

# **Competition and Coexistence in Spatially Subdivided Habitats**

ZONG-LING WANG\*<sup>†</sup>, JING-GUANG ZHANG\* AND XIN-MIN LIU<sup>‡</sup>

\*State Key Laboratory of Arid Agroecology, Lanzhou University, Lanzhou 730000, Gansu,

People's Republic of China

Shapotou Experimental Station of Desert Research, Chinese Academy of Sciences, Zhongwei 751702, Ningxia, People's Republic of China

(Received on 10 June 1999, Accepted in revised form on 4 May 2000)

While non-spatial models predict that like species cannot stably coexist, empirical studies suggest that similar species have similar distributions due to shared habitat requirements. A model is developed to discuss competition and coexistence in subdivided but locally stable habitats. The model predicts that in some cases it is possible for one species to exclude the other species from a geographic region, while in other cases two competing species can stably coexist. The equilibrium level and the fraction of doubly occupied patches, if there is coexistence, are determined by the strength of competition on colonization and exclusion in such a system. Also, it is possible for two ecologically identical species to stably coexist, and two asymmetrically competing species can coexist when there is a trade-off between local competition ability and invasion ability. When rescue effects are considered, the stable region at internal equilibrium point would be reduced, but the fraction of doubly occupied patches would be enlarged.

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## 1. Introduction

Although Gause's law has become widely accepted, the mechanism of coexistence of competitive species still remains a central problem that attracts the attention of many ecologists (Begon *et al.*, 1996; Wang & Zhang, 1997). On the one hand, the Lotka–Volterra model of interspecific competition predicts that two ecologically identical species cannot coexist at equilibrium in a stable environment. This acts as the theoretical ground for the competitive exclusion principle. On the other hand, it has been suggested that similar species have similar distributions due to

†Author to whom correspondence should be addressed. Present address: First Institute of Oceanography, State Oceanic Administration, Xianxialing Road, Qingdao, 266061, Shandong, P. R. China. E-mail: wangzl@lzu.edu.cn shared habitat requirements. Empirical studies show that, in stable environments, many like species may live together to compete for limiting resources, and the strength of the competition will increase with increasing productivity (Brown & Davidson, 1977). For example, more than 100 species coexist with little bluestem in grasslands and native prairie in which nitrogen is the only limiting resource (Tilman, 1994).

Of course, there are no two identical species in nature, but the competitive exclusion principle is of great theoretical importance for understanding the role of competition and coexistence in community ecology. In recent years, it has been considered that the heterogeneity of environments is an essential factor controlling the species dynamics and biodiversity of many communities (Gilpin & Hanski, 1991; Tilman, 1994; Hanski & Gilpin, 1997; Tilman *et al.*, 1997). Theoretical models have demonstrated that heterogeneous environments may allow competing species, two congruent species (Levins & Culver, 1971; Slatkin, 1974; Hanski, 1983) or a fugitive species and a superior competitor (Nee & May, 1992; Hanski Gilpin, 1997), to stably coexist as metapopulations. In spatially fragmented habitats, coexistence on the local time-scale may be transitory, but regional coexistence may be maintained through immigration and patch dynamics (Hanski, 1983; Wilson, 1992).

Models of competition in spatially structured habitats are the extensions of the original metapopulation model of Levins (1969, 1970). Assume there is a large network of similar small patches, with local dynamics occurring on a fast timescale in comparison with metapopulation dynamics. The patches can be colonized by all the species under consideration. The local populations in this system are assumed to be subject to stochastic extinctions. 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. In these models, the relevant variables are not the number of individuals of each species within a community, but the number of habitats in a region that are colonized by each species (Slatkin, 1974).

The difference between the Lotka-Volterra model and the metapopulation model is not one of mechanism but of scale. For example, in Slatkin's competition models (Slatkin, 1974; see also Taneyhill, 1999), it is assumed that the dynamics of two competing species within a doubly occupied patch can be roughly described by the Lotka-Volterra equations or similar competition models on the local time-scale. The predictions of these equations could be related to the extinction and colonization probabilities. From the models of metapopulations, we may conclude that not only the movements of individuals among the patches but also the patch dynamics (local population turnover) play a critical role in the coexistence phenomena. Two like species may stably coexist through both the ability of invasion of the other's patches and the ability of colonizing empty patches. A fugitive species may coexist with a superior species through the ability of colonizing empty patches.

However, in nature, not all habitats are always in the danger of local population turnover and the biodiversity will increase with increasing net primary production. Experimental studies also indicate that like species may stably coexist in spatially subdivided but locally stable habitats. In a recent paper, Gotelli (1997) reported results from a set of experiments that were conducted in several patchy habitats, without explicit local population turnover, to examine the coexistence of competing species. The species he used were ant lion larvae of Myrmeleon crudelis and M. immaculatus. There are three larval instars of each species and overlapping generations of larvae coexist. In the experiments, the presence of third-instar larvae did not affect recruitment or survivorship of first-instar larvae. So, the excluded elder-instars of a species can be recolonized by first-instars, and the coexistence is maintained. There is no relation between the coexistence and the local-scale dynamics (local population turnover).

The results of Gotelli's experiments indicate that it is only the abilities of the two similar species to colonize the patches occupied by its competitors that play a key role in the coexistence phenomena. Now, the question is whether it is a general pattern in such a system, or further, a general pattern in all ecological communities. When and how can two competing species stably coexist? In this paper, we will modify the basic metapopulation model in order to explore the interactions of two competing species.

## 2. An Analytical Model of Two Competing Species

Let us consider a habitat composed of a large number of distinct patches. Each patch acts as a stable microhabitat, within which environmental stochasticity is neglected. First, only one species in such an environment is considered. Let p be the fraction of patches occupied by the species and we have

$$\frac{\mathrm{d}p}{\mathrm{d}t} = mp(1-p),\tag{1}$$

where *m* is the colonization rate. This states that the rate of change in site occupancy (dp/dt)

depends on the rate of propagule production (mp) multiplied by the proportion of currently open sites (1 - p). Equation (1) has the same form as the logistic equation of single species in limited habitat. The solution of eqn (1) can be written directly as

$$p(t) = \frac{1}{1 + (1 - p(0))e^{-mt}/p(0)},$$
 (2)

where p(0) is the initial fraction of occupied patches. With time tending to infinity  $(t \to \infty)$ , all the patches tend to be occupied  $(p \to 1)$ . In the case of no local extinction, a single species will occupy all the habitats.

Now, as two competing species in such an environment are considered, suppose that each species can colonize the remaining patches, neglecting the presence of another species. However, the colonization rate will be decreased by the presence of the competitor. The persistence of one species in a patch is also affected by the presence of its competitor.

Let  $p_1$  be the fraction of habitat patches occupied by species 1 only,  $p_2$  the fraction of patches occupied by species 2 only,  $p_3$  the fraction of patches occupied by both species together, and  $p_0$  the fraction of empty patches.

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, with a constant of proportionality  $m_1$ . Similarly, the rate of colonization of a habitat occupied by species 2 is proportional to  $Y_1$  with a decreased constant of proportionality  $\mu_1(\mu_1 < m_1)$ . We are assuming that the propagules are equally likely to come from any occupied habitat. The effect of spatial arrangement of the habitat 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 local population extinction of either species in a patch is caused only by competitive displacement. Let  $e_1$  be the extinction rate of species 1 in the presence of species 2. The extinction of species 1 in the absence of species 2 is ignored.  $m_2$ ,  $\mu_2$  and  $e_2$  are defined in the same way.

Thus, we get the following deterministic equations for this system:

$$\frac{\mathrm{d}p_0}{\mathrm{d}t} = -\left(m_1 Y_1 + m_2 Y_2\right) p_0,\tag{3a}$$

$$\frac{\mathrm{d}p_1}{\mathrm{d}t} = m_1 Y_1 p_0 - \mu_2 Y_2 p_1 + e_2 p_3, \tag{3b}$$

$$\frac{\mathrm{d}p_2}{\mathrm{d}t} = m_2 Y_2 p_0 - \mu_1 Y_1 p_2 + e_1 p_3, \qquad (3c)$$

$$\frac{\mathrm{d}p_3}{\mathrm{d}t} = \mu_1 Y_1 p_2 + \mu_2 Y_2 p_1 - (e_1 + e_2) p_3. \quad (3\mathrm{d})$$

The equilibrium points of these equations can be solved analytically. Obviously,  $p_0$  is a decreasing function of time until  $p_0 = 0$  and we have that at equilibrium

$$\hat{p}_0 = 0.$$
 (4)

That is to say that at equilibrium all patches will be occupied. Then, we have  $\hat{p}_1 + \hat{p}_2$  $+ \hat{p}_3 = 1$ . So, there are only two of the three factors  $\hat{p}_1$ ,  $\hat{p}_2$  and  $\hat{p}_3$  being independent of each other. It is easy to find that there are three nontrivial equilibrium solutions of the system

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

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

$$\hat{p}_{1} = \frac{1}{2} \left( 1 + \frac{2e_{2}}{\mu_{2}} - \sqrt{1 + \frac{4e_{1}e_{2}}{\mu_{1}\mu_{2}}} \right),$$

$$\hat{p}_{2} = \frac{1}{2} \left( 1 + \frac{2e_{1}}{\mu_{1}} - \sqrt{1 + \frac{4e_{1}e_{2}}{\mu_{1}\mu_{2}}} \right),$$

$$\hat{p}_{3} = -\left( \frac{e_{1}}{\mu_{1}} + \frac{e_{2}}{\mu_{2}} \right) + \sqrt{1 + \frac{4e_{1}e_{2}}{\mu_{1}\mu_{2}}}.$$
(5c)

The first, we interpret as species 1 being present in the region alone, the second as species 2 present in the region alone, the third as the coexistence of the two species. Under the conditions of coexistence, the fraction of patches occupied by one species or two species together depends on  $e_1/\mu_1$  and  $e_2/\mu_2$  only. We call  $e_i/\mu_i$ (i = 1 or 2) the competition coefficient. It measures the competitive effect of species 2 (or 1) on species 1 (or 2). The position of the factor of  $e/\mu$  in the model is just as  $\alpha$  in the Lotka–Volterra model.

The question we are concerned with is when can two competing species coexist in the region at equilibrium? What are the general conditions that permit the coexistence of competitors, and what circumstances lead to competitive exclusion in all regions? Can a patch occupied by one species be invaded by a competing species? It is instructive to discuss the stability of each equilibrium point. If only one boundary equilibrium is stable and the other boundary equilibrium point and the internal equilibrium point are unstable, the two competing species cannot coexist. If only the internal equilibrium point is stable, the two competing species can stably coexist and a species can always invade a region occupied by its competitor. If both boundary equilibrium points are stable and the internal equilibrium is unstable, the two competing species can never coexist and the outcome of competition depends on the initial fractions of the habitats occupied by each of the species.

Considering a small perturbation from any one of the three equilibrium points, we let

$$p_{0} = \hat{p}_{0},$$

$$p_{1} = \hat{p}_{1} + p'_{1},$$

$$p_{2} = \hat{p}_{2} + p'_{2},$$

$$p_{3} = \hat{p}_{3} - (p'_{1} + p'_{2}).$$
(6)

Substituting eqn (6) into eqn (3) and considering the first order of  $p'_i$  (i = 1 or 2), we get the linear differential equations of the system

$$\frac{\mathrm{d}}{\mathrm{d}t} \begin{pmatrix} p_1' \\ p_2' \end{pmatrix} = A \begin{pmatrix} p_1' \\ p_2' \end{pmatrix},\tag{7}$$

where

$$A = \begin{bmatrix} -\mu_2 - e_2 + 2\mu_2 \hat{p}_1 & -e_2 \\ -e_1 & -\mu_1 - e_1 + 2\mu_1 \hat{p}_2 \end{bmatrix}.$$
(8)

The stability of an equilibrium point is determined by the eigenvalues of A. From this, we can easily get the stability condition of each

equilibrium solution (Table 1). It is not surprising that the stable condition at internal equilibrium point is just the unstable conditions of two boundary equilibrium points (Fig. 1). The stable conditions depend on  $e_1/\mu_1$  and  $e_2/\mu_2$  only. When  $(e_1/\mu_1 - e_2/\mu_2)^2 < 1$ , the two species can stably coexist.  $(e_1/\mu_1 - e_2/\mu_2)^2 < 1$  means that neither species has the absolute predominance in the competition. Both the species have the chance to exclude its competitor from any given patches, and have the ability to colonize the patches occupied by its competitor. Though a species may be excluded from a patch, it may succeed in another patch. In this case, coexistence is maintained.

For two ecologically identical species, we have  $\mu_1 = \mu_2 = \mu$ ,  $e_1 = e_2 = e$ . In this case, the expression  $(e_1/\mu_1 - e_2/\mu_2)^2 < 1$  is truly satisfied. That is to say, two identical species will stably coexist regionally in such system. Because, as assumed, there are no difference between inter- and intraspecific competition of two identical species, both species have the chance to succeed in competition in a given patch and the ability to colonize the patches occupied by its competitor. So, through the process of exclusion-colonization, a dynamic equilibrium of coexistence will be maintained. Similar species have the same patterns of dispersal and the same food requirements would be more likely to exclude each other from local patches. However, because of the ability to invade the patches occupied by its competitor, coexistence in the region can be maintained.

It is also possible for two competing species with unequal competitive ability to stably coexist, when there is a trade-off between local competition ability and invasion ability. In this case, though the stronger competitor has a higher

TABLE 1 Stability conditions of different equilibrium solutions [eqn (5)]

PI	$P_{\mathrm{II}}$	$P_{C}$
$\frac{\overline{e_2}}{\mu_2} > 1 + \frac{e_1}{\mu_1}$	$\frac{e_1}{\mu_1} > 1 + \frac{e_2}{\mu_2}$	$\left(\frac{e_1}{\mu_1} - \frac{e_2}{\mu_2}\right)^2 < 1$

*Note.*  $P_{I}$ , the boundary equilibrium point of only species 1 present;  $P_{II}$ , the boundary equilibrium point of only species 2 present;  $P_{C}$ , the internal equilibria of the coexistence of two competing species.



FIG. 1. The stability regions of the internal equilibria of two competing species in parameter space. The real line is for the analytical model and the dotted line for the consideration of rescue effects ( $\omega_1 = \omega_2 = 0.3$ ). The stable region at internal equilibrium point is reduced due to the rescue effects.

chance to succeed in local competition  $(e_1 < e_2)$ , the weaker competitor may have higher probability in colonization  $(\mu_1 < \mu_2)$ , so that the stability condition  $(e_1/\mu_1 - e_2/\mu_2)^2 < 1$  can be maintained. In this case, the coexistence is just like the coexistence of two like species.

When  $(e_1/\mu_1 - e_2/\mu_2)^2 < 1$  is not satisfied, either  $e_2/\mu_2 > 1 + e_1/\mu_1$  or  $e_1/\mu_1 > 1 + e_2/\mu_2$ , and coexistence can never occur. That is to say that a species with weak competitive ability and low ability to colonize can never coexist with its competitor. This is different from the result of metapopulation models that a completely superior competitor and a completely fugitive species can stably coexist regionally (Nee & May, 1992).

## 3. The Rescue Effects on the Model of Two Competing Species

In the basic model, we have assumed that there is no correlation between the probability of competitive exclusion and p. However, as Hanski (1983) pointed out, the probability of extinction often decreases with increasing p. Because of emigration and colonization, average local abundance of species is usually positively correlated with p. When p is small, many local populations are small and prone to be excluded. When p is large, most local populations are large and unlikely to be excluded rapidly. Because of this correlation between exclusion probability and population size and between average population size and p, the exclusion probability and p are also correlated.

Let us consider the rescue effect and assume that the correlation between the exclusive probability and p is linear. In this case, eqn (3) should be rewritten as

$$\frac{\mathrm{d}p_0}{\mathrm{d}t} = -(m_1 Y_1 + m_2 Y_2)p_0, \qquad (9a)$$

$$\frac{\mathrm{d}p_1}{\mathrm{d}t} = m_1 Y_1 p_0 - \mu_2 Y_2 p_1 + e_2 p_3 (1 - \omega_2 Y_2),$$
(9b)

$$\frac{\mathrm{d}p_2}{\mathrm{d}t} = m_2 Y_2 p_0 - \mu_1 Y_1 p_2 + e_1 p_3 (1 - \omega_1 Y_1), \quad (9c)$$

$$\frac{\mathrm{d}p_3}{\mathrm{d}t} = \mu_1 Y_1 p_2 + \mu_2 Y_2 p_1 - (e_1(1 - \omega_1 Y_1) + e_2(1 - \omega_2 Y_2))p_3, \qquad (9d)$$

where  $0 \le \omega_1 \le 1$  and  $0 \le \omega_2 \le 1$  are the slopes of the declining extinction rate with increasing  $Y_1$  and  $Y_2$ , respectively, and are usually interpreted as the effect of different time-scale for extinction and recolonization. It is easy to find that there should be  $\hat{p}_0 = 0$  at equilibrium points, and then there are only two of the three factors  $\hat{p}_1$ ,  $\hat{p}_2$  and  $\hat{p}_3$  being independent of one another. It is obvious that there are two boundary equilibria

and

$$\hat{p}_1 = 1, \qquad \hat{p}_2 = 0, \qquad \hat{p}_3 = 0$$
 (10a)

$$\hat{p}_1 = 0, \qquad \hat{p}_2 = 1, \qquad \hat{p}_3 = 0.$$
 (10b)

However, it is difficult to find the internal equilibria of eqn (9). Here, we just discuss the stability of the two boundary equilibrium points and argue whether either is stable. If either boundary equilibrium is unstable, coexistence may occur. Sufficient and necessary conditions for the stability of the boundary equilibrium points are

$$\frac{e_2}{\mu_2} > 1 + \frac{e_1}{\mu_1} (1 - \omega_1)$$

for species 1 present, (11a)

$$\frac{e_1}{\mu_1} > 1 + \frac{e_2}{\mu_2} (1 - \omega_2)$$

for species 2 present. (11b)

When expression (11a) is satisfied, the equilibrium solution of expression (10a) is stable and species 1 can prevent species 2 from invading. If it is not satisfied, the point is unstable and species 2 can invade the region occupied by species 1. When the rescue effects are concerned, the stability condition is not only related to  $e_i/\mu_i$  (i = 1 and 2) but related to the strength of rescue effects also. The rescue effect enlarges the stable region of boundary equilibria (Fig. 1). A weaker competitor may invade a region occupied by a stronger competitor, but it will not invade the region anymore when there are rescue effects.

In the limiting case  $\omega = 1$ , expression (11a) reduces to  $e_2/\mu_2 > 1$ . That is to say that when the invasion rate of species 2 in the presence of species 1 is less than the exclusion rate, species 2 will eventually be excluded.

Considering two like species in the values for their parameters, we set  $\mu_1 = \mu_2 = \mu$  and  $e_1 = e_2 = e$ . In this case, condition (11a) reduces to

$$0 > 1 - \frac{e_1 \omega_1}{\mu_1}.$$
 (12)

Obviously, eqn (12) can never be satisfied for any circumstance. Therefore, we would predict that one species could always invade a region occupied by a similar species. Based on this conclusion, we can expect that two identical species would coexist in the region and at least one stable equilibrium point would exist. Of course, the presence of the competing species could greatly reduce its competitor's abundance.

When both expressions (11) are not satisfied, there should be at least one stable internal equilibrium solution and there may be coexistence. Further, we may discuss some aspects of internal equilibrium points by using the results of the basic model. Let

$$p_0^* = 0,$$
 (13a)

$$p_1^* = \frac{1}{2} \left( 1 + \frac{2e_2}{\mu_2} - \sqrt{1 + \frac{4e_1e_2}{\mu_1\mu_2}} \right), \quad (13b)$$

$$p_2^* = \frac{1}{2} \left( 1 + \frac{2e_1}{\mu_1} - \sqrt{1 + \frac{4e_1e_2}{\mu_1\mu_2}} \right), \quad (13c)$$

$$p_3^* = -\left(\frac{e_1}{\mu_1} + \frac{e_2}{\mu_2}\right) + \sqrt{1 + \frac{4e_1e_2}{\mu_1\mu_2}}.$$
 (13d)

Substituting eqn (13) into the right-hand side of eqn (9), we have

$$\frac{\mathrm{d}p_0}{\mathrm{d}t}_{P=P^*} = 0, \qquad (14a)$$

$$\frac{\mathrm{d}p_1}{\mathrm{d}t}_{P=P^*} = -e_2\omega_2 p_3^*(p_2^* + p_3^*), \qquad (14b)$$

$$\frac{\mathrm{d}p_2}{\mathrm{d}t}_{P=P^*} = -e_1\omega_1 p_3^*(p_1^* + p_3^*), \qquad (14\mathrm{c})$$

$$\frac{\mathrm{d}p_3}{\mathrm{d}t}_{P=P^*} = e_1 \omega_1 p_3^* (p_1^* + p_3^*) + e_2 \omega_2 p_3^* (p_2^* + p_3^*), \qquad (14d)$$

where,  $P = P(p_0, p_1, p_2, p_3)$  and  $P^* = P^*(p_0^*, p_1^*, p_2^*, p_3^*)$ . Obviously, there are  $dp_1/dt_{P=P^*} < 0$ ,  $dp_2/dt_{P=P^*} < 0$  and  $dp_3/dt_{P=P^*} > 0$ . Then we may expect that at internal equilibrium point

$$\hat{p}_1 < \frac{1}{2} \left( 1 + \frac{2e_2}{\mu_2} - \sqrt{1 + \frac{4e_1e_2}{\mu_1\mu_2}} \right),$$
 (15a)

$$\hat{p}_2 < \frac{1}{2} \left( 1 + \frac{2e_1}{\mu_1} - \sqrt{1 + \frac{4e_1e_2}{\mu_1\mu_2}} \right),$$
 (15b)

$$\hat{p}_3 > -\left(\frac{e_1}{\mu_1} + \frac{e_2}{\mu_2}\right) + \sqrt{1 + \frac{4e_1e_2}{\mu_1\mu_2}}.$$
 (15c)

That is to say that, when the rescue effects are considered, the proportion of doubly occupied patches  $\hat{p}_3$  will be enlarged.

#### 4. Discussion

Many mechanisms have been proposed to explain the coexistence of identical species since the birth of the competitive exclusion principle. These mechanisms can be divided into two categories (Chesson, 1991). The first is to prolong coexistence by postponing the inevitable extinction of some competitors (e.g. Hubbell, 1979; Hubbell & Foster, 1986). The second is to truly promote long-term coexistence by giving each species an advantage when it is at low densities (e.g. Atkinson & Shorrocks, 1981; Hanski, 1981; Chesson & Huntly, 1988, 1989; Ives, 1988). However, because all the mechanisms that fall into the second category require that each species has an advantage when it is at low densities, they are not truly identical species. In recent years, metapopulation models have made some success in explaining the coexistence of competing species. Taneyhill (1999) analysed the competition in metapopulations, and proved the conditions under which a metapopulation structure invalidates Gause's law for regionally similar competitors. Taneyhill's results suggest that coexistence of like species within a metapopulation is possible if and only if there is recolonization from doubly occupied patches, and rescue effects may make competitive coexistence impossible via the creation of a saddle point equilibrium having one-dimensional stable and unstable manifolds.

In this paper, we constructed an analytical model to evaluate the coexistence of competitive species in subdivided but locally stable habitats. The conditions of the model can be seen in some real-world scenarios where extinction events are relatively rare; colonization of newly created habitat, or in the habitat where local stochastic extinction takes place on a time-scale that is much longer than that of local competitive displacements are examples. Given that there is no local extinction of each patch when only one species exists, species invading into this environment will occupy all patches. The presence of a competing species will affect both the colonization rates and the persistence of the competitor. The present model is not just a simplified form of the four-state metapopulation competition models (Slatkin, 1974; Taneyhill, 1999). In the model, we prove that the coexistence of very like species do not depend on environmental stochasticity. This may contribute to understand the phenomenon of coexistence on a regional scale.

Our model predicts that the conditions of stability of coexistence and the proportion of patches of coexistence are only related to the ratios  $e_1/\mu_1$  and  $e_2/\mu_2$ , not  $e_1$ ,  $\mu_1$ ,  $e_2$  and  $\mu_2$ , respectively. The condition  $(e_1/\mu_1 - e_2/\mu_2)^2 < 1$ implies that, if there is coexistence of two competing species, there should not be much difference in their competitive abilities. So, two identical species always coexist, and two unalike competing species, if there is a trade-off between local competition ability and invasion ability. Similar species that have the same patterns of dispersal and the same food requirements would be most likely to exclude each other from a local patch. Their coexistence thus depends on their invasion abilities in the presence of the competitors. So, the mechanism of coexistence in such system is not the ability of the species to colonize the empty patches but the ability to invade the patches occupied by its competitor.

It has been considered that, in metapopulation models, "too much" migration can be as bad for metapopulation persistence as "too little" migration and species with an intermediate rate of migration are the ones which tolerate best habitat fragmentation (Hanski & Zhang, 1993). And, further, increased movements between habitat patches do not necessarily facilitate regional coexistence, because increased movements may critically decrease the difference between the local (usually fast) and regional (usually slow) time scales (Hanski, 1983). However, the results of the present model indicate that increasing movements will increase the chance of successful invasion into its competitor's patch, and eventually facilitate regional coexistence.

When considering rescue effects, both the stable regions at boundary equilibrium points and the fraction of doubly occupied patches at the internal equilibrium point will be enlarged. For two stably coexisting species, rescue effects can decrease the local competitive displacement rate, and thus reduce the competitive impact of its competitor. We may expect that the fraction of doubly occupied patches would increase when considering rescue effects. On the other hand, because the rescue effects increase with the increase in the proportion of occupied patches, the relative difference between two unalike competitors would also be enlarged. In this case, rescue effects may change the interior equilibrium from a stable node to an unstable saddle.

We may extend the results of the present model to the more general case. As we have defined  $\mu$  as the rate of colonization of a habitat occupied by a competitor, it is related to the dispersal ability of the species, the local competitive ability in the presence of a competitor, and the chance of success of dispersing individuals in finding new patches. So, for a certain pair of competitors, when the density of the patches increases or the distances among patches decreases, both  $\mu_1$  and  $\mu_2$  will increase, and eventually the proportion of patches occupied by both species will increase. Thus, we may expect that there are highest coexistence in a spatially structured habitat, in which individuals can invade other patches freely while the extinction caused by competition occurs only within doubly occupied patches. In fact, the restricted condition of the spatially structured habitats can also be removed in many cases. Within any habitat, an individual organism is more likely to interact with neighbouring organisms than with more distant ones, especially for terrestrial plants, many marine invertebrates, corals and other sessile organisms (Pacala, 1986a, b; Goldberg, 1987; Pacala & Silander, 1990; see Tilman, 1994). So, we can expect that individual exclusion will be mostly caused by its neighbours. In this case, the restrictive condition of spatially subdivided habitats in the model will have no meaning, and we can expect that two identical species can stably coexist in homogenous environments. This is different from the Lotka-Volterra model's predictions. The classical model assumes 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. The population dynamics of two completely competing species is a stochastic displacement process between species and the outcomes of competition are also stochastic. Thus,

two identical species cannot stably coexist in Lotka-Volterra model.

competitive exclusion However, because always occurs locally and individual colonization may occur in a much different spatial scale, local extinction caused by interspecific competition may be recolonized by other individuals of the locally excluded species. In this case, two identical species may regionally coexist in a state of dynamic equilibrium of locally competitive displacement and recolonization. So, in our model, though local population competitive exclusion is still a stochastic process, the exclusion can be compensated by recolonization. The abilities to invade its competitor's manor may play the role of "restoring force". When there is any deviation against the equilibrium point, the recolonization will occur.

We thank Prof. D.-Y. Zhang, Prof. G. Wang and Prof. Z.-Z. Li for their constructive suggestions. Prof. I. Hanski for his inspiring lectures in Lanzhou University, and the anonymous reviewers for their useful comments on this manuscript. This work was supported by a grant (No. 39800022) from the National Natural Science Foundation of China, and a grant from Shapotou Desert Experimental Research Station of Chinese Academy of Sciences.

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