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Global Migration Can Lead to Stronger Spatial Selection than Local Migration

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Abstract The outcome of evolutionary processes depends on population structure. It is well known that mobility plays an important role in affecting evolutionary dynamics in group structured populations. But it is largely unknown whether global or local migration leads to stronger spatial selection and would therefore favor to a larger extent the evolution of cooperation. To address this issue, we quantify the impacts of these two migration patterns on the evolutionary competition of two strategies in a finite island model. Global migration means that individuals can migrate from any one island to any other island. Local migration means that individuals can only migrate between islands that are nearest neighbors; we study a simple geometry where islands are arranged on a one-dimensional, regular cycle. We derive general results for weak selection and large population size. Our key parameters are: the number of islands, the migration rate and the mutation rate. Surprisingly, our comparative analysis reveals that global migration can lead to stronger spatial selection than local migration for a wide range of parameter conditions. Our work provides useful insights into understanding how different mobility patterns affect evolutionary processes.

Keywords Evolutionary dynamics · Population structure · Mathematical biology · Evolutionary game theory

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1 Introduction

How particles interact has been long studied in physics [1, 2], yet exploring the fundamental law governing the evolution of living systems, ranging from multicellular organisms to humans, poses a grand challenge for the 21st century [3, 4]. Darwinian theory of evolution provides a unifying framework to studying this issue. Natural selection, as well as mutation, is the driving force for genetical and cultural evolution. Cooperation is needed for evolution to construct new levels of complexity [5]. Therefore, understanding how cooperation evolves is of primary significance [6, 7].

In recent years, a wide variety of social dynamics have been extensively studied (see an excellent review, for example, in Ref. [8]). Among them, the evolution of cooperation has attracted increasing attention not just from evolutionary biologists (see a review in Ref. [9] and a more recent one in Ref. [5]), but also from physicists [10–21] (see a recent review in Ref. [22]).

Evolutionary game theory is a useful tool for studying frequency-dependent selection [23–29]. Unlike constant selection [30–33], the fitness of an individuals depends on its strategy and the frequency of other strategies in the population. Evolutionary game theory can be used to study host-parasite interactions [34], evolution of metabolic pathways [35], and virus competition [36]. Recent theoretical advances go beyond replicator dynamics [37] and are centered on stochastic dynamics in finite populations [38–41]. Various evolutionary updating rules, such as the frequency-dependent Moran process [42], Wright-Fisher process [43], and the pairwise comparison rule [10, 44] have been investigated.

Inspired by spatial games [45], there has been much growing interest in studying evolutionary dynamics in structured populations [46–63] (see a recent review in Ref. [64]). Departing from the well-mixed scenario, populations are often exquisitely structured. Interactions are not random but limited to neighboring individuals (games on graphs [49]) or individuals belonging to the same set (games on sets [54]). Much effort has been made on quantifying the impact of population structure on the mutation-selection equilibrium [53–56, 58, 60, 63]. Noteworthy, other topics explored include, but are not limited to, learning in games [65, 66], the heterogeneity in population structure [67–70], and coevolutionary games [71–78].

Weak selection is a helpful concept for the analytical study of evolutionary game dynamics [38, 79–82]. In this limit, the fitness differences between individuals are small, and thus evolutionary dynamics can be calculated on the basis of neutral drift [56, 81]. Weak selection is often used in population genetics [30, 31, 83]. Moreover, the approach of adaptive dynamics for studying phenotypic evolution also assumes that the mutant phenotype is drawn from an infinitesimally small neighborhood around the resident phenotype [84–87], and as a consequence, the fitness differences are very small.

In particular, when it comes to structured populations, weak selection proves very fruitful. A series of recent theoretical findings pave the way for calculating evolutionary dynamics in structured populations [49, 53–56, 58, 60]. In these work, it is shown that for weak selection, population configurations can be approximated by correlations obtained at neutrality. If one is merely interested in the question which strategy is more abundant in the long run, then the condition for strategy selection can be expressed as a linear inequality of payoff matrix entries with coefficients summarizing the effects of population structure. For a detailed description of this new machinery we refer to Refs. [53, 54, 58].

Most recently, there has been a surge of interest in examining the role migration plays in evolutionary dynamics. In Ref. [88], the authors investigate the impact of migration on biological diversity using rock-paper-scissors games. In Ref. [89], the authors consider the outbreak of cooperation under success-driven migration. Reference [90] addresses the impact of migration on cooperation in spatial public goods games. We note that in these prior work, it is not possible for more than two individuals to habitat in the same site, and that individuals can only migrate to empty sites.

Therefore, in order to quantify the impact of migration on the evolutionary competition, it seems more plausible to consider subdivided or group structured populations [91–101]. In this case, multiple individuals can reside in the same site (group, island, set). Moreover, the connections between sites regulate the pathways of migration. Two distinct, simple schemes of migration naturally arise: restrained local migration versus unrestricted global migration. In the former scheme, sites are connected via a cycle and individuals can only migrate to the two nearest-neighbor sites. In the latter, sites are fully connected and individuals can migrate to any other site. The question is: which migration structure leads to a stronger spatial effect and hence to a stronger boost for the evolution of cooperation.

To address this question, we derive analytical conditions for the evolution of cooperation under these two simple migration schemes. We further conduct comparative analysis to determine the parameter region under which one migration scheme is more in favor of cooperation than the other. Our present work utilizes the general results of strategy selection in structured populations as detailed in Refs. [53–56, 58].

2 Model

Let us first define the population structure and evolutionary dynamics. We investigate evolutionary game dynamics in a population of finite size, N. Individuals are distributed over M sites. Such sites are referred to as islands in population genetics [91] or as patches (or demes) in ecological studies [92, 95]. Within each site, individuals play evolutionary games and accrue payoff from pairwise interactions. At each time step, an individual is chosen, with probability proportional to its fitness, to reproduce an offspring. Reproduction is subject to mutation. With probability u, the offspring mutates to a random strategy; otherwise its strategy is identical to its parent. Following reproduction, a random individual in the population dies. Thus the total population size remains constant. The newly reproduced offspring has a chance to migrate to other sites.

For the local migration case, sites are situated on a one-dimensional, regular cycle with each site connected to two nearest-neighbor sites (Fig. 1a). Individuals migrate to the two nearest-neighbor sites with equal probability $v/2$; otherwise they stay at the parental site with probability $1 - v$ $(0 < v < 1)$.

In comparison to local migration, we also consider global migration where individuals migrate to any one of the other $(M - 1)$ sites with equal probability $v/(M - 1)$. In this latter case, the sites are connected with a complete graph (Fig. 1b).

We are interested under what conditions global migration leads to stronger spatial effect than local migration. It is useful to consider the rescaled strategy mutation rate, $\mu = Nu$, and the rescaled migration rate, $\nu = Nv$, in the theoretical analysis. For weak selection and large population size, we can derive general results for the evolutionary competition of two strategies under these two migration patterns. We will also study the conditions for the evolution of cooperation in the simplified Prisoner's Dilemma.

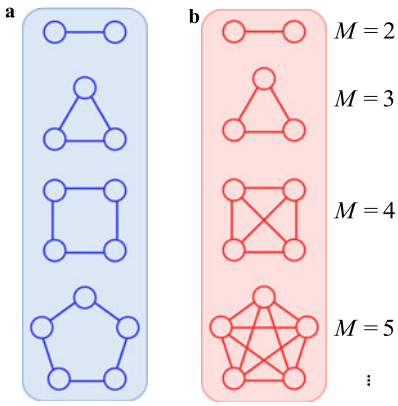

Fig. 1 Evolutionary game dynamics in finite islands. The individuals of a population are distributed over a finite number of sites, M. Individuals play games with others who reside in the same site and payoffs are accrued in these interactions. Reproduction is proportional to payoff. Offspring can migrate to other sites. In this paper, we aim to address the impact of migration patter on the evolutionary competition. To this end, we consider (**a**) local migration and (**b**) global migration. In (**a**), sites are connected by a one-dimensional ring and individuals can only migrate to the two nearest-neighbor sites, whereas in (**b**) sites are fully connected and individuals can migrate to any other site. As shown here, for $M = 2, 3$ the two migration patterns lead to exactly the same results, but differences arise for $M \geq 4$

3 Results

3.1 Prisoner's Dilemma

Let us start with the simplified Prisoner's Dilemma. A cooperator pays cost c for a recipient to receive benefit b ($b > c > 0$). A defector pays no cost and distributes no benefits. The payoff matrix (for the column player) is given by

$$\begin{array}{c|cc} & C & D \\ \hline C & b-c & -c \\ D & b & 0 \end{array}. \tag{1}$$

Denote by $\langle x_C \rangle$ and $\langle x_D \rangle$ the average frequency of cooperators and defectors in the mutation-selection equilibrium. In the limit of weak selection the condition for cooperators to be favored over defectors is $\langle x_C \rangle > 1/2 > \langle x_D \rangle$. This condition is equivalent to the benefit-to-cost ratio exceeding a critical size $b/c > (b/c)^*$. We are interested in calculating this critical benefit-to-cost ratio under weak selection and for large population size.

For global migration the critical benefit-to-cost ratio is given by [58]:

$$\text{Global migration:} \quad \left(\frac{b}{c}\right)^* = \frac{M+\mu+2}{M-1} + \frac{(\mu+1)(\mu+3)}{(\mu+2)\nu} + \frac{M\nu}{(M-1)^2} - \frac{M(\mu+1)}{(\mu+2)((M-1)(\mu+2)+M\nu)}. \tag{2}$$

For $M = 2$ and $M = 3$ our local and global migration models are identical (see Fig. 1). Therefore the above condition also holds for the local migration model for $M = 2$ and $M = 3$. Differences arise for $M \geq 4$. As shown in the Appendix we can derive explicit expressions for the local model for any M, but the resulting formulas are lengthy. Here we

present some specific examples for the limit of low mutation $\mu \to 0$ (which best characterizes the effect of pure selection).

For local migration and $M = 4$ we obtain

$$\left(\frac{b}{c}\right)^*_{\mu\to 0, M=4} = \frac{52}{25} + \frac{3}{2\nu} + \frac{2\nu}{5} + \frac{27 - 94\nu - 382\nu^2 - 202\nu^3}{50(12 + 51\nu + 78\nu^2 + 48\nu^3 + 10\nu^4)}. \tag{3}$$

For local migration and $M = 5$ we obtain

$$\left(\frac{b}{c}\right)^*_{\mu\to 0, M=5} = \frac{19}{10} + \frac{3}{2\nu} + \frac{\nu}{4} + \frac{216 + 476\nu + 100\nu^2 - 65\nu^3}{10(96 + 296\nu + 340\nu^2 + 160\nu^3 + 25\nu^4)}. \tag{4}$$

For local migration and $M = 6$ we obtain

$$\begin{aligned}\left(\frac{b}{c}\right)^*_{\mu\to 0, M=6} &= \frac{316}{175} + \frac{3}{2\nu} + \frac{6\nu}{35} \\ &\quad - \frac{3(-10728 - 61252\nu - 128540\nu^2 - 114680\nu^3 - 33906\nu^4 + 941\nu^5)}{350(288 + 1752\nu + 4180\nu^2 + 4980\nu^3 + 3126\nu^4 + 959\nu^5 + 105\nu^6)}.\end{aligned} \tag{5}$$

For any finite M the critical b/c ratio diverges as ν approaches 0 and ∞. There exists an intermediate optimum migration rate that minimizes the critical b/c ratio. For $M = 4$, the optimum value is $\nu \approx 1.93$. For $M = 5$ it is $\nu \approx 2.55$. For $M = 6$ it is $\nu \approx 3.22$. The optimum migration rate increases with M and diverges as $M \to \infty$.

For $\mu \to 0$ and $M \to \infty$, the critical b/c ratio for local migration is given by:

$$\left(\frac{b}{c}\right)^*_{\mu\to 0, M\to\infty} = \frac{(3 + 4\nu)\sqrt{3 + 2\nu} + (1 + 2\nu)\sqrt{3 + 6\nu}}{(1 + 2\nu)\sqrt{3 + 6\nu} - \sqrt{3 + 2\nu}}. \tag{6}$$

This result is the same as the one derived for the Wright-Fisher process in Ref. [53]. Further letting ν approach infinity, we obtain [53]

$$\left(\frac{b}{c}\right)^* = 1 + \frac{2}{\sqrt{3}}. \tag{7}$$

3.2 General 2×2 Games

Let us now consider a general payoff matrix for a game between two strategies A and B:

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array} \tag{8}$$

The values a, b, c, d denote the entries of the payoff matrix. They can be positive, zero or negative. Our results hold for any payoff matrix.

For weak selection, natural selection favors A over B if the following linear inequality holds [56]

$$\langle x_A \rangle > \langle x_B \rangle \quad \Leftrightarrow \quad \sigma a + b > c + \sigma d. \tag{9}$$

The structural coefficient σ quantifies the effect of spatial selection (and to some extent the level of assortment among individuals who use the same strategy) [56]. For our model the value of σ depends on the number of sites, M, the mutation rate, μ, and the migration

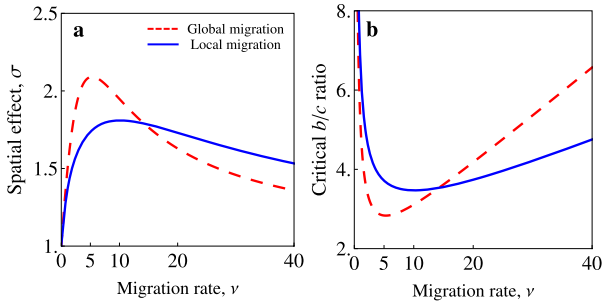

Fig. 2 Evolutionary conditions for the evolution of cooperation. Here, we study the competition of two strategies, A versus B, with the payoff matrix $[a, b; c, d]$. Strategy A is favored over B by natural selection if the σ-dominance condition holds [56]: $\sigma a + b > c + \sigma d$, where the coefficient σ summarizes the effects of population structure. For the simplified prisoner's dilemma, a cooperator pays a cost c to benefit a recipient b, whereas a defector neither pays costs nor distributes benefits. In this particular case, cooperation is favored over defection if the benefit-to-cost ratio, b/c, is greater than $(\sigma + 1)/(\sigma - 1)$. Shown in panel (**a**) is the dependence of σ value on the migration rate, ν. Panel (**b**) plots the dependence of the critical b/c ratio on ν. The larger σ, the stronger the level of positive assortment, thus resulting in a smaller critical b/c ratio for cooperation to evolve. For both migration patterns, there exists an intermediate optimum migration rate. There also exists a crossover of the two curves shown in (**a**) and (**b**): for low migration rates, global migration leads to stronger spatial selection (and hence leads to a stronger boost of cooperation) than local migration while the order is reversed for high migration rates. Parameters: $M = 10$, $\mu = 2$

rate, ν. The specific value of σ can be derived simply by using the critical b/c ratio given above [56]:

$$\sigma = \frac{(\frac{b}{c})^* + 1}{(\frac{b}{c})^* - 1}. \tag{10}$$

As presented in the Appendix, we calculate the structural coefficient σ, respectively, for local and global migrations. Larger σ value corresponds to stronger spatial effect, and therefore cooperators have greater chance to prevail [64]. In what follows, we present our main results based on the comparison of σ values for different mobility patterns and varying model parameters.

3.3 Comparative Analysis of Local and Global Migration

As shown in Fig. 2a, there exist intermediate optimum migration rates that lead to the strongest spatial effects for global and local migrations. Interestingly, we find a crossover of the two σ values with increasing ν. Depending on the model parameters, M and μ, there exists a critical migration rate, ν_c. For $\nu < \nu_c$ global migration leads to a stronger spatial effect than local migration, whereas for migration rates $\nu > \nu_c$ the order is reversed (Fig. 2).

This result can be intuitively understood as follows. If the migration rate is small, then global dispersal is more efficient in promoting the establishment of islands that are populated by a single type (A or B). As a result, global migration leads to a stronger spatial effect than local migration in this case. On the other hand, if the migration rate is large, then local migration is more efficient at keeping individuals of the same type together on neighboring islands. In this case, local migration leads to better assortment resulting in a stronger spatial effect.

Figure 3 demonstrates that the spatial effect becomes stronger as the number of sites M increases. At low migration rates, for any number of sites $M \geq 4$, global migration leads to

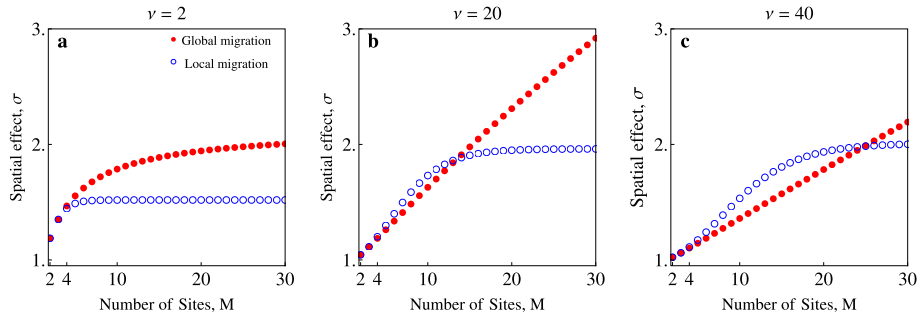

Fig. 3 The spatial effect, σ, depends on the number of sites, M. For both local (○) and global (●) migrations, the value of σ monotonically increases with M. For $M = 2, 3$, the two migration patterns lead to exactly the same σ value, while difference arises for $M \geq 4$. The value of σ reaches a plateau (asymptotic value) at smaller values of M under local migration than global migration. Panel (**a**) shows that for low migration, global migration is always better than local migration in eliciting spatial effect. Panels (**b**) and (**c**) show that with increasing migration rates, there exists a crossover of the two σ values with respect to varying M. At small M, local migration is better whereas for high M, global migration is better. Parameters: $\mu = 2$, (**a**) $\nu = 2$, (**b**) $\nu = 20$, (**c**) $\nu = 40$

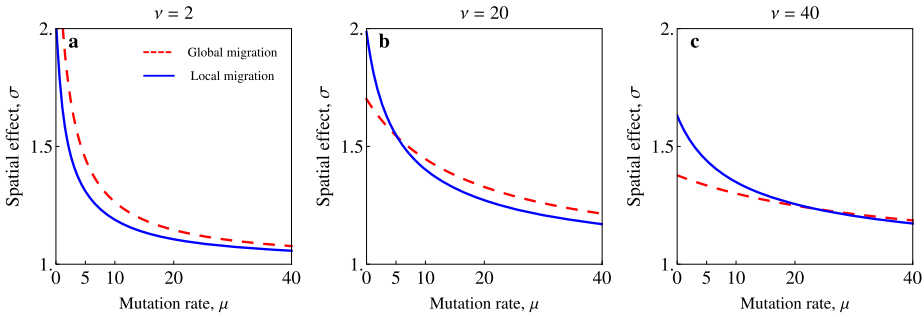

Fig. 4 Mutation diminishes the spatial effect. For both local (*solid*) and global (*dashed*) migrations, the value of σ monotonically decreases with the strategy mutation rate, μ. Panel (**a**) shows that for low migration, global migration always leads to larger σ values, thus better in promoting cooperation than local migration. Panels (**b**) and (**c**) show that with increasing migration rates, there exists a crossover of the two σ values with respect to varying μ. At small μ, local migration is better whereas global migration is better for high μ. Parameters: $M = 10$, (**a**) $\nu = 2$, (**b**) $\nu = 20$, (**c**) $\nu = 40$

stronger spatial effect than local migration (Fig. 3a). With larger migration rates (Figs. 3b and 3c), local migration is better than global migration if the number of sites is fewer than a certain threshold, M_c. The value of M_c increases as the migration rate increases (cf. Figs. 3b and 3c). Together with Fig. 2, Fig. 3 corroborates that global migration does have an advantage over local migration in eliciting a stronger spatial effect for larger numbers of sites and for lower migration rates.

As shown in Fig. 4, increasing the strategy mutation rate, μ, diminishes the spatial effect in both migration patterns. Similarly, in Figs. 2 and 3, the crossover of the two σ values as function of μ arises only for large migration rates (cf. Figs. 4a and 4b). The threshold, μ_c, at which the two σ's values are equal, increases with ν (cf. Figs. 4b and 4c). Only for $\mu < \mu_c$ does local migration lead to a stronger spatial effect. In short, global migration is

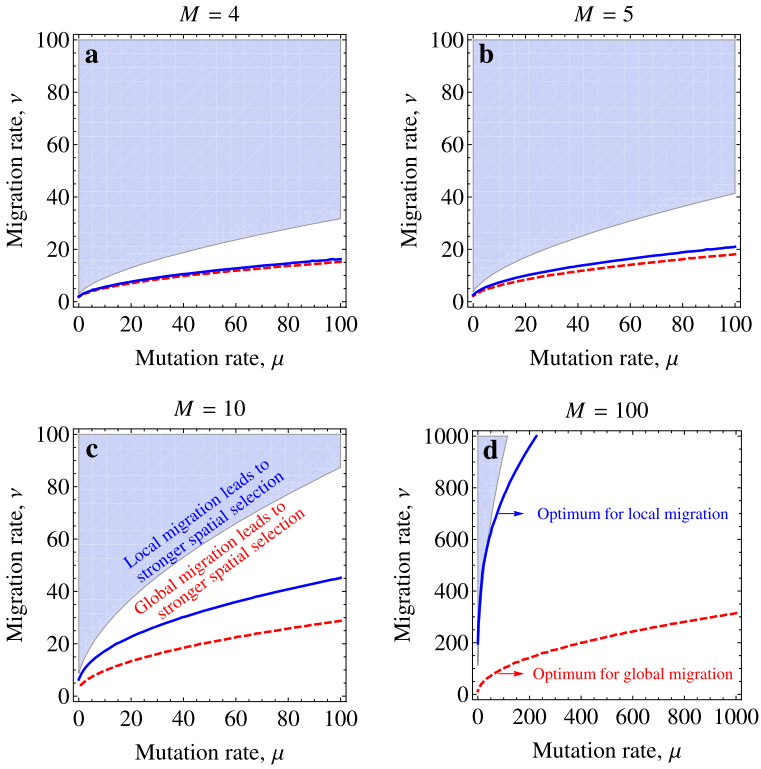

Fig. 5 Full comparison of local and global migration across the parameter space (μ, ν). The *colored region* in (**a**)–(**d**) shows the combinations of (μ, ν) under which local migration leads to stronger spatial effect (*i.e.*, higher σ values), compared to global migration for a given population size. As the number of sites M increases, the *shaded area* shrinks. The *solid lines* (*dashed*) represent the optimal migration rate as a function of mutation rate for local migration (global migration). While both optimal migration rates monotonically increase with mutation rate μ, they are always within in the region where global migration is better. The optimal migration rate is always smaller in global migration than in local migration, and the difference of the two optima becomes even larger with increasing the number of sites. The mutation and migration rates are both scaled with the population size N, $\mu = Nu$ and $\nu = Nv$ (see text for details). Parameters: (**a**) $M = 4$, (**b**) $M = 5$, (**c**) $M = 10$, (**d**) $M = 100$ (Color figure online)

more robust against the detrimental effect of high mutations on spatial selection than local migration.

We further compare the spatial effects induced by global and local migration across the model parameter space (μ, ν) for a given number of sites, M. In the shaded parameter region shown in Fig. 5, local migration results in greater values of σ than global migration. This shaded area shrinks with increasing number of sites (cf. Figs. 5a–5d). Only for small M, small μ, and large ν, is local migration better than global migration in eliciting spatial effect. In other words, global migration leads to stronger spatial selection than local migration for a wide range of parameters. It is worth noting that for excessively small migration rates (lower than a certain threshold), global migration always does better than local migration in eliciting spatial effect for any $\mu < 0$ and $M \geq 4$. Moreover, for both migration patterns, the optimum migration rate that leads to the strongest spatial selection is always located in the parameter region where global migration is better (Fig. 5).

As a particular example, we can apply these general results to the evolution of cooperation (Fig. 2b). Larger value of σ corresponds to stronger spatial effect and therefore smaller critical b/c ratio is required for cooperators to be favored over defectors. Both for local and global migration, the analytical calculations show that for any finite number of sites, the critical b/c ratio diverges as $\nu \to 0$ and $\nu \to \infty$, and reaches a minimum at some certain intermediate value of ν. We note that both critical b/c ratios monotonically decrease with ν for infinitely many sites ($M \to \infty$). Comparing the impacts of local and global migration on cooperation, we find that for low migration rates $\nu < \nu_c$ global migration is more in favor of cooperation than local migration. In contrast, local migration is better than global migration in promoting cooperation for $\nu > \nu_c$. As depicted in Fig. 5, the critical migration rate, ν_c, is an increasing function of the mutation rate, μ, and the number of sites, M. Furthermore, in the limit of low mutation and infinitely many sites, global migration is always better than local migration at promoting cooperation for any migration rate, ν.

4 Discussion

The finite island model in our study resembles the well-studied stepping stone models in population genetics [91, 102, 103]. Most prior work assumes infinitely many islands and is based on neutral drift, whereas the current study calculates the strategy selection condition for arbitrary number of islands under frequency-dependent selection. Unlike previous studies [96, 104], the number of individuals in each island is not constant in our model and natural selection operates on the individual level. It is possible that some islands are abandoned at a time and re-populated later on. Individuals are often found clustering in a few islands, leading to dynamic, heterogeneous island population size distribution which may help overcome the tragedy of commons in some circumstances [97].

To study the competition of two strategies, we utilize the strategy selection condition, $\sigma a + b > c + \sigma d$, with the structural parameter, σ, specifically calculated for our case [56]. Note that the parameter σ quantifies the magnitude of the spatial effect [55, 56]. A larger value of σ indicates stronger spatial selection, and corresponds to a lower critical benefit-to-cost ratio required for the evolution of cooperation. Although the current analysis is focused on discrete binary strategies, extending to arbitrary number of strategies is straightforward [58, 82].

Our results show that the spatial effect depends crucially on the number of sites, M. For both migration patterns, the larger M the stronger the spatial effect. Surprisingly, we find that global migration leads to stronger spatial effect than local migration for large M (Fig. 3). The parameter region of (μ, ν), under which local migration results in a larger value of σ than global migration, shrinks precipitously with increasing the number of sites. From this perspective, global migration can lead to stronger spatial selection than local migration for a wide range of parameter conditions.

There is an ongoing debate about the usefulness and limitation of inclusive fitness theory [7, 100, 105–107]. It is possible that some of the results presented in this paper can be reformulated in terms of inclusive fitness theory, if one uses sufficiently abstract notions of 'cost', 'benefit' and 'relatedness'. This does not alter the fact that inclusive fitness theory is a limited approach that works only in specific circumstances and whenever it works it can at best reformulate what has been calculated with a direct analysis of natural selection [100]. We note that inclusive fitness is obviously not needed for any of the calculations presented in this paper.

In the present model, individuals migrate in a stochastic manner, and thus the migration rate can be seen as the intensity of randomness (noise) in population structure. The

existence of an intermediate optimum migration rate resembles the stochastic resonance phenomenon widely observed in chemical and physical systems [108]. Previous studies have reported the optimality of cooperation with respect to varying noise intensity in a variety of cases, including randomness in network topology [109], noise in strategic imitation [110, 111], and the interplay between strategy updating and network rewiring [112]. It is worthwhile to note that there always exists an optimum migration rate for any finite number of sites, but the optimality is lacking in the limiting case of infinitely many sites (where the critical b/c ratio is monotonically decreasing with migration rate as also shown in Ref. [53]).

Studying mobility pattern and its impact on various spreading phenomena, such as the transmission of contagious diseases, has attracted increasing interests [113, 114]. Along this line, our present work focuses on two simple migration patterns, and compares the conditions for the evolution of cooperation under local and global migration. We show that only for the combination of low strategy mutation, small number of sites and high migration rates, does local migration provide a more favorable condition for evolution of cooperation than global migration. For a wide range of parameter conditions, global migration induces a stronger spatial effect than local migration. In this way, our results quantify the impact of migration pattern on evolutionary game dynamics in an island model.

In summary, we have studied evolutionary game dynamics in a finite island model. Individuals play games with others located in the same site. We present a comparative study of how different migration patterns, local versus global, affect the evolutionary outcomes. Specifically, for local migration, sites are connected by a regular cycle and individuals migrate between neighboring sites. In contrast, for the global migration, all sites are connected and individuals can migrate from one site to any other. Our derivations account for all 2×2 games. As a particular example we study the simplified Prisoner's Dilemma. We derive analytical conditions for cooperation to be favored in the limit of weak selection. Furthermore, our comparative analysis shows that global migration can lead to stronger spatial effect than local migration for a wide range of the model parameters, especially when the number of sites is large. Our results shed some light on the role of mobility in evolutionary game dynamics.

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Appendix

In this appendix, we present details for studying evolutionary competition of two strategies in finite islands with local migration. The case of global migration can be analyzed in a similar fashion.

Specifically, let us consider two binary strategies A and B with the 2×2 payoff matrix, which gives the payoff for the column player:

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array} \tag{11}$$

Denote by x_A (x_B) the fraction of A (B) individuals, and we have $x_A + x_B = 1$. Denote by x_A^i (x_B^i) the fraction of A (B) individuals in the site i, and we have $\sum_{i=1}^{M} x_A^i = x_A$ and

$\sum_{i=1}^{M} x_B^i = x_B$. The interaction pattern of strategies is characterized by $[I_{AA}, I_{AB}; I_{BA}, I_{BB}]$, where I_{XY} denotes the total number of interactions between X and Y. By symmetry, we have $I_{AB} = I_{BA}$. The payoff of an A-individual is $P_A = (aI_{AA} + bI_{AB})/(Nx_A)$ and its fitness is given by $f_A = \exp(\beta P_A)$, where β denotes the intensity of selection.

Perturbation method has proved to be particularly useful for studying evolutionary dynamics in the limit of weak selection. Following previous practice [53, 56, 81], we can obtain the equilibrium fraction of A individuals (up to the first order of the selection strength β):

$$\langle x_A \rangle = \frac{1}{2} + \frac{\beta(1-u)}{Nu} \langle x_B F_A - x_A F_B \rangle_0, \tag{12}$$

where F_A and F_B are the total payoff of A and B, respectively, and the subscript "0" indicates that $\langle \cdot \rangle$ is averaged from all possible population configurations at neutrality with $\beta = 0$.

Natural selection favors A over B if $\langle x_A \rangle > 1/2$. This condition is equivalent to

$$\langle x_B F_A - x_A F_B \rangle_0 > 0, \tag{13}$$

which can further boil down to

$$a\langle x_B I_{AA} \rangle_0 + b\langle x_B I_{AB} \rangle_0 > c\langle x_A I_{BA} \rangle_0 + d\langle x_A I_{BB} \rangle_0. \tag{14}$$

At neutrality, the two types A and B act like different colors of individuals, and thus index permutations do not bring in any changes. We have $\langle x_B I_{AA} \rangle_0 = \langle x_A I_{BB} \rangle_0$ and $\langle x_B I_{AB} \rangle_0 = \langle x_A I_{BA} \rangle_0$. Therefore, we get the following σ-dominance condition for A to be favored [56]:

$$\sigma a + b > c + \sigma d, \tag{15}$$

where the coefficient σ summarizes the spatial effect, and its formula can be given by [55]

$$\sigma = \frac{\langle x_B I_{AA} \rangle_0}{\langle x_B I_{AB} \rangle_0}. \tag{16}$$

For the simplified prisoner's dilemma, cooperation is favored by selection if the benefit-to-cost ratio satisfies:

$$\frac{b}{c} > \frac{\langle x_B I_{AA} \rangle_0 + \langle x_B I_{AB} \rangle_0}{\langle x_B I_{AA} \rangle_0 - \langle x_B I_{AB} \rangle_0}. \tag{17}$$

Substituting $I_{AA} = N^2 \sum_{i=1}^{M} x_A^i x_A^i$, $I_{AB} = N^2 \sum_{i=1}^{M} x_A^i x_B^i$ into the above inequality, we can obtain the critical $(\frac{b}{c})^*$:

$$\left(\frac{b}{c}\right)^* = \frac{\langle x_B x_A^i x_A^i \rangle_0 + \langle x_B x_B^i x_A^i \rangle_0}{\langle x_B x_A^i x_A^i \rangle_0 - \langle x_B x_B^i x_A^i \rangle_0}. \tag{18}$$

We note that for notational simplicity, we drop the sums and cancel the common factor N^2 in the above equation.

Using the symmetry condition under neutrality, we can further simplify the above condition. To be concrete, $\langle x_B x_A^i x_A^i \rangle_0 + \langle x_B x_B^i x_A^i \rangle_0 = \langle x_B x_*^i x_A^i \rangle_0 = \langle x_B x_*^i x_*^i \rangle_0 - \langle x_B x_B^i x_*^i \rangle_0$, where x_*^i denotes the fraction of individuals in the site i. The first term $\langle x_B x_*^i x_*^i \rangle_0$ can be interpreted as the probability that for three randomly chosen individuals, the first individual is a B strategist, and the second and the third are in the same site. The second term $\langle x_B x_B^i x_*^i \rangle_0$ represents the probability that for three randomly chosen individuals, the first and the second individuals have the same B strategy while the second and the third belong to the same site.

Using the fact that both strategies A and B are equally present in the population, $\langle x_B x_*^i x_*^i\rangle_0 - \langle x_B x_B^i x_*^i\rangle_0$ can be equivalently written as $\frac{1}{2}\,\mathrm{Prob}\{G_i = G_j\} - \frac{1}{2}\,\mathrm{Prob}\{S_i = S_j, G_j = G_k\}$. In a similar way, $\langle x_B x_A^i x_A^i\rangle_0 - \langle x_B x_B^i x_A^i\rangle_0 = \langle x_A^i x_A^i\rangle_0 - \langle x_A x_A^i x_A^i\rangle_0 - (\langle x_B x_B^i x_*^i\rangle_0 - x_B x_B^i x_B^i\rangle_0) = \langle x_A^i x_A^i\rangle_0 - \langle x_B x_B^i x_*^i\rangle_0 = \frac{1}{2}\,\mathrm{Prob}\{S_i = S_j, G_i = G_j\} - \frac{1}{2}\,\mathrm{Prob}\{S_i = S_j, G_j = G_k\}$. Therefore we get the critical b/c ratio in the following form [53]:

$$\left(\frac{b}{c}\right)^* = \frac{\mathrm{Prob}\{G_i = G_j\} - \mathrm{Prob}\{S_i = S_j, G_j = G_k\}}{\mathrm{Prob}\{S_i = S_j, G_i = G_j\} - \mathrm{Prob}\{S_i = S_j, G_j = G_k\}}, \tag{19}$$

where these pair/triplet correlations are taken at neutral evolution. The key for these calculations is to calculate $\mathrm{Prob}\{G_i = G_j\}$, the probability that any two randomly individuals are from the same site.

To calculate these quantities using coalescent theory [115], it is useful to consider the rescaled mutation and migration rates, $\mu = Nu$ and $\nu = Nv$.

Let us label the M sites from $0, \ldots, M-1$. Taking into accounting the fact that these sites are located at a regular ring with periodic boundary conditions, we can use an integer $l \in (-\infty, \infty)$, computed modulo M, to denote an individual i's site number G_i as $G_i = l \bmod M$. In this way, we can regard the migration of an individual between neighboring sites as an unbiased random walk on a one-dimensional plane with integer coordinates $l \in (-\infty, \infty)$.

After their coalescence, the signed displacement at time τ, $d = G_i(\tau) - G_j(\tau)$, between any randomly chosen two individuals i and j, follows the probability distribution

$$\mathrm{Prob}\{G_i - G_j = d | t = \tau\} = e^{-\nu\tau} I_{|d|}(\nu\tau), \tag{20}$$

where $I_{|d|}(\nu\tau)$ is the modified Bessel function of its first kind. It is easy to see that individuals i and j are in the same site if and only if $d \bmod M = 0$. Thus, we can calculate the pair correlation $\mathrm{Prob}\{G_i = G_j\}$ as follows:

$$\begin{aligned}\mathrm{Prob}\{G_i = G_j\} &= \sum_{i=-\infty}^{\infty} \int_0^{\infty} d\tau e^{-\tau} e^{-\nu\tau} I_{|Mi|}(\nu\tau) \\ &= \frac{\nu^M + (1+\nu+\sqrt{1+2\nu})^M}{\sqrt{1+2\nu}((1+\nu+\sqrt{1+2\nu})^M - \nu^M)}.\end{aligned} \tag{21}$$

$\mathrm{Prob}\{S_i = S_j, G_i = G_j\}$ can be calculated as follows.

$$\begin{aligned}&\mathrm{Prob}\{S_i = S_j, G_i = G_j\} \\ &= \sum_{i=-\infty}^{\infty} \int_0^{\infty} d\tau e^{-\tau}\left(e^{-\mu\tau} + \frac{1}{2}\left(1 - e^{-\mu\tau}\right)\right) e^{-\nu\tau} I_{|Mi|}(\nu\tau) \\ &= \frac{1}{2\sqrt{1+2\nu}} \frac{(1+\nu+\sqrt{1+2\nu})^M + \nu^M}{(1+\nu+\sqrt{1+2\nu})^M - \nu^M} \\ &\quad + \frac{1}{2\sqrt{1+\mu}\sqrt{1+\mu+2\nu}} \frac{(1+\mu+\nu+\sqrt{(1+\mu)(1+\mu+2\nu)})^M + \nu^M}{(1+\mu+\nu+\sqrt{(1+\mu)(1+\mu+2\nu)})^M - \nu^M}.\end{aligned} \tag{22}$$

Calculating the remaining quantity $\mathrm{Prob}\{S_i = S_j, G_j = G_k\}$ requires a little bit more work, but we are able to obtain the explicit expression (however, it is too tedious to be included here). Substituting these quantities into Eq. (19), we obtain the explicit formula for the critical b/c ratio.

For completeness, we show the explicit expression of the structural coefficient $\sigma_l = c_1/c_2$ for the local migration case, where c_1 and c_2 are given by

$$
\begin{aligned}
c_1 = {} & \mu\sqrt{(1+\mu)(1+2\nu)(1+\mu+2\nu)}\left(-1+\left(\frac{\nu}{1+\nu+\sqrt{1+2\nu}}\right)^M\right) \\
& \times\left(-1+\left(\frac{\nu}{1+\mu+\nu+\sqrt{(1+\mu)(1+\mu+2\nu)}}\right)^M\right) \\
& \times\left(\frac{5}{(2+3\mu+\mu^2)\sqrt{(3+\mu)(3+\mu+2\nu)}}-\frac{2}{(2+\mu)\sqrt{1+2\nu}(-1+(\frac{\nu}{1+\nu+\sqrt{1+2\nu}})^M)}\right. \\
& -\frac{2(\frac{\nu}{1+\nu+\sqrt{1+2\nu}})^M}{(2+\mu)\sqrt{1+2\nu}(-1+(\frac{\nu}{1+\nu+\sqrt{1+2\nu}})^M)} \\
& +\frac{6}{(2+3\mu+\mu^2)\sqrt{(3+\mu)(3+\mu+2\nu)}(-1+(\frac{\nu}{3+\mu+\nu+\sqrt{(3+\mu)(3+\mu+2\nu)}})^M)} \\
& +\frac{\mu(1+(\frac{\nu}{3+\mu+\nu+\sqrt{(3+\mu)(3+\mu+2\nu)}})^M)}{(2+3\mu+\mu^2)\sqrt{(3+\mu)(3+\mu+2\nu)}(-1+(\frac{\nu}{3+\mu+\nu+\sqrt{(3+\mu)(3+\mu+2\nu)}})^M)} \\
& +\frac{2\sqrt{1+2\nu}+3\sqrt{(3+\mu)(3+\mu+2\nu)}-2\sqrt{1+2\nu}(\frac{\nu}{1+\nu+\sqrt{1+2\nu}})^M}{(1+\mu)(2+\mu)\sqrt{(3+\mu)(1+2\nu)(3+\mu+2\nu)}(-1+(\frac{\nu}{1+\nu+\sqrt{1+2\nu}})^M)} \\
& \left.+\frac{3\sqrt{(3+\mu)(3+\mu+2\nu)}(\mu+(1+\mu)(\frac{\nu}{1+\nu+\sqrt{1+2\nu}})^M)}{(1+\mu)(2+\mu)\sqrt{(3+\mu)(1+2\nu)(3+\mu+2\nu)}(-1+(\frac{\nu}{1+\nu+\sqrt{1+2\nu}})^M)}\right)
\end{aligned}
\tag{23}
$$

$$
\begin{aligned}
c_2 = {} & \sqrt{1+2\nu}-\sqrt{(1+\mu)(1+\mu+2\nu)}-\sqrt{1+2\nu}\left(\frac{\nu}{1+\nu+\sqrt{1+2\nu}}\right)^M \\
& -\sqrt{(1+\mu)(1+\mu+2\nu)}\left(\frac{\nu}{1+\nu+\sqrt{1+2\nu}}\right)^M \\
& \times\sqrt{1+2\nu}\left(\frac{\nu}{1+\mu+\nu+\sqrt{(1+\mu)(1+\mu+2\nu)}}\right)^M \\
& +\sqrt{(1+\mu)(1+\mu+2\nu)}\left(\frac{\nu}{1+\mu+\nu+\sqrt{(1+\mu)(1+\mu+2\nu)}}\right)^M \\
& -\sqrt{1+2\nu}\left(\frac{\nu^2}{(1+\nu+\sqrt{1+2\nu})(1+\mu+\nu+\sqrt{(1+\mu)(1+\mu+2\nu)})}\right)^M \\
& \times\sqrt{(1+\mu)(1+\mu+2\nu)} \\
& \times\left(\frac{\nu^2}{(1+\nu+\sqrt{1+2\nu})(1+\mu+\nu+\sqrt{(1+\mu)(1+\mu+2\nu)})}\right)^M.
\end{aligned}
\tag{24}
$$

For the global migration case, the formula for σ_g can be given by

$$
\begin{aligned}
\sigma_g = {} & 1+\frac{2(3-6M+3M^2+\mu-2M\mu+M^2\mu)}{(3+M+\mu+M\mu)(-3+3M-\mu+M\mu+M\nu)} \\
& +2\big(1-3M+3M^2-M^3+\mu-3M\mu+3M^2\mu-M^3\mu \\
& +M\nu-2M^2\nu+M^3\nu+M\mu\nu-2M^2\mu\nu+M^3\mu\nu\big)
\end{aligned}
$$

$$\times \big((3 + M + \mu + M\mu)$$
$$\times \big(1 - 2M + M^2 + \mu - 2M\mu + M^2\mu - 2\nu + 2M\nu - \mu\nu + M\mu\nu + M\nu^2\big)\big)^{-1} \tag{25}$$

For low mutation and infinitely many sites, the above formulae for σ_g and σ_l can be greatly simplified

$$\sigma_l = \frac{(1+2\nu)(3+2\nu+\sqrt{3}\sqrt{(1+2\nu)(3+2\nu)})}{2(1+\nu)(3+2\nu)}, \tag{26}$$

$$\sigma_g = \frac{(1+\nu)(3+2\nu)}{3+\nu}. \tag{27}$$

It is easy to check that $\sigma_l < \sigma_g$ holds for any $\nu > 0$ in above equations. Therefore, for low mutation and infinitely many sites, global migration always leads to stronger spatial effect than local migration.

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