Coupling of two competitive systems via density dependent migration

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Coupling of two Lotka–Volterra type competition systems with density-dependent migration was surveyed. We assumed that species x and y are each exclusively superior in subhabitat 1 and subhabitat 2, respectively, and that population densities that exert intra-and interspecific competitive effects also impose pressures for migration of individuals from a subhabitat. If the two species are, respectively, abundant in the subhabitats in which either species is competitively superior, and the migration has a mixing effect, then, it would be intuitively expected that, as potential migration rates increase, the two species are mixed well and coexist in the whole habitat. An analysis of this competitive situation using our model under the assumption of linear diffusion predicted that, even though weak mixing maintains coexistence in the whole habitat, strong mixing collapses coexistence and leads to the exclusion of one species. The assumption that migrations occur due to self- and cross-population pressures provides different predictions: (i) weak dominance and strong mixing destabilize the coexistence state and lead to a monopolizing equilibrium of either species (bi-stability of monopolizing equiliblia); (ii) conspicuous weakness of the inferior species makes the mixing equilibrium stable, regardless of the potential migration rate; and (iii) tri-stability exists in between situations (i) and (ii). In the third case, the attainable state is the mixing equilibrium or either of the monopolizing equilibria, depending on the initial state. Migration mechanisms with self- and cross-population pressures tends to mediate spatial segregation and makes coexistence possible, even with strong mixing.

Key words: bi-stability; migration; mixing equilibrium; monopolizing equilibria; mono-stability; self- and cross-population pressures; tri-stability.

INTRODUCTION

Competitive interaction has been addressed to explain the coexistence and exclusion of species (Lotka 1925; Gause 1934; MacArthur 1958; Hutchinson 1961; MacArthur & Levins 1967; Lack 1971; May 1972; Park 1962). The classical theoretical work on two-species competition (Lotka–Volterra [L–V] type ordinary differential equations) tells us the ecological conditions of three typical behaviors of the interaction: (i) coexistence; (ii) bi-stability (either species predominates depending on the initial condition); and (iii) dominance (one species predominates and excludes the other species, irrespective of the initial condition) (Yodzis 1989; Gotelli 1998). Even though criticism exists that the L–V model is descriptive and needs to take into account more mechanistic models (Huisman & Weissing 1999; MacArthur 1972; Tilman *et al.* 1981), the L–V model still plays an important role in population and community ecology (Lawton & Hassel 1981; Kingsland 1985; Yodzis 1989; Hastings 1996; Yodzis 1996; Hughes & Roughgarden 1998). In this paper, we address the issue of coexistence/predominance in two species that compete according to the L–V model in a habitat that consists of two adjoining subhabitats between which migration is possible.

Levin (1974) carried out a classic study that incorporates migration into the L–V model. He

argued for the stability condition of coexistence of two competitive species in a habitat that is comprised of two identical subhabitats in which the bi-stability condition holds. He assumed that migration between the subhabitats occurs as a simple linear diffusion process (i.e. movements of individuals are proportional to the differences in species densities between the two subhabitats, with common dispersal constants). When the dispersal constants are non-zero (but not large), two competitive species coexist stably in each subhabitat. Large dispersal constant values make the coexistence equilibrium unstable, and either species will monopolize both of the subhabitats, depending on the initial conditions. His model tried to answer the question of species coexistence in a patchwork habitat of similar environments.

The reaction–diffusion equations model is a general extension of the study of competition/migration in continuous space (Levin 1974). The pattern of spatial distribution of two competitive species has been studied assuming various associations of competitive abilities, and initial and boundary conditions (Pao 1981). Assumptions of dispersive force have been modified differently. Shigesada et al. (1979), and Mimura & Kawasaki (1980) assumed that per capita emigration at each point in space occurs not only as random diffusion, but also by intra- and interspecific population pressures at the point. Even though several types of competition/migration models have been presented (Shigesada et al. 1979; Mimura & Kawasaki 1980; Namba 1989), no thorough studies on subsets of the full model have been conducted because of mathematical difficulties, divergence of submodels and/or restricted interest in the biological processes.

Our model postulates two species and two different subhabitat types, with the assumption that one species is competitively superior in one subhabitat and the other species is competitively superior in the other subhabitat. If there is no migration between the two subhabitats, competitive segregation would occur between the two subhabitats. If the two subhabitats were adjacent, migration of individuals between the two subhabitats would occur by various mechanisms. Movement of individuals from a certain point could be assumed depending on the conditions at the point of departure (Namba 1989; Okubo 1980).

Our model also postulates that the per capita emigration rate is determined by intra- and interspecific population pressures in the subhabitats, and the dispersive movement of a species is proportional to the difference in the total emigration rates between the two adjacent subhabitats. Our assumption of individual migration is homologous to Namba (1989; equation 1), in which random diffusion effects were removed from the full nonlinear diffusion model presented by Shigesada et al. (1979; equation 26).

Competitive segregation is not necessarily maintained if migration acts to join adjacent subhabitats. Immigrants from an adjacent subhabitat may lead to the prevention of extinction of an inferior species in a subhabitat and the maintenance of the coexistence of two species. Reciprocal immigration of dominant species between two subhabitats should collapse any allopatiric coexistence and lead to either species monopolizing both subhabitats. In the present study, we address how intra- and interspecific population pressures on the migration of individuals may have an effect on segregation, mixing and monopolization of two competitive species in two subhabitats.

We postulate a system in which species x is competitively superior to species y in subhabitat 1, and species y is competitively superior to species x in the adjacent subhabitat 2, and individuals of both species migrate from their home subhabitat to the adjoining one due to a crowding effect in their home subhabitat. Without migration, species x would exclude species y in subhabitat 1, and species y would exclude species x in subhabitat 2. We analyze how equilibrium states (coexistence/exclusion of two species in each subhabitat) change with migration, competition coefficients and initial conditions.

THE MODEL

The dynamics of two competitive species (x and y) are examined in a habitat that consists of two subhabitats, with the assumptions that the two subhabitats adjoin each other, and species x and y exist in a certain assemblage in both subhabitats in an initial condition.

Instantaneous change in the population density of species x in subhabitat i is divided into the three

components: (i) birth and death within the sub-habitat; (ii) emigration to the adjoining sub-habitat; and (iii) immigration from the adjoining subhabitat. We assume that intra- and interspecific competition with density dependence regulates the birth and death of the focal species within the subhabitat, and the process follows a L–V competition equation:

$$r_{x_i}\left(1-\frac{x_i+\gamma_{y_i}y_i}{K_{x_i}}\right)x_i, \quad \{1,2\}\ni i, \qquad (1)$$

where x_i is the density (or population number) of species x, y_i is the density of species y, y_{x_i} is the intrinsic increasing rate of species x, K_{x_i} is the carrying capacity of species x, and γ_{y_i} is a competition coefficient of y to x (a conversion factor of y into x as density) in subhabitat i, respectively.

Emigration of species x from a subhabitat is caused by intra- and interspecific population pressures within the subhabitat. The instantaneous per capita migration rate of species x can be assumed to be an increasing function of the effective density of species x in the subhabitat. The effective density of species x is defined as the density of x plus the density of y that is converted as the density of x by the competition coefficient. Here, we define the instantaneous per capita emigration rate of a focal species as a function of the effective density:

$$f(X) = pX^n \qquad (2)$$

where p is the potential per capita instantaneous migration rate ($0 < p$), X is the effective density of the focal species standardized by the carrying capacity of the species in the subhabitat, and n is the exponent characterizing the non-linearity of density dependence ($0 < n$). As intra- and inter-specific competition lead to a decrease in the population growth rates in closed populations, we assume that intra- and interspecific competitions work as pressures on the individuals to move from the subhabitat. Thus, the standardized effective density for species x in subhabitat i, is defined as:

$$X_i = \frac{x_i+\gamma_{y_i}y_i}{K_{x_i}}.$$

Assuming that no mortality during migration exists (there is a one-to-one correspondence of emigrants from one subhabitat and immigrants into the other subhabitat), the process of instantaneous emigration and immigration of species x in subhabitat i adjacent to subhabitat j is expressed as:

$$\underbrace{-f(X_i)x_i}_{\text{emigration}}+\underbrace{f(X_j)x_j}_{\text{immigration}} \quad (\{1,2\}\ni\{i,j\}, \text{ and } i\neq j)$$

Thus, the dynamics of species x in subhabitat i, which adjoins habitat j, is:

$$\frac{dx_i}{dt} = r_{x_i}\left(1-\frac{x_i+\gamma_{y_i}y_i}{K_{x_i}}\right)x_i - f(X_i)x_i + f(X_j)x_j. \qquad (3)$$

Similarly, we can define the dynamics of species x in subhabitat j and the dynamics of species y in subhabitats i and j.

Since our interest is focused on the qualitative effects of migration intensity and competition relations between the two species on the fate of the two competitive species in two subhabitats, for analytical simplicity we assume that the intrinsic rates of increase and carrying capacities are identical in both subhabitats and for both species. The carrying capacity is standardized as unity. We assume that $n = 1$ to express a simple positive density dependent migration process in equation (2), and each species employs identical migration mechanisms in both subhabitats. We further assume that the two species have identical migration mechanisms. The full form of the dynamics of species x and species y in subhabitat 1 and subhabitat 2 are;

$$\frac{dx_1}{dt} = r(1-x_1-\gamma_{y_1}y_1)x_1 - p(x_1+\gamma_{y_1}y_1)x_1$$
$$+ p(x_2+\gamma_{y_2}y_2)x_2$$

$$\frac{dy_1}{dt} = r(1-y_1-\gamma_{x_1}x_1)y_1 - p(y_1+\gamma_{x_1}x_1)y_1$$
$$+ p(y_2+\gamma_{x_2}x_2)y_2$$

$$\frac{dx_2}{dt} = r(1-x_2-\gamma_{y_2}y_2)x_2 - p(x_2+\gamma_{y_2}y_2)x_2$$
$$+ p(x_1+\gamma_{y_1}y_1)x_1$$

$$\frac{dy_2}{dt} = r(1-y_2-\gamma_{x_2}x_2)y_2 - p(y_2+\gamma_{x_2}x_2)y_2$$
$$+ p(y_1+\gamma_{x_1}x_1)y_1 \qquad (4)$$

If we suppose that species x and species y are each exclusively superior in subhabitat 1 and subhabitat 2, respectively, the following conditions should be satisfied: $\gamma_{y_1}< 1 <\gamma_{x_1}$, and $\gamma_{x_2} < 1 <\gamma_{y_2}$,

(Yodzis 1989; Gotelli 1998). This implies that the per capita competitive influence of heterospecifics is lower than that of conspecifics for superior species, and vice versa. For simplicity, we assume that the competition between the two species is symmetrical in the two subhabitats, and denote that $\gamma_{y_1} = \gamma_{x_2} = \gamma_1$ and $\gamma_{x_1} = \gamma_{y_2} = \gamma_2$ $(0 < \gamma_1 < 1 < \gamma_2)$. An initial condition is that there are non-zero numbers of both species in each subhabitat.

RESULTS

When the potential migration rate (p) is zero, the two subhabitats are completely separate. In this system, there exists only one stable equilibrium, $E_1 = (\hat{x}_1, \hat{y}_1, \hat{x}_2, \hat{y}_2) = (1, 0, 0, 1)$. Complete competitive exclusion occurs in both subhabitats. Species x monopolizes subhabitat 1 and species y monopolizes subhabitat 2, and segregation occurs in the habitat. Any pulse perturbation cannot change the attainable state (except for a complete replacement perturbation or a complete exclusion perturbation).

Mixing equilibrium and local stability

When the potential migration rate takes a non-zero value, the two subhabitats are coupled by two-way migrations due to density dependence factors in home subhabitats. Intuitively, it makes sense that the effect of migration is a mixing equilibrium. In the new equilibrium, the two species mix in a certain proportion in each subhabitat, with the proportion influenced by the competition coefficients and the potential migration rate. We studied the mixing equilibrium for the parameter set (ρ, γ_1, γ_2), where ρ is the standardized potential migration rate (the ratio of the potential migration rate to the intrinsic increase rate, p/r). Since our analysis is restricted to a symmetrical system, the trivial mixing equilibrium is symmetrical, $E'_1 = (\hat{e}_1, \hat{e}_2, \hat{e}_2, \hat{e}_1)$. E_1 can be considered to be a special case of E'_i. In the equilibrium, as ρ becomes large, predomination of the competitively superior species is relaxed. Because the inferior species excluded by competition in one subhabitat is supplemented by immigration from the other subhabitat (where the species is competitively superior), the larger the ρ the higher the degree of mixing in the two subhabitats at equilibrium (Fig. 1).
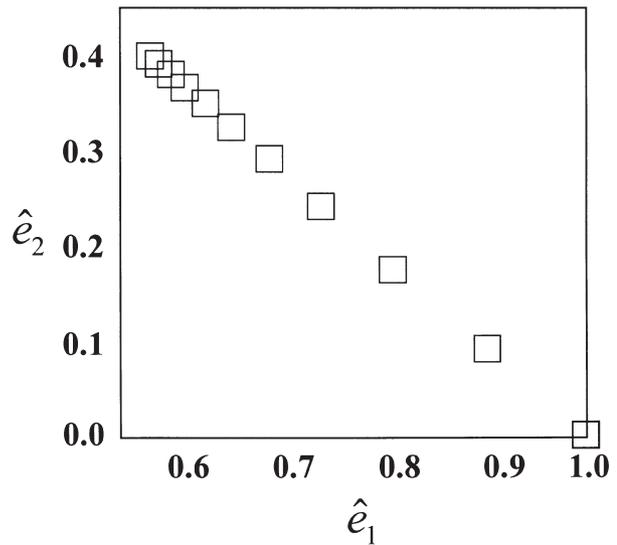

Fig. 1. The mixing equilibrium population sizes, $\hat{e}_1 = \hat{x}_1 = \hat{y}_2$ and $\hat{e}_2 = \hat{x}_2 = \hat{y}_1$. The competition coefficients are $\gamma_1 = 0.91$, $\gamma_2 = 1.01$. From the lower right to the upper left ρ is designated from 0 to 0.1 with every 0.01 step.
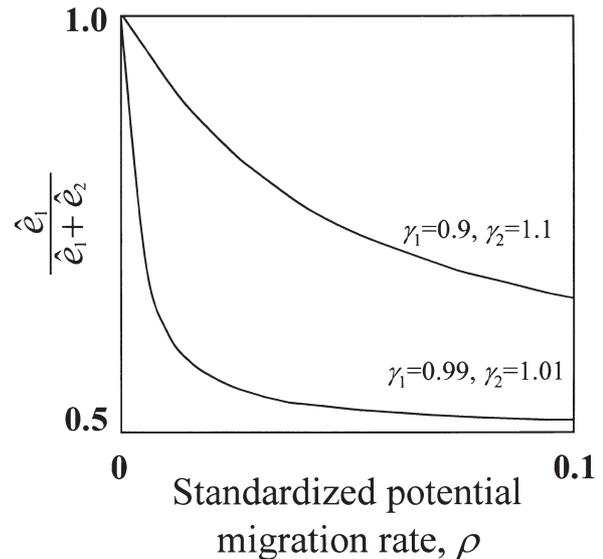

Fig. 2. The proportion of superior species to the total population in each subhabitat as a function of the standardized potential migration rate at the mixing equilibrium.

We surveyed species mixing for different competition coefficient sets and different potential migration rates. Figure 2 shows the proportion of the predominant species to the total population of each subhabitat ($\hat{e}_1/(\hat{e}_1 + \hat{e}_2)$). The mixing effect works well with high migration and/or weak competitive dominance.
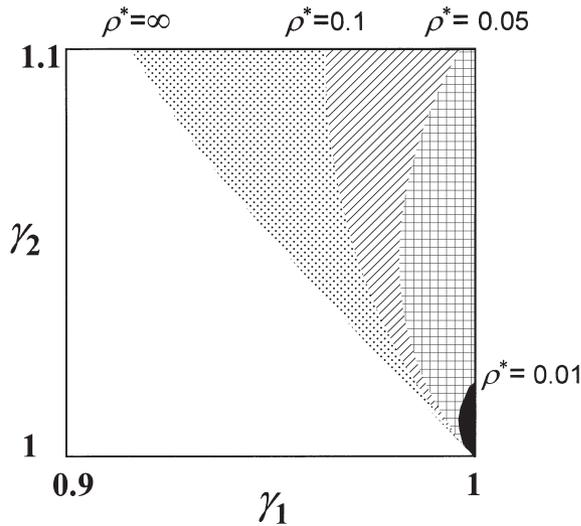
Fig. 3.   Parameter sets (γ_1, γ_2) that locally stabilize or destabilize the mixing equilibrium for given values of ρ. The mixing equilibrium is locally stabilized in the white region irrespective of ρ. The mixing equilibrium is locally unstable in the right-side regions of the boundaries for ρ larger than ρ^*.

It is not necessarily guaranteed that the equilibrium is stable for any parameter values. To examine the local stability of equilibrium , we conducted a numerical calculation of eigenvalues of a linear approximation of the system [equations (4)] at equilibrium. For the parameters, $0 < \rho$ and $0 < \gamma_1 < 1 < \gamma_2$, we calculated the eigenvalues of the Jacobian matrix of equations (4) at equilibrium and evaluated the signs of the largest element of the eigenvalues in the parameter space $(\rho, \gamma_1, \gamma_2)$ using the manual *Mathematica* (Wolfram 1996).

Figure 3 shows the stability and instability of the mixing equilibrium for the parameter sets. The mixing equilibrium is not always stable for migration rates that are non-zero. Migration tends to destabilize the mixing equilibrium in certain combinations of competition coefficients. Weak competitive dominance and high migration rates destabilize the mixing equilibrium. Minor superiority of the dominant species facilitates stabilization of the mixing equilibrium.

Monopolizing equilibria and local stability

Equations (4) have two other equilibrium states, $(\hat{x}_1, \hat{y}_1, \hat{x}_2, \hat{y}_2) = E_2 = (1, 0, 1, 0)$ and $E_3 = (0, 1, 0, 1)$. In these states, either species x or species y would monopolize the subhabitat where it is com-

petitively superior, and also the other subhabitat where it is competitively inferior. We conducted local stability analyses of the monopolizing equilibria, E_2 and E_3.

We can analytically survey the local stability of the equilibria. The eigenvalues of the Jacobian matrix of the linearized system of equation (4) at equilibria, E_2 and E_3, are identical: $(-1, -1 -4\rho, \ D_-, \ D_+)$, where $D_\pm = \frac{1}{2}((2 - \gamma_2 - \gamma_1) - (\gamma_2 + \gamma_1)\rho \pm \sqrt{\Delta})$ and $\Delta = (\gamma_2 + \gamma_1)^2\rho^2 + 2(\gamma_2 - \gamma_1)^2 \rho + (\gamma_2 - \gamma_1)^2$. For $0 < \rho$ and $0 < \gamma_1 < 1 < \gamma_2$, Δ is positive and a monotonically increasing function of ρ, and thus, all eigenvalues are real, and D_+ is the largest eigenvalue. When the sign of D_+ is positive, the equilibria are unstable and vice versa.

Since $D + (\rho_{=0}) = (1-\gamma_1) > 0$, if $D_+(\rho) = 0$ has a single positive root, ρ^*, the largest eigenvalue is positive for $0 \leq \rho < \rho^*$ and negative for $\rho^* < \rho$, and the equilibria are unstable for $0 \leq \rho < \rho^*$ and stable for $\rho^* < \rho$. The threshold standardized migration rate ρ^* is given as,

$$\rho^* = \frac{(1-\gamma_1)(1-\gamma_2)}{(\gamma_1 + \gamma_2) - 2\gamma_1\gamma_2}, \qquad (5)$$

if the denominator is negative. Therefore, the necessary conditions for which there exists a positive ρ^* above which the monopolizing equilibria are locally stable are:

$$\frac{1}{2} < \gamma_1 \ \text{and} \ \frac{\gamma_1}{-1 + 2\gamma_1} < \gamma_2, \qquad (6)$$

for the permitted range of γ_1 and γ_2. However, if $\frac{1}{2} < \gamma_1$ and $\frac{\gamma_1}{-1 + 2\gamma_1} < \gamma_2$, or $\gamma_1 \leq \frac{1}{2}$ for any value of γ_2 hold, there exists no ρ-value that satisfies $D_+ = 0$ and $0 < D_+$ is satisfied for any positive ρ. In these cases of the permitted range of γ_1 and γ_2, the monopolizing equilibria are destabilized for any migration rate.

The equilibria, E_2 and E_3, become locally stable or unstable depending on the parameters set $(\rho, \gamma_1, \gamma_2)$ given that inequalities (6) hold. Equation (5) implies that a threshold standardized potential migration rate is a function of competition coefficients. For given competition coefficients, $\hat{\gamma}_1$ and $\hat{\gamma}_2$ that satisfy equations (6), the threshold standardized migration rate ρ^* is determined. If the standardized migration rate is greater than ρ^* at $(\hat{\gamma}_1, \hat{\gamma}_2)$, the equilibria are locally stable. However,
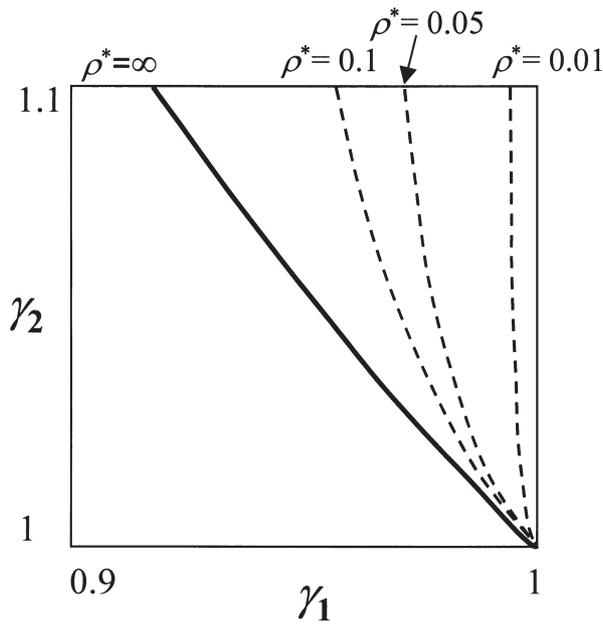
Fig. 4. Parameter sets (γ_1, γ_2) that locally stabilize or destabilize the monopolizing equilibria for given values of ρ. The monopolizing equilibria are locally unstable in the left-side region of the solid boundary curve ($\gamma_1/(-1 + 2\gamma_1) = \gamma_2$) irrespective of ρ. The monopolizing equilibria are locally stable in the right-side region of each dashed line for ρ larger than ρ^*.

if the standardized migration rate is less than ρ^* at ($\hat{\gamma}_1$, $\hat{\gamma}_2$), the equilibria are locally unstable. If the standardized migration rate is equal to ρ^* at ($\hat{\gamma}_1$, $\hat{\gamma}_2$), the equilibria are neutrally stable. Insignificant weakness and/or dominance of the inferior or superior species lessens the threshold migration rate, and stabilizes the monopolizing equilibria.

Mono-stability, bi-stability and tri-stability

We checked numerically that the mixing equilibrium is stable if the monopolizing equilibria are unstable. The parameter space of competition coefficients is divided into three regions depending on the combinations of local stability/unstability of the two types of equilibrium (mixing or monopolizing) (Fig. 4).

1. A distinct weakness of the inferior species tends, locally, to stabilize the mixing equilibrium and destabilize the monopolizing equilibria. This situation implies that there is mono-stability of the mixing equilibrium.

2. Indefinite weaknesses and/or weak dominances of the inferior and superior species facilitates the stabilization of the monopolizing equilibria and the destabilization of the mixing equilibrium. This situation implies bi-stability of the equilibria, and an attainable monopolizing state depending on the initial state.

3. In between 1 and 2, both the mixing and the monopolizing equilibria are locally stable. This tri-stability situation implies that the mixing equilibrium, or any of the monopolizing equilibria, can be attainable depending on the initial state.

We found numerically that two unstable interior equilibria also exist, E_4 and E_5, in the tri-stability situation. The characteristics of the two unstable equilibria will be mentioned in the next section. Among them, a high potential migration rate widens the region of bi-stability of the monopolizing equilibria on the γ_1-γ_2 plane (Fig. 5).

We calculated numerically the proportion of the superior species to the total population of the sub-habitat in the mixing equilibrium on the γ_1-γ_2 plane for a given ρ (Fig. 5). It is intuitively appealing that a high potential migration rate and/or inconspicuous differences in competitive abilities favor strong mixing (the weaker the competitive dominance, the closer the proportion to 0.5; however, the equilibrium becomes destabilized). However, low migration and/or conspicuous differences in competitive abilities favor weak mixing, and the superior species will predominate in each subhabitat.

When the potential migration rate is low, the equilibrium proportion would be affected by the competition coefficient of the superior species. When the potential migration rate is high, the equilibrium proportion would be affected by the competition coefficients of both the superior and the inferior species.

Global stability of the mixing equilibrium and monopolizing equilibria

In the system analyzed here, if a unique equilibrium exists that is locally stable, the equilibrium would also be globally stable. If multiple equilibria exist that are locally stable, then attainable states of trajectories of dynamics will depend on
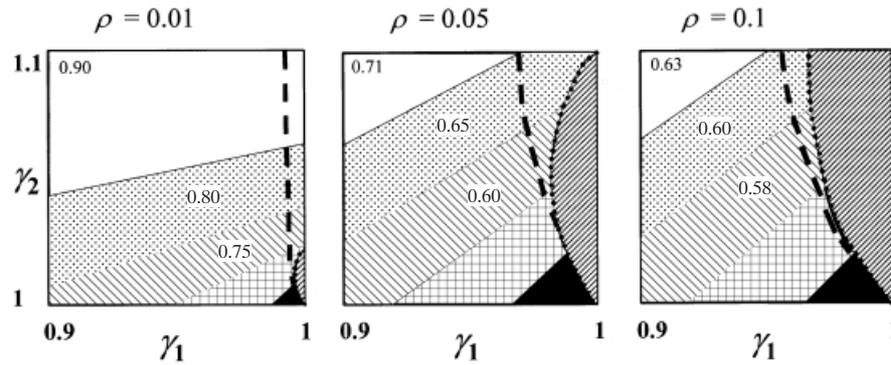
$\rho = 0.01$ $\rho = 0.05$ $\rho = 0.1$

Fig. 5. Stability and instability of the mixing and the monopolizing equilibria on the competition coefficients plane for given values of ρ. Mono-stability region: only the mixing equilibrium is locally stable on the left side of the dashed lines. Bi-stability region: only the monopolizing equilibria are locally stable on the right side of the dotted lines. Tri-stability region: in between the dashed and dotted lines, both the mixing equilibrium and the monopolizing equilibria are locally stable. The numbers on the contours indicate the proportion of dominant species to the total population in each subhabitat at the mixing equilibrium. At the area near $(\gamma_1, \gamma_2) = (1, 1)$, there is no difference in competitive ability between the two species and at the mixing equilibrium, each species exists with a proportion of 0.5.
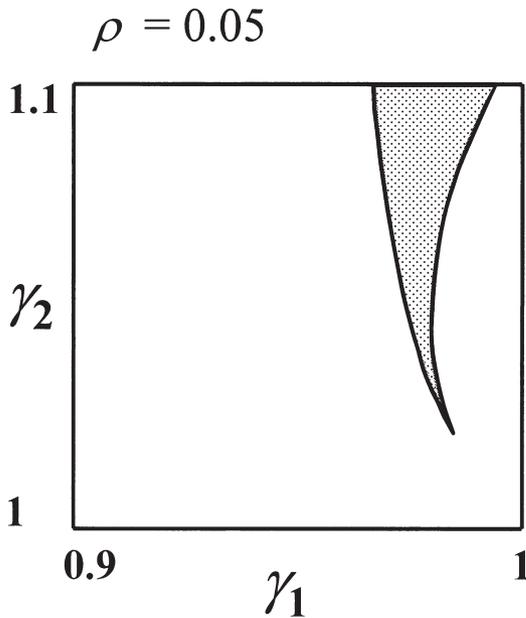

$\rho = 0.05$

Fig. 6. Number of interior equilibria on the competition coefficient plane for $\rho = 0.05$. The shaded area has one stable and two unstable interior equilibria. Outside of the shaded area, there exists a unique interior equilibrium. Fig. 5b showed the local stability of the equilibrium.

the initial conditions and on thre scale of the attractor domains of the equilibria.

In the tri-stability case, two monopolizing equilibria and one mixing equilibrium (all of which are locally stable), and two interior unstable equilbria

exist (Fig. 6). For example, in the case of $\gamma_1 = 0.98$, $\gamma_2 = 1.1$ and $\rho = 0.05$ (located in between the dashed and the dotted lines of Fig. 5b), we find the numerical solutions for interior equilibria. The locally stable mixing equilibrium is $E_1' = (\hat{x}_1, \hat{y}_1, \hat{x}_2, \hat{y}_2) = (0.6638, 0.3190, 0.3190, 0.6638)$. The interior unstable equilibria are $E_4 = (0.2573, 0.7278, 0.0909, 0.9022)$ and $E_5 = (0.9022, 0.0909, 0.7278, 0.2573)$.

We analyzed domains of attraction of the three locally stable equilibria, numerically. We considered a restricted situation in which the two species divided the carrying capacities of subhabitats with arbitrary combinations in the initial state. The initial state was chosen from $(x_1, y_1 | x_1 + y_1 = K_1)$, and $(x_2, y_2 | x_2 + y_2 = K_2)$.

Figure 7 shows the boundaries between basins of the three attractors. The attractor of the mixing equilibrium is placed around the region where the sum of species x (or species y) in both subhabitats is K ($K_1 = K_2 = K$). This implies that, regardless of the degree of segregation, the existence of the two species in roughly equal numbers within the whole habitat maintains the dynamics in a coexistence state, and leads the dynamics to a mixing equilibrium. When high proportions are allocated to the subhabitat where each species is competitively dominance (high segregation in the initial state), the mixing equilibrium is robustly obtainable, despite the distortion of equal numbers of the
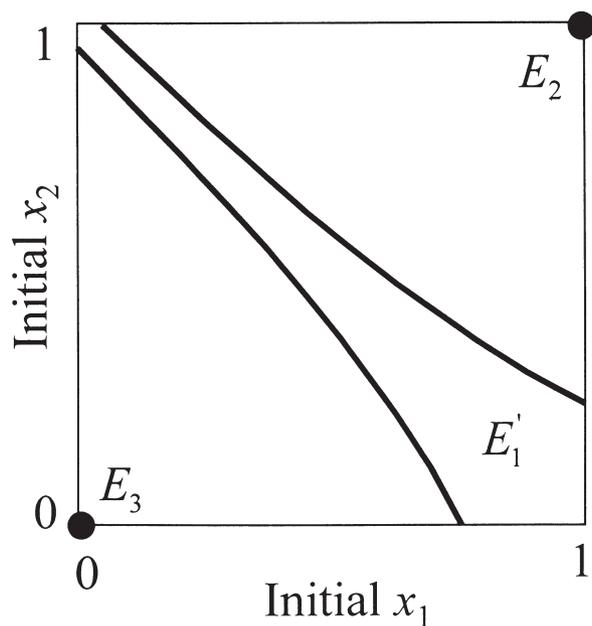
Fig. 7. Domains of attractors of the mixing equilibrium, and either of the monopolizing equilibria. The horizontal and the vertical axes each indicate proportion of species x in subhabitat 1 and subhabitat 2, respectively.

competitive species within the whole habitat as an initial condition.

When the initial species distribution is far from equal numbers, the monopolizing equilibrium of the species initially predominating in the total population is attainable. The proportion of species x to the total population is 0.176 and 0.824 at the unstable equilibriums E_4 and E_5, respectively. Therefore, each of the two unstable interior equilibria would be contained in the domain of attractor of either monopolizing equilibrium.

DISCUSSION

Certain species may be competitively dominant to other species in a subhabitat, but competitively subordinate to other species in other subhabitats. Such competitive reciprocal dominance is observed in brook char (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) in North America (Nagel 1991; Magoulick & Wilzbach 1997). Generally, brook char is competitively dominant in the headwaters of a river, and rainbow trout is competitively dominant downstream (Larson *et al*. 1995).

Exclusion, segregation and mixing of competitive species in a habitat that is comprised of two adjacent subhabitats (in which one species is competitively dominant in one subhabitat and the other species is competitively dominant in the other subhabitat) is determined by competitive dominance and the migration balance. In a sympatric region containing brook char and rainbow trout, complete exclusion of one species in the river habitat, segregation of the two species in two types of subhabitats (upstream and downstream), and weak mixing of the two species in both subhabitats have all been observed (Flebbe 1994; Strange & Habera 1998). Complete exclusion of one species in a river might be caused by insufficient specialization to either of subhabitats, or be due to the high migration rate between the subhabitats.

The cause of migration is associated with the state of the point of departure. Crowding can facilitate activity to leave a place (Crisp 1993; Fonseca & Hart 1996), and movement from a place is considered to be influenced by non-random self- and cross-population pressures.

It is expected, intuitively, that segregation would be maintained between subhabitats if competitive depression of an inferior species overwhelms its immigration from another subhabitat, even if migration between the two subhabitats is considerable. If migration takes place, two species become mixed in certain proportions. Thus, if migration exists, superficially segregated coexistence would be expected with little mixing of the two species. If the migration rate becomes high, two species would be expected to be mixed well in both subhabitats, with species coexisting.

However, mixing is not a uniquely feasible state. Migration may facilitate the mixing of two species, but it also destabilizes the coexistence state. When the subordination of the inferior species is minimal, the mixing effect of a high migration rate destroys coexistence and excludes one of the species, depending on the initial conditions. Conspicuous weakness of the inferior species and/or strong dominance of the superior species tends to maintain segregation with a certain degree of mixing between two subhabitats. In cases where each species is not heavily depressed by its competitor in the main habitat in which they are competitively superior (i.e. $\gamma_1 \ll 1$), the monopolizing equilibria are destabilized, irrespective of

the degree of suppression of the inferior competitor in the main habitat and of migration rate. In such situations, competitive exclusion does not occur and the mixing equilibrium is stabilized.

Tri-stability conditions exist in terms of competitive relations and migration rates. The conditions that satisfy tri-stability include roughly equal numbers of competitive species, regardless of the distribution patterns within the whole habitat, which helps to maintain coexistence and leads to a mixing equilibrium.

Coexistence/exclusion of competitive species in spatially structured habitats has been studied under the assumptions of continuous or discrete habitat space and varying biological states. Partial differential diffusion models address aspects of the existence of stable spatially non-homogeneous positive distributions of competitive species. Several types of competition and migration have been assumed (Shigesada *et al.* 1979; Mimura & Kawasaki 1980; Bertsch *et al.* 1984; Namba 1989; Mimura & Fang 1991). Many studies assume that (i) the competitive relationship between two species is spatially homogeneous; and (ii) the causes of movement of individuals are self- and/or cross-population pressures, and/or random drift (linear diffusion) with a spatially homogeneous function. Several discrete habitat–migration models have also adopted assumption (ii) of the diffusion models, with the additional assumptions: (i) that competitive relationships are different or identical between subhabitats; and (ii) that carrying capacities of competitive species are different or identical between subhabitats and between species. This diversification of assumptions has led to the creation of several varieties of submodels according to biological interests.

Takeuchi (1989) analyzed the coexistent condition of competitive species with random diffusion between two subhabitats. With a condition similar to our assumption of the competition relationship, his model suggests that a mixing equilibrium is unstable for larger migration rates. In our model, in which movement is caused by self- and cross-population pressures, individuals forced to emigrate from their main subhabitat to the other subhabitat (in which they are competitively inferior) can also immigrate into their main subhabitat. Competitively inferior species is suppressed in the subhabitat, but is evacuated to their main subhabitat. Reinforcement of this mechanism by population pressures may serve to allow species to coexist within the whole habitat, even if the mixing effect of movement predominates.

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