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# Implementation of the lattice model in the coexistence of species and its potential consequences on environment

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**Abstract**--The population dynamics of a system of two competing species have been investigated in the mean-field and lattice approximation. The two species are denoted by A and B. Each site of the square lattice is either occupied by an individual or vacant. The two species compete for vacant sites to reproduce. There is a reproduction only to the nearest neighbours. We consider the invasion of a rare species into a population composed of a resident species based on a pair – approximation method in which the dynamics of both average densities and nearest neighbour correlations are

considered. The results are then compared with those obtained by the mean-field approximation. When species B contain intraspecific interaction term, invasion of the rare species A into resident species B becomes easier in lattice structured populations. But the rare species B invading species A is difficult in lattice models in comparison to mean-field approximation. The overall coexistence of species is enhanced in lattice models. These results were verified by simulation on a square lattice although the range of the enhancement of the species coexistence is reduced. This calls for the attention that pair-approximation is an oversimplification of the real situation. However, with the presence of commensalism (when A helps B), the range of species coexistence is reduced in lattice habitat in comparison to the mixed population case.

**Keywords**---lattice models, the coexistence of species, Species biodiversity, Conservation, mean-field model, Spatial pattern, Global change.

## Introduction

An individual organism usually interacts with a higher probability with the neighbouring organisms than the distant ones. Spatial structure can influence the population dynamics when the organisms have a limited dispersal range. As the gametes of sessile organisms like plants usually disperse to neighbouring sites, the effect of the spatial structure becomes important. These spatial influences can also lead to increased coexistence between two or more competing species. For two populations having the same overall density, the growth rates can be different depending on whether their distributions are random or have a spatial pattern. The spatial distributions can also be spontaneously formed by certain ecological processes. Spatial dynamics are known to have important effects on competitive coexistence in model systems (Levins and Culver, 1971; Levin, 1974; Hastings, 1980; Hanski, 1983; Levin *et al.*, 1984; Chesson, 1985; Pacala, 1986; Adler and Nuernberger, 1994; Tilman, 1994; Gandhi *et al.*, 1998). The spatial models are usually investigated via simulation. Traditionally, most ecological models have assumed that all individuals of all species experience a well-mixed homogeneous habitat in which similar compositions can be found in all the neighbourhoods. This conceptually simple description is called the mean-field model. It assumes that the global averages are good substitutes for the local population distributions. Durrett & Levin (1994) have shown that this mean-field description sometimes fails to correctly describe the dynamics of the system. There are a variety of models that try to overcome the drawbacks of the mean field models. In patch models, individuals comprising a population are divided among patches; there is complete mixing within a patch and limited dispersal among patches. Models such as interacting particle systems (Durrett and Levin, 1994) and probabilistic cellular automata (Rand *et al.*, 1995) consider the effect of stochasticity and spatial extension of natural populations. Metapopulation models are known to increase the persistence of species through spatial dynamics (Gilpin and Hanski, 1991). Cellular automata models have been investigated to model spatially explicit population dynamics (Hassel *et al.*, 1991; De Roos *et al.*, 1991;

Sato and Iwasa, 1993). Sometimes spatial structure has been neglected (Caswell and Etter, 1992), but the predictions become qualitatively different from the lattice simulation (Harada and Iwasa, 1996; Durrett and Levin, 1997). It is difficult to examine parameter dependence clearly from direct simulation on a lattice. In the lattice model, pair-approximation is a method to construct a closed dynamical system of global densities and local densities. The method has been applied successfully to various dynamical models with lattice structures, such as predator-prey dynamics (Matsuda *et al.*, 1992), host-pathogen systems (Sato *et al.*, 1994) and the evolution of altruism (Matsuda *et al.*, 1987; Nakamura *et al.*, 1997).

In this paper, we discuss the competition between two species living in a spatially structured habitat. They compete for vacant sites to reproduce. The basic purpose of our analysis is to examine whether a spatially explicit model has a species-coexistence range different from a perfectly mixed system. We aim to show under what situation spatial structure can increase the coexistence of species. We provide one example of where it happens. We also give another model where the reverse situation occurs. The two different models are- i) one species has intraspecific interactions and ii) one species helps another through commensalism. To analyze the population dynamics, we have considered the dynamical system of overall population density and local density, the latter representing the nearest neighbour correlation (Harada and Iwasa, 1994; Harada and Iwasa, 1996). We have used pair-approximation (Matsuda *et al.*, 1992) which is a valuable tool to analyze lattice models (Sato *et al.*, 1994; Harada *et al.*, 1995; Nakamura *et al.*, 1997). We have also conducted computer simulations on a lattice to compare with the analytical result based on pair approximation. In section 2, the model is formulated; the results are presented in section 3 followed by concluding remarks in section 4.

## Model

We consider two types of species, denoted by A and B. The habitat is a two-dimensional lattice. Each site has  $Z$  neighbours, where  $Z = 4$  (we have adopted the Neuman neighbourhood). Each site is either occupied by type A, occupied by type B, or vacant, which we call an A-site, a B-site and an E-site, respectively. The average fractions of the sites of states A, B and E are designated  $\rho_A$ ,  $\rho_B$  and  $\rho_E$ . These are called global densities (21, 24). For example,  $q_{A/B}$  is the fraction of A among the neighbours of a randomly chosen B-site. In general,  $q_{i/j}$  is the local density of  $i$  in the nearest neighbours of  $j$ -site ( $i, j = A, B$  or  $E$ ). The states of the neighbours become positively correlated as reproduction occurs only to neighbours. Let  $d_A$  be the rate of transition from site A to E, and  $d_B$  be that from B to E, which are the mortalities of species A and species B, respectively. An individual of species A can produce offspring only if it is adjacent to a vacant site, and the reproduction rate per vacant neighbouring site is  $b_{A/z}$ , where  $b_{A/z}$  is the maximum reproductive rate achieved when all the neighbours are vacant. The rate of successful reproduction of A is proportional to the number of vacant sites E in the neighbourhood of the A-site. Hence the reproductive rate of a randomly chosen A-site is  $b_A q_{E/A}$ , which is the product of the maximum birth rate and the

fraction of E- sites in the neighbourhood of the A-site. Similarly, the rate of successful reproduction of an average B-site is  $b_B q_{E/B}$ .

(a) *Intraspecies interaction*

We shall investigate a model where species B have intraspecific interaction in addition to competition for vacant sites between species A and species B. We have considered intraspecies interaction in one species only because it is easier to manage the mathematical equations.

The rate of change in global densities  $\rho_A$  and  $\rho_B$  are given by

$$\frac{d\rho_A}{dt} = -d_A\rho_A + b_A q_{E/A}\rho_A, \quad (1a)$$

$$\frac{d\rho_B}{dt} = -d_B\rho_B + b_B q_{E/B}\rho_B - c q_{B/B}\rho_B. \quad (1b)$$

In the above equations,  $q_{E/A}$  and  $q_{E/B}$  are local densities and  $c$  is a coefficient which measures the strength of intraspecific interaction.

**Mean- field approximation:**

Mean-field approximation is to neglect the correlation between sites. The dynamics based on mean-field approximation can be regarded as those for the population

mixed completely by additional external forces. Under mean-field approximation, local density is replaced by global density, for example  $q_{E/A}$  and  $q_{B/B}$  are replaced by  $\rho_E$  and  $\rho_B$

respectively. Equations (1a) and (1b) are then rewritten as

$$\frac{d\rho_A}{dt} = [(b_A - d_A) - b_A\rho_A - b_A\rho_B]\rho_A, \quad (2)$$

and

$$\frac{d\rho_B}{dt} = [(b_B - d_B) - b_B\rho_A - (b_B + c)\rho_B]\rho_B. \quad (3)$$

Which is a special case of Lotka-Volterra competition model with intraspecific interaction? After doing phase plane analysis of  $\rho_A$  and  $\rho_B$  isoclines, the following conditions can be obtained.

A can invade if

$$1 - \frac{d_A}{b_A} > \frac{b_B - d_B}{b_B + c}. \quad (4)$$

B can invade if

$$1 - \frac{d_B}{b_B} > 1 - \frac{d_A}{b_A}. \quad (5)$$

### Lattice model with pair approximation:

To make a closed dynamical system of global and local densities, the pair-approximation postulates:  $q_{A/EA} \cong q_{A/E}$ . In general, quantity  $q_{i/jk}$  is the conditional probability for a site to be  $i$  given that it is a neighbour of a  $j$ -site whose another neighbour is  $k$  ( $i, j$ , and  $k$  are in  $\{A, B, E\}$ ). Pair-approximation is  $q_{i/j} \cong q_{i/jk}$  (Sato *et al.*, 1994).

The dynamics of two global densities in Eq. (1) can be rewritten as:

$$\frac{d\rho_A}{dt} = [-d_A + b_A(1 - q_{A/A} - q_{B/A})]\rho_A, \quad (6a)$$

and

$$\frac{d\rho_B}{dt} = \left[ -d_B + b_B \left( 1 - \frac{\rho_A}{\rho_B} q_{B/A} - q_{B/B} \right) - cq_{B/B} \right] \rho_B. \quad (6b)$$

(See Appendix A).

### Invasion condition:

(i) *A invades B:*

Here we consider the conditions for invasion by a rare type, say  $A$ , to the population dominated by the other type  $B$ . We shall examine whether a rare invader  $A$  can increase in frequency in the equilibrium population dominated by type  $B$ . Equation (1a) shows that the Malthusian parameter of a rare invader depends only on  $q_{E/A}$ , the availability of vacant sites adjacent to invader individual  $A$ .

$A$  can invade if  $q_{E/A} > d_A / b_A$ , where the local density should be estimated at the equilibrium composed only of resident species  $B$ . The procedures to calculate invasibility are: (1) the equilibrium of the dynamics of  $\rho_B$  and  $q_{B/B}$  are obtained with  $\rho_A = 0$ ; (2) using these three variables we construct the dynamics of two local densities  $q_{A/A}$  and  $q_{B/A}$ , and calculate the stable equilibrium of these two local densities; and finally (3) the inequality  $q_{E/A} > d_A / b_A$  is examined (Matsuda *et al.*,

1992). By means of these procedures, the condition for species A to invade species B can be calculated (see appendix B). The condition turns out to be

$$b_A > \frac{d_A [z\{b_B(d_B + c) + d_A(b_B + c)\} + b_B\{z(b_B - d_B) - (b_B + c)\}]}{[z\{b_B(d_B + c) + d_A(b_B + c)\} - \{b_B(d_B + c) + d_A(b_B + c)\} - d_A\{z(b_B - d_B) - (b_B + c)\}]} \quad (7)$$

If the reverse inequality holds, species A must decrease in population dominated by species B, and hence invasion is not possible. The birth rate of species B must satisfy the following constraints. It is found that  $b_B > 4/3 d_B + 1/3 c$  by using  $0 < \rho_B < 1$  and equation (B.2). Similarly,  $b_B > d_B$  is obtained from equation (B.1) and  $0 < q_{B/B} < 1$ .

(ii) *B invades A:*

Here we consider the conditions for invasion by a rare type B to the resident The population of type A. Equation (1b) shows that B can invade if

$$q_{E/B} > \frac{1}{b_B} [d_B + cq_{B/B}] \quad (8)$$

where the local density should be estimated at the equilibrium composed only of resident species A. The condition for invasibility is calculated by following the procedure of the previous section (see appendix C). The condition for Species B to invade Species A is given by (from equation C.5)

$$\begin{aligned} & \frac{1}{b_B} (d_B + cx_1) + \frac{1}{2c} \left[ \left\{ (2d_B + cx_1)^2 + 2c(d_B + cx_1) \right\}^{1/2} - (2d_B + cx_1) \right] \\ & + \frac{(b_A + b_B) \frac{1}{b_B} (d_B + cx_1) \left( \frac{3}{4} - \frac{d_A}{b_A} \right)}{(d_A + d_B + cx_1)} - 1 < 0. \quad (9) \end{aligned}$$

$q_{B/B} = x_1$  can be determined numerically by solving the two coupled equations (C.3a) and (C.3b) at equilibrium.  $b_A$  must satisfy the following constraints:  $q_{A/A} > 0$  and equation (C.1) imply that  $b_A > d_A$  and  $\rho_A > 0$  with equation (C.2) give  $b_A > 4/3 d_A$ .

**Commensalism:**

We have also analyzed a two-species competition model with one way helping interaction where species A helps species B. The rate of change in global densities are

$$\frac{d\rho_A}{dt} = -d_A\rho_A + b_A q_{E/A}\rho_A, \quad (10a)$$

and

$$\frac{d\rho_B}{dt} = -d_B\rho_B + b_B q_{E/B}\rho_B + c' q_{A/B}\rho_B. \quad (10b)$$

In Eq.(10b),  $c'$  represents the strength of one-way helping interaction. By following the same procedure as before one can find the invasion conditions in the mean-field approximation. A can invade B if

B can invade A if

$$\frac{b_B - d_B}{b_B - c_1} > 1 - \frac{d_A}{d_B} \frac{b_A}{b_B}. \quad (11)$$

$$\frac{b_A}{d_A} > \frac{b_B}{d_B}. \quad (12)$$

In the lattice formulation with pair approximation, by following the previous procedure, it can be found that A can invade B if

$$\frac{b_A}{d_A} > \frac{b_B}{d_B}. \quad (13)$$

This invasion condition is the same as in the mean-field case (see Eq. 11). In a similar manner the condition can be calculated when species B invades species A (see appendix D).

### Lattice simulation:

We have also investigated the invasibility of a rare species in a population dominated by the resident species using computer simulation on a square lattice. The chief purpose was to check the range of validity of the pair approximation. A 25 by 25 grid (625 cells) was modelled. In the computer program, an empty lattice cell was assigned 0 while those occupied by species A and B were designated as 1 and 2 respectively. The rare species was chosen with a low probability  $p_i (= 0.01)$  initially. A lattice cell was chosen at random, and its birth process to neighbours and death with certain probabilities were conducted. Then another cell was chosen at random, and a similar process was repeated. In one time step, the cells were chosen at random 625 times and birth and death processes were evaluated. The simulation was allowed to run for 6-time steps. Then the frequency of the rare species was examined. If it was more than the initial frequency, then we had concluded that the rare species was able to invade a population of resident species. Since it was a random process, the result was taken as the average of 12 samples. Let  $p_f$  be the final probability of the rare species 'A,' after some time steps and  $b_A$  its birth rate. After one-time step  $p_i$  and  $p_f$  were nearly equal for different birth rates  $b_A$  but  $p_f$  changed as the number of time steps increased. After 6-time steps,  $p_f$  tended to zero for low  $b_A$ , became equal to  $p_i$  for some

intermediate value of  $b_A$  and attained a value greater than  $p_i$  for a higher value of  $b_A$ . A was able to invade successfully when its birth rate was beyond a certain critical value. The critical value of  $b_A$  was slightly increased with the increase of the number of time steps but it gradually attained an asymptotic value. The number of time steps was limited to 6 (which was good enough for theoretical investigation) to save computational time.

## Results

The primary concern of our analysis was to compare the results of invasibility between mean field and lattice models. Figure 1 shows that species A can invade species B easily in the lattice model. Invasion becomes still easier when the intraspecies interaction strength of species B increases.

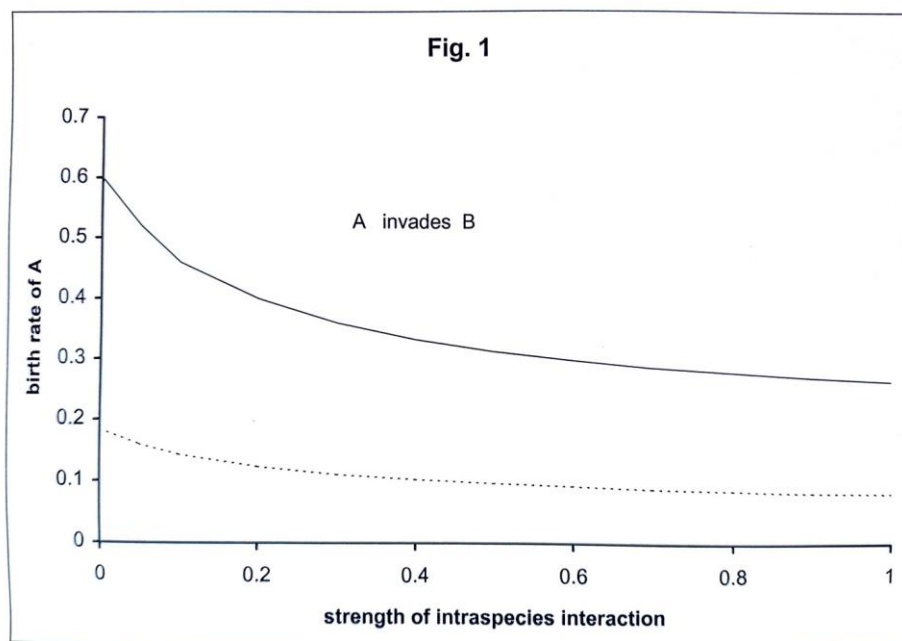


Fig. 1: The invasion of species A as a function of intraspecies interaction strength inspecies B. The solid lines represent the mean field case, and the dashed line shows the lattice results. A can invade B in the region above the solid and dashed lines.  $b_B = 0.6$

However, the invasion becomes more difficult with a higher birth rate of species B (data not shown). Figure 2A illustrates the change of the birth rate of species A as a function of the birth rate of species B. Species A can easily invade species B in spatial models in comparison to the mean field case. The invasion is easy when the intraspecies interaction is strong. The invasion of the rare species B into resident species A is difficult in lattice habitat when compared with the



continuum approximation (Fig. 2B). Figure 3 shows that the species coexistence region is enhanced in the lattice model with pair approximation. However, the range of the coexistence region is reduced in the case of lattice simulation. Figure 4 depicts the coexistence region of the two species when commensalism is present (species A helps species B). It shows that the coexistence region is reduced in the lattice habitat.

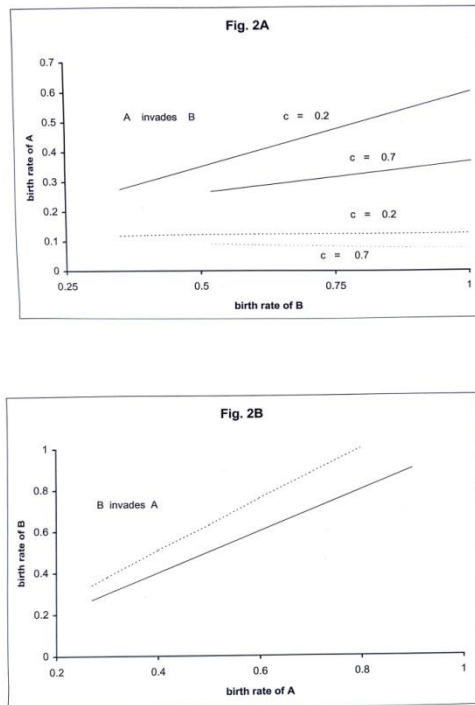


Fig. 2A: The invasion of species A with the birth rate of species B. The allowed birth rate of species B is more for the higher value of the intraspecies interaction strength. The solid line represents the mean field case and the dashed line shows the lattice results.

Fig. 2B: The invasion of species B into a resident species A. The solid and dashed lines are for mean field and lattice cases, respectively.  $c = 0.2$ .

## Discussion

Determining how regional dynamics of competition and mobility significantly affect species coexistence is an important challenge in ecology. Clusters are spatial formations that arise. To ensure constant coexistence for two species, population models in a patch structured habitat must include specific extra mechanisms favoring rare species, such as niche differentiation (Chesson, 1981; Chesson, 1991). The parameters for a rare species' successful invasion into a population dominated by resident species were investigated (Takenaka et al., 1997). Studies have concluded that there is no possibility for the stable coexistence of two distinct types in the lattice model. It has also shown that there is no equilibrium in which both types coexist stably in the mean field

approximation. We have shown that the addition of intraspecies interaction can not only make a stable coexistence possible but can improve the range of species coexistence in lattice structured habitat in comparison to a completely mixed population model. The spatial effects are important when intraspecific interaction is present. The clustering effect becomes important due to reproduction to the nearest neighbours. However, the coexistence region is somewhat reduced when the result is computed through simulation (Fig. 3). This shows that pair-approximation is not a particularly good approximation. The result of computer simulation should lie between continuum approximation and lattice model with pair approximation. This should be the general feature of any system. As intraspecies interaction in species B increases, A invading B becomes easier in the mean-field model in comparison to the lattice case. When this is combined with the fact that species B invading species A is independent of the intraspecies interaction term in the mean-field model, the following picture emerges. When the intraspecies interaction in species B is increased, the coexistence region in the mean-field model becomes greater while in the lattice model it is relatively reduced. Consequently, the advantage in the lattice model in terms of species coexistence is reduced.

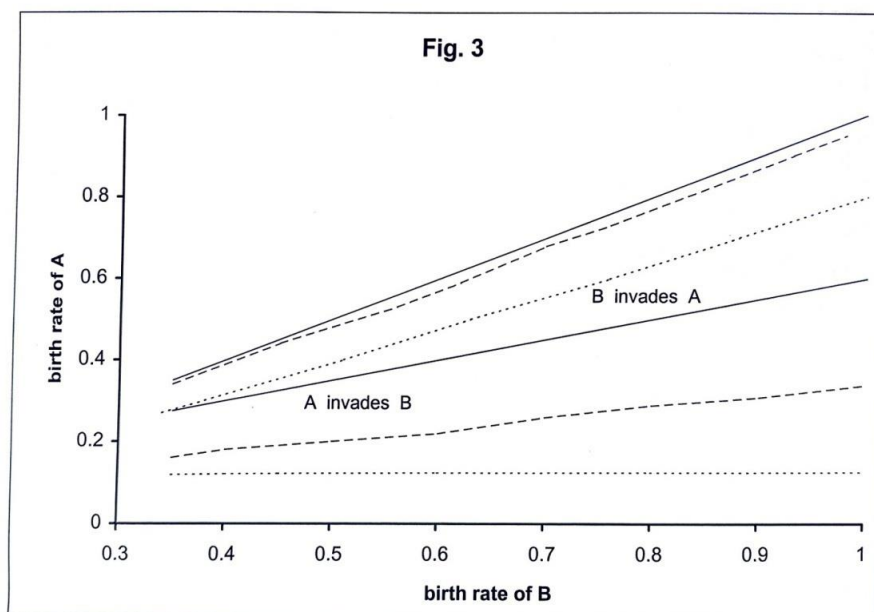


Fig. 3: The coexistence region for both the species. The different lines show the following cases: solid (mean field), dashed (lattice model with pair approximation) and long dashed (lattice model with simulation). Species A can invade species B above the three lower lines and species B can invade species A below the upper three lines.  $c = 0.2$ .

When species A helps species B, clusters of A's are formed surrounding A as reproduction occurs to nearest neighbours in the lattice habitat. As a result,

species B invading species A becomes more difficult in the lattice model than in the mean-field case. So, when species A helps one another, the range of coexistence is reduced in spatial models (Fig. 4). The same result will be true when both the species survive by helping each other through mutualistic interaction. We have simulated a lattice size of 25 by 25. In a lattice size of 50 by 50 (with fixed birth rate  $b_A$ ), the final frequency of the rare invading species at successive time steps is slightly lower in comparison to the case with a lattice size of 25 by 25. So, the critical birth rate beyond which value the rare species can invade is a little higher. We have also shown by simulation that mutualism can evolve through spatial effects (in preparation).

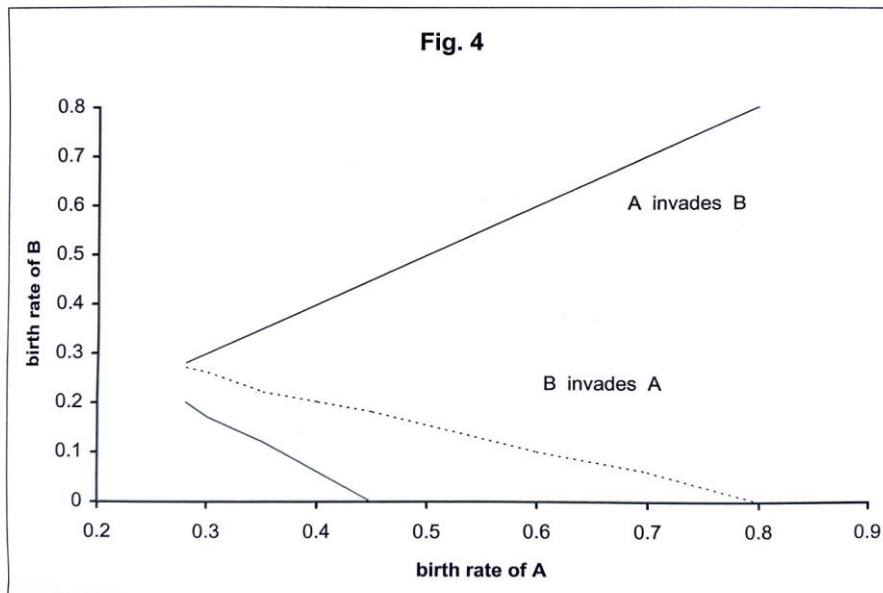


Fig. 4: The coexistence region when species A helps species B. The condition for rare species A invading the resident species B is the same for both the mean field and lattice models. The upper solid line represents both cases. Species A can invade species B below the upper solid line. Species B can invade species A above the dashed line (lattice model) and above the lower solid line (mean field model).  $c = 0.4$ .

In a two species system, when each survives by helping the other, mutualism cannot evolve in the mean-field approximation. But mutualism can evolve due to spatial effects when the benefit of helping each other is high and the associated cost is low. This happens due to cluster formation around mutualistic pairs of species as reproduction occurs to the nearest neighbours. The incorporation of spatially explicit dynamics provides an important insight to understand the coexistence of competing species. We conjecture that our present conclusion will also hold good when  $n$ -species interact through competition with intraspecies interaction. Spatial effects can improve the coexistence of species.

### **Environmental impact:**

We study how ecological variations, or the lack thereof, may impact other patterns of species living together and population dynamics since not all species cohabit. We investigate the changes from species invasions to range modifications; we exhibit how massive change is influencing species coexistence at both rare and dominant levels. Finally, we consider how adaptive progression and morphological flexibility could influence species' responses to climate change and coexistence. We may never know if coexistence approaches can maintain the planet's vast diversity of life. Nonetheless, we suggest that conservationists worried about the consequences of global transformation on species diversity should focus on increasing their knowledge.

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### Appendix A:

There are three global densities ( $\rho_A$ ,  $\rho_B$  and  $\rho_E$ ) and nine local densities ( $q_{A/A}$ ,  $q_{B/A}$ , ...,  $q_{E/E}$ ) but not all of them are independent of each other. We have the following seven constraints:

$$\rho_A + \rho_B + \rho_E = 1, \quad (\text{A.1a})$$

$$q_{A/i} + q_{B/i} + q_{E/i} = 1 \quad (i = A, B \text{ or } E), \quad (\text{A.1b})$$

and

$$q_{i/j} \rho_j = q_{j/i} \rho_i \quad (i, j = A, B \text{ or } E). \quad (\text{A.1c})$$

Hence there are only five independent variables. We can choose  $\rho_A$ ,  $\rho_B$ ,  $\rho_{A/A}$ ,  $\rho_{B/A}$ ,  $\rho_{B/B}$ , as independent variables and express all the others in terms of these five.

Let the density of AA-sites be  $\rho_{AA}$ , i.e., a randomly chosen pair of nearest neighbours are both A. This is called ‘‘doublet density’’ (22). From its definition as a conditional probability, we can express local density as  $q_{A/A} = \rho_{AA} / \rho_A$ , the ratio of doublet density to (singlet) global density. In general, we denote the density of ‘‘ij’’- pairs as  $\rho_{ij}$  ( $i$  or  $j = A, B$  or  $E$ ). Using this notation, we can express the local density as simply the ratio of doublet density to singlet density:  $q_{i/j} = \rho_{ij} / \rho_j$ . To calculate the dynamics of local density, for example  $q_{A/A}$ , we first calculate the dynamics of doublet density  $\rho_{AA}$ . They are:

$$\frac{d\rho_{AA}}{dt} = -2d_A \rho_{AA} + 2\rho_{AE} b_A \left( \frac{1}{z} + \frac{z-1}{z} q_{A/EA} \right), \quad (\text{A.2})$$

Where the first term of the right-hand side indicates the rate at which an AA-pair is lost by the death of either one of the two A’s, each occurring at rate  $d_A$ . The second term is the formation of new AA bonds from AE, which is possible by two ways:

first by the reproduction of the A-site of the pair to the E-site, or second by the reproduction of an A existing in one of the other  $Z-1$  neighbours of the E other than the A-site of the pair. The rate of reproduction is defined as  $b_{A/Z}$  per AE bond. As shown by Eq (A.2), calculating the dynamics of the number of AA-pairs requires a higher order local conditional probability  $q_{A/EA}$ , which is the probability for a randomly chosen nearest neighbour of an E-site to be A, given one of the other neighbours of the E-site is an A,

We can choose  $\rho_A$ ,  $\rho_B$ ,  $q_{A/A}$ ,  $q_{B/A}$ , and  $q_{B/B}$  as independent variables and express all the others in terms of these five:

$$\rho_E = 1 - \rho_A - \rho_B, \quad (\text{A.3a})$$

$$q_{E/B} = 1 - \frac{\rho_A}{\rho_B} q_{B/A} - q_{B/B}, \quad (\text{A.3b})$$

$$q_{A/B} = \frac{\rho_A}{\rho_B} q_{B/A}, \quad (\text{A.3c})$$

$$q_{E/A} = 1 - q_{A/A} - q_{B/A}, \quad (\text{A.3d})$$

$$q_{A/E} = \frac{\rho_A}{1 - \rho_A - \rho_B} (1 - q_{A/A} - q_{B/A}), \quad (\text{A.3e})$$

$$q_{B/E} = \frac{\rho_B}{1 - \rho_A - \rho_B} \left( 1 - \frac{\rho_A}{\rho_B} q_{B/A} - q_{B/B} \right), \quad (\text{A.3f})$$

and

$$q_{E/E} = \frac{1 - 2\rho_A - 2\rho_B + \rho_A q_{A/A} + \rho_B q_{B/B} + 2\rho_A q_{B/A}}{1 - \rho_A - \rho_B}, \quad (\text{A.3g})$$

(a) *Interspecific interaction:*

The rate of change of doublet densities and local densities are calculated as follows by using pair approximation.

$$\begin{aligned} \frac{d\rho_{AB}}{dt} &= -(d_A + d_B)\rho_{AB} + \rho_{AE}b_B \frac{z-1}{z} q_{B/EA} + \rho_{BE}b_A \frac{z-1}{z} q_{A/EB} - cq_{B/BA}\rho_{AB} \\ &= -(d_A + d_B)\rho_{AB} + (b_A + b_B)\rho_E \frac{z-1}{z} q_{A/E} q_{B/E} - cq_{B/B}\rho_{AB} \end{aligned} \quad (\text{A.4})$$

$$\frac{d\rho_{BB}}{dt} = -2d_B\rho_{BB} + 2\rho_{BE}b_B \left( \frac{1}{z} + \frac{z-1}{z} q_{B/EB} \right) - 2cq_{B/BB}\rho_{BB}$$



$$= -2d_B \rho_{BB} + 2\rho_{BE} b_B \left( \frac{1}{z} + \frac{z-1}{z} q_{B/E} \right) - 2c q_{B/B} \rho_{BB}. \quad (\text{A.5})$$

$$\begin{aligned} \frac{dq_{A/A}}{dt} &= \frac{1}{\rho_A} \frac{d\rho_{AA}}{dt} - \frac{1}{\rho_A^2} \rho_{AA} \frac{d\rho_A}{dt} \\ &= -2d_A q_{A/A} + 2b_A (1 - q_{A/A} - q_{B/A}) \left[ \frac{1}{z} + \frac{z-1}{z} \frac{\rho_A}{1 - \rho_A - \rho_B} (1 - q_{A/A} - q_{B/A}) \right] \end{aligned}$$

$$\begin{aligned} \frac{dq_{B/B}}{dt} &= \frac{1}{\rho_B} \frac{d\rho_{BB}}{dt} - \frac{1}{\rho_B^2} \rho_{BB} \frac{d\rho_B}{dt} \\ &= -(d_A + d_B) q_{B/A} + \frac{z-1}{z} \frac{\rho_B}{1 - \rho_A - \rho_B} (b_A + b_B) (1 - q_{A/A} - q_{B/A}) \end{aligned} \quad (\text{A.6})$$

$$- c q_{B/B} q_{B/B} - q_{B/B} [-d_B + b_B (1 - q_{A/B} - q_{B/B})] \quad (\text{A.7})$$

$$= -2d_B q_{B/B} + 2b_B (1 - q_{A/B} - q_{B/B}) \left\{ \frac{1}{z} + \frac{z-1}{z} \frac{\rho_B}{1 - \rho_A - \rho_B} (1 - q_{A/B} - q_{B/B}) \right\}$$

$$\left(1 - \frac{\rho_A}{\rho_B} q_{B/A} - q_{B/B}\right) - c q_{B/B} q_{B/A} - q_{B/A} [-d_A + b_A (1 - q_{A/A} - q_{B/A})] \quad (\text{A.8})$$

$$\begin{aligned} \frac{dq_{B/A}}{dt} &= \frac{dq_{A/B}}{dt} \frac{d\rho_{AB}}{d\rho_B} \frac{1}{\rho_A^2} \frac{d\rho_{AB}}{d\rho_A} \rho_{AB} \frac{d\rho_A}{d\rho_B} \frac{d\rho_B}{dt} \\ &= -d_A q_{A/B} + \frac{z-1}{z} (b_A + b_B) \frac{\rho_A}{1 - \rho_A - \rho_B} \left(1 - q_{A/A} - \frac{\rho_B}{\rho_A} q_{A/B}\right) \end{aligned}$$

$$(1 - q_{A/B} - q_{B/B}) - b_B q_{A/B} (1 - q_{A/B} - q_{B/B}) \quad (\text{A.9})$$

(b) *Commensalism:*

The rate of change of doublet densities and local densities can be calculated in a equivalent manner when there is one way helping interaction (see Eq. 10)

## Appendix B:

The condition for species A to invade species B in lattice model can be calculated as follows.

(1) Global and local densities of the resident species:

We put  $\rho_A=0$  in  $dp_B/dt = 0$  in Eq.(6b) and get

$$q_{B/B} = \frac{b_B - d_B}{b_B + c}. \quad (\text{B.1})$$

After putting  $\rho_A=0$  in  $dq_{B/B}/dt = 0$ ,

it is found that

$$\rho_B = \frac{z(b_B - d_B) - (b_B + c)}{(z-1)(b_B + c) - (d_B + c)}. \quad (B.2)$$

(2) Local densities for the rare invades:

With  $\rho_A = 0$ , Eq. (B.1) and Eq. (B.2) the dynamics of local densities  $q_{A/A}$  and  $q_{B/A}$  become as follows: (if we abbreviate  $x = q_{A/A}$  and  $y = q_{B/A}$ ):

$$\frac{dx}{dt} = -d_A x + b_A(1-x-y) \left( \frac{z}{z} - x \right), \quad (B.3a)$$

and

$$\frac{dy}{dt} = -d_B y + k(1-x-y) - y b_A(1-x-y) - c q_{B/B} y, \quad (B.3b)$$

where

$$k = \frac{z-1}{z} \frac{\rho_B}{1-\rho_B} (b_A + b_B)(1 - q_{B/B})$$

$$= \frac{1}{z} \frac{(b_A + b_B)}{(b_B + c)} [z(b_B - d_B) - (b_B + c)] \quad (B.3c)$$

is a constant. An autonomous dynamical system given by Eq. (B.3a and B.3b) has single positive equilibrium ( $0 < x < 1$ ,  $0 < y < 1$ ) that is stable and obtained as follows. Using  $w = 1 - x - y$ , we can express the equilibrium values of  $x$  and  $y$  as:

$$x = \frac{2 \frac{b_A}{Z} w}{d_A + b_A w} \quad \text{and} \quad y = \frac{k w}{\frac{b_B (d_B + c)}{b_B + c} + b_A w}. \quad (\text{B.4})$$

Then  $1 = w + x + y$  becomes

$$1 = w + \frac{2 \frac{b_A}{z} w}{d_A + b_A w} + \frac{k w}{\frac{b_B (d_B + c)}{b_B + c} + b_A w}. \quad (\text{B.5})$$

The equilibrium of Eqs. (B.3a) is calculated from Eqs. (B.4) with  $w$  obtained from Eq. (B.5) and  $0 < w < 1$ .

(3) Examine the sign of the Malthusian parameter for rare invaders:

The solution  $w$  of Eq. (B.5) corresponds to the fraction of vacant sites among the neighbours of the random rare invader,  $w = q_{E/A}$ . If we regard the right-hand side of Eq. (B.5) as a function of  $w$ , denoted by  $f(w)$ , it satisfies  $f(0) = 0$  and  $f(1) > 1$  and  $df(w)/dw > 0$  under certain conditions.

Hence there is the unique solution of Eq. (B.5) satisfying  $0 < w < 1$ . The inequality

$q_{E/A} > d_A / b_A$  implies that the invasion is possible if and only if  $w$  is larger than  $d_A / b_A$ , which is equivalent to  $f(d_A / b_A) < 1$ . This can be rewritten by using Eq. (B.5) as

$$\frac{d_A}{b_A} + \frac{1}{z} + \frac{kd_A(b_B + c)}{b_A[b_B(d_B + c) + d_A(b_B + c)]} < 1. \quad (B.6)$$

### Appendix C:

The condition for species B to invade species A in the lattice model can be found by following the procedure of the previous section.

After putting  $\rho_B = 0$  in  $d\rho_A/dt$  of Eq.(6a), it is found that

$$q_{A/A} = 1 - \frac{d_A}{b_A}. \quad (C.1)$$

Then we put  $\rho_B = 0$  in  $dq_{A/A}/dt = 0$  to find

$$\rho_A = \frac{(z-1)b_A - zd_A}{(z-1)b_A - d_A}. \quad (C.2)$$

With  $\rho_B = 0$  in  $dq_{B/B}/dt$  and  $dq_{A/B}/dt$  (after abbreviating  $q_{B/B} = x_1$  and  $q_{A/B} = y_1$ ),

$$\frac{dx_1}{dt} = -d_B x_1 + \frac{2}{z} b_B (1 - x_1 - y_1) - b_B x_1 (1 - x_1 - y_1) - c x_1^2, \quad (C.3a)$$

and

$$\frac{dy_1}{dt} = -d_A y_1 + k_1 (1 - x_1 - y_1) - b_B y_1 (1 - x_1 - y_1), \quad (C.3b)$$

where

$$k_1 = (b_A + b_B) \left( \frac{z-1}{z} - \frac{d_A}{b_A} \right) \quad (C.3c)$$

is a constant.

Using  $w = 1 - x_1 - y_1$ , the equilibrium values of  $x_1$  and  $y_1$  can be expressed as:

$$x_1 = \frac{-(d_B + b_B w) + \sqrt{(d_B + b_B w)^2 + 8 \frac{c}{z} b_B w}}{2c}, \quad (C.4a)$$

and

$$y_1 = \frac{k_1 w}{d_A + b_A w}. \quad (C.4b)$$

Using  $f(w) = w + x + y$  and following the same procedure as in previous section the invasion condition becomes

$$f\left[\frac{1}{b_B}(d_B + c q_{B/B})\right] < 1. \quad (C.5)$$

Appendix D:

We shall consider a situation where there is commensalism (A helps B). By following the previous procedure, the following condition can be found for species B to invade species A in the lattice model,

B can invade A if

$$\begin{aligned} \frac{1}{b_B}(d_B - c_1 q_{A/B}) + \frac{\frac{2}{z}(d_B - c_1 q_{A/B})(d_A + d_B - c_1 q_{A/B})}{(d_A + d_B - c_1 q_{A/B})(2d_B - c_1 q_{A/B}) - \frac{c_1 k_2}{b_B}(d_B - c_1 q_{A/B})} \\ + \frac{\frac{k_2}{b_B}(d_B - c_1 q_{A/B})}{(d_A + d_B - c_1 q_{A/B})} - 1 < 0 \quad (D.1) \end{aligned}$$

where

$$k_2 = \frac{z-1}{z} \frac{\rho_A}{1-\rho_A} (b_A + b_B) \frac{d_A}{b_A} \quad (D.2a)$$

and

$$\rho_A = \frac{b_A(z-1) - zd_A}{b_A(z-1) - d_A}. \quad (D.2b)$$

$q_{A/B}$  should be determined from the two coupled equations at equilibrium given below.

$$\frac{dq_{A/B}}{dt} = -d_A q_{A/B} + (k_1 - b_B q_{A/B})(1 - q_{A/B} - q_{B/B}), \quad (D.3a)$$

and

$$\frac{dq_{B/B}}{dt} = -d_B q_{B/B} + (1 - q_{A/B} - q_{B/B})b_B \left( \frac{2}{z} - q_{B/B} \right) + c_1 q_{A/B} q_{B/B}. \quad (D.3b)$$