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Does spatial structure facilitate coexistence of identical competitors?

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Abstract

In an apparent violation of Gause's principle of competitive exclusion, many metapopulation models of interspecific competition make the claim that identical species can coexist in spatially structured habitats. In these models, it is assumed that extinction and colonization parameters are always the same for both species, independent of the relative abundance of the two species in doubly occupied patches. We show that it is this simplifying assumption that gives an unfair advantage to the regionally rarer species. More realistic assumptions in these models would lead to different conclusions, which indicate that two identical species cannot coexist regionally in a network of many habitat patches.
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1. Introduction

Environmental heterogeneity has long been suggested as an important mechanism promoting coexistence of similar species. It is widely accepted that two species that can not coexist locally in a homogenous habitat may nonetheless coexist stably in a network of many habitat patches. This notion has been discussed using metapopulation models of the Levins (1969) type for competing species. In these models, local dynamics are ignored for the sake of mathematical tractability, and only changes in the fractions of habitat patches occupied by the two species are modeled. It is worth noting that there are two alternative approaches to the modeling of interspecific competition in metapopulations, depending on whether jointly occupied patches are taken into account. One modeling approach considers asymmetric competition between a superior competitor and an inferior competitor, in

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which the superior competitor can completely displace the inferior competitor from patches which it occupies (Nee and May, 1992; Hanski and Zhang, 1993; Tilman, 1994; Nee et al., 1997). Assuming that the asymmetry in competitive ability is inversely correlated with an asymmetry in colonization ability, it is not difficult to show that metapopulation-level coexistence can be achieved. This mechanism of coexistence is the classical scenario of fugitive coexistence, first studied by Hutchinson (1951) and Skellam (1951).

Another way to construct metapopulation models of interspecific competition is to assume that both species may colonize the same patches and interspecific competition can affect the colonization and extinction rates of each species. This kind of models was first analyzed by Slatkin (1974), and later by many authors e.g. Hanski (1983), Taneyhill (2000), and Wang et al. (2000, 2002). The main conclusion from these models is that species with similar or even identical colonization and extinction parameters may coexist regionally, contrary to a key result of the classical competition theory, the principle of competitive exclusion, which states that identical species cannot coexist (Hardin, 1960; Hutchinson, 1978; but see Zhang and Jiang, 1995; Zhang and Hanski, 1998; Zhang et al., 2004). Do habitat heterogeneity and regional processes (extinction and colonization) really promote coexistence so much that a fundamental result of the competition theory is overturned? Hanski (1999) has already pointed out that the answer is no; in this article we provide some further clarifying observations. We shall demonstrate that the previous conclusion of stable coexistence of identical competitors is an artifact of the assumptions made in previous metapopulation models, and that more realistic revisions would lead to different conclusions.

2. The model and its predictions

The metapopulation models with which interspecific competition has been analyzed are straightforward extensions of the original single-species model of Levins (1969), in which local dynamics are ignored, and only changes in the fractions of habitat patches occupied by the two species are modeled. There are four kinds of patches, namely those occupied by species 1 only (p_1), patches occupied by species 2 only (p_2), patches jointly occupied by species 1 and species 2

(p_3), and empty patches (p_0). The following four equations describe the rates of the change of the fractions of different types of patches (Slatkin, 1974; Taneyhill, 2000):

$$\frac{\mathrm{d}p_0}{\mathrm{d}t} = -(m_1\gamma_1 + m_2\gamma_2)p_0 + \varepsilon_1 p_1 + \varepsilon_2 p_2$$

$$\frac{\mathrm{d}p_1}{\mathrm{d}t} = m_1\gamma_1 p_0 - [\varepsilon_1 + \mu_2\gamma_2]p_1 + (\varepsilon_2 + \varepsilon_{21})p_3$$

$$\frac{\mathrm{d}p_2}{\mathrm{d}t} = m_2\gamma_2 p_0 - [\varepsilon_2 + \mu_1\gamma_1]p_2 + (\varepsilon_1 + \varepsilon_{12})p_3$$

$$\frac{\mathrm{d}p_3}{\mathrm{d}t} = \mu_1\gamma_1 p_2 + \mu_2\gamma_2 p_1 - (\varepsilon_1 + \varepsilon_{12} + \varepsilon_2 + \varepsilon_{21})p_3 \tag{1}$$

where m_i and ε_i are the single-species rate of recolonization and extinction, respectively, for species i; μ_i be the rates of colonization of species i to a habitat occupied by the other species; parameters ε_{ij} denote the addition to the extinction rate of species i within doubly occupied patches via interaction with species j. $\gamma_i = p_i + \alpha p_3$, and $0 \le \alpha \le 1$ is the proportion of doubly occupied patches that contribute to recolonization. Assuming that production of propagules from doubly occupied patches was identical to that from singly occupied patches, Slatkin (1974) analyzed a special case of Eq. (1) with $\alpha = 1$. Taneyhill (2000) provided a thorough analysis of the dynamical behavior of the model, and found that identical species can stably coexist within a metapopulation so long as there is recolonization from doubly occupied patches (i.e. $\alpha > 0$).

However, it is important to bear in mind that model (1) is based on the assumption that local dynamics within a patch occurs on a much faster time scale than regional dynamics of extinction and recolonization within the metapopulation (Hanski, 1999). This assumption, combined with a prerequisite of doubly occupied patches for regional coexistence in Eq. (1) (Christiansen and Fenchel, 1977; Taneyhill, 2000), effectively requires that two species coexist locally within a patch, hence making the whole argument for coexistence circular. Thus, to overcome this shortcoming one has to consider local coexistence as transient, merely to allow for dispersal to new patches (e.g. Lett et al., 2003), with relative species abundance following a random walk (cf. Hubbell, 2001). Though not explicitly pointed out, this scenario is, we guess, what most modelers would have in mind when working with the Levins-type metapopulation models of interspecific competition. Under this scenario, however, the values of α and ε are no longer the same for common and rare

species, because local abundances of the two species in doubly occupied patches are likely different (Hanski, 1999). The regionally rarer species in doubly occupied patches should have a higher extinction rate (larger ε_{ij}) and contribute less to recolonization (smaller α) than the commoner species. Assuming that the values of these parameters are equal for two species effectively gives an unfair advantage to the rarer species. As will be made clear in data given below, two identical species cannot coexist locally or regionally in a landscape of many habitat patches in spite of stochastic extinctions and recolonizations.

To take into account the effects of local abundance on extinction and recolonization, the model is accordingly modified as follows. The local competitive extinction was modeled as Wang et al. (2002). Let ε_1 and e_1^0 be the extinction rate of species 1 caused by local stochastic extinction and by competitive effects of species 2 in doubly occupied patches when the two competing species have the same initial local density (Wang et al., 2002), respectively. ε_2 and e_2^0 are defined in the same way. In doubly occupied patches, a species that happens to have a higher local abundance will contribute more to recolonization. Since the regionally more common species is more likely to arrive first at a given patch, it should enter into local competition with a higher local abundance. It is an empirical generalization that 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). Thus, to make the model more realistic, we assume that there exists a positive relationship between a species' distribution and its contribution to recolonization, and the model can be written as:

$$
\frac{\mathrm{d}p_0}{\mathrm{d}t} = -m_1 \left(p_1 + p_3 \frac{Y_1}{Y_1 + Y_2} \right) p_0 \\
- m_2 \left(p_2 + p_3 \frac{Y_2}{Y_1 + Y_2} \right) p_0 + \varepsilon_1 p_1 + \varepsilon_2 p_2
$$
(2a)

$$
\frac{\mathrm{d}p_1}{\mathrm{d}t} = m_1 \left(p_1 + p_3 \frac{Y_1}{Y_1 + Y_2} \right) p_0 + \varepsilon_2 p_3 \\
+ e_2^0 p_3 \frac{2Y_1}{Y_1 + Y_2} - \varepsilon_1 p_1 \\
- \mu_2 \left(p_2 + p_3 \frac{Y_2}{Y_1 + Y_2} \right) p_1
$$
(2b)

$$
\frac{\mathrm{d}p_2}{\mathrm{d}t} = m_2 \left(p_2 + p_3 \frac{Y_2}{Y_1 + Y_2} \right) p_0 + \varepsilon_1 p_3 \\
+ e_1^0 p_3 \frac{2Y_2}{Y_1 + Y_2} - \varepsilon_2 p_2 \\
- \mu_1 \left(p_1 + p_3 \frac{Y_1}{Y_1 + Y_2} \right) p_2
$$
(2c)

$$
\frac{\mathrm{d}p_3}{\mathrm{d}t} = \mu_1 \left(p_1 + p_3 \frac{Y_1}{Y_1 + Y_2} \right) p_2 \\
+ \mu_2 \left(p_2 + p_3 \frac{Y_2}{Y_1 + Y_2} \right) p_1 \\
- \left(\varepsilon_1 + \varepsilon_2 + e_1^0 \frac{2Y_2}{Y_1 + Y_2} + e_2^0 \frac{2Y_1}{Y_1 + Y_2} \right) p_3
$$
(2d)

where $Y_i = p_i + p_3$, represents the total proportions of the occupied patches by species i. Here we express the contribution of species 1 and 2 in doubly occupied patches to recolonization as $p_3 Y_1/(Y_1 + Y_2)$ and $p_3 Y_2/(Y_1 + Y_2)$, respectively. The meaning of the two forms is straightforward. When two competing species have a similar distribution, they will have similar average local abundance and, both of them, on average, will contribute equally to recolonization from the doubly occupied patches. When the two species have much different regional distributions, the species with the narrower distribution will contribute less, while its competitor will contribute more to recolonization from the doubly occupied patches.

Because of the complicated form of Eq. (2), it is not practical to find an analytical solution for all of the equilibrium points. Here, following Slatkin (1974), we only discuss the stability of two boundary equilibrium points.

Since $p_0 + p_1 + p_2 + p_3 = 1$, only three equations are independent in the above model. The present boundary equilibrium point of species 1 can be written directly as:

$$
\hat{p}_0 = \frac{\varepsilon_1}{m_1}, \quad \hat{p}_1 = 1 - \frac{\varepsilon_1}{m_1}, \quad \hat{p}_2 = 0, \text{ and } \hat{p}_3 = 0
$$
(3)

Following Hanski (1983), the system's linear differential equations are as follows:

$$\frac{d}{dt}\begin{pmatrix} p'_1 \\ p'_2 \\ p'_3 \end{pmatrix} = A \begin{pmatrix} p'_1 \\ p'_2 \\ p'_3 \end{pmatrix}$$

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 elements of A are the partial derivatives of the right-hand side of Eq. (2) (Hanski, 1983) as:

$$A = \begin{bmatrix} -m_1\hat{p}_1 & -m_1\hat{p}_1 - \mu_2\hat{p}_1 & m_1 + \varepsilon_2 + e_2 - 2m_1\hat{p}_1 \\ 0 & m_2\hat{p}_2 - m_2\hat{p}_1 - \mu_1\hat{p}_1 & \varepsilon_1 \\ 0 & \mu_1\hat{p}_1 + \mu_2\hat{p}_1 & -(\varepsilon_1 + \varepsilon_2 + e_2) \end{bmatrix}$$

where $e_1 = 2e_1^0$ and $e_2 = 2e_2^0$ for simplification. $\hat{p}_1 = 1 - \varepsilon_1/m_1$ and $\hat{p}_2 = 1 - \varepsilon_2/m_2$ are the precompetitive distributions of species 1 and species 2, respectively. Since $a_{21} = a_{31} = 0$ and $a_{11} = -m_1\hat{p}_1$, one of the Eigen values of A is real and negative. Thus, the local stability of the boundary equilibrium point depends on two conditions:

$$a_{22} + a_{33} < 0 \tag{5a}$$

$$a_{23}a_{32} < a_{22}a_{33} \tag{5b}$$

If both conditions are satisfied, the boundary equilibrium point of species 1 is stable. Otherwise, it is unstable. Now we will first demonstrate that two like (identical) species can never stably coexist in such systems. Then, following Slatkin (1974) and Hanski (1983), we will analyze the cases of pure migration competition and pure extinction competition. It will be seen that metapopulation structure does not, as commonly perceived, promote competitive coexistence.

2.1. Two like species

Let $m_1 = m_2 = m$, $\mu_1 = \mu_2 = \mu$, $\varepsilon_1 = \varepsilon_2 = \varepsilon$, and $e_1 = e_2 = e$, then we have:

$$a_{22} + a_{33} = -(\mu\hat{p} + e + 2\varepsilon) \tag{6a}$$

$$a_{22}a_{33} - a_{23}a_{32} = \mu\hat{p}e \tag{6b}$$

where $\hat{p} = 1 - \varepsilon/m$. Obviously, when $e > 0$, conditions (5) are always true. In this case, the boundary

equilibrium is always stable. When $e = 0$, there are $a_{22} + a_{33} < 0$ and $a_{22}a_{33} - a_{23}a_{32} = 0$. This is a neutral stable point. That is to say, two like species can never stably coexist in such systems. This result is different from those that are obtained from the previous two-species metapopulation models, but well in line with the competitive exclusion principle (Gause, 1934; Hardin, 1960).

2.2. Migration competition

Let $e_1 = e_2 = 0$, then we have:

$$\tag{4}$$

$$a_{22} + a_{33} = m_2\hat{p}_2 - m_2\hat{p}_1 - \mu_1\hat{p}_1 - (\varepsilon_1 + \varepsilon_2) \tag{7a}$$

$$a_{22}a_{33} - a_{23}a_{32} = m_2(m_2 + \mu_1)$$
$$\times \left(\frac{\varepsilon_2}{m_2}\hat{p}_1 - \frac{\varepsilon_1 + \varepsilon_2}{m_2 + \mu_1}\hat{p}_2 \right)$$
$$+ \varepsilon_1(m_2 - \mu_2)\hat{p}_1 \tag{7b}$$

It is easy to prove that when $a_{23}a_{32} < a_{22}a_{33}$, there is always $a_{22} + a_{33} < 0$. Let $a_{23}a_{32} < a_{22}a_{33}$, we get the stable condition of the boundary equilibrium point of species 1 as:

$$(\varepsilon_2(m_2 + \mu_1) + \varepsilon_1(m_2 - \mu_2))\hat{p}_1$$
$$- m_2(\varepsilon_1 + \varepsilon_2)\hat{p}_2 > 0 \tag{8}$$

Similarly, the stability condition for the boundary equilibrium point of species 2 is:

$$(\varepsilon_1(m_1 + \mu_2) + \varepsilon_2(m_1 - \mu_1))\hat{p}_2$$
$$- m_1(\varepsilon_1 + \varepsilon_2)\hat{p}_1 > 0 \tag{9}$$

Thus, the unstable condition of the boundary point of species 2 is:

$$(\varepsilon_1(m_1 + \mu_2) + \varepsilon_2(m_1 - \mu_1))\hat{p}_2$$
$$- m_1(\varepsilon_1 + \varepsilon_2)\hat{p}_1 < 0 \tag{10}$$

After some mathematical rearrangements, it can be proved that Eq. (10) is always true when Eq. (8) is

satisfied. That is to say, the unstable condition of the boundary point of species 2 is just the stable condition of the boundary point of species 1. In other words, the two competitors can never coexist stably.

Eq. (8) can also be written as $\hat{p}_2 < [(1 + \mu_1\varepsilon_2 - \mu_2\varepsilon_1)/(m_2(\varepsilon_1 + \varepsilon_2))]\hat{p}_1$. Because $\mu_1\varepsilon_2 - \mu_2\varepsilon_1$ can be either positive or negative, there are some chance that when $\hat{p}_1 < \hat{p}_2$ Eq. (8) can still be satisfied. So, $\hat{p}_1 > \hat{p}_2$ is not a necessary condition for the stability of the boundary point of species 1 in pure migration competition.

2.3. Extinction competition

Let $\mu_1 = m_1$ and $\mu_2 = m_2$, we then have:

$$a_{22} + a_{33} = m_2\hat{p}_2 - m_2\hat{p}_1 - m_1\hat{p}_1 - (\varepsilon_1 + \varepsilon_2 + e_2)$$
(11a)

$$a_{22}a_{33} - a_{23}a_{32} = m_2(m_2 + m_1)$$
$$\times \left(\left(\frac{e_2}{m_2}\hat{p}_1 - \frac{e_2}{m_2 + m_1}\hat{p}_2 \right) \right.$$
$$\left. + \left(\frac{\varepsilon_2}{m_2}\hat{p}_1 - \frac{\varepsilon_1 + \varepsilon_2}{m_2 + m_1}\hat{p}_2 \right) \right)$$
(11b)

Obviously, when $\hat{p}_1 > \hat{p}_2$, there are always $a_{22} + a_{33} < 0$ and $a_{22}a_{33} - a_{23}a_{32} > 0$. This means that the boundary point of species 1 is a stable equilibrium, or species 1 can always prevent species 2 from invasion when $\hat{p}_1 > \hat{p}_2$. By the same token, we can show that the boundary point of species 2 is a stable equilibrium when $\hat{p}_2 > \hat{p}_1$. Therefore, in extinction competition, a species with widely precompetitive distribution can completely prevent the invasion of its competitor with narrow precompetitive distribution.

From the above analysis we can conclude that the two-species metapopulation model generally does not facilitate coexistence. This conclusion is radically different from that of previous models (Slatkin, 1974; Hanski, 1983; Taneyhill, 2000; Wang et al., 2000, 2002). We believe that the difference lies crucially in our assumption that a species contribution to recolonization is positively related to its regional distribution. In this way, the unfair advantages to the rarer species in previous models are effectively removed.

An assumption to the model is that occupied patches are biologically saturated with individuals of either species. Two species may harm each other only through local preemption of resources, with colonization and extinction being unaffected, which may be called preemption competition.

2.4. Preemption competition

Let $e_1 = e_2 = 0$, $m_1 = \mu_1$, and $m_2 = \mu_2$, from Eq. (4) we get:

$$a_{22} + a_{33} = m_2\hat{p}_2 - m_2\hat{p}_1 - m_1\hat{p}_1 - (\varepsilon_1 + \varepsilon_2)$$
(12a)

$$a_{22}a_{33} - a_{23}a_{32} = m_2(m_2 + m_1)$$
$$\times \left(\frac{\varepsilon_2}{m_2}\hat{p}_1 - \frac{\varepsilon_1 + \varepsilon_2}{m_2 + m_1}\hat{p}_2 \right)$$
(12b)

Obviously, Eq. (12) has the similar behavior with Eq. (11). We can conclude that if two competing species only reduce each other's population size in doubly occupied patches, the two species can never stably coexist. A species with widely precompetitive distribution can completely prevent the invasion of a competitor with narrow precompetitive distribution.

3. Discussion

A key result of classical competition theory, generally known as Gause's principle, or the principle of competitive exclusion (Gause, 1934; Hardin, 1960), states that identical species cannot stably coexist (but see Zhang and Jiang, 1995; Zhang and Hanski, 1998; Zhang et al., 2004). In other words, stable coexistence of competing species is possible only if the species are sufficiently distinct ecologically. To see why this is the case, consider two competing species of which one is common and one happens to be temporally rarer. If they are to coexist, the rarer species must be able to increase in relative abundance; otherwise it becomes extinct. If there is no difference between individuals of different species, an individual's competitive action harms equally both conspecifics and heterospecifics, and there can be no advantage to membership in one species over another. The relative abundances of ecologically

identical species are thus expected to follow a random walk until one of them goes extinct (Chesson, 1991).

The above argument is rather powerful and quite independent of the spatial and/or temporal scales under consideration. Failure to fully appreciate the significance of this simple notion has led many researchers to wrongly conclude that identical competitors can stably coexist in their models. As shown in Chesson (1991) and above, models purportedly demonstrating stable coexistence of identical species in fact either implicitly assume ecological distinctions between individuals of different species or have to resort to some invalid prerequisite conditions, which would confer some unfair advantages to the rarer species.

In metapopulation models, there are only a small fraction of patches that are occupied by two competitors at the same time, so it has been customary to think that spatial heterogeneity will lessen the importance of species interactions or limit their role in community structuring. However, the present model demonstrates that habitat heterogeneity in fact does not promote coexistence, in square contrast to previous two-species metapopulation models. Two species that cannot coexist locally within a patch cannot coexist regionally in a network of many such habitat patches. In other words, habitat patchiness can promote coexistence only when it creates new niche opportunities (Huston and DeAngelis, 1994; Chesson and Huntly, 1997; Goreaud et al., 2002; Klausmeier and Tilman, 2002). Klausmeier and Tilman (2002) recently discussed how spatial aspects of competition can be captured in theoretical models and how they affect coexistence. Along with the exposition of these new ideas about coexistence may come an illusion that Gause's principle of competitive exclusion has been refuted by spatial and/or temporal heterogeneity. As we have made explicit in the above analysis, spatial structure per se does not promote stable coexistence of identical competitors, and some other mechanisms are very well required (Zhang and Jiang, 1995; Zhang and Hanski, 1998; Zhang et al., 2004).

Another important result from the present model is that a species' invasion ability may play a more important role than the locally competitive displacement ability in determining its success in regional competition. In pure extinction competition, a species' precompetitive distribution determines its success in regional competition. In the case of pure migration competition, though a species' success in regional competition is still largely determined by its precompetitive distribution, the ability to invade its competitor's patches may increase the chance of a species' success in regional competition. If a species has high invasion abilities to its competitor's patches and, simultaneously, can effectively prevent its competitor from invasion, the species will get a prerogative in regional competition. Perhaps the ability to prevent its competitor from invasion is more efficient than the ability to drive out the competitor from its territories.

An important assumption of the present model is that species with wide distributions tend to be locally more abundant in doubly occupied patches than species with narrow distributions. This assumption is intuitively realistic, as the regionally more common species is more likely to arrive first at a given patch, and the first-arriving species enters into local competition with a higher initial local abundance than the later-arriving species. This assumption can also gain some support from the empirical generalization of a positive relationship between the fraction of occupied patches and the average size of local populations (Hanski, 1982, 1999; Brown, 1984; Lawton, 1993; Hanski and Gyllenberg, 1997). The present model reconfirms Hanski's (1999) assertion that ignoring local dynamics and local species abundance, may be badly misleading in the case of two species, although it may represent a sensible first approximation in a single-species metapopulation model.

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