



Research article

Population persistence under two conservation measures: Paradox of habitat protection in a patchy environment

Nariyuki Nakagiri^{1,*}, Hiroki Yokoi², Yukio Sakisaka^{3,4} and Kei-ichi Tainaka⁵

¹ School of Human Science and Environment, University of Hyogo, Himeji 670-0092, Japan

² Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Yokohama 236-8648, Japan

³ Division of Early Childhood Care and Education, Nakamura Gakuen University Junior College, Fukuoka 814-0198, Japan

⁴ Institute of Preventive and Medicinal Dietetics, Nakamura Gakuen University, Fukuoka 814-0198, Japan

⁵ Department of Mathematical and Systems Engineering, Shizuoka University, Hamamatsu 432-856, Japan

* **Correspondence:** Email: nakagiri@shse.u-hyogo.ac.jp; Tel: +81792929420; Fax: +81792929420.

Abstract: Anthropogenic modification of natural habitats is a growing threat to biodiversity and ecosystem services. The protection of biospecies has become increasingly important. Here, we pay attention to a single species as a conservation target. The species has three processes: reproduction, death and movement. Two different measures of habitat protection are introduced. One is partial protection in a single habitat (patch); the mortality rate of the species is reduced inside a rectangular area. The other is patch protection in a two-patch system, where only the mortality rate in a particular patch is reduced. For the one-patch system, we carry out computer simulations of a stochastic cellular automaton for a “contact process”. Individual movements follow random walking. For the two-patch system, we assume an individual migrates into the empty cell in the destination patch. The reaction-diffusion equation (RDE) is derived, whereby the recently developed “swapping migration” is used. It is found that both measures are mostly effective for population persistence. However, comparing the results of the two measures revealed different behaviors. i) In the case of the one-patch system, the steady-state densities in protected areas are always higher than those in wild areas. However, in the two-patch system, we have found a paradox: the densities in protected areas can be lower than those in wild areas. ii) In the two-patch system, we have found another paradox: the total density in both

patches can be lower, even though the proportion of the protected area is larger. Both paradoxes clearly occur for the RDE with swapping migration.

Keywords: habitat conservation; stochastic cellular automaton; contact process; reaction-diffusion equation; swapping migration; birth and death processes; metapopulation model

1. Introduction

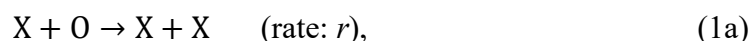
Species extinctions are ongoing due to various factors, such as habitat destruction and climate change [1–3]. The development of conservation policies for endangered species is one of the most urgent issues [4,5]. In the present article, we focus on the simplest system consisting of one species. To save the species, we consider the following two conservation measures: (i) Partial protection in a one-patch system, wherein the target species lives in a single habitat, a partial region is protected and individuals can move around randomly; (ii) Patch protection in a two-patch system, wherein the species lives in two patches, one of which is protected, and the individuals can migrate between both patches. In the two-patch system, we report on “paradoxes of habitat protection”. So far, paradoxes have often been observed when systems contain plural species [6–9]. However, paradoxes may be rare in systems composed of only one species.

In a one-patch system, an agent- or individual-based model is applied [4,5,7,10–16]. Given our choice of a model ecosystem, we apply a “contact process” (CP), which exhibits the phase transition between survival and extinction phases [10,17,18]. CP model, which contains a single species, is a local-interaction version of a logistic equation because the well-mixed population (mean-field theory) of CP corresponds to logistic equations. In the present study, we added migration to CP. The movements of individuals are basic characteristics of animals and humans [19,20].

In a two-patch system, we study the population dynamics, which involve individuals migrating between spatially separated patches. Modeling such dynamics in a patch environment, which is presented as a metapopulation model, has long been studied in ecology [21–23]. In recent years, metapopulation dynamics have been extensively studied in many fields [9,24–27]. Traditionally, the dynamics have been described by the reaction-diffusion equation (RDE), which is composed of reaction and diffusion (migration) terms. Between the patches, individuals (agents) can freely migrate. In the present study, however, we assume the capacities of patches are finite. Individuals migrate into empty cells in the destination patch. For this reason, we apply nonlinear (or “swapping”) migration [28,29].

2. Preliminary

CP is a well-known model in various fields, such as mathematics [17,30], physics [31–33] and epidemiology [17,34–36]. In ecology, CP is regarded as a simple ecosystem consisting of a single species [10,13]. The target species (X) lives on a square lattice. Each lattice site (cell) is either occupied (X) or vacant (O). CP model is defined as follows:



Here, Reactions (1a) and (1b) denote reproduction and death processes, respectively. The parameters

r and μ respectively denote the reproduction and death rates. Simulations are usually carried out by considering either local or global interaction. For the former, Reaction (1a) occurs between adjacent cells. On the other hand, for the latter, it occurs between any pair of cells.

In the case of global interaction, the population dynamics are described by the mean-field theory:

$$dx/dt = rx(1 - x) - \mu x, \quad (2)$$

where $x(t)$ is the density of X at time t . The first and second terms on the right side denote the birth and death process, respectively. Eq (2) can be rewritten as a logistic function:

$$dx/dt = Rx(1 - x/K). \quad (3)$$

Here, we set $R = r - \mu$ and $K = 1 - \mu/r$. Hence, we can say that CP is a lattice version of the logistic equation.

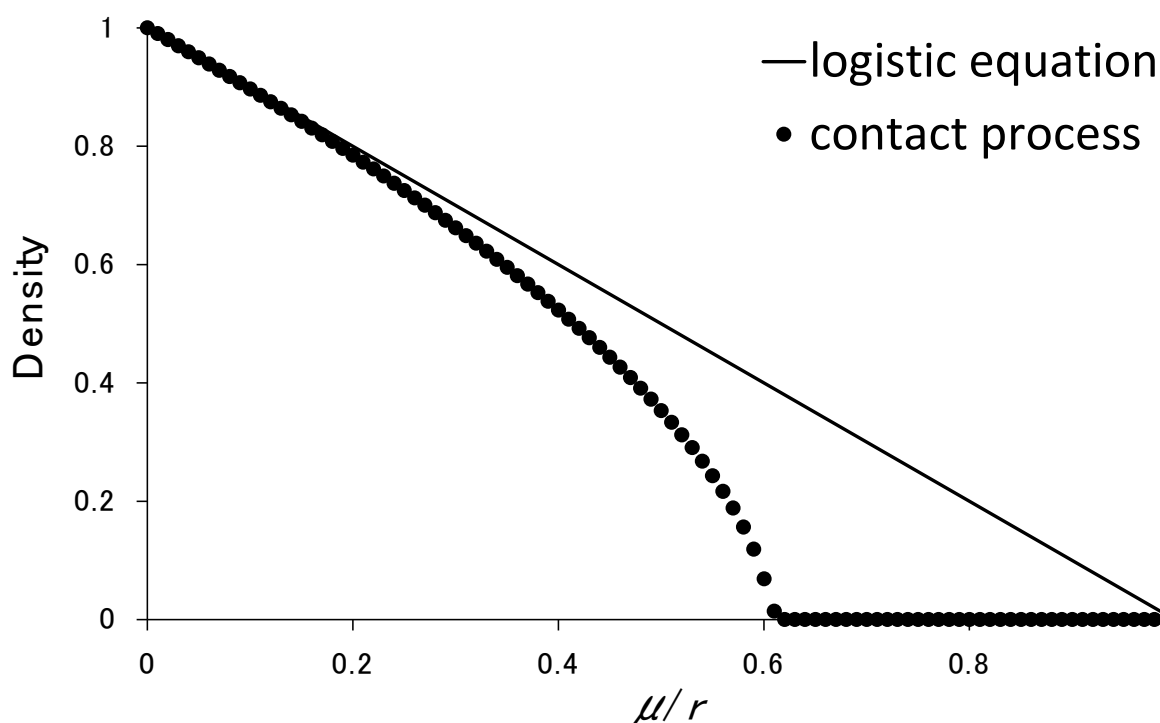


Figure 1. Results of simulating the contact process (CP). The steady-state densities of CP are plotted against (μ/r) . The straight line indicates the results of the logistic equation (well-mixed population).

In Figure 1, the simulation results for local and global interactions are shown. The steady-state densities of local interactions (CP) are plotted against (μ/r) . For the sake of comparison, the results of global interactions (logistic growth: well-mixed population) are represented by a straight line. Figure 1 reveals a phase transition between the survival and extinction phases. The critical value (c) of survival is known to be $c = 1$ for global interaction (logistic equation). However, the rigorous value of c is unknown for local interaction. Figure 1 indicates $c \approx 0.62$ for CP [31,32]. When $\mu/r < c$, the species X survives; in contrast, for $\mu/r \geq c$, the species X goes extinct. To save the species, it is necessary to increase the reproduction rate or decrease the death rate.

3. Models and methods

In Figure 2, two measures of species protection are depicted. Figure 2(a) represents partial protection in a one-patch system; the mortality rate of a species is reduced inside the rectangular (grey) area. On the other hand, Figure 2(b) shows patch protection in a two-patch system; only the mortality rate in the grey patch is reduced. The mortality rate (μ_P) in a protected region is less than μ_W , where μ_W denotes the mortality rate in a wild region: $\mu_P < \mu_W$. Let us define g as the protection ratio (fraction of the protected area relative to the whole area). It measures the degree of habitat protection. In Table 1, the parameters and variables are listed.

Table 1. Descriptions of symbols and parameters.

Symbols and parameters	Descriptions
X	biospecies
O	vacant (empty) cell
r	reproduction (birth) rate
μ_P	mortality rate in protected region
μ_W	mortality rate in wild region
g	protection ratio
D	migration rate
x_1	density of X in Patch 1
x_2	density of X in Patch 2

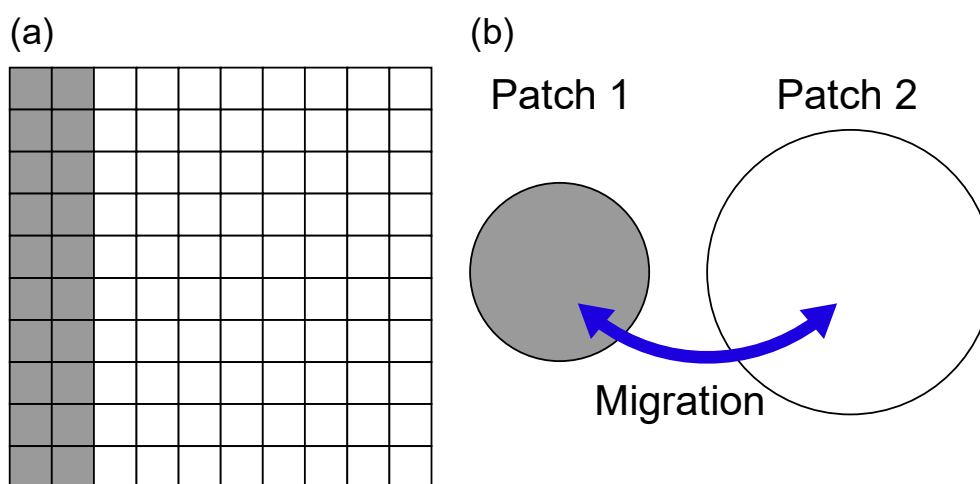
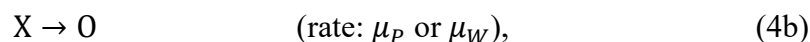
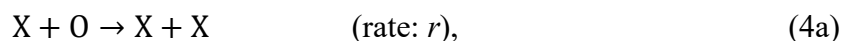


Figure 2. Two types of habitat protection systems. (a) Partial protection in a one-patch system. A species lives on a single lattice. The protection sites, which form a rectangle, are colored grey. (b) Patch protection in a two-patch system. Patch 1 (grey) is protected, while Patch 2 (white) is not protected.

3.1. One-patch system

We want to carry out the simulations on each lattice in consideration of both local and global interactions. We apply a CP model with migration as follows [37]:



Both Reactions (4a) and (4b) are the same as CP. Note that the mortality rate takes different values. If an individual is located in a protected region (grey area in Figure 2(a)), the mortality rate takes μ_P ; otherwise, it takes μ_W . Reaction (4c) denotes the movement (random walk). The lattice is updated as follows:

- 1) Initially, we randomly distribute the biospecies X on a square lattice in such a way that each cell is occupied by only one individual or vacant cell. Here, we employ periodic boundary conditions.
- 2) Each reaction process is performed by applying the following procedures:
 - i) Initiate the reproduction process given by Reaction (4a). We randomly choose a single site on the lattice. When the chosen cell is X, we select one more cell from four adjacent sites. If the latter cell is O, the latter cell is changed to X at a rate r .
 - ii) Initiate the death process given by Reaction (4b). We randomly choose one site on the lattice. If the site is X, then it becomes O because of a different mortality rate. When the selected cell is located in a protected area (or a wild area), the mortality rate takes μ_P (or μ_W).
 - iii) Initiate the diffusion (migration) process given by Reaction (4c). We randomly choose one site on the lattice. If the cell is X, then we choose one more cell from four adjacent sites. If the latter cell is O, then X migrates into O at a rate D . After the migration, both X and O are exchanged (swapped).
- 3) Repeat Steps i), ii) and iii) for 2000 Monte Carlo steps (MCS), where 1 MCS means that the steps i), ii) and iii) are repeated $L \times L$ times [7,38]. Here, L^2 is the lattice size; we set $L = 100$.

For the global interaction, the reproduction process (Reaction (4a)) and migration process (Reaction (4c)) occur between any pair of sites. In this case, the mean-field theory holds. We define $x_P(t)$ and $x_W(t)$ as the densities in protected and wild regions at time t , respectively. The densities can be described by

$$\begin{aligned} \frac{dx_P(t)}{dt} = & r(1 - x_P(t) - x_W(t))x_P(t) - \mu_P x_P(t) \\ & + [D_{PW}x_W(t)(g - x_P(t)) - D_{WP}x_P(t)(1 - g - x_W(t))], \end{aligned} \quad (5a)$$

$$\begin{aligned} \frac{dx_W(t)}{dt} = & r(1 - x_P(t) - x_W(t))x_W(t) - \mu_W x_W(t) \\ & + [D_{WP}x_P(t)(1 - g - x_W(t)) - D_{PW}x_W(t)(g - x_P(t))], \end{aligned} \quad (5b)$$

where D_{PW} and D_{WP} are the rates of migration from a wild to protected region and from a protected to wild region, respectively. The first and second terms on the right-hand side of Eqs (5a) and (5b) represent the reproduction and death processes, respectively. The last term denotes the migration process. The total density $x(t)$ is given by $x(t) = x_P(t) + x_W(t)$.

3.2. Two-patch system

We consider a two-patch model consisting of a protected area (Patch 1) and wild area (Patch 2) (see Figure 2(b)). Let C_1 and C_2 be the capacities of Patches 1 and 2, respectively. For example, Patch 1 contains C_1 cells. Each cell is either occupied (X) or empty (O). All cells are assumed to be well mixed. Hence, the fraction (g) of protection is represented by $g = C_1/(C_1 + C_2)$. In order to define the density (x_j) in Patch j . (For $j = 1, 2$, we set X_j as the number of X cells in Patch j .) The densities in Patches 1 and 2 are defined as $x_1 = X_1/(C_1 + C_2)$ and $x_2 = X_2/(C_1 + C_2)$, respectively. Hereafter, we normalize as $C_1 + C_2 = 1$. The dynamics are described by the mean-field theory. According to the traditional RDE, we get

$$\frac{dx_1(t)}{dt} = r(g - x_1(t))x_1(t) - \mu_P x_1(t) + [D_{12}x_2(t) - D_{21}x_1(t)], \quad (6a)$$

$$\frac{dx_2(t)}{dt} = r(1 - g - x_2(t))x_2(t) - \mu_W x_2(t) + [D_{21}x_1(t) - D_{12}x_2(t)], \quad (6b)$$

where D_{ij} is the rate of migration from patch j to i ($i = 1, 2$ and $i \neq j$). The first and second terms of the right side of Eqs (6a) and (6b) represent the logistic equation. The last term denotes the migration (net flow), which is expressed by a linear function of densities.

In the present article, we take into account the capacities of patches. The migration is defined by Reaction 4(c). For example, when an agent (X) migrates from Patch 1 to 2, the agent X goes into the empty cell (O) in Patch 2; thus, the occupied cell (X) in Patch 1 and empty cell (O) in Patch 2 are exchanged (swapped). Note that both patch capacities remain the same over time. In this case, we have

$$\frac{dx_1(t)}{dt} = r(g - x_1(t))x_1(t) - \mu_P x_1(t) + f_{12}(g, x_1, x_2), \quad (7a)$$

$$\frac{dx_2(t)}{dt} = r(1 - g - x_2(t))x_2(t) - \mu_W x_2(t) + f_{21}(g, x_1, x_2), \quad (7b)$$

where the function $f_{ij}(g, x_1, x_2)$ represents the net flow from Patch j to Patch i . From Reaction (4c),

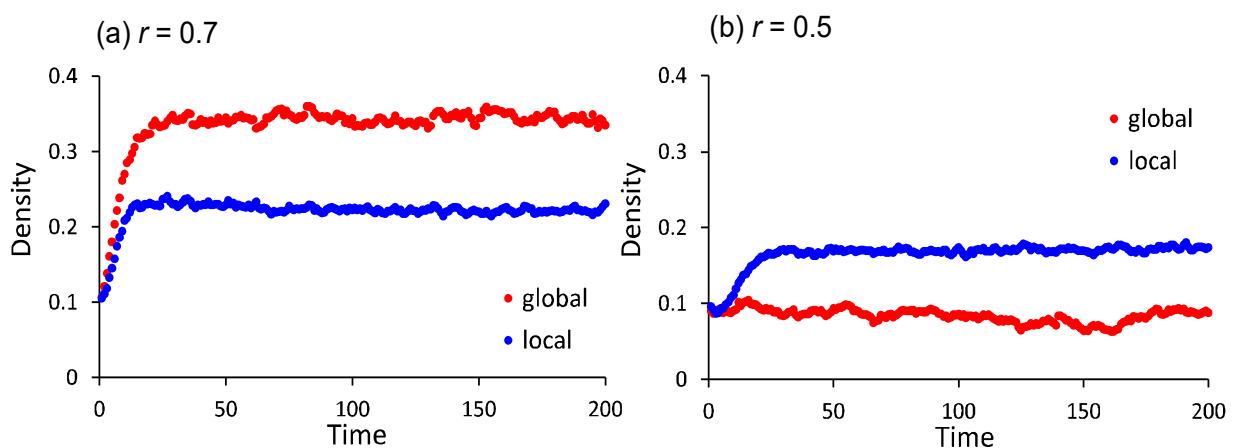


Figure 3. Results for one-patch model. In the present study, we always set $\mu_P = 0.2$, $\mu_W = 0.6$ and $D = 1$. Population dynamics are depicted for local (blue plots) and global (red plots) interactions. (a) $r = 0.7$ and $g = 0.3$, (b) $r = 0.5$ and $g = 0.3$.

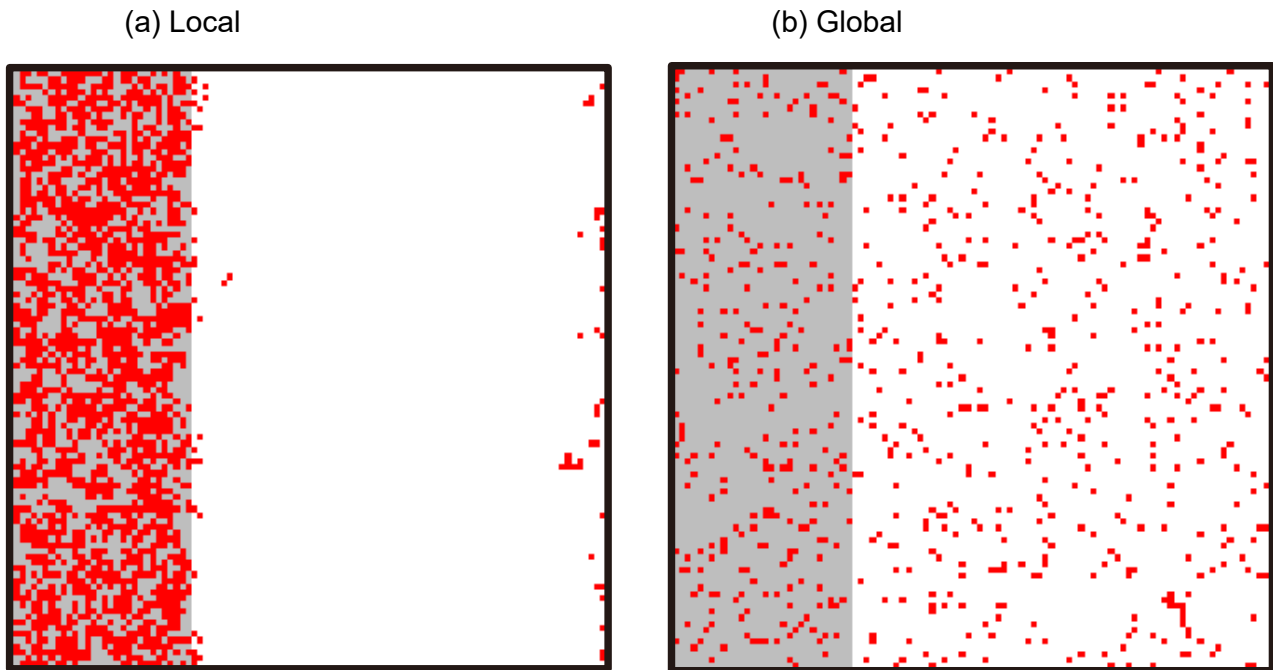


Figure 4. Typical spatial patterns in a stationary state ($r = 0.5$ and $g = 0.3$). Spatial distributions are shown for (a) local interaction and (b) global interaction. The grey rectangles denote the protected areas, and the red cells represent individuals. The total density is higher in (a) than in (b).

We have

$$f_{ij}(g, x_1, x_2) = [D_{ij}x_j(t)e_i(t) - D_{ji}x_i(t)e_j(t)], \quad (8)$$

where $e_j(t)$ means the empty density in Patch j :

$$e_1(t) = g - x_1(t), \quad e_2(t) = 1 - g - x_2(t). \quad (9)$$

It should be emphasized that Eq (8), which denotes the migration term, is generally the nonlinear function of densities.

4. Results

4.1. Results for one-patch system

The simulation results for local and global interactions are reported. Hereafter, we apply the model parameters as follows: $\mu_p = 0.2$, $\mu_w = 0.6$ and $D = 1$. In Figure 3, the typical population dynamics in a one-patch system are plotted, where (a) $r = 0.7$ and $g = 0.3$, and (b) $r = 0.5$ and $g = 0.3$. In both cases, the system is found to evolve into a stationary state. We can confirm that the results of global interaction agree well with the prediction of Eqs (5a) and (5b). The population dynamics in Figure 3(b) reveal an unexpected result that differs from the previous results of CP. Namely, we can observe that the steady-state density for local interactions is higher than that for a well-mixed population (global interaction). To elucidate the mechanism of such an unexpected result, we identified the spatial patterns in a stationary state. Figure 4(a),(b) show snapshots of the distributions of individuals from the

perspectives of local and global interactions, respectively. Here, we set $r = 0.5$ and $g = 0.3$. It is shown in Figure 4(a) that individuals are distributed at high densities inside the protected area. On the contrary, in the case of global interaction, individuals are randomly distributed everywhere (see Figure 4(b)).

In Figure 5, the steady-state densities are plotted against g for a one-patch model. The consecutive dots and lined curves show the results for the local and global interactions, respectively. When r is large, the densities for local interactions are smaller than those for global interactions. On the other hand, when r takes a small value (i.e., $r = 0.5$), we find the opposite result: the densities for local interactions can be larger than those for global interactions. Moreover, in the case of local interactions (spatial model), the biospecies never goes extinct for nearly any value of g .

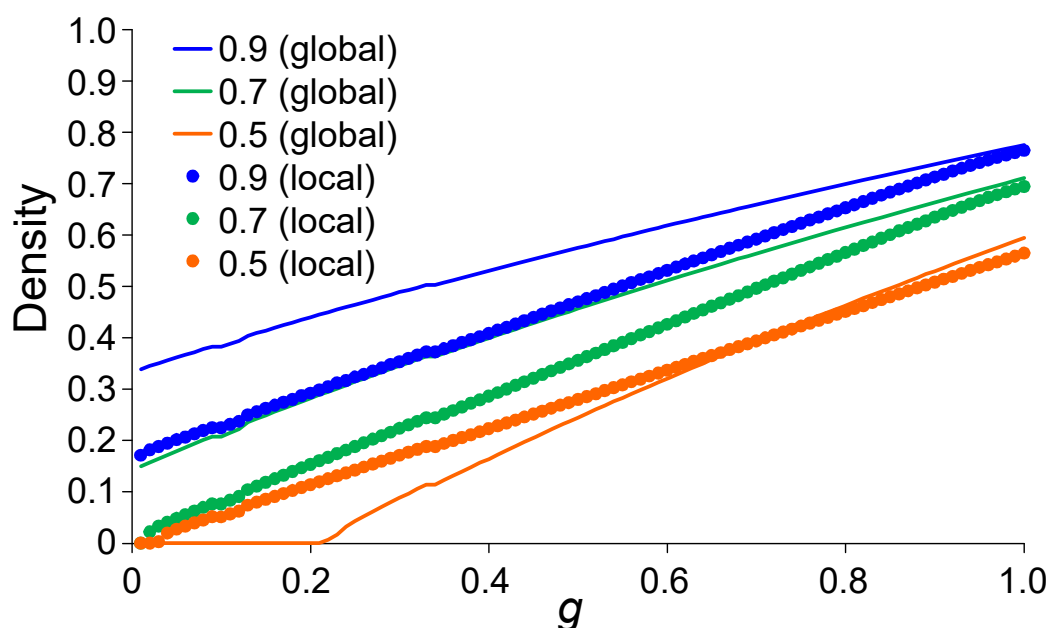


Figure 5. Steady-state densities for local and global interactions are plotted against the protection rate (g). The consecutive dots represent the simulation results for local interactions for $r = 0.9, 0.7$ and 0.5 , while the lined curves indicate the results for global interactions. Each curve reflects the average over the interval $1000 < t \leq 2000$.

4.2. Results for two-patch system

The numerical results for the RDE are reported. For simplicity, we set $D_{12} = D_{21} = 1$. Two types of solutions are obtained. The first solution can be calculated by using the traditional RDE (Eqs (6a) and (6b)). The second solution can be obtained by using the RDE with swapping migration (Eqs (7a) and (7b)). The population dynamics in a two-patch system exhibit the results similar to those in a one-patch system. Namely, the system eventually evolves into a stationary (equilibrium) state. The steady-state density can be calculated by performing numerical analysis ($t = 10^6$). In Figure 6, the steady-state densities are plotted against the protection ratio g , where (a) and (b) are the results for traditional and swapping migrations ($r = 0.7$). In both cases, the steady-state density tends to increase as the protection ratio g increases. However, when g is small, a clear difference can be observed between the migration types in Figure 6(a),(b). In the case of swapping migration (Figure 6(b)), we can observe two paradoxes

that are not seen in a one-patch system. (i) When $g \approx 0.05$, we can find that $x_1 < x_2$. Namely, the densities in the protected areas (green curves) are lower than those in the wild areas (orange curves). (ii) The total density does not always increase with the increase of g . The density can decrease in spite of an increase of g . We refer to both (i) and (ii) as “paradoxes of habitat protection”.

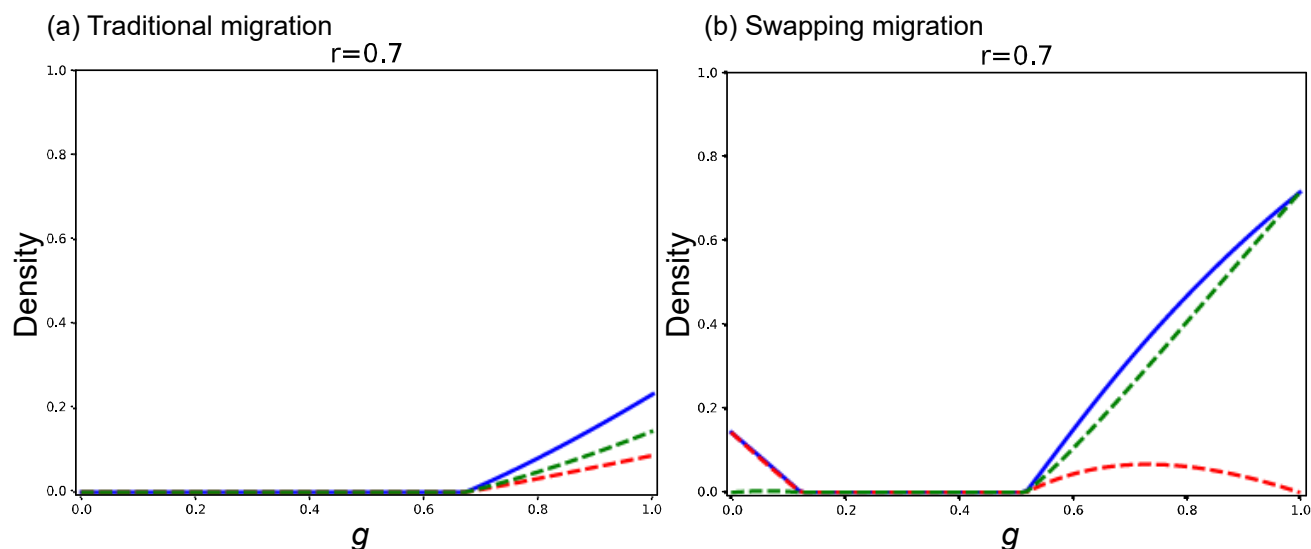


Figure 6. Results for two-patch model ($D_{12} = D_{21} = 1$). The steady-state (equilibrium) densities are plotted against the protection ratio g ; (a) traditional migration and (b) swapping migration. The green and orange curves are the numerical results for the densities in Patches 1 and 2, respectively ($t = 10^6$). The blue curves denote the total density in both patches. The initial values are fixed at $x_1(0) = x_2(0) = 0.1$.

5. Discussion

For the one-patch system, we have applied a CP model as a simple ecosystem and dealt with the reaction processes described by Reactions (4a)–(4c). The effects of the random walk on CP in a homogeneous lattice has been studied by Harada et al. [37]. If the migration rate D takes a value of zero, then the steady-state density becomes the same as the result of CP in Figure 1. Conversely, if $D \rightarrow \infty$, the density approaches the prediction of the logistic equation in Figure 1. Hence, the density under the condition of a random walk always takes a lower value than the outcomes for global interaction. On the other hand, we investigated CP under the conditions of a heterogeneous environment (Figure 2(a)). In this case, we obtained the opposite result: the densities for local interactions can be larger than those for global interactions (see Figures 4 and 5). Hence, we have found that the spatial heterogeneity of habitats promotes the survival of a species [18,39].

In the case of the two-patch system, the metapopulation dynamics was studied. In most cases, the RDE ignores the difference in patch capacities, as shown in Eqs (6a) and (6b). To take into account the patch difference, Zou and Wang [40] and Wei and Wang [41] corrected the RDE. In their formulas, the migration terms are still the linear function of densities. In the present study, however, we have applied “swapping migration”, which highlights the exchange between occupied and empty cells. The migration terms in Eqs (7a) and (7b) generally form the nonlinear functions of densities. An individual

can only migrate when there are empty cells in the destination patch.

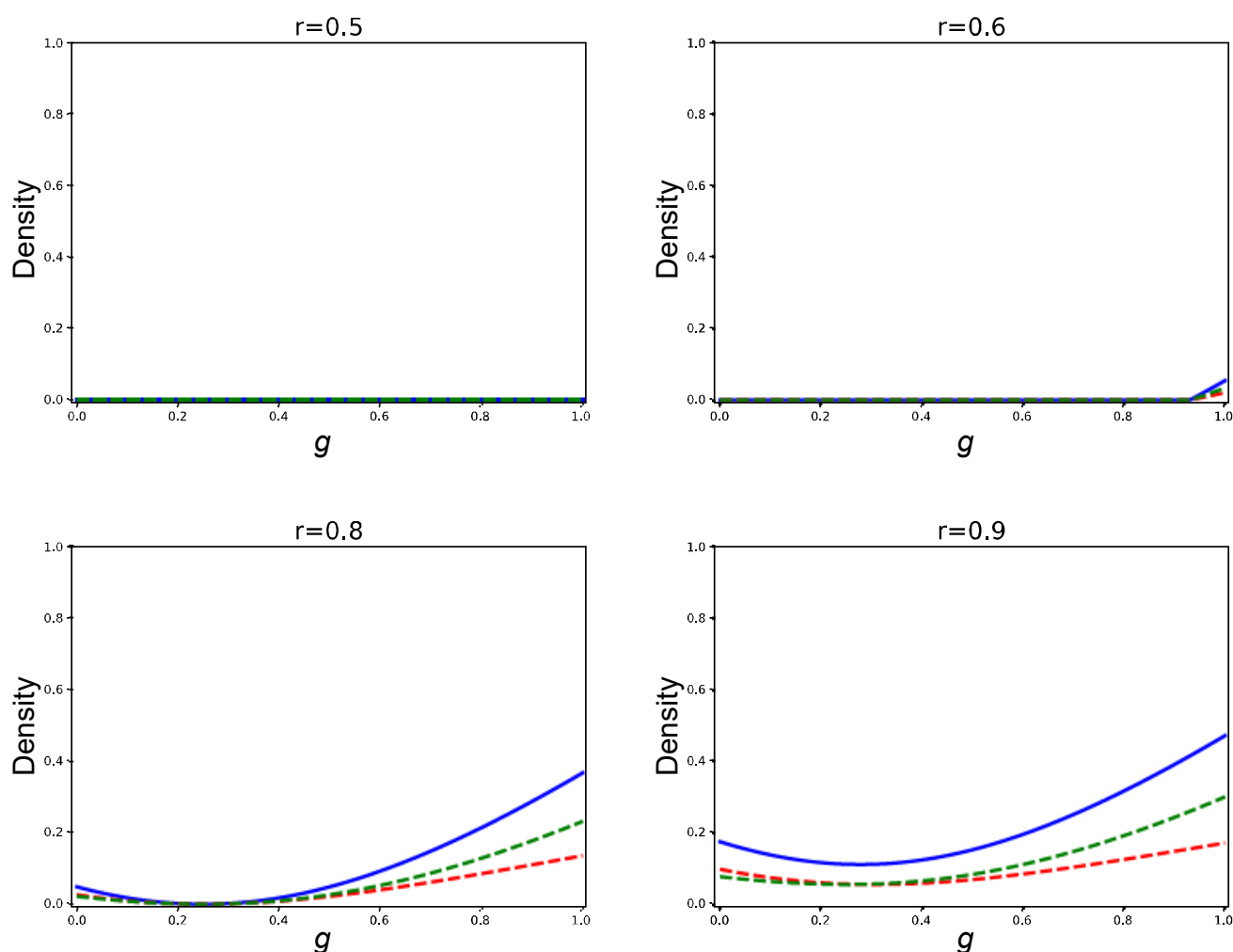


Figure 7. Summary of traditional migration. It is generally the same as in Figure 6(a), but r takes various values.

The paradoxes of habitat protection can be observed for swapping migration. We shall discuss the mechanism of paradoxes. First, we will consider the special case of $D = 0$ (no migration) in Eqs (7a) and (7b). When $g \approx 0.5$, the species can survive in Patch 1, but it goes extinct in Patch 2. Conversely, when g takes a small value (e.g., $g \approx 0.05$), the species only survives in Patch 2. These results are sensitive to the density of empty cells. If the migration occurs ($D \neq 0$), the paradoxes emerge due to the combined effect of three processes: birth, death and migration. Regarding parameter dependence, we have explored the behavior of density for various values of the reproduction rate (r). In Figures 7 and 8, the r dependencies of density are displayed for traditional and swapping migrations, respectively. From Figure 7, we can find paradoxes in the cases of $r = 0.8$ and $r = 0.9$. Hence, both paradoxes of habitat protection can be confirmed even for traditional migration. In the case of swapping migration, however, the paradoxes are clearly observed for $r \geq 0.7$.

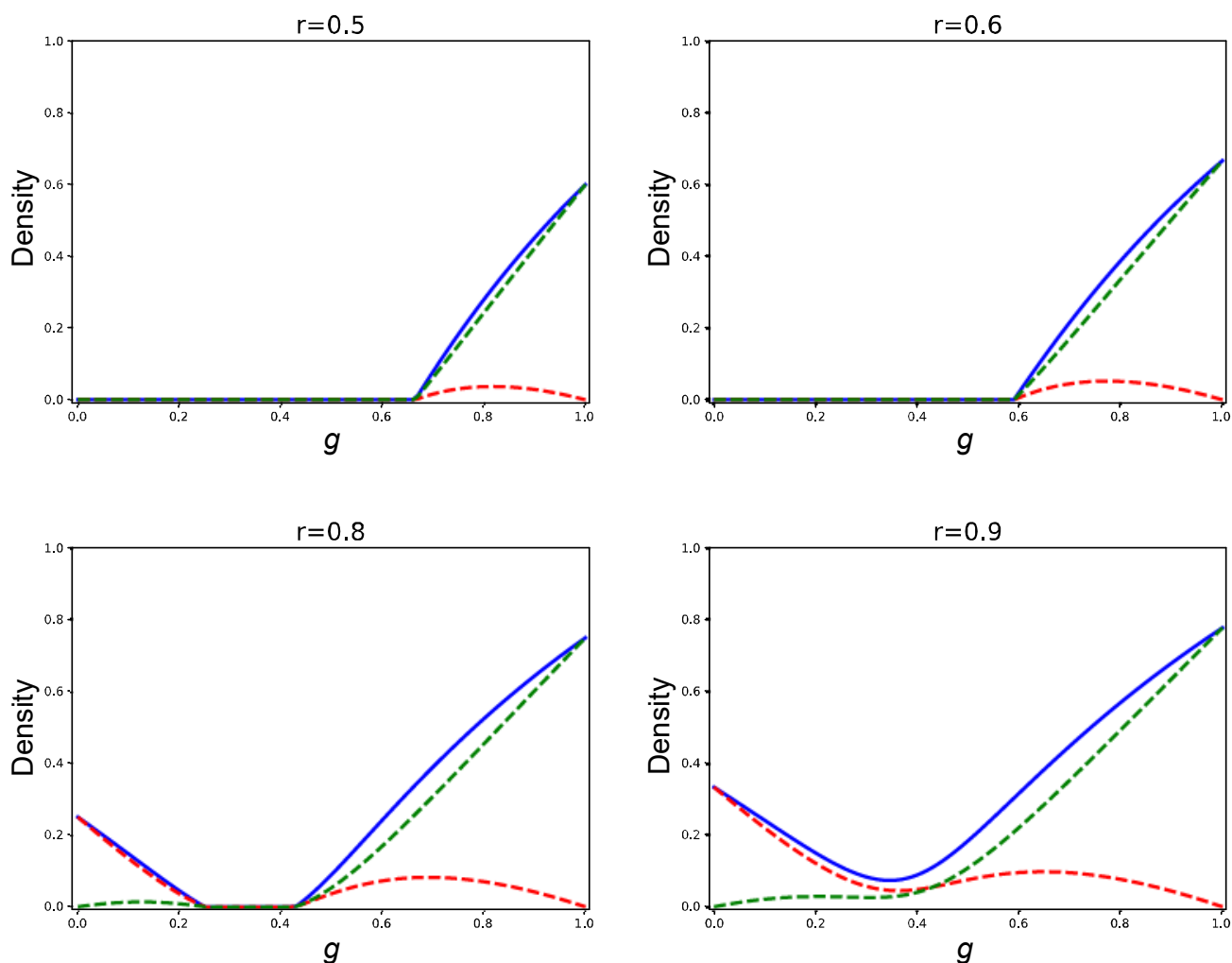


Figure 8. Summary of swapping migration. It is generally the same as in Figure 6(b), but r takes various values.

Here, we discuss the parameter dependencies of D_{12} and D_{21} . We assumed $D_{12} = D_{21}$ to obtain the results for the two-patch system. Under this assumption, the migration term in Eqs (7a) and (7b) becomes the linear function of densities. In other words, the swapping migration becomes linear for $D_{12} = D_{21}$. We have explored more general cases of $D_{12} \neq D_{21}$. It can be seen that, whether the migration term in Eqs (7a) and (7b) is linear or nonlinear, there is no significant effect on the results. For example, we set $D_{12} = 1$ and $D_{21} = 1.2$ (nonlinear migration). In this case, the results were almost the same as those obtained for $D_{12} = D_{21} = 1$; the shapes of the curves in Figures 6–8 were unchanged.

6. Conclusions

We have developed a model of population dynamics under two conservation measures: partial protection in a one-patch system and patch protection in a two-patch system. We found that habitat protection is generally effective with both measures. In the case of the one-patch system, the conservation of a species effectively functions by setting the species protection. Extinction can be avoided because many individuals survive in the protected area (see Figure 4(a)). However, in the case of the two-patch system, we found two paradoxes of habitat protection. (i) The density in the protected

patch not always higher than that in the wild patch. (ii) The steady-state density of a species can decrease in spite of an increase in the protection ratio (g). Such paradoxes were clearly observed for the RDE with swapping migration (see Figure 8). Paradox (i) can be observed experimentally. However, Paradox (ii) cannot be observed because the patch capacity cannot be changed artificially.

Conflict of interest

The authors declare that there is no conflict of interest.

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