a small local population (Hubbell 1979; Hubbell and Foster 1986). However, seeds of higher plants can colonize patches that are a little far from the maternal plants (Begon et al. 1996). In this case, competition does not have an appreciable effect on properties of communities such as species composition, diversity, and niche overlap. It is consistent with the assumption that niche differentiation is not an important mechanism of coexistence in plant communities (Hubbell 1979; Aarssen 1983; Shmida and Ellner 1984; Hubbell and Foster 1986; Silvertown and Law 1987; Mahdi et al. 1989; Goldberg and Barton 1992; Laurie and Cowling 1994), although all green plants have similar resource requirements (light, carbon dioxide, and water) and the same mineral nutrients (Grubb 1977). The coexistence in a local patch may be transitory, but regional coexistence may be maintained through immigration. The coexistence of very similar species in regional habitats is a stable state. It is a dynamic equilibrium of locally competitive displacement and recolonization.

The results that two similar species can regionally coexist in heterogenous environments obviously invalidate the competitive exclusion principle. The validity of competitive exclusion principle, as well as of its theoretical implications, is primarily confined to homogeneous environments and to environments of restricted extent (Ekschmitt and Breckling 1994). In heterogenous environments, not only the competition intensity between two competition pairs but also their colonization and local stochastic extinction can produce large effects on two species' competing dynamics. Maybe that is why most of the laboratory experiments support the principle, while many empirical observations invalidate it. It is not surprising that, when the habitats are artificially structured in laboratory experiments, two originally excluded species may stably coexist (Gotelli 1997). It is also possible that large parts of classical ecological theory mainly apply to artificial laboratory situations.

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