

Phase separation in spatial coordination games

Guanlin Li*

*Interdisciplinary Graduate Program in Quantitative Biosciences,
Georgia Institute of Technology, Atlanta, GA, USA and
School of Physics, Georgia Institute of Technology, Atlanta, GA, USA*

Gabi Steinbach*

School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA, USA

Yao Yao

Department of Mathematics, National University of Singapore, Singapore

Joshua S. Weitz[†]

*School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA, USA
School of Physics, Georgia Institute of Technology, Atlanta, GA, USA and
Institut d'Biologie École Normale Supérieure, Paris, France*

(Dated: August 16, 2022)

Microbes interact in crowded, complex communities. Microbe-microbe interactions can span antagonistic to cooperative, and can vary between and across microbial species and strains. Differences in microbe-microbe interactions are critical to structuring coexistence at population scales. For example, it is often assumed that stable microbial communities are enabled by cooperative (or neutral) interactions. However, in recent work, studies of high-density colonies of *Vibrio cholerae* revealed a mechanism by which strain-dependent antagonistic interactions enabled coexistence amongst diverse microbes. Notably, these microbes utilize a proximity-based secretion system to kill individuals of other types without killing microbes of the same type. Such strain-dependent killing led to the emergence of distinct patches which grew in size and structure with spatiotemporal dynamics whose scaling was consistent with ‘Model A’ coarsening. Here, we build upon these findings and ask: to what extent is mutual killing required to enable the emergence and coarsening of cellular patches? To do so, we explore a dynamic stochastic spatial game model, focusing our attention on coordination games, such that individuals do better when playing (*i.e.*, interacting) with individuals of the same type and do worse when playing with individuals of a different type. Such coordination games include mutual killing mechanisms as well as cooperative mechanisms. Using this framework, we show that the emergence of ‘Model A’ coarsening is universal for symmetric, spatial coordination games. We also show that coarsening is maintained for cases where symmetry is broken, but that strong asymmetries in interaction payoffs lead to dominance by one type rather than the stable coexistence of distinct types in coarsening patches. Finally, we derive a PDE equivalent of the spatial stochastic game, showing how local interactions can modify the reaction components of the underlying PDE model, and confirming the basis for both the double-well nature of spatial coordination games and the potential for asymmetric payoffs to disrupt coarsening. Our findings of generic coarsening are relevant to microbial interactions and potentially to the dynamics of cellular assemblages within developing multi-cellular organisms. Altogether, this work extends the generality of prior findings on the link between type-dependent microbial interactions and population structure and suggests a greater range of interaction mechanisms are likely to lead to the emergence and growth of cellular groups.

I. INTRODUCTION

Microbes live in dense and diverse communities. As a result, microbes have evolved a variety of mechanisms to communicate and interact within and across species. Microbial interactions are often competitive [1, 2] but they can also be symbiotic (positive), facilitating protection against environmental threats, exchanging resources, or by producing public goods [3, 4]. The valence of microbial interactions can also be contingent on context, *e.g.*,

turning from cooperative to antagonistic as strains compete for resources and space [5].

One common consequence of these interactions among and across different species is the emergence of spatial structure such as coarsening dynamics, where members of the same strain and taxa accumulate and form spatially defined interfaces to non-kin strains over time [6]. Emerging spatial structures, in return, impact the frequency of contacts between kin and non-kin members and, thus, may change the global efficiency of kin or non-kin microbial interactions over time. Such complex population dynamics have been studied for a variety of specific scenarios. Yet, it remains challenging to compare scenarios with different interactions due to the lack of a general

* These authors contributed equally

[†] jsweitz@gatech.edu; <https://weitzgroup.biosci.gatech.edu>

understanding of the dynamics.

The population dynamics in crowded systems of interacting bacterial strains is a direct result of the local actions taken by individuals. The survival of each strain depends on the ‘strategy’ they utilize, the interaction intensity (the probability of deploying an interaction), and the payoff of the interaction. This type of problem is broadly studied in game theory. Here, we propose a game-theoretic framework to study the coarsening dynamics of an initially random ordered microbial system leading to coherent patterns of single-strain domains that can appear in a broad range of ecological contexts.

Specifically, we analyze numerical studies on the spatial dynamics of a two-player game with opponents that may or may not kill each other. The work is motivated by recent studies of two-player games of *Vibrio cholerae* [7], which can kill each other by injecting toxic effectors on contact. As shown in [7], initially well-mixed populations of *Vibrio* strains undergo phase separation (‘coarsening’) upon mutual killing and clonal reproduction. Domain formation emerges as cells within genetically uniform groups (locally surrounded by the same type) no longer risk contact-mediated death. In agreement with numerical simulations, it was further shown that the phase separation of equal or similar competitors exhibit hallmarks of a universal order-disorder transition that is part of the ‘Model A’ class [7], a universality class that describes systems lacking conservation and was originally developed to describe the interaction of atomic ‘spin’ systems [8, 9]. We hypothesized that mutual killing is only a subset of possible microbial interaction scenarios that phase separate following the universal Model A transition. We propose an ecologically-based stochastic game-theoretic framework (interactions can be positive or negative) to model cooperation (or coordination) with kin and show that ‘Model A’ coarsening occurs for spatial ecological systems where species have incentives to coordinate with kin (i.e., via a synergistic interaction).

Our stochastic game model is an individual-based model involving two players, but where the birth-death step is decoupled from the game step [10]. First, we derive transition rules in the mean-field limit and show that the system converges to the replicator dynamics. Next, we adapt the same transition rules to study phase separation in these coordination games in a spatial system. Finally, we derive a reaction diffusion equation as a limit of spatially distributed game systems. Our results demonstrate that a variety of interaction patterns in microbial communities can be modeled with the same game-theoretic framework. Further, we find that coarsening is a universal characteristic in coordination games, where kin members exhibit synergistic interactions, and even exhibit the same scaling law in the case of symmetric interaction potentials.

II. A GAME-THEORETIC APPROACH

II.1. Stochastic games

We consider a two-player game where the players utilize different strategies 1 and 2. The payoff matrix, A , can be written as follows

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}. \quad (1)$$

In this game, a focal player with strategy 1 receives a payoff of a_{11} or a_{12} when playing against opponent players with strategies 1 (kin) or 2 (non-kin), respectively. Similarly, focal players with strategy 2 receive a payoff of a_{21} or a_{22} when playing against opponent players with strategies 1 or 2, respectively. The payoff values (a_{ij} ’s) can be any real positive or negative number. Here we use the convention that in a biological context, a negative payoff value can lead to death and that a positive payoff value can lead to reproduction. Diagonal elements in the matrix A define intra-specific interactions, i.e. those that occur between individuals of the same species, while off-diagonal elements define inter-specific interactions that occur between members across species. Throughout, we focus our analysis on the case where A belongs to the class of coordination games, that is, where $a_{11} > a_{21}$ and $a_{22} > a_{12}$.

The community dynamics in the spatial system emerges from the accumulation of local birth and death events. Consider a community with N members, with a population size N_1 of players with strategy 1 and a population size N_2 of players with strategy 2 such that $N = N_1 + N_2$. Further, consider a continuous-time birth-death process $\{N_i(t), t \geq 0\}$ taking on values in $\mathcal{S} = \{0, 1, \dots, N\}$, where $N_i(t)$ is the number of players with strategy $i = 1, 2$ at time t . At any given time $t \geq 0$, the focal player with strategy i plays a game against an opponent with strategy j . When $a_{ij} > 0$, the focal player reproduces and replaces a randomly chosen individual with an offspring at rate a_{ij} ; when $a_{ij} < 0$, the focal player dies and is replaced by a randomly chosen individual at rate $|a_{ij}|$.

In Appendix A, we derive the mean field dynamics for the frequency of player 1, $x := N_1/N$ as $N \rightarrow \infty$, from the master equation,

$$\dot{x} = x(1-x)[(a_{11} - a_{21})x - (a_{22} - a_{12})(1-x)], \quad (2)$$

where \dot{x} denotes the time derivative of x . The replicator dynamics is recovered from the individual game rules. The first-order system in Eq. 2 can be rewritten as a gradient system, $\dot{x} = -dV/dx$ with the interaction potential $V(x)$. Coordination games, i.e., $a_{11} > a_{21}$ and $a_{22} > a_{12}$, lead to a double-well potential with two local minima of $V(x)$ at $x = 0, 1$ that correspond to locally stable equilibria, and one local maximum at $x = x_m \in (0, 1)$ corresponding to an unstable equilibrium, a mixed Nash

equilibrium, given by

$$x_m = \frac{a_{22} - a_{12}}{(a_{11} - a_{21}) + (a_{22} - a_{12})}. \quad (3)$$

Therefore, the double-well potential $V(x)$ provides a bistable system, and it is symmetric if $(a_{11} - a_{21}) = (a_{22} - a_{12})$, where $x_m = 1/2$.

II.2. Spatial, stochastic games

To study the pattern formation of coordination games in a spatial environment, we applied the stochastic games formalism (see Sect. II III.1) on a two-dimensional fully occupied lattice with length L per dimension and $N = L^2$ sites. We apply periodic boundary conditions, *i.e.*, the system is a torus in \mathbb{Z}^2 . Each site $x \in \mathbb{Z}^2$ is occupied by a player with either strategy 1 or strategy 2. In this model, every focal player plays with an opponent player that is randomly chosen from adjacent sites (we use a von Neumann neighborhood throughout, *i.e.*, the four adjacent sites). Given the strategies of the focal player and the opponent player, the payoff for the focal player is determined by the payoff matrix A . If the focal player plays strategy i and the opponent plays strategy j , then focal player receives payoff a_{ij} . If $a_{ij} > 0$, then the focal player reproduces at rate a_{ij} and replaces a randomly chosen adjacent individual with an offspring. If $a_{ij} < 0$, then the focal player dies with rate $|a_{ij}|$ and is replaced by an offspring of a randomly chosen, adjacent individual. Note that the offspring will always play the same strategy as their parent. The proposed spatial interactions of players can be formally described as interacting particle systems [11], the details are given in Appendix D. The pseudo-code of the Monte Carlo simulation can be found in Appendix B.

II.3. Ecological interactions in coordination games

For a two-player game, the sign of a_{ij} can be interpreted as the ecological impact of player with strategy j on player with strategy i . Specifically, ecological interactions can be defined as either intra-specific or inter-specific. Intra-specific interactions are those that occur between individuals of the same type, while interactions that occur between two types are called inter-specific interactions. Note that the intra-specific or inter-specific interactions usually refer to the ecological interactions between two species instead of two types. For example, a scenario of mutual killers (such as for killing-proficient *Vibrio* strains in [7]) can be modeled via a two-player coordination game with positive diagonal elements and negative off-diagonal elements, that correspond to positive intra-specific interactions and negative inter-specific interactions. Here, we map the coordination games to

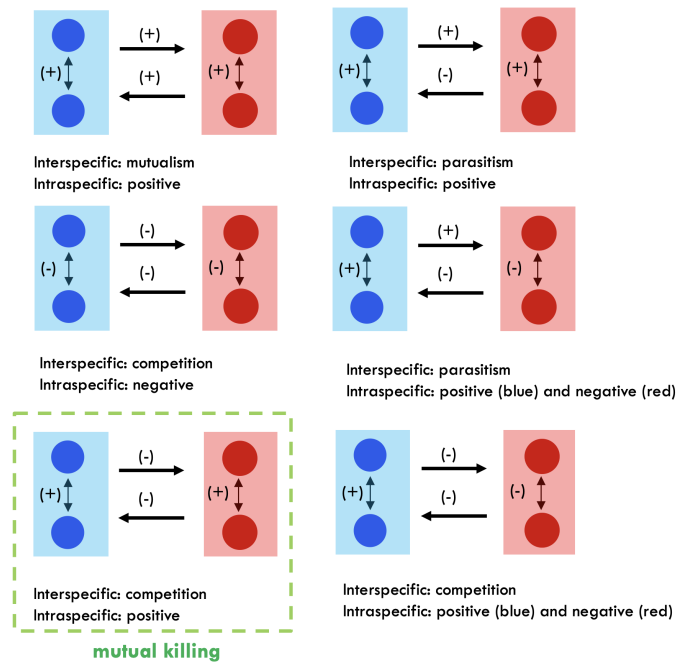


FIG. 1: Partitioning coordination games into inter- and intra-specific interactions. The sign (+/-) of payoff values correspond to the positive (+) and negative (-) interactions. For example, the mutual killing system (boxed with dashed green line) has positive intra-specific interactions $a_{ij} > 0$ if $i = j$, and negative inter-specific interactions $a_{ij} < 0$ if $i \neq j$.

a broad range of intra-/inter-specific ecological interactions, including but not limited to the mutual-killer system. The classes of intra-/inter-specific ecological interaction can be characterized by the sign of payoff values. There are four payoff values in the two-player payoff matrix A , so there are 2^4 possible games besides coordination games (classified by the sign of payoff values, each payoff value a_{ij} is either positive or negative), see Fig. A.1 in Appendix A. We summarize all distinct classes of intra-/inter-specific ecological interaction, that can be mapped to coordination games, in Fig. 1.

Using the proposed spatial coordination game-theoretic framework, in the following, we investigate the ‘coarsening’ behavior of coordination games in a broad range of ecological contexts. The key point of coordination games is that the intra-specific interactions are always preferred over inter-specific interactions, *i.e.*, synergistic effects of coordination games. Motivated by mutual killer scenarios, we hypothesize that coarsening occurs for any spatial ecological systems if strains have incentives to coordinate with kin. We further analyze the requirements for a universal order-disorder transition.

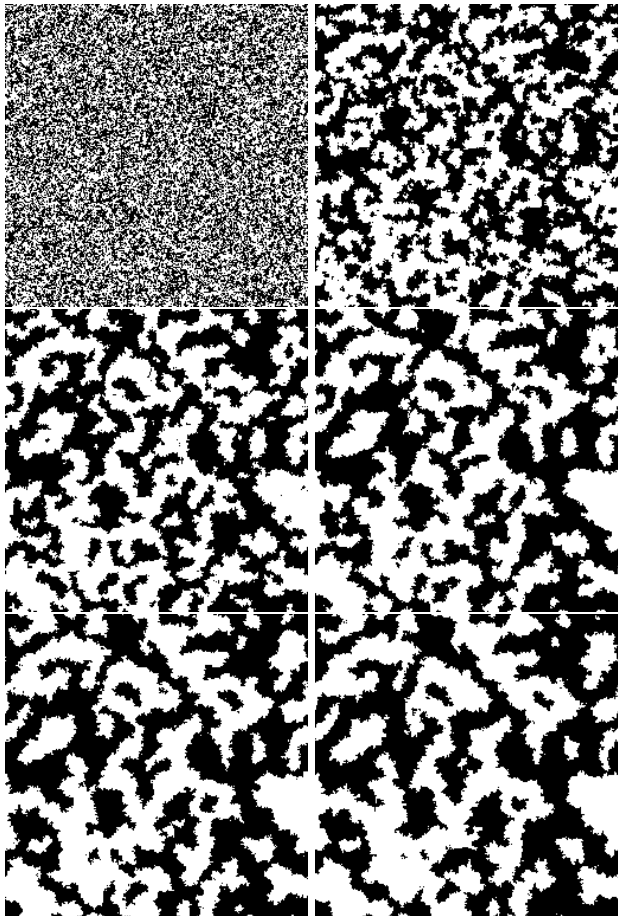


FIG. 2: Time lapse images of a two player coordination game. The images show the spatial configuration (lattice size $L = 256$) at $t = 0, 2, 4, 6, 8, 10$ with $dt = 0.05$. The payoff matrix is given as $A = [10, -5; -5, 10]$. White corresponds to player 1 and black is player 2. Starting from well mixed initial condition, initial fraction of player 1 is 0.5, the two players separate into domains whose characteristic length scales grow over time.

III. PHASE SEPARATION

To demonstrate coarsening behavior in a spatial, stochastic coordination game, we first present results on a game scenario of equal mutual killers, *i.e.* we model a spatial game with a symmetric payoff matrix and negative off-diagonal elements. We observe rapid phase separation in Fig. 2, similar to the observation for mutual killer biofilms presented in [7]. Domains of kin members (players with the same strategy) form and grow over time.

Next, we determine whether the phase separation undergoes the same type of order-disorder transition as was reported for mutual killers in [7]. We quantitatively examine the dynamics of phase separation as follows. We first compute the Fourier transform of the phase separation

images obtained from simulation as shown in Fig. 2. This transforms the image from real space into wave space with wave number coordinates $q = [q_x, q_y]^T$, providing the spatial frequencies in the x and y directions, respectively. Next, we calculate the structure factor $S(q)$ by radially integrating the real part of the Fourier transformed image (see Appendix B for more details) and calculate the characteristic wavenumber as $q_m = \int q S(q) dq / \int S(q) dq$. As a hallmark for ‘Model A’ transitions, q_m should scale as $q_m \sim t^{-1/2}$, and $S(q_m)$ scales as $S(q_m) \sim t$ with time t . This also provides a time-independent scaling relationship of $S(q_m) \sim q_m^{-2}$. Indeed, we find that the coordination game of mutual killers undergoes phase separation that follows these Model A hallmarks, see spatial structure analysis of mutual-killer game in Fig. 3.

Next, we show that any the spatial coordination games with symmetric double well potential (*i.e.*, the potential of mean-field replicator dynamics is in symmetric double-well shape, see Sect. II) leads to ‘Model A’ coarsening. To do so, we arbitrarily choose a payoff matrix from each class of intra-/inter-specific interaction shown in Fig. 1 that is associated with a symmetric double well potential, *i.e.*, $(a_{11} - a_{21}) = (a_{22} - a_{12}) > 0$. We perform a spatial coordination game for each case and conduct the spatial structural analysis on that process. We find that for each type of game the system undergoes phase separation. Moreover, the curves of the structural analysis of all games collapse (see Fig. 3), and their temporal progression is consistent with ‘Model A’ order-disorder phase separation process. In Appendix C, we present the generalized coarsening behaviors in spatial coordination games when the double-well potential functions are not perfectly symmetric. We find that the coarsening behavior of coordination games that with a small deviation from symmetric potential (low degree of asymmetry) still closely follows the ‘Model A’ coarsening. In contrast, for the coordination games with high degree asymmetric potential, we can still observe coarsening (clusters are formed), however, the coarsening is not consistent with ‘Model A’ order-disorder phase separation, see Appendix C for details.

IV. HYDRODYNAMIC LIMIT

In continuous space, phase separation processes that follow ‘Model A’ order-disorder transition can be described by a reaction-diffusion equation, the Allen-Cahn equation [12]). To compare and connect this theory with our game theoretic approach, we need to extend our model to include cellular migration; players at neighboring sites will be allowed to exchange sites with a certain probability. With this ingredient, we can derive the partial differential equation (PDE) limits of spatial games by assuming high exchange rates and scaling the lattice appropriately, *i.e.*, the hydrodynamic limit of an interacting particle system. We consider a lattice with spacing ϵ

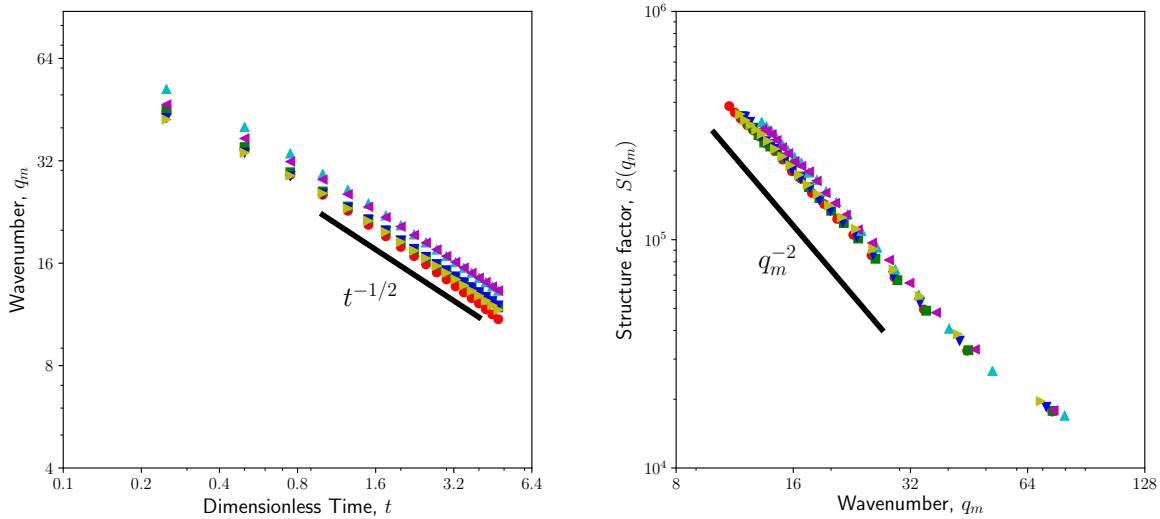


FIG. 3: Structural analysis of simulated spatial coordination games. For both panels (top and bottom), there are 6 different colors, every color corresponds to one type of ecological species interactions in Fig. 1. We choose one example payoff matrix from each class of ecological interactions, every data point is averaged over 50 realizations. The payoff matrices are $[10, 2; 5, 7]$ (red circle), $[10, -3; 5, 2]$ (green square), $[10, -7; 5, -2]$ (blue triangle), $[2, -1; -3, 4]$ (cyan triangle), $[2, -7; -3, -2]$ (magenta triangle) and $[-5, -7; -10, -2]$ (yellow triangle). The relationship between q_m and t is summarized in top panel, all the processes follow a universal $t^{-1/2}$ trend. Similarly, $S(q_m)$ curves collapse when $S(q_m)$ is plotted versus q_m , all the games are undergoing the same coarsening process.

between the lattice sites, which provides a diffusion constant of $4\epsilon^{-2}$. This means that individual players perform ‘random walks’ at rate $4\epsilon^{-2}$ on a lattice with spacing ϵ . Since the lattice is fully occupied, individual players swap with one of their nearest players (with distance ϵ) with equal probability at rate $4\epsilon^{-2}$. Let $u^\epsilon(t, x)$ and $v^\epsilon(t, x)$ be the mean number of player 1 and player 2 at x at time t , where $v^\epsilon(t, x) = 1 - u^\epsilon(t, x)$. We can write the time derivative of the population of player 1 as

Theorem 1. *As $\epsilon \rightarrow 0$, $u^\epsilon(t, x) \rightarrow u(t, x)$ is the solution of*

$$\begin{aligned} \frac{\partial u}{\partial t} = & \frac{3}{4}u(1-u)[(a_{12} - a_{22})(1-u) \\ & + (a_{11} - a_{21})u + \frac{1}{3}(a_{12} - a_{21})] + \Delta u. \end{aligned} \quad (4)$$

The proof of Theorem 1 can be found in Appendix E. The diffusive term, Δu , emerges as individual, adjacent players perform ‘random swaps’ (in analogy to random walks but in fully occupied space). The central limit theorem suggests that in the limit players perform Brownian motion (by appropriate scaling). The reaction term in Eq. 4 is a cubic polynomial. Let us define the potential W as

$$W(u) = - \int_0^u f(s) ds, \quad (5)$$

where f is the reaction term in Eq. 4. If W has two local minima at $u = 0$ and $u = 1$, and a local maximum at $u = \theta$ where $\theta \in (0, 1)$, then W is a double-well potential (see Appendix E for the condition of W being a double-well potential). The reaction-diffusion equation in Theorem 1 takes the form of an Allen-Cahn equation [12]. When Eq. 4 is defined on a two dimensional torus \mathbb{T}^2 (periodic boundary condition), the evolution of Eq. 4 can be viewed as the L^2 -gradient flow of the Ginzburg-Landau free energy functional [13, 14]

$$\mathcal{E}[u] = \int_{\mathbb{T}^2} \frac{1}{2} |\nabla u|^2 + W(u) dx, \quad (6)$$

i.e., $u_t = -\nabla_{L^2(\mathbb{T}^2)} \mathcal{E}[u]$. The free energy is non-increasing in time (see Appendix E). Note that the free energy $\mathcal{E}[u]$ contains two terms, where the gradient term penalizes spatial variation (thus has a smoothing effect), while the potential W (which has a double-well shape with two local minima) drives the system to undergo phase separation. This perspective is supported by the linear stability analysis of a mixed-strategy homogeneous steady state \bar{u} , see Appendix E.

V. DISCUSSION

Microorganisms commonly live in complex, spatially-organized communities with different strains and taxa.

Microbes have evolved an abundance of mechanisms to interact within or across species. Those interactions can enhance or diminish reproduction, and might be mutual or unilateral. The variety in interaction patterns combined with the interaction-induced structure formation of the communities pose challenges to understand of the link between process and pattern. In this work, we present a spatial coordination game model that utilizes a game theoretica framework to evaluate the link between possible combinations of interactions in a multi-species community with emergent spatiotemporal patterns. This approach enabled us to compare different interaction scenarios and find common characteristics and hallmarks of emerging structures and assortment in microbial communities.

In doing so, we focus on coordination games where members of the same species coordinate with kin and we restrict interactions to nearest neighbors. We find spatially explicit interactions can lead to ‘coarsening’ (*i.e.*, phase separation) in the class of coordination games. This means that phase separation is independent of the ‘quality’ of the interaction (whether it promotes or diminishes reproduction of the focal player). It only requires that intra-strain interactions are favored over inter-strain interactions. This suggests that in an ecological context microbes need to balance the investment into both, intra-strain and inter-strain interactions, to govern the population and community dynamics. This is particularly important as upon phase separation the frequency of contacts between self increases and the contacts between non-self decreases. The switch in social contexts suggests a selection pressure both for functional traits that contribute to initial phase separation and the formation of clonal domains and for functional traits which

stabilize locally similar, microbial domains [15].

Further, our quantitative spatial analysis showed that phase separation following spatial coordination games belong to the same type of an order-disorder transition - the ‘Model A’ universality class - if the payoff matrix corresponds to a symmetric potential. In two-player games, this case arises when the sum of the entries in each row on the payoff matrix are equal. This universal behavior has already been shown for the specific case of two-player mutual killer scenarios with equal killing rates [7]. Based on our results from coordination games, we find that the universality class is more general. In addition to equally competitive mutual-killing strains, we find that a broad range of two-species ecological interactions can lead to ‘Model A’ coarsening provided that the interaction potential is symmetric.

At the core of our findings is a derivation of a reaction-diffusion equation that represents the hydrodynamic limit of spatially distributed games. In doing so, we find that the limiting reaction-diffusion equation associated with the spatial game system is different from one obtained by adding a diffusion term to the replicator dynamics (*i.e.* to the mean-field limit of the corresponding non-spatial system). This observation recapitulates the findings in [16] and reinforces the importance of assessing how microscopic spatial interactions transform the emergence of spatiotemporal patterns in biological systems.

ACKNOWLEDGMENTS

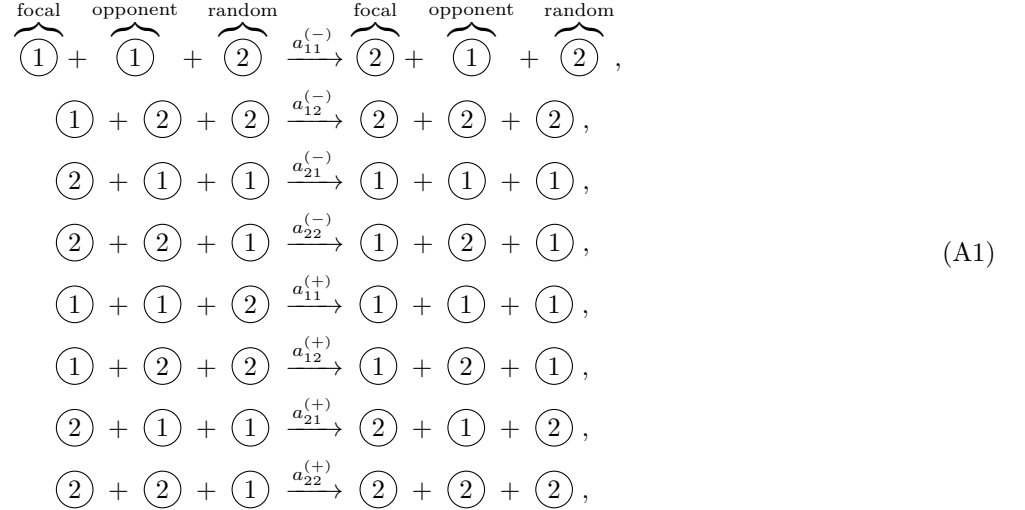
JSW acknowledges support from the Army Research Office (W911NF1910384) and the Chaire Pascal program of the Ile-de-France region.

-
- [1] K. R. Foster and T. Bell, Competition, not cooperation, dominates interactions among culturable microbial species, *Current biology* **22**, 1845 (2012).
 - [2] K. Z. Coyte, J. Schluter, and K. R. Foster, The ecology of the microbiome: networks, competition, and stability, *Science* **350**, 663 (2015).
 - [3] C. D. Nadell, K. Drescher, and K. R. Foster, Spatial structure, cooperation and competition in biofilms, *Nature Reviews Microbiology* **14**, 589 (2016).
 - [4] S. Mukherjee and B. L. Bassler, Bacterial quorum sensing in complex and dynamically changing environments, *Nature Reviews Microbiology* **17**, 371 (2019).
 - [5] M. E. Hibbing, C. Fuqua, M. R. Parsek, and S. B. Peterson, Bacterial competition: surviving and thriving in the microbial jungle, *Nature Reviews Microbiology* **8**, 15 (2010).
 - [6] D. Yanni, P. Márquez-Zacarías, P. J. Yunker, and W. C. Ratcliff, Drivers of spatial structure in social microbial communities, *Current Biology* **29**, R545 (2019).
 - [7] L. McNally, E. Bernardy, J. Thomas, A. Kalzigi, J. Pentz, S. P. Brown, B. K. Hammer, P. J. Yunker, and W. C. Ratcliff, Killing by type vi secretion drives genetic phase separation and correlates with increased cooperation, *Nature communications* **8**, 1 (2017).
 - [8] G. Steinbach, C. Crisan, S. L. Ng, B. K. Hammer, and P. J. Yunker, Accumulation of dead cells from contact killing facilitates coexistence in bacterial biofilms, *Journal of the Royal Society Interface* **17**, 20200486 (2020).
 - [9] M. O. Lavrentovich and D. R. Nelson, Nucleation of antagonistic organisms and cellular competitions on curved, inflating substrates, *Physical Review E* **100**, 042406 (2019).
 - [10] Y.-H. Lin and J. S. Weitz, Spatial interactions and oscillatory tragedies of the commons, *Physical review letters* **122**, 148102 (2019).
 - [11] R. Durrett, Ten lectures on particle systems, in *Lectures on Probability Theory* (Springer, 1995) pp. 97–201.
 - [12] S. M. Allen and J. W. Cahn, A microscopic theory for antiphase boundary motion and its application to antiphase domain coarsening, *Acta metallurgica* **27**, 1085 (1979).
 - [13] R. V. Kohn, F. Otto, M. G. Reznikoff, and E. VandenEijnden, Action minimization and sharp-interface limits for the stochastic allen-cahn equation, *Communications on Pure and Applied Mathematics: A Journal Issued by*

- the Courant Institute of Mathematical Sciences **60**, 393 (2007).
- [14] M. A. Peletier, Variational modelling: Energies, gradient flows, and large deviations, arXiv preprint arXiv:1402.1990 (2014).
 - [15] D. B. Borenstein, P. Ringel, M. Basler, and N. S. Wingreen, Established microbial colonies can survive type vi secretion assault, *PLOS Computational Biology* **11**, e1004520 (2015).
 - [16] R. Durrett and S. Levin, The importance of being discrete (and spatial), *Theoretical population biology* **46**, 363 (1994).
 - [17] C. Ratzke, J. Barrere, and J. Gore, Strength of species interactions determines biodiversity and stability in microbial communities, *Nature Ecology Evolution* [10.1038/s41559-020-1099-4](https://doi.org/10.1038/s41559-020-1099-4) (2020).
 - [18] M. Wong, X. Liang, M. Smart, L. Tang, R. Moore, B. Ingalls, and T. G. Dong, Microbial herd protection mediated by antagonistic interaction in polymicrobial communities, *Applied and environmental microbiology* **82**, 6881 (2016).
 - [19] D. F. Anderson and T. G. Kurtz, Continuous time markov chain models for chemical reaction networks, in *Design and analysis of biomolecular circuits* (Springer, 2011) pp. 3–42.
 - [20] S. M. Krone, Spatial models: stochastic and deterministic, *Mathematical and computer modelling* **40**, 393 (2004).
 - [21] A. De Masi, P. A. Ferrari, and J. L. Lebowitz, Reaction-diffusion equations for interacting particle systems, *Journal of statistical physics* **44**, 589 (1986).
 - [22] N. G. Van Kampen, *Stochastic processes in physics and chemistry*, Vol. 1 (Elsevier, 1992).

Appendix A: Derivation of mean-field limit

In the notion of chemical reactions [19], with $\textcircled{1}$ denoting a player with strategy 1 and $\textcircled{2}$ denoting a player with strategy 2, then the possible combinations of players involved in a game (a focal player, an opponent and a randomly selected third player that is not the opponent) in which there is a change in the state N_1 are



the reaction rates $a_{ij}^{(-)}$ and $a_{ij}^{(+)}$ are shorthands of $-a_{ij}\mathbf{1}_{\{a_{ij}<0\}}$ and $a_{ij}\mathbf{1}_{\{a_{ij}>0\}}$, where $\mathbf{1}_{\{E\}}$ is the indicator function; $\mathbf{1}_{\{E\}} = 1$ if event E is true and $\mathbf{1}_{\{E\}} = 0$ otherwise. Technically, for any given payoff matrix $A \in \mathbb{R}^{2 \times 2}$, only four reactions in Eq. A1 are realized. Next, we derive the mean-field limit of above stochastic games by following a similar exercise in [10].

The transition rates of Eq. A1 are

$$\begin{aligned}
Q_{N_1, N_1+1} &= a_{21}^{(-)} N_2 \frac{2 \binom{N_1}{2}}{(N-1)^2} + a_{22}^{(-)} N_2 \frac{\binom{N_2-1}{1} \binom{N_1}{1}}{(N-1)^2} + a_{11}^{(+)} N_1 \frac{\binom{N_1-1}{1} \binom{N_2}{1}}{(N-1)^2} + a_{12}^{(+)} N_1 \frac{2 \binom{N_2}{2}}{(N-1)^2} \\
&\quad + a_{21}^{(-)} N_2 \frac{N_1}{(N-1)^2} + a_{12}^{(+)} N_1 \frac{N_2}{(N-1)^2}, \\
Q_{N_1, N_1-1} &= a_{12}^{(-)} N_1 \frac{2 \binom{N_2}{2}}{(N-1)^2} + a_{11}^{(-)} N_1 \frac{\binom{N_1-1}{1} \binom{N_2}{1}}{(N-1)^2} + a_{22}^{(+)} N_2 \frac{\binom{N_1}{1} \binom{N_2-1}{1}}{(N-1)^2} + a_{21}^{(+)} N_2 \frac{2 \binom{N_1}{2}}{(N-1)^2} \\
&\quad + a_{12}^{(-)} N_1 \frac{N_2}{(N-1)^2} + a_{21}^{(+)} N_2 \frac{N_1}{(N-1)^2},
\end{aligned} \tag{A2}$$

where $Q_{n, n'}$ represents the transition rate from state n to state n' . Note that $Q_{n, n'} = 0$ if $|n - n'| > 1$. For each equation in (A2), the first four terms on the right hand sides correspond to the cases in (A1), whereas the last two terms correspond to the case where the randomly selected third player coincides with the opponent. The evolution of state N_1 is governed by the master equation, which has a gain-loss form [10, 22]

$$\frac{d}{dt} \mathbb{P}(N_1, t) = Q_{N_1-1, N_1} \mathbb{P}(N_1-1, t) + Q_{N_1+1, N_1} \mathbb{P}(N_1+1, t) - (Q_{N_1, N_1-1} + Q_{N_1, N_1+1}) \mathbb{P}(N_1, t). \tag{A3}$$

Then, multiplying Eq. A3 with N_1 and summing over N_1 , we obtain

$$\sum_{N_1=0}^N N_1 \frac{d}{dt} \mathbb{P}(N_1, t) = \sum_{N_1=0}^{N-1} Q_{N_1, N_1+1} \mathbb{P}(N_1, t) - \sum_{N_1=1}^N Q_{N_1, N_1-1} \mathbb{P}(N_1, t). \tag{A4}$$

Thus, we have found for the average of the stochastic variable $N_1(t)$,

$$\frac{d}{dt} \langle N_1(t) \rangle = \langle Q_{N_1, N_1+1} \rangle - \langle Q_{N_1, N_1-1} \rangle. \tag{A5}$$

Assume $N, N_1, N_2 \gg 1$, we note that

$$\begin{aligned}\langle Q_{N_1, N_1+1} \rangle &\approx a_{21}^{(-)} \langle \frac{N_1^2 N_2}{N^2} \rangle + a_{22}^{(-)} \langle \frac{N_2^2 N_1}{N^2} \rangle + a_{11}^{(+)} \langle \frac{N_1^2 N_2}{N^2} \rangle + a_{12}^{(+)} \langle \frac{N_1 N_2^2}{N^2} \rangle + a_{21}^{(-)} \langle \frac{N_1 N_2}{N^2} \rangle + a_{12}^{(+)} \langle \frac{N_1 N_2}{N^2} \rangle, \\ \langle Q_{N_1, N_1-1} \rangle &\approx a_{12}^{(-)} \langle \frac{N_2^2 N_1}{N^2} \rangle + a_{11}^{(-)} \langle \frac{N_1^2 N_2}{N^2} \rangle + a_{22}^{(+)} \langle \frac{N_2^2 N_1}{N^2} \rangle + a_{21}^{(+)} \langle \frac{N_2 N_1^2}{N^2} \rangle + a_{12}^{(-)} \langle \frac{N_1 N_2}{N^2} \rangle + a_{21}^{(+)} \langle \frac{N_1 N_2}{N^2} \rangle.\end{aligned}\quad (\text{A6})$$

Here, we define $x = N_1/N$, and thus $N_2/N = 1 - x$. Plugging the expressions of averaged transition rates in Eq. A6 into Eq. A5, then we normalize the system via dividing both sides of Eq. A5 by N , we find

$$\begin{aligned}\frac{d}{dt} \langle x \rangle &= a_{21}^{(-)} \langle x^2(1-x) \rangle + a_{22}^{(-)} \langle x(1-x)^2 \rangle + a_{11}^{(+)} \langle x^2(1-x) \rangle + a_{12}^{(+)} \langle x(1-x)^2 \rangle \\ &\quad - a_{12}^{(-)} \langle x(1-x)^2 \rangle - a_{11}^{(-)} \langle x^2(1-x) \rangle - a_{22}^{(+)} \langle x(1-x)^2 \rangle - a_{21}^{(+)} \langle x^2(1-x) \rangle \\ &\quad + \frac{a_{21}^{(-)} \langle x(1-x) \rangle + a_{12}^{(+)} \langle x(1-x) \rangle}{N} - \frac{a_{12}^{(-)} \langle x(1-x) \rangle + a_{21}^{(+)} \langle x(1-x) \rangle}{N}.\end{aligned}\quad (\text{A7})$$

Since $N \gg 1$, the last two terms in the order of $1/N$ are dropped, and Eq. A7 becomes

$$\frac{d}{dt} \langle x \rangle = \delta_{11} \langle x^2(1-x) \rangle - \delta_{21} \langle x^2(1-x) \rangle + \delta_{12} \langle x(1-x)^2 \rangle - \delta_{22} \langle x(1-x)^2 \rangle, \quad (\text{A8})$$

where $\delta_{ij} = a_{ij}^{(+)} - a_{ij}^{(-)}$. Note that $a_{ij}^{(+)} - a_{ij}^{(-)} = a_{ij}(\mathbf{1}_{\{a_{ij}>0\}} + \mathbf{1}_{\{a_{ij}<0\}}) = a_{ij}$. In the large N limit, the normalized system converges to the deterministic dynamics, *i.e.*, the fluctuations around the average value $\langle x \rangle$ are negligible. We thus omit the angular brackets in Eq. A8, and obtain

$$\frac{dx}{dt} = x(1-x) [(a_{11} - a_{21})x + (a_{12} - a_{22})(1-x)], \quad (\text{A9})$$

which recovers the standard replicator dynamics.

The details of mapping from two-player games to intra-/inter-specific ecological interactions are shown in Fig. A.1.

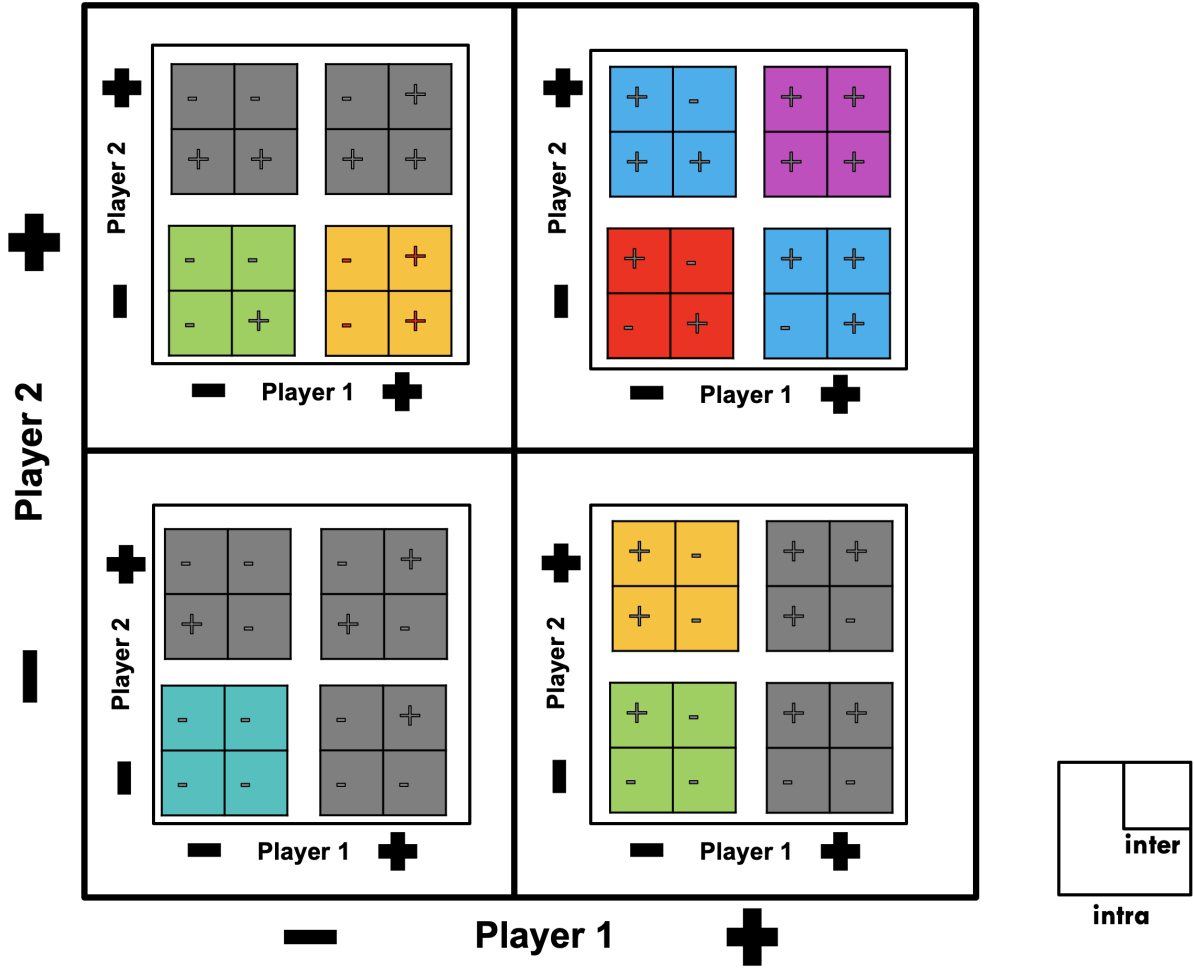


FIG. A.1: Mapping from two-player games to inter- and intra-specific interactions. The sign (+/-) of payoff values correspond to the positive (+) and negative (-) interactions. There are two layers, the outer-layer represents the intra-specific interactions and the inner-layer represents the inter-specific interactions. Some intra-/inter-specific ecological interactions cannot be mapped to any coordination games (gray blocks), e.g., an example of *anti-coordination game* with $\text{sign}\{A\} = [-, +; -, +]$. Some pairs of games are symmetric (blocks with same color), *i.e.*, one can be transformed to another via swapping player 1 and player 2. Hence, there are six distinct inter-/intra-specific ecological interactions are mapped to coordination games that are shown in Fig. 1 in main text.

Appendix B: Simulation of spatial games and spatial structure analysis

The simulation details of spatial games are summarized in Algorithm 1.

Algorithm 1: Simulation protocol of spatial games

Input : lattice size: $N = L \times L$
a 2×2 payoff matrix A with entries $A[i, j] = a_{ij}$
time step: dt
final time: t_f
game generations: $T = t_f/dt$
initial ratio of player 1: $x_0 = \#\{\text{players 1}\}/N$

Output : evolution of spatial configuration $\{\xi_t\}$

Initialization: $\xi_0 = [\xi(x_{ij})]_{L \times L}$ with $x_{ij} \in \{1, 2, \dots, L\}^2$ and $\xi(x_{ij}) \in \{1, 2\}$

for $t = 1$ **to** T **do**

for $n = 1$ **to** N **do**

- Select a random focal player, x_F
- Select a random opponent player, x_O , at an adjacent site of x_F
- Identify payoff $\alpha = A[\xi(x_F), \xi(x_O)]$ and define rate of the game, $\lambda = |\alpha|$
- compute the probability of the game given duration dt , $\beta = \lambda dt$

if $\alpha > 0$ **then**
Update ξ correspondingly: the focal player reproduces with probability β and replaces a randomly selected adjacent individual with an offspring.

else if $\alpha < 0$ **then**
Update ξ correspondingly: the focal player dies with probability β and is replaced by an offspring of a randomly chosen, adjacent individual.

end for
Save configuration ξ_t

end for

return $\xi_0, \xi_1, \dots, \xi_T$

The workflow of the image processing and analysis of structure factor is shown in Fig. B.1.

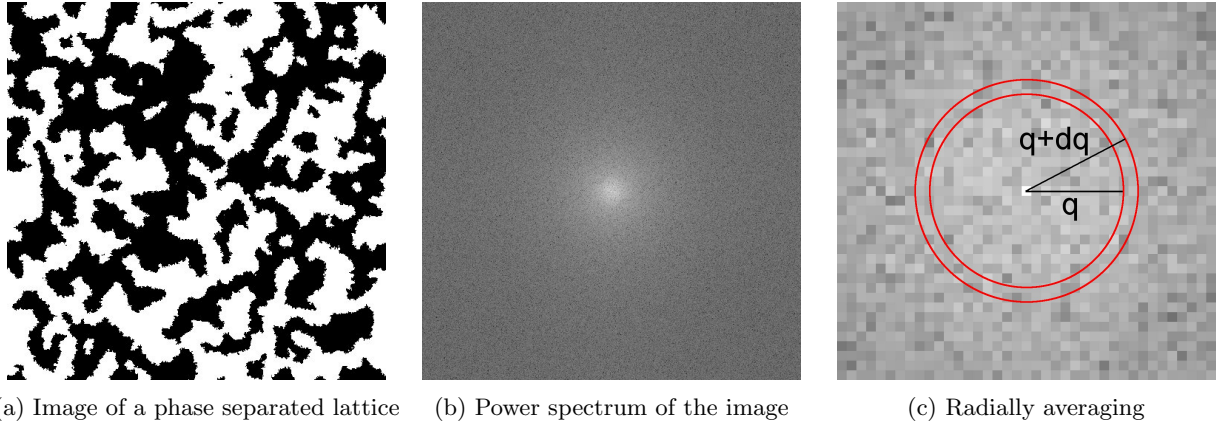
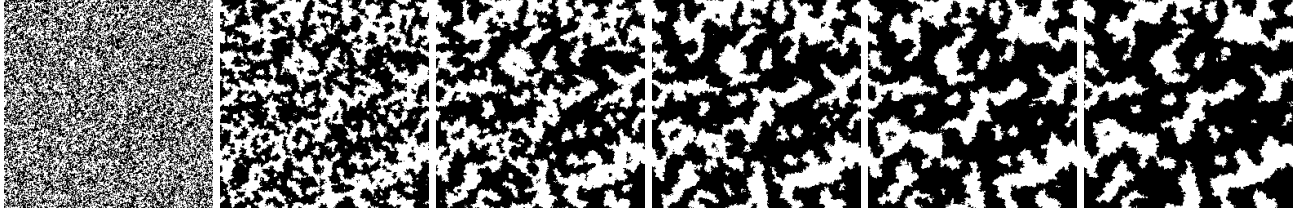


FIG. B.1: Workflow of the image processing and analysis. (a) Black-white image of a phase separated lattice, and (b) the power spectrum of the Fourier transformed image in (a), displayed with logarithmic scaling. (c) Magnified cutout of the center of the Fourier transformed image (b) illustrating the radial integration for calculating the structure factor $S(q)$. Intensities of pixels between concentric circles of q and $q + dq$ (red) are integrated and normalized by the number of pixels in this ring. This procedure performed for the whole range of q -values provides the radial $S(q)$ as a function of distance q from the center of the Fourier transformed image. Note that the radial axis is displayed with a logarithmic scale, and the image center corresponds to $q = 0$.

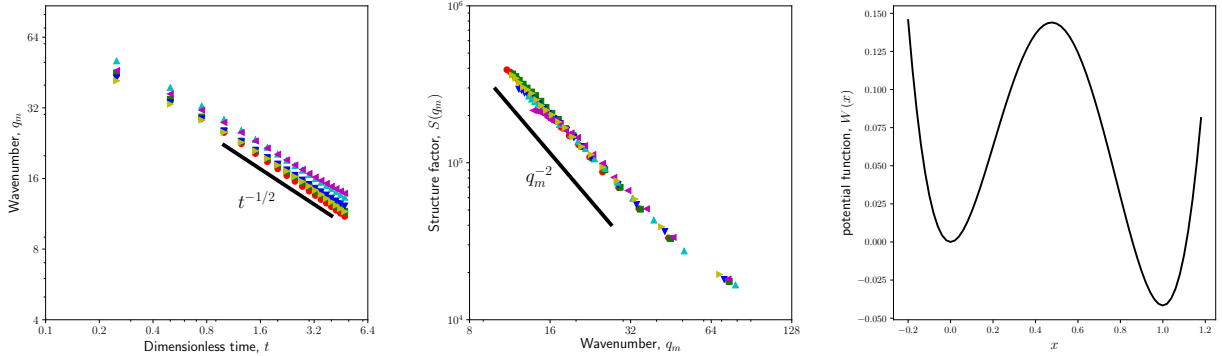
Appendix C: Coarsening in spatial coordination games when the double-well potential is not perfectly symmetric

In this section, we consider two classes of asymmetric double-well potential: symmetric double-well potential with a small or large deviation. In the main text Fig. 3, we choose one example payoff matrix that with symmetric double-well potential from each class of ecological interactions, every data point is averaged over 50 realizations. The payoff matrices are $[10, 2; 5, 7]$, $[10, -3; 5, 2]$, $[10, -7; 5, -2]$, $[2, -1; -3, 4]$, $[2, -7; -3, -2]$ and $[-5, -7; -10, -2]$. The relative fitness values (or the intra-/inter-specific interaction payoff differences for two types of player) are same, *i.e.*, $(a_{11} - a_{21}) = (a_{22} - a_{12}) = 5$. For simplicity, we consider these payoff matrices are the baseline cases. Then, we add a deviation factor η to control the degree of asymmetry. For example, adding η to symmetric potential payoff matrix $A = [10, 2; 5, 7]$ yields $A_\eta = [10, 2; 5 - \eta, 7]$. In our numerical experiments and coarsening analysis, we use $\eta = 0.5$ for low degree of asymmetry and $\eta = 3$ for high degree of asymmetry.

The coarsening behavior of coordination games that with a small deviation from symmetric potential still closely follows the ‘Model A’ coarsening, see Fig. C.1. For the coordination games with high degree of asymmetrical potential, we can still observe coarsening behavior, black clusters are growing and white clusters are shrinking in time, see Fig. C.2a, however, the coarsening is not consistent with ‘Model A’ order-disorder phase separation, see Fig. C.2b.

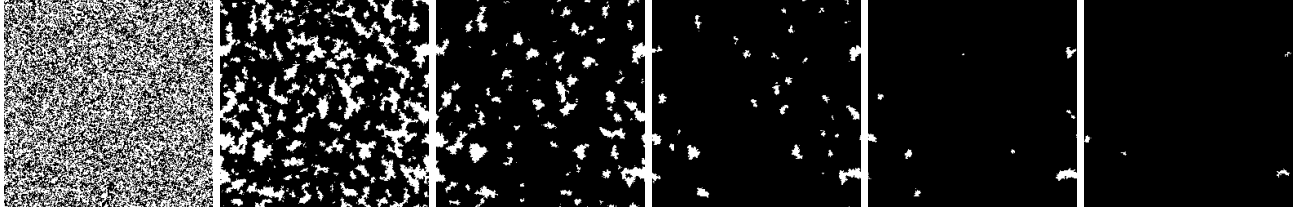


(a) Simulation of spatial coordination games with low degree asymmetric potential function.

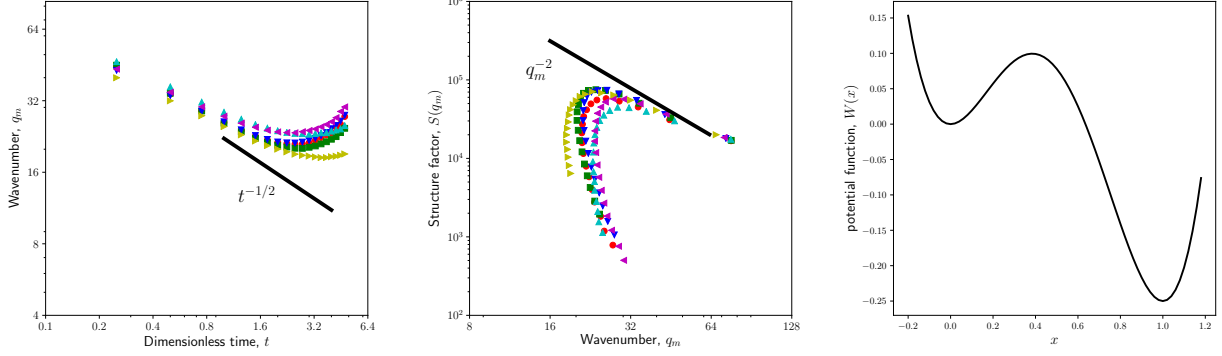


(b) Spatial structure analysis of spatial coordination games with low degree asymmetric potential function.

FIG. C.1: (a) Time lapse images of a two player coordination game with payoff matrix $A = [10, -5; -5.5, 10]$. The images show the spatial configuration (lattice size $L = 256$) at $t = 0, 2, 4, 6, 8, 10$ with $dt = 0.05$. White corresponds to player 1 and black is player 2. Starting from a well mixed initial condition, initial fraction of player 1 is 0.49 (unstable equilibrium of corresponding replicator equation), the two players separate into domains which grow over time. (b) Structural analysis of simulated spatial coordination games that correspond to asymmetric potentials with a small deviation ($\eta = 0.5$). For both panels (top and bottom), there are 6 different colors, every color corresponds to one type of ecological species interactions in Fig. 1. We choose one example payoff matrix from each class of ecological interactions, every data point is averaged over 50 realizations. The payoff matrices are $[10, 2; 4.5, 7]$ (red circle), $[10, -3; 4.5, 2]$ (green square), $[10, -7; 4.5, -2]$ (blue triangle), $[2, -1; -3.5, 4]$ (cyan triangle), $[2, -7; -3.5, -2]$ (magenta triangle) and $[-5, -7; -10.5, -2]$ (yellow triangle). The relationship between q_m and t is summarized in left panel, all the processes closely follow a universal $t^{-1/2}$ trend. Similarly, $S(q_m)$ curves collapse when $S(q_m)$ is plotted versus q_m , all the games are undergoing the same coarsening process, see middle panel. The plot of potential function shows the low degree of asymmetrical, see right panel.



(a) Simulation of spatial coordination games with high degree asymmetric potential function.



(b) Spatial structure analysis of spatial coordination games with high degree asymmetric potential function.

FIG. C.2: (a) Time lapse images of a two player coordination game with payoff matrix $A = [10, -5; -8, 10]$. The images show the spatial configuration (lattice size $L = 256$) at $t = 0, 2, 4, 6, 8, 10$ with $dt = 0.05$. White corresponds to player 1 and black is player 2. Starting from a well mixed initial condition, initial fraction of player 1 is 0.45 (unstable equilibrium of corresponding replicator equation), the two players separate into domains which grow over time. (b) Structural analysis of simulated spatial coordination games that correspond to asymmetric potentials with a large deviation ($\eta = 3$). For both panels (top and bottom), there are 6 different colors, every color corresponds to one type of ecological species interactions in Fig. 1. We choose one example payoff matrix from each class of ecological interactions, every data point is averaged over 50 realizations. The payoff matrices are $[10, 2; 2, 7]$ (red circle), $[10, -3; 2, 2]$ (green square), $[10, -7; 2, -2]$ (blue triangle), $[2, -1; -6, 4]$ (cyan triangle), $[2, -7; -6, -2]$ (magenta triangle) and $[-5, -7; -13, -2]$ (yellow triangle). The relationship between q_m and t is summarized in left panel, all the processes closely follow a universal $t^{-1/2}$ trend. Similarly, $S(q_m)$ curves collapse when $S(q_m)$ is plotted versus q_m , all the games are undergoing the same coarsening process, see middle panel. The plot of potential function shows the high degree of asymmetrical, see right panel.

Appendix D: Theoretical framework of spatial games, interacting particle systems

The spatial interactions of players can be modeled using the framework of interacting particle systems [11]. Here, we consider a lattice with L sites per dimension with periodic boundary conditions. In two dimensions, this is a torus in \mathbb{Z}^2 with $N = L^2$ lattice sites. For each site x , it's occupied by a player with either strategy 1 or strategy 2. So, the state space of each site is $\mathcal{A} = \{1, 2\}$, the configuration of system at time t is $\xi_t : \mathbb{Z}^2 \rightarrow \mathcal{A}$. Then, we define an interaction neighborhood of site x :

$$\mathcal{I}(x) = \bigcup_{y \in \mathcal{N}(x)} \mathcal{N}(y), \quad (\text{D1})$$

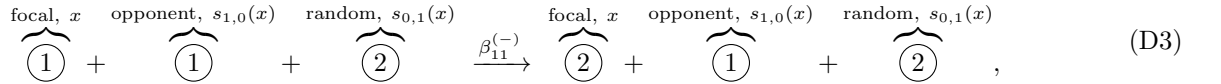
where $\mathcal{N}(x)$ is 4 nearest neighbors of x : $\mathcal{N}(x) = \{y \in \mathbb{Z}^2 : \|y - x\|_1 = 1\}$. Only one event is allowed at one time, and the other sites remain (temporarily) as they were, *i.e.*, a regular Markov jump process. We define $c_{ij}(x, \xi)$ as the rate at which site x at state $i \in \mathcal{A}$ flips to state $j \in \mathcal{A}$. The flip rate $c_{ij}(x, \xi)$ only depends on the configuration ξ through the states of some interaction neighborhood $\mathcal{I}(x)$ of site x . We refer this flip event as the particle flip dynamics. The focal player's position x is selected at random, and the opponent's position is chosen randomly from the nearest neighborhood $\mathcal{N}(x)$. As we apply the game rules in Eq. A1, the third player's position is randomly chosen from $\mathcal{N}(x)$ as well. Note that the opponent in a game could be chosen as the third player with some nonnegligible probability $\frac{1}{4}$ (in contrast to the mean field limit of non-spatial games). For convenience, we define the translation of a site x as

$$s_{k,\ell}(x) = x + (k, \ell) = (x_1 + k, x_2 + \ell). \quad (\text{D2})$$

We denote the positions of the focal player, the opponent and the randomly chosen third player as x_F , x_O and x_R respectively. We formulate the spatial dynamics by listing all the possible 'local' games that may result in a state flip on site x .

First, we assume $\xi(x) = 1$ and the position of the focal player is x , then discuss following scenarios.

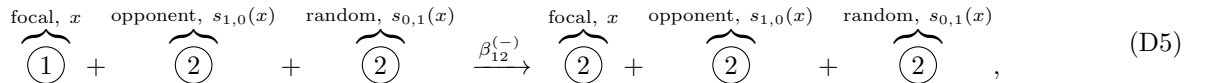
- The position of the focal player is x , *i.e.*, $x_F = x$, the opponent is from one of its nearest neighbor sites and it has the same strategy as the focal player, *i.e.*, $\xi(x_O) = \xi(x_F) = 1$. Suppose the focal player loses a game and gets replaced by a randomly chosen third player in $\mathcal{N}(x)$ (other than the opponent) with a different strategy, *i.e.*, $\xi(x_R) = 2$. So, we require $\xi(x) = 1$, $\xi(x_O) = 1$ and $\xi(x_R) = 2$. With $x_F = x$ fixed, there are 12 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{x, s_{1,0}(x), s_{0,1}(x)\}$, the reaction (flip dynamics) is



where the flip rate $\beta_{11}^{(-)}$ is

$$\beta_{11}^{(-)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,0}(x)} \times \underbrace{a_{11}^{(-)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=s_{0,1}(x)}. \quad (\text{D4})$$

- The position of the focal player is x , *i.e.*, $x_F = x$, the opponent is from $\mathcal{N}(x)$ and it has a different strategy from the focal player, *i.e.*, $\xi(x_O) = 2$. Suppose the focal player loses a game and gets replaced by a randomly chosen third player (other than the opponent) with same strategy as the opponent, *i.e.*, $\xi(x_R) = 2$. So, we require $\xi(x) = 1$, $\xi(x_O) = 2$ and $\xi(x_R) = 2$. With $x_F = x$ fixed, there are 12 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{x, s_{1,0}(x), s_{0,1}(x)\}$, the reaction (flip dynamics) is



where the flip rate $\beta_{12}^{(-)}$ is

$$\beta_{12}^{(-)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,0}(x)} \times \underbrace{a_{12}^{(-)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=s_{0,1}(x)}. \quad (\text{D6})$$

- The position of focal player is x , *i.e.*, $x_F = x$, the opponent is from $\mathcal{N}(x)$ and it has a different strategy from the focal player, *i.e.*, $\xi(x_O) = 2$. Suppose the focal player loses a game and gets replaced by an offspring of the opponent, *i.e.*, $x_R = x_O$. So, we require $\xi(x) = 1$ and $\xi(x_O) = 2$. With $x_F = x$ fixed, there are 4 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{x, s_{1,0}(x), s_{1,0}(x)\}$, the reaction (flip dynamics) is

$$\begin{array}{c} \text{focal, } x \\ \widehat{\textcircled{1}} \end{array} + \begin{array}{c} \text{opponent, } s_{1,0}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{random, } s_{1,0}(x) \\ \widehat{\textcircled{2}} \end{array} \xrightarrow{\beta_{12}^{(-)}} \begin{array}{c} \text{focal, } x \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{opponent, } s_{1,0}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{random, } s_{1,0}(x) \\ \widehat{\textcircled{2}} \end{array}, \quad (\text{D7})$$

where the flip rate $\beta_{12}^{(-)}$ is

$$\beta_{12}^{(-)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,0}(x)} \times \underbrace{a_{12}^{(-)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=s_{1,0}(x)}. \quad (\text{D8})$$

Now, we still assume $\xi(x) = 1$, and consider the case where the position of the focal player is $s_{k,\ell}(x)$, where $|k| + |\ell| = 1$, *i.e.*, the focal player is one of the nearest neighbors of x . (Note that there are 4 possible positions of the focal player.) For example, when $(k, \ell) = (0, 1)$, the following three scenarios may result in a state flip on site x .

- The position of the focal player is $s_{0,1}(x)$, *i.e.*, $x_F = s_{0,1}(x)$, and the strategy of the focal player is 2, *i.e.*, $\xi(x_F) = 2$. The opponent is one of its nearest neighbors (except x) and it has the same strategy as x_F , *i.e.*, $\xi(x_O) = 2$. Suppose the focal player wins a game and reproduces and replaces the player at x (the third player), *i.e.*, $x_R = x$. So, we require $\xi(x_F) = 2$, $\xi(x_O) = 2$ and $\xi(x) = 1$. With $x_R = x$ and $x_F = s_{0,1}(x)$ fixed, there are 3 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{s_{0,1}(x), s_{1,1}(x), x\}$, the reaction (flip dynamics) is

$$\begin{array}{c} \text{focal, } s_{0,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{opponent, } s_{1,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{random, } x \\ \widehat{\textcircled{1}} \end{array} \xrightarrow{\beta_{22}^{(+)}} \begin{array}{c} \text{focal, } s_{0,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{opponent, } s_{1,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{random, } x \\ \widehat{\textcircled{2}} \end{array}, \quad (\text{D9})$$

where the flip rate $\beta_{22}^{(+)}$ is

$$\beta_{22}^{(+)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,1}(x)} \times \underbrace{a_{22}^{(+)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=x}. \quad (\text{D10})$$

- The position of the focal player is $s_{0,1}(x)$, *i.e.*, $x_F = s_{0,1}(x)$, and the strategy of the focal player is 2, *i.e.*, $\xi(x_F) = 2$. The opponent is one of its nearest neighbor sites (except x) and it has a different strategy as x_F , *i.e.*, $\xi(x_O) = 1$. Suppose the focal player wins a game and reproduces and replaces the player at x (the third player), *i.e.*, $x_R = x$. So, we require $\xi(x_F) = 2$, $\xi(x_O) = 1$ and $\xi(x) = 1$. With $x_R = x$ and $x_F = s_{0,1}(x)$ fixed, there are 3 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{s_{0,1}(x), s_{1,1}(x), x\}$, the reaction (flip dynamics) is

$$\begin{array}{c} \text{focal, } s_{0,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{opponent, } s_{1,1}(x) \\ \widehat{\textcircled{1}} \end{array} + \begin{array}{c} \text{random, } x \\ \widehat{\textcircled{1}} \end{array} \xrightarrow{\beta_{21}^{(+)}} \begin{array}{c} \text{focal, } s_{0,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{opponent, } s_{1,1}(x) \\ \widehat{\textcircled{1}} \end{array} + \begin{array}{c} \text{random, } x \\ \widehat{\textcircled{2}} \end{array}, \quad (\text{D11})$$

where the flip rate $\beta_{21}^{(+)}$ is

$$\beta_{21}^{(+)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,1}(x)} \times \underbrace{a_{21}^{(+)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=x}. \quad (\text{D12})$$

- The position of the focal player is $s_{0,1}(x)$, *i.e.*, $x_F = s_{0,1}(x)$, and the strategy of the focal player is 2, *i.e.*, $\xi(x_F) = 2$. The position of the opponent is x , *i.e.*, $x_O = x$. Suppose the focal player wins a game and reproduces and replaces player at x (the third player), *i.e.*, $x_R = x$. So, we require $\xi(x_F) = 2$, $\xi(x) = 1$. With $x_O = x_R = x$ and $x_F = s_{0,1}(x)$ fixed, there is only 1 feasible combination of positions $\{s_{1,0}(x), x, x\}$, and the reaction (flip dynamics) is

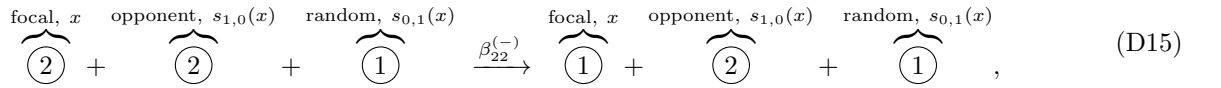
$$\begin{array}{c} \text{focal, } s_{0,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{opponent, } x \\ \widehat{\textcircled{1}} \end{array} + \begin{array}{c} \text{random, } x \\ \widehat{\textcircled{1}} \end{array} \xrightarrow{\beta_{21}^{(+)}} \begin{array}{c} \text{focal, } s_{0,1}(x) \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{opponent, } x \\ \widehat{\textcircled{2}} \end{array} + \begin{array}{c} \text{random, } x \\ \widehat{\textcircled{2}} \end{array}, \quad (\text{D13})$$

where the flip rate $\beta_{21}^{(+)}$ is

$$\beta_{21}^{(+)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=x} \times \underbrace{a_{21}^{(+)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=x}. \quad (\text{D14})$$

Second, we assume $\xi(x) = 2$ and the position of focal player is x , and discuss the following scenarios that may result in a state flip on site x . Note that the following scenarios are parallel with the ones that we discussed above with $\xi(x) = 1$, except that states 1 and 2 are interchanged.

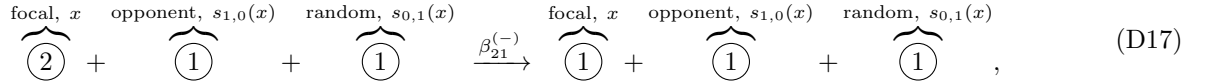
- The position of the focal player is x , *i.e.*, $x_F = x$, the opponent is from one of its nearest neighbor sites and it has the same strategy as the focal player, *i.e.*, $\xi(x_O) = \xi(x_F) = 2$. Suppose the focal player loses a game and gets replaced by a randomly chosen third player in $\mathcal{N}(x)$ (other than the opponent) with a different strategy, *i.e.*, $\xi(x_R) = 1$. So, we require $\xi(x) = 2$, $\xi(x_O) = 2$ and $\xi(x_R) = 1$. With $x_F = x$ fixed, there are 12 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{x, s_{1,0}(x), s_{0,1}(x)\}$, the reaction (flip dynamics) is



where the flip rate $\beta_{22}^{(-)}$ is

$$\beta_{22}^{(-)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,0}(x)} \times \underbrace{a_{22}^{(-)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=s_{0,1}(x)}. \quad (\text{D16})$$

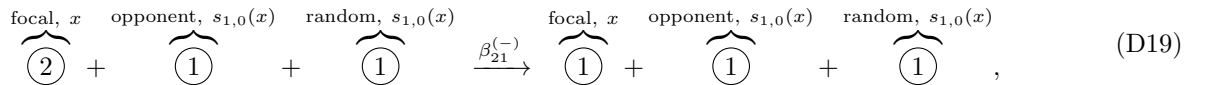
- The position of the focal player is x , *i.e.*, $x_F = x$, the opponent is from $\mathcal{N}(x)$ and it has a different strategy from the focal player, *i.e.*, $\xi(x_O) = 1$. Suppose the focal player loses a game and gets replaced by a randomly chosen third player (other than the opponent) with same strategy as the opponent, *i.e.*, $\xi(x_R) = 1$. So, we require $\xi(x) = 2$, $\xi(x_O) = 1$ and $\xi(x_R) = 1$. With $x_F = x$ fixed, there are 12 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{x, s_{1,0}(x), s_{0,1}(x)\}$, the reaction (flip dynamics) is



where the flip rate $\beta_{21}^{(-)}$ is

$$\beta_{21}^{(-)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,0}(x)} \times \underbrace{a_{21}^{(-)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=s_{0,1}(x)}. \quad (\text{D18})$$

- The position of focal player is x , *i.e.*, $x_F = x$, the opponent is from $\mathcal{N}(x)$ and it has a different strategy from the focal player, *i.e.*, $\xi(x_O) = 1$. Suppose the focal player loses a game and gets replaced by an offspring of the opponent, *i.e.*, $x_R = x_O$. So, we require $\xi(x) = 2$ and $\xi(x_O) = 1$. With $x_F = x$ fixed, there are 4 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{x, s_{1,0}(x), s_{1,0}(x)\}$, the reaction (flip dynamics) is

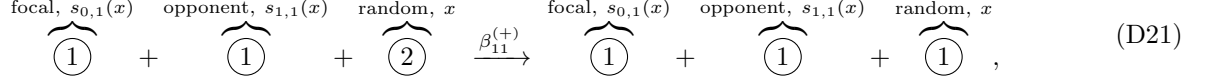


where the flip rate $\beta_{21}^{(-)}$ is

$$\beta_{21}^{(-)} = \underbrace{\frac{1}{4}}_{\text{probability of } x_O=s_{1,0}(x)} \times \underbrace{a_{21}^{(-)}}_{\text{rate of game}} \times \underbrace{\frac{1}{4}}_{\text{probability of } x_R=s_{1,0}(x)}. \quad (\text{D20})$$

Next, we still assume $\xi(x) = 2$, and consider the case where the position of the focal player is $s_{k,\ell}(x)$, where $|k| + |\ell| = 1$, *i.e.*, the focal player is one of the nearest neighbors of x . (Note that there are 4 possible positions of the focal player.) For example, when $(k, \ell) = (0, 1)$, the following three scenarios may result in a state flip on site x .

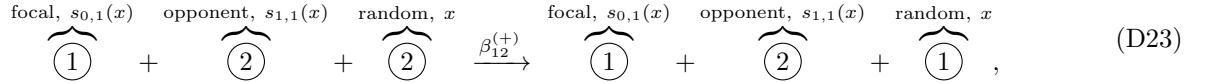
- The position of the focal player is $s_{0,1}(x)$, *i.e.*, $x_F = s_{0,1}(x)$, and the strategy of the focal player is 1, *i.e.*, $\xi(x_F) = 1$. The opponent is one of its nearest neighbors (except x) and it has the same strategy as x_F , *i.e.*, $\xi(x_O) = 1$. Suppose the focal player wins a game and reproduces and replaces the player at x (the third player), *i.e.*, $x_R = x$. So, we require $\xi(x_F) = 1$, $\xi(x_O) = 1$ and $\xi(x) = 2$. With $x_R = x$ and $x_F = s_{0,1}(x)$ fixed, there are 3 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{s_{0,1}(x), s_{1,1}(x), x\}$, the reaction (flip dynamics) is



where the flip rate $\beta_{11}^{(+)}$ is

$$\beta_{11}^{(+)} = \overbrace{\frac{1}{4}}^{\text{probability of } x_O=s_{1,1}(x)} \times \overbrace{a_{11}^{(+)}}^{\text{rate of game}} \times \overbrace{\frac{1}{4}}^{\text{probability of } x_R=x}. \quad (\text{D22})$$

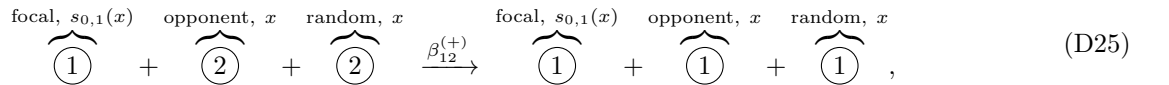
- The position of the focal player is $s_{0,1}(x)$, *i.e.*, $x_F = s_{0,1}(x)$, and the strategy of the focal player is 1, *i.e.*, $\xi(x_F) = 1$. The opponent is one of its nearest neighbor sites (except x) and it has a different strategy as x_F , *i.e.*, $\xi(x_O) = 2$. Suppose the focal player wins a game and reproduces and replaces the player at x (the third player), *i.e.*, $x_R = x$. So, we require $\xi(x_F) = 1$, $\xi(x_O) = 2$ and $\xi(x) = 2$. With $x_R = x$ and $x_F = s_{0,1}(x)$ fixed, there are 3 feasible combinations of positions $\{x_F, x_O, x_R\}$. For every feasible combination, say $\{s_{0,1}(x), s_{1,1}(x), x\}$, the reaction (flip dynamics) is



where the flip rate $\beta_{12}^{(+)}$ is

$$\beta_{12}^{(+)} = \overbrace{\frac{1}{4}}^{\text{probability of } x_O=s_{1,1}(x)} \times \overbrace{a_{12}^{(+)}}^{\text{rate of game}} \times \overbrace{\frac{1}{4}}^{\text{probability of } x_R=x}. \quad (\text{D24})$$

- The position of the focal player is $s_{0,1}(x)$, *i.e.*, $x_F = s_{0,1}(x)$, and the strategy of the focal player is 1, *i.e.*, $\xi(x_F) = 1$. The position of the opponent is x , *i.e.*, $x_O = x$. Suppose the focal player wins a game and reproduces and replaces player at x (the third player), *i.e.*, $x_R = x$. So, we require $\xi(x_F) = 1$, $\xi(x) = 2$. With $x_O = x_R = x$ and $x_F = s_{0,1}(x)$ fixed, there is only 1 feasible combination of positions $\{s_{1,0}(x), x, x\}$, and the reaction (flip dynamics) is



where the flip rate $\beta_{12}^{(+)}$ is

$$\beta_{12}^{(+)} = \overbrace{\frac{1}{4}}^{\text{probability of } x_O=x} \times \overbrace{a_{12}^{(+)}}^{\text{rate of game}} \times \overbrace{\frac{1}{4}}^{\text{probability of } x_R=x}. \quad (\text{D26})$$

Appendix E: Hydrodynamic limit of spatial, stochastic games

In addition to the partial flip dynamics described above, we introduce another type of dynamics, namely the particle exchange dynamics. Consider the scaled lattice $\mathbb{Z}_\epsilon^2 = \epsilon\mathbb{Z}^2 = \{x : x \in \mathbb{Z}^2\}$. Assume the states at site x and y are exchanged at rate $\kappa\epsilon^{-2}$, where $\|x - y\|_1 = \epsilon$ and κ is the *diffusion constant*. This is equivalent to say that the player

at position x tries to swap with another nearest player (chosen at random with equal transition probability $1/4$) at rate $2\kappa\epsilon^{-2}$. Specifically, the rate of x, y swapping, given x is the center and y is the neighbor, that is $\frac{1}{2}\kappa\epsilon^{-2}$, the same swap event could also occur in the case of y is the center and x is the neighbor which also has rate $\frac{1}{2}\kappa\epsilon^{-2}$, so that the total rate of x, y swapping is $\kappa\epsilon^{-2}$. The configuration of the scaled system at time t is denoted by $\xi_t^\epsilon : \mathbb{Z}_\epsilon^2 \rightarrow \mathcal{A}$.

In an appropriately scaled limit, in which the lattice spacing goes to zero ($\epsilon \rightarrow 0$) and the speed of stirring goes to infinity ($\epsilon^{-2} \rightarrow \infty$), the densities of the different types of particles converge to continuous densities which are solutions of a reaction-diffusion equation [11, 20, 21]. The term ‘reaction’ corresponds to the particle flip dynamics and the term ‘diffusion’ corresponds to the scaled particle exchange dynamics (fast stirring). In the next theorem, we will derive the reaction-diffusion equation as the hydrodynamic limit of the interacting particle system, where the particle exchange dynamics is as above, and the particle flip dynamics is described as in Appendix D.

Theorem 2. *Consider an interacting particle system on the scaled lattice \mathbb{Z}_ϵ^2 . Let the particle flip dynamics be given in Eqs. D3 - D26, and the particle exchange dynamics are given by the symmetric nearest neighbor stirring with scaled rate $2\kappa\epsilon^{-2}$. Suppose $\xi_0^\epsilon(x)$, $x \in \mathbb{Z}_\epsilon^2$, are independent (product measure) and let $u^\epsilon(t, x) = \mathbb{P}(\xi_t^\epsilon(x) = 1)$. If $u^\epsilon(0, x) = g(x)$ is continuous then as $\epsilon \rightarrow 0$, $u^\epsilon(t, x)$ converges to the hydrodynamic limit $u(t, x)$, where $u(t, x)$ is the bounded solution of*

$$\begin{aligned} \frac{\partial u}{\partial t} &= f(u) + \kappa \Delta u, \\ u(x, 0) &= g(x), \end{aligned} \tag{E1}$$

where the reaction term $f(u)$ is

$$f(u) = \frac{3}{4}u(1-u) \left((a_{12} - a_{22})(1-u) + (a_{11} - a_{21})u + \frac{1}{3}(a_{12} - a_{21}) \right). \tag{E2}$$

Proof. According to theory of hydrodynamic limits of interacting particle systems [11, 20, 21], the reaction term $f(u)$ is

$$f(u) = \overbrace{\langle c_{21}(x, \xi) \mathbf{1}_{\{\xi(x)=2\}} \rangle_u}^{\text{flip from state 2 to state 1}} - \overbrace{\langle c_{12}(x, \xi) \mathbf{1}_{\{\xi(x)=1\}} \rangle_u}^{\text{flip from state 1 to state 2}}, \tag{E3}$$

where $\langle \cdot \rangle_u$ denotes the expected value under product measure in which states 1 and 2 have densities u and $1-u$ respectively, i.e., $\mathbb{P}(\xi(x) = 1) = u$ and $\mathbb{P}(\xi(x) = 2) = 1-u$. Recall the flip dynamics that are associated with $\xi(x) = 2$, Eqs. D15 - D26, the first term $\langle c_{21}(x, \xi) \mathbf{1}_{\{\xi(x)=2\}} \rangle_u$ becomes

$$\begin{aligned} \langle c_{21}(x, \xi) \mathbf{1}_{\{\xi(x)=2\}} \rangle_u &= (1-u) \left(12\beta_{22}^{(-)}u(1-u) + 12\beta_{21}^{(-)}u^2 + 4\beta_{21}^{(-)}u \right) \\ &\quad + 4(1-u) \left(3\beta_{11}^{(+)}u^2 + 3\beta_{12}^{(+)}u(1-u) + \beta_{12}^{(+)}u \right) \\ &= u(1-u) \left(\frac{3}{4}a_{22}^{(-)}(1-u) + \frac{3}{4}a_{21}^{(-)}u + \frac{1}{4}a_{21}^{(-)} + \frac{3}{4}a_{11}^{(+)}u + \frac{3}{4}a_{12}^{(+)}(1-u) + \frac{1}{4}a_{12}^{(+)} \right) \\ &= u(1-u) \left(\frac{3}{4}(1-u) \left(a_{22}^{(-)} + a_{12}^{(+)} \right) + \frac{3}{4}u \left(a_{11}^{(+)} + a_{21}^{(-)} \right) + \frac{1}{4} \left(a_{12}^{(+)} + a_{21}^{(-)} \right) \right). \end{aligned} \tag{E4}$$

Similarly, we let $\xi(x) = 1$, using Eqs. D3 - D14, the second term $\langle c_{12}(x, \xi) \mathbf{1}_{\{\xi(x)=1\}} \rangle_u$ becomes

$$\begin{aligned} \langle c_{12}(x, \xi) \mathbf{1}_{\{\xi(x)=1\}} \rangle_u &= u \left(12\beta_{11}^{(-)}u(1-u) + 12\beta_{12}^{(-)}(1-u)^2 + 4\beta_{12}^{(-)}(1-u) \right) \\ &\quad + 4u \left(3\beta_{22}^{(+)}(1-u)^2 + 3\beta_{21}^{(+)}u(1-u) + \beta_{21}^{(+)}(1-u) \right) \\ &= u(1-u) \left(\frac{3}{4}a_{11}^{(-)}u + \frac{3}{4}a_{12}^{(-)}(1-u) + \frac{1}{4}a_{12}^{(-)} + \frac{3}{4}a_{22}^{(+)}(1-u) + \frac{3}{4}a_{21}^{(+)}u + \frac{1}{4}a_{21}^{(+)} \right) \\ &= u(1-u) \left(\frac{3}{4}(1-u) \left(a_{22}^{(+)} + a_{12}^{(-)} \right) + \frac{3}{4}u \left(a_{11}^{(-)} + a_{21}^{(+)} \right) + \frac{1}{4} \left(a_{12}^{(-)} + a_{21}^{(+)} \right) \right). \end{aligned} \tag{E5}$$

Plugging the Eqs. E4 - E5 into Eq. E3, we have

$$f(u) = u(1-u) \left(\frac{3}{4}(1-u) (\delta_{12} - \delta_{22}) + \frac{3}{4}u (\delta_{11} - \delta_{21}) + \frac{1}{4}(\delta_{12} - \delta_{21}) \right), \tag{E6}$$

where $\delta_{ij} = a_{ij}^{(+)} - a_{ij}^{(-)} = a_{ij}$. □

Remark 1. Comparing Eqs. E1–E2 with Eq. 2, we point out that the limiting reaction-diffusion equation associated with the spatial game system is different from simply adding a diffusion term to the mean-field replicator dynamics. This observation recapitulates the findings in [16]. This is because for each spatial game in dimension 2, there is a $1/4$ probability that the random third player coincides with the opponent, which is not negligible. As a contrast, without spatial effects the probability would be $1/N$ (here N is the total number of players), which goes to zero as $N \rightarrow \infty$. In addition, in dimension d , a similar derivation leads to a reaction term

$$f(u) = \left(\frac{2d-1}{2d}\right) u(1-u) \left((a_{12} - a_{22})(1-u) + (a_{11} - a_{21})u + \frac{1}{2d-1}(a_{12} - a_{21}) \right), \quad (\text{E7})$$

which recovers the replicator dynamics when d is large, $\left(\frac{2d-1}{2d}\right) \rightarrow 1$ as $d \gg 1$.

On the other hand, we can modify the game rules such that the opponent player cannot be identified as the random selected third player in Eqs. D3 - D26, i.e., we guarantee the random selected third player is not opponent, then the hydrodynamics PDE takes the form of Eq. E1 with reaction term Eq. E7.

The reaction term $f(u)$ in Eq. E2 is a cubic polynomial. Let us define the potential function W associated to f as

$$W(u) = - \int_0^u f(s) ds. \quad (\text{E8})$$

If W has two local minima at $u = 0$ and $u = 1$, and a local maximum at $u = \theta$ where $\theta \in (0, 1)$, then we refer to W as a *double-well potential*. In the following proposition, we give a sufficient condition for W to be a double-well potential.

Proposition E.1. For the spatial game in dimension d , suppose the 2×2 payoff matrix A satisfies

$$\begin{aligned} (a_{12} - a_{22}) + \left(\frac{1}{2d-1}\right) (a_{12} - a_{21}) &< 0, \\ (a_{11} - a_{21}) + \left(\frac{1}{2d-1}\right) (a_{12} - a_{21}) &> 0. \end{aligned} \quad (\text{E9})$$

Then, the potential function $W(u)$ in Eq. E8 is a double-well potential.

Proof. To ensure the potential function W has a double-well shape, we restrict $f(u) = 0$ when $u = 0, 1$ and θ , where $\theta \in (0, 1)$, and $f'(0) < 0$, $f'(1) < 0$, $f'(\theta) > 0$. Note that $f(u) = 0$ whenever $u = 0, 1$ given the form of $f(u)$ in Eq. E7. Define a linear function h on $[0, 1]$ as

$$h(u) = (a_{12} - a_{22})(1-u) + (a_{11} - a_{21})u + \left(\frac{1}{2d-1}\right) (a_{12} - a_{21}),$$

so that $f(u) = \frac{2d-1}{2d} u(1-u)h(u)$. To have $f(\theta) = 0$ with $\theta \in (0, 1)$, we require $h(\theta) = 0$ for some $\theta \in (0, 1)$. Since h is linear, we need $\text{sign}\{h(0)\} \neq \text{sign}\{h(1)\}$ to ensure the existence of such a θ , moreover, we need $h(0) < 0$ and $h(1) > 0$ so that $f'(\theta) > 0$. In doing so, we obtain Eq. E9. \square

Decay of free energy. The reaction-diffusion equation in Theorem 2 takes the form of an Allen-Cahn equation [12]. When Eq. E1 is defined on a two dimensional torus \mathbb{T}^2 , the evolution of Eq. E1 can be viewed as the L^2 -gradient flow of the Ginzburg-Landau free energy functional [13, 14]

$$\mathcal{E}[u] = \int_{\mathbb{T}^2} \frac{1}{2} |\nabla u|^2 + W(u) dx, \quad (\text{E10})$$

i.e., $u_t = -\nabla_{L^2(\mathbb{T}^2)} \mathcal{E}[u]$. Taking the derivative of $\mathcal{E}[u]$ with respect to time yields

$$\begin{aligned} \frac{d}{dt} \mathcal{E}[u] &= \int_{\mathbb{T}^2} \nabla u \cdot \nabla u_t - f(u)u_t dx \\ (\text{integration by parts}) &= \int_{\mathbb{T}^2} \nabla \cdot (u_t \nabla u) - u_t \Delta u - f(u)u_t dx \\ &= - \int_{\mathbb{T}^2} u_t (f(u) + \Delta u) dx + \int_{\mathbb{T}^2} \nabla \cdot (u_t \nabla u) dx \\ (\text{divergence theorem}) &= - \int_{\mathbb{T}^2} |u_t|^2 dx + \int_{\partial \mathbb{T}^2} (u_t \nabla u) \cdot \vec{n} dS \\ (\text{periodic boundary condition}) &= - \int_{\mathbb{T}^2} |u_t|^2 dx \\ &\leq 0. \end{aligned} \quad (\text{E11})$$

Therefore, the free energy is non-increasing in time. Note that the free energy $\mathcal{E}[u]$ contains two terms, where the gradient term penalizes spatial variation (thus has a smoothing effect), whereas the potential W (which has a double-well shape with two local minima) drives the system to undergo phase separation.

Linear stability analysis. For Eq. E1, note that the constant solution $u(x, t) \equiv \bar{u}$ is a steady state for any $\bar{u} \in (0, 1)$, and it corresponds to a mixed strategy that is spatially homogeneous. Now let us consider a solution that has a small fluctuation around \bar{u} , that is, $u(x, t) = \bar{u} + \delta u(x, t)$, where $|\delta u| \ll 1$. Substituting this solution to the evolution equation Eq. E1 and omitting the terms of order $(\delta u)^2$ or higher, we find that an arbitrary tiny perturbation δu evolves as follows (a linear evolution equation):

$$\frac{\partial \delta u}{\partial t} = f'(\bar{u})\delta u + \kappa \Delta \delta u.$$

The general solution of a constant-coefficient linear evolution equation can be written as $\delta u(x, t) = v e^{\sigma t} e^{iqx}$, where v is some nonzero constant vector, σ is growth rate and $q = [k\pi/\ell, j\pi/\ell]^T$ is the wave vector (qx is a dot product). Substituting $\delta u(x, t) = v e^{\sigma t} e^{iqx}$ into the above linear evolution equation and canceling common terms from both sides, we find that

$$\sigma(q) = f'(\bar{u}) - \kappa |q|^2.$$

The growth rate σ is then determined as a function of wave vector. Those associated wavelengths with positive growth rates are unstable, and those with negative growth rates are stable; the parameters of the system determine which, if any, of the wavelengths fall into each category. The small fluctuation term could lead to phase diverge from homogeneous equilibrium if the largest growth rate is positive, *i.e.*, $\max \sigma(q) > 0$. The largest growth rate corresponds to the wave vector $q = [\pi/\ell, \pi/\ell]$, so that $\sigma_{max} = f'(\bar{u}) - 2\kappa(\pi/\ell)^2$, where the second term indicates that diffusion is stabilizing the phase from diverging.