Mesoscopic Interactions and Species Coexistence in Evolutionary Game Dynamics of Cyclic Competitions

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Evolutionary dynamical models for cyclic competitions of three species (e.g., rock, paper, and scissors, or RPS) provide a paradigm, at the microscopic level of individual interactions, to address many issues in coexistence and biodiversity. Real ecosystems often involve competitions among more than three species. By extending the RPS game model to five (rock-paper-scissors-lizard-Spock, or RPSLS) mobile species, we uncover a fundamental type of mesoscopic interactions among subgroups of species. In particular, competitions at the microscopic level lead to the emergence of various local groups in different regions of the space, each involving three species. It is the interactions among the groups that fundamentally determine how many species can coexist. In fact, as the mobility is increased from zero, two transitions can occur: one from a five- to a three-species coexistence state and another from the latter to a uniform, single-species state. We develop a mean-field theory to show that, in order to understand the first transition, group interactions at the mesoscopic scale must be taken into account. Our findings suggest, more broadly, the importance of mesoscopic interactions in coexistence of great many species.

As fundamental problems of continuous interest in evolutionary biology and biodiversity, competition among species, their coexistence, and the underlying self-organized pattern formation processes have attracted much interest1–4. Earlier models were based on population dynamical equations, which provided a macroscopic picture of species competition5–7. Recent years have witnessed a great deal of effort in the microscopic model and mechanism of species competition and coexistence at the level of individual interactions8–10,13–35,37. In this regard, a paradigm is the three-species cyclic game model (rock-paper-scissor, or RPS) to address the role of population mobility in coexistence, a basic parameter in the dynamical evolution of realistic ecosystems ranging from bacteria run and tumble to animal migration. A landmark result was the emergence of coexistence for sufficiently small values of the mobility. Specifically, say in a two-dimensional spatial region three species can disperse and compete cyclically for survival. Then, coexistence can occur in the form of entangled rotating spiral waves in the region3. The spiral wave patterns have since been viewed as the basic dynamical structure supporting coexistence. Subsequently, various pertinent issues have been addressed such as noise and correlation8, conservation laws9,10, strength of competition11, emergence and stability of spatial patterns12–15, basins of coexistence state16,17, long-range migration18,19, local habitat suitability20, intraspecific competition21, role of inhomogeneous reaction rates22–26, multi-strategy competition due to two-toxins bacterial interaction27, simultaneous epidemic spreading28, effects of spatial extent and population size29–31, low dimensional behaviors32,33, and extension to arbitrary number of species34,35, as reviewed in Ref.36.

The macroscopic and microscopic pictures represent two extreme settings to probe into the dynamics of species competition and coexistence. In particular, the macroscopic description is based on the dynamical evolution of the entire population of each species involved, and the interaction occurs at the global or collective level of all individuals in the population. In contrast, the microscopic framework is based on interactions at the individual level. In nature, species interactions at a scale somewhere between the two extreme cases are also possible, e.g., interactions among groups of individuals. Such group interactions are in fact quite common in real social and ecosystems38–42 of e.g., human beings, ants, and bees, where social or
group interaction rules emerge from the microscopic interactions among the individuals. Group interactions are also ubiquitous in microorganisms. For example, communities of microorganisms bred from different tributaries may interact under the confluence to the main stream. Another example is adaptation of a living body to a new environment with the invasion of new bacteria set (or flora), which may disturb its own intestinal bacterial flora (originally organized into stable configurations) due to the interaction between the two stable bacterial floras. For convenience, we use the term “mesoscopic” to refer to interactions at the group level.

There have been recent works on group interactions at the mesoscopic scale, such as the study of defensive alliances formed by several different species to avoid external invasion. However, a systematic framework to investigate the effects of mesoscopic interactions on species coexistence has been missing. In this paper, we address this fundamental problem by using an evolutionary-game model of cyclic competition among five species, the so-called “Rock-paper-scissors-lizard-Spock” (RPSLS) game. We identify the emergence of mesoscopic groups, each involving three species, and find that the group interactions are key to coexistence. Spatially, there are five distinct local spiral wave patterns, and it is the interactions among the spirals that lead to coexistence (or extinction). Utilizing the mean field theory, we develop a set of rate equations governing the time evolution of the spiral densities, which enable prediction of extinction of species. In particular, for small mobility, all five species coexist through stable mesoscopic interactions among the five types of spirals. As the mobility is increased through a critical value, extinction of four types of spirals occurs due to mesoscopic fluctuations, with one single type of spiral left to maintain coexistence but only for three species. As the mobility is increased further through another critical point, two more species become extinct, leading to a uniform state of one species. This route from coexistence to extinction can be fully understood based on our mean-field framework. Our results provide understanding of coexistence of more than three species through interactions at the mesoscopic level, which go beyond the conventional microscopic model of three species, and provide new insights into the fundamental problem of coexistence and biodiversity.

Results

Rules of microscopic dynamical evolution. The RPSLS game involves five species competing with one another in a cyclic manner, which is a direct (but nontrivial) extension of the classic three species cyclic-competition game originally proposed by May and Leonard, widely known as the RPS game. The RPSLS game has more complicated predator-prey relationships than the RPS game. In particular, the ten game rules are: scissors cut paper, paper covers rock, rock crushes lizard, lizard eats paper, paper disproves Spock, Spock vaporizes rock, Spock smashes scissors, scissors decapitate lizard, lizard eats paper, paper disproves Spock, Spock vaporizes rock, and Rock crushes scissors.

![Figure 1 | Schematic illustration of five-species competition.](image)

Figure 1 shows the game rules: scissors cut paper, paper covers rock, rock crushes lizard, lizard eats paper, paper disproves Spock, Spock vaporizes rock, Spock smashes scissors, scissors decapitate lizard, lizard eats paper, paper disproves Spock, Spock vaporizes rock, and Rock crushes scissors.

Species coexistence and mesoscopic interactions. Figure 2 shows typical snapshots of individual distributions of the five species in space for different mobility values, where the lattice size is $N = 1000 \times 1000$. We observe the following features: (1) the individuals of species form a spiral wave pattern, and interactions among different species are characterized by entanglement of the corresponding spirals, (2) the basic, self-organized spiral wave patterns are those associated with different combinations of three species, and (3) as demonstrated in previous works, the wavelength of the spiral wave tends to increase with the mobility $M$ (in fact proportional to $\sqrt{M}$).

Figure 2 shows two kinds of extinction probability $P_{\text{ext}}$ versus $M$, where the solid and open symbols denote the cases of extinction from the five-species and three-species states, respectively. In particular, for near zero mobility, all five species coexist. Due to the symmetry of the game dynamics and the requirement to maintain cyclic competition, extinction occurs through pair of species. As $M$ is increased through a critical value (denoted by $M_{\text{c1}}$), two species are extinct, leaving behind three species, which is defined as the event of five-species extinction. As $M$ is further increased through another critical value, denoted by $M_{\text{c2}}$, two more species become extinct, leading to a uniform state of one species in the system. This signifies
Figure 2 | Effect of mobility on dynamics. (a) Typical snapshots of spatial patterns of five species competition game for different values of the mobility $M$. Each color represents one of the five species and white denotes empty sites. The system size is $N = 1000 \times 1000$. (b) Extinction probabilities $P_{\text{ext}}$ of the 5 and 3 species states as a function of $M$, represented by the solid and open symbols, respectively, for systems of sizes $N = 50 \times 50$ (red circles), $100 \times 100$ (blue triangles), $150 \times 150$ (green diamonds), and $200 \times 200$ (violet squares). The thick solid curve is theoretical estimation of the extinction probability from the five species coexistence state in the thermodynamic limit (i.e., $N \to \infty$) through an equivalent dynamical model based on spiral or group interaction at the mesoscopic level.

The critical points of (light gray region), and finally to a single species state (gray region). species coexist (white region), to a three-species coexistence state that, as $M$ is increased, the system is first in the state where all five species coexist (white region), to a three-species coexistence state (light gray region), and finally to a single species state (gray region). The critical points of $M$ are: $M_{c5} \approx 1.5 \times 10^{-3}$, and $M_{c3} \approx (4.0 \pm 0.5) \times 10^{-4}$. We note that the values of $M_{c3}$ agree well with the critical mobility value for loss of coexistence in the classic three-species RPS game model in Ref. 3.

A remarkable phenomenon is that coexistence of the five species in the low mobility regime is supported by the competition among the diversified three-species spirals. In particular, from the first snapshot in Fig. 2(a), we see that several different kinds of three-species spirals (e.g., those consisting of species 2, 3, and 4, or species 4, 5, and 1, etc.) coexist and are located in different spatial regions. Extinction from the five species coexistence state corresponds to the disappearance of certain spirals. This phenomenon thus points to the importance of spiral interactions, i.e., group interactions at the mesoscopic scale, in species coexistence. As shown in Fig. 3, there are in total five different kinds of three-species spirals or groups, each containing three cyclically competitive species. Transition from five- to three-species coexistence state at $M_{c5}$ can be understood through the interactions among the five groups.

As indicated in Fig. 3, we define three types of group interactions among all the five groups (or spirals): nearest-neighbor group interaction (e.g., interaction between spiral 123 and 234, denoted by 123-234), next-nearest-neighbor group interaction (e.g., 123-345), and self-interaction (e.g., 123-123). By designing proper numerical experiment, we can observe the spatiotemporal patterns associated with the distinct types of group interactions. The specifically designed Monte-Carlo simulations are as follows. We divide the entire region into two subregions of equal size. In each subregion, the populations are first allowed to reach thermal equilibrium, which can be realized by placing individuals in each subregion and evolving the dynamics according to the RPSLS competition rules until a steady state is reached. When the populations in both subregions reach thermal equilibrium, the partition between the two subregions are removed, initiating interactions between the individuals from the two subregions. This allows the three types of group interactions to be monitored. Figure 4 shows examples of the nearest and next-nearest neighbor interactions among the spirals. For the nearest-neighbor interaction (123-234), since the two kinds of spirals touch each other, 234 keep invading 123 until 123 becomes extinct. We name the nearest-neighbor interaction process as “incipience”, which reduces the diversity of spirals and consequently species diversity. For the next-nearest-neighbor interaction (123-345), two new kinds of spirals (234 and 451) are generated, which is then a kind of “reaction” that serves to improve the spiral diversity. Additionally, we observe that the spirals of the individuals from the same species coexist regardless of the mobility value, indicating that self-interactions have little effect on competitions at the spiral or group level.

The spiral interactions can be characterized by the spiral interaction graph (SIG), as shown in Fig. 3, which specifies the detailed interactions among the five kinds of spirals, including incursion between the nearest-neighbor spirals (blue thick arrows) and reaction between the next nearest-neighbor spirals (gray dashed lines). Compared with the microscopic interactions among the five species (c.f., Fig. 1), the SIG in Fig. 3 describes interactions at a higher level. We find numerically that the SIG is independent of the value of the mobility in the regime of coexistence.

Figure 5 presents snapshot examples from simulation with random initial configuration of species, where the five types of spirals arise in the entire spatial domain. When certain spirals are invaded
and 234 with incursion (234 under Fig. 3 provides a framework to investigate coexistence of the vulnerable one. Compared with the microscopic level interaction at the mesoscopic scale. We develop a mean field theory based on numerical results is essential to understanding and prediction the dynamics of the multi-species competition system. For example, for a four-species competition system, we can conclude immediately from Fig. 3 that the system is not stable, because four species can form at most two kinds of three-species spirals, corresponding to reaction that generates two new spirals. Each spiral is composed of three species as distinguished by colors and numbers. The framework of spiral (group) interactions that we establish based on numerical results is essential to understanding and predicting the dynamics of the multi-species competition system. For example, for a four-species competition system, we can conclude immediately from Fig. 3 that the system is not stable, because four species can form at most two kinds of three-species spirals, corresponding to reaction that generates two new spirals. Each spiral is composed of three species as distinguished by colors and numbers.

A mean-field theoretical analysis is given in section Methods to understand the spiral (group) interactions. The rate equations for the densities of the five spirals effectively describes the dynamics of the system at the mesoscopic level. Fig. 2(b) plots the extinction probability of the five-species state as a function of $M$ (solid curve) predicted from our mesoscopic mean-field theory.

**Conclusions**

In a complex ecological system consisting of a large number of competing species populations, interactions can occur at different scales (or levels). At the large, macroscopic scale, the entire populations compete with one another which, mathematically, can be described by population dynamics governed by a set of coupled ordinary differential equations, one for each distinct population. This approach usually leads to qualitative understanding of the problem of coexistence versus extinction. A representative example of the macroscopic approach is the population dynamics of three cyclically competing species, the so-called RPS dynamics. At the opposite extreme is the relatively recent, microscopic approach based on evolutionary game dynamics, which treats species interactions at the individual level. This approach can lead to significant insights into phenomena such as the coexistence of mobile, cyclically competing species in the low mobility regime and extinction in the high mobility regime. In between the microscopic and macroscopic scales lies the mesoscopic scale. To our knowledge, interactions at the mesoscopic scale, how they emerge and affect coexistence/extinction were not well understood.

We present a case study to gain significant insights into species interactions at the mesoscopic scale. We take the system of five cyclically competing species described by the RPSLS game dynamics, and observe the emergence of distinct groups of three cyclically interacting species, which appear as localized spiral wave patterns in different regions of the spatial domain. Interactions among different cyclic groups, dynamically manifested as interactions among different spirals, determine how many species can coexist for different regimes of mobility. In particular, as the mobility is increased from zero, two critical transitions occur, at which the number of coexisting species changes relatively suddenly. For sufficiently small mobility, all five species can coexist. At the first transition, two species are extinct, resulting in a state where three species coexist. As the mobility is increased further, the second transition occurs at which two more species become extinct, leaving behind a uniform, single-species state. Based on extensive numerical computations, we demonstrate that, while the second transition can be understood in the microscopic framework, the first transition from five to three coexisting species can be understood only by resorting to group or spiral interactions at the mesoscopic scale. We develop a mean field theory that enables us to predict the transition point and the extinction probability.

![Figure 3 | Spiral interaction graph (SIG).](image-url)

The SIG lists the interaction rules among the five different kinds of spirals (or groups). The nearest neighbor interaction (blue thick arrows) specifies "incursion" from one to another, and the next-nearest neighbor interaction (gray dashed lines) corresponds to reaction that generates two new spirals. Each spiral is composed of three species as distinguished by colors and numbers. The difference between the second and third ($t = 24000$) snapshots is the generation of 451 in the reaction region between 512 and 345. The state of the system at the spiral level is determined by the trade-off between the two types of interaction, leading to enhancement or destruction of certain spirals during the dynamical evolution.

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![Figure 4 | Pattern evolution due to spiral interactions.](image-url)

(a) Nearest neighbor interaction in SIG (Fig. 3), e.g., the interaction between spirals 123 and 234 with incursion (234 $\rightarrow$ 123). (b) Next-nearest neighbor interaction, e.g., between spirals 123 and 345, that generates two products (e.g., the new spirals 234 and 451). The system is composed of two $N = 500 \times 500$ sublattices and the two different kinds of spirals are separated initially to within the left and right sublattices. The color legend of species is the same as in Fig. 2.
Biodiversity typically involves coexistence of a large number of species. In this sense the microscopic theory based on the RPS game dynamics provides a starting point to address the coexistence problem. Our results indicate that, in order to fully understand the consequences of interactions among many species, interactions at the mesoscopic scale must be taken into account. We hope the results reported in this paper will stimulate further efforts in this direction.

**Methods**

We develop a theory to understand the spiral (group) interaction dynamics in systems hosting more than three species. From numerical simulations, we see that the effective interactions among the spirals are incursion between nearest-neighbor spirals and reaction between next-nearest-neighbor spirals, while self-interactions have no effect on interactions at the spiral level. To gain insight, we consider the scenario of interaction between two spirals of well-mixed species. As shown in Fig. 6, we denote all possible reactions between the two spirals using arrows and list all the products correspondingly on the right-hand side. For example, the species 2 and 4 in 234 may invade and replace 1 in 123, generating the products 223 and 423, respectively. There are seven possible products from the pairs of spirals with nearest neighbors relationship (e.g., 123 + 234), and eight products from those of next-nearest neighbors (e.g., 123 + 345). However, only the products with three cyclic-competition species can self-sustain, which are underlined (red). We see that the product from 123 + 234 is simply 423 (i.e., 234), which actually implies the incursion from 234 to 123. The products from 123 + 345 are 423 and 145, which coincide with the simulation results (Fig. 4). The well-mixed scenario of elementary interactions is thus reasonable to certain extent, since randomness in the boundaries and the phase difference among the spirals may induce all possible elementary interactions. Assuming that each elementary interaction takes place equally probably when two spirals contact, we can define the relative rate of the incursion process to be ζ = 1/8, while the relative rate of the reaction process for each of the two products to be ζ = 1/8.

For a spatially extended ecosystem self-organized into three-species spiral patterns, the number $N_i$ of certain kind of spirals (i = 1, 2, ..., 5) changes with time due to the interactions among them. However, the total number of spirals, $N = \sum N_i$, is approximately invariant. For a system with a large population of spirals (e.g., at the thermodynamic limit $N_i \to \infty$), intrinsic fluctuations in the spiral interaction dynamics (i.e., the mesoscopic fluctuations) can be neglected, and the mean-field rate equations for the spirals can be used to describe the dynamics of the system. From the interaction rules in Fig. 3, we arrive at the following set of deterministic rate equations for the densities $n_i = N_i/N$, of the five kinds of spirals:

\[
\begin{align*}
\dot{e}_1 n_1 &= \zeta ([n_1 n_2] - [n_3 n_4] - [n_5]), \\
\dot{e}_2 n_2 &= \zeta ([n_2 n_3] - [n_4 n_5] - [n_1 n_5]), \\
\dot{e}_3 n_3 &= \zeta ([n_3 n_4] - [n_5] - [n_1 n_2]), \\
\dot{e}_4 n_4 &= \zeta ([n_4 n_5] - [n_1 n_3] - [n_2 n_3]), \\
\dot{e}_5 n_5 &= \zeta ([n_5] - [n_1 n_4] - [n_2 n_4]).
\end{align*}
\]

where, in each equation, the first item with rate $\zeta$ represents the incursion processes and the second item with rate $\zeta$ represents the reaction processes. The rate equations are symmetric and the solution denoted by $n = (n_1, n_2, n_3, n_4, n_5)$ is not sensitive to the values of $\zeta$ and $\zeta$. Equation (2) possesses one reactive fixed point $n^* = \left\{ \frac{1}{5}, 1, 1, 1, 1 \right\}$ associated with the coexistence of all five spirals, and 6 absorbing fixed points with one kind of spiral persisting, e.g., $n = (1, 0, 0, 0, 0), (0, 1, 0, 0, 0), ..., (0, 0, 0, 0, 1)$, or with no spiral left (0, 0, 0, 0, 0). Due to the reaction processes, the six absorbing fixed points cannot actually be reached during the dynamical evolution from the initial configuration with more than three nonzero $n_i$ for $N_i \to \infty$.

The dynamics in the vicinity of the reactive fixed point $n^*$ can be studied by linearizing Eq. (2) and then determining the eigenvalues of the corresponding Jacobian matrix. Let $\delta n = n - n^*$ be an infinitesimal deviation from the reactive fixed point. Since the number of spirals is conserved, we can eliminate one of the infinitesimal variables, say $\delta n_5$, leading to the reduced vector $\delta x = (\delta n_1, \delta n_2, \delta n_3, \delta n_4)$. The linearized Eq. (2) can then be written in the following form:

\[
\dot{\delta x} = A \delta x.
\]

The reactive fixed point $n^*$ turns out to be a stable focus as the complex eigenvalues of $A$ have negative real parts.

Figure 7(a) shows the time evolution of the spirals’ densities from the solutions of Eq. (2). Even when the initial spiral configuration is heterogeneous (e.g., three nonzero densities with one of them dominant), the system exhibits exponential convergence to the stable focus $n^*$ (Sidebar: The envelopes of $n_i$ converge exponentially to 1/5). The behaviors of the system in the two-dimensional subspace defined as $n_3 = n_4$ and $n_1 = n_5$ are also shown in Fig. 7(a). We see that, the rate equations at the level of spiral interaction predict the existence of $n^*$, i.e., the coexistence of the five types of spirals, implying coexistence of five species. However, simulation results of the five species game dynamics in Fig. 2(b) show two transitions as the value of mobility $M$ is increased, each responsible for extinction of two species, i.e., the transitions from white to light gray, then to gray regions. Thus, the disappearance of the five-species state from simulation in fact signifies the loss of spiral diversity, in contrast to the prediction $n^*$ from rate equations Eq. (2).

**Figure 7** | Illustrations of elementary spiral interactions. Possible elementary interactions and products between a pair of nearest neighbor spirals (upper) and next-nearest neighbor spirals (bottom). The red underlined products are self-sustained through the formation of the spiral patterns.
Spiral density $n_i$ from mesoscopic interaction dynamics. Numerically obtained spiral densities (a) from the rate equations Eq. (2) and (b) from the corresponding stochastic simulations. Simulations are carried out for the systems composed of $N_i = 10^6$, $10^3$, and $10^2$ spirals, respectively.

What is the dynamical mechanism underlying the transition from five- to three-species state as $M$ is increased? We find that the transition can be explained as due to a phenomenon at the mesoscopic level, namely, fluctuations in the spiral interaction dynamics due to the finite number of spirals $N_i$, which is characteristically different from the known mechanism responsible for the transition from three-species to uniform states. Figure 7(b) shows the spiral density $n_i$ from direct stochastic simulations of the mesoscopic spiral interaction system defined according to Fig. 3, with $N_i = 10^6$, $10^3$, and $10^2$ spirals. It is worth emphasizing that, the elements in simulation are the $N_i$ spirals that assumed to be well-mixed but not spatially distributed. We see that, at the mesoscopic level, as the number of spirals approaches infinity, the system exhibits essentially the same behavior predicted from the rate equations Eq. (2), i.e., there is a stable focus $n^*$ with five coexisting species. We articulate that finitesize effect is responsible for the difference between the predictions of the two types of models. In particular, for small $N_i$, the intrinsic fluctuations may drive the system into an absorbing state, e.g., $n = (0, 0, 0, 0, 1)$ with only one kind of spiral left, corresponding to coexistence of three species. In stochastic simulations of spiral interactions, the relative fluctuation in the spiral density $n_i$ is

$$f = \sigma_n / \langle n_i \rangle = \sqrt{5/N_i},$$

which decreases with $N_i$, as shown also in Fig. 7(b). Here, $\sigma_n$ and $\langle n_i \rangle$ are the standard deviation and the expected value of $n_i$, respectively. Spiral diversity is doomed to be lost when the two remaining spirals have the incursion relationship (the nearest-neighbor spirals in Fig. 3) by chance. Take the case in Fig. 7(b) (the right-hand side panel) as an example, the strong fluctuation leads $n_i$ to zero firstly, and as a consequence, $n_i$ and $n_2$ decrease to zero, with the spirals 1 and 5 left (containing merely four species). The five-species state thus is extinct. Moreover, due to the incursion relationship between spiral 1 and spiral 5, the state possessing four species is not stable and finally reaches three species state as the spiral 5 has.

For the spatially extended five-species competition system self-organized into three-species spiral patterns, the number $N_s$ of spirals can decrease with increasing mobility $M$. Specifically, the spiral wave length $\lambda$ increases with $M$ as ref. 8, with

$$\lambda = 2\pi a_2 \sqrt{a_1^{-1} M (1 - \lambda^2)}^{-1},$$

where

$$a_1 = \frac{\sigma \mu}{2(3\sigma + \mu)}, \quad a_2 = \frac{\sqrt{3} (18\sigma + 5\mu)}{48\sigma + 11\mu}.$$  

The transition from three- to one-species state can be attributed to $\lambda$’s approaching the linear size of the system around the critical mobility $M_c$. In addition, the area (number of individuals) occupied by each spiral scales with $\lambda$ as $\lambda^2$. For a system of a given number of individuals, the number of spirals can be estimated as

$$N_s \sim 1/\lambda^2 \sim 1/M.$$  

From the spiral interaction dynamics at the mesoscopic level, the shrinking population of spirals with $M$ enhances the intrinsic fluctuations. As a result, the probability of extinction of spirals, i.e., the extinction probability $P_{ext}$ of five species at the microscopic level, increases with $M$.

Spiral interaction dynamics at the mesoscopic level is thus equivalent to the microscopic species competition game dynamics. Thus, based on the mesoscopic level theory, we can also estimate the extinction probability $P_{ext}$ as a function of $M$ for the limiting case of $N \to \infty$ [see the solid curve in Fig. 2(b)]. First, the relationship between the number of spirals $N_i$ and $M$, as $N_i = N_i(M)$ can be estimated from Eq. (7), and then can be verified directly by the spatial patterns of species obtained from simulation of the five-species competition game. Secondly, as we know, the spiral extinction probability in the mesoscopic level, denoted by $P_{N_i}$, is dependent on the number of spirals $N_i$ and the evolutionary time of the system. Thus, the probability $P_{ext}$ is related to $M$. The case that satisfies

$$\lim_{M \to M_c} P_{N_i} = 1.0,$$  

can be obtained by setting proper evolutionary time in the spiral interaction dynamics. Then, the value of $P(M)$ for $M < M_c$, which equals to $P_{ext}$, can be estimated [the solid curve in Fig. 2(b)]. The $P_{ext}$ obtained directly from simulation of the microscopic level model of different systems sizes $N$ are also plotted (solid symbols) in Fig. 2(b). For a system of larger population size $N$, the intrinsic noise level is lower, and so the spiral pattern is formed with higher resolution, leading to smaller extinction probability for a given $M$. The $P_{ext}$ of the system with $N \to \infty$ approaches the value estimated by the mesoscopic level theory.

It is worth emphasizing that the group-interaction dynamics we investigate here concerns the effects of intrinsic random fluctuations at the mesoscopic level due to the finite number $N_i$ of spirals on spiral destruction. It is different from the intrinsic fluctuation from the finite $N$ of individuals at the microscopic level. Our analysis at the mesoscopic level of group-interaction dynamics is approximate as it is strictly valid only for the limiting case of $N \to \infty$.

1. Kerr, B., Riley, M. A., Feldman, M. W. & Bohannan, B. J. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. Nature 418, 171–174 (2002).
2. Czárán, T. L., Hoekstra, R. F. & Pagie, L. Chemical warfare between microbes promotes biodiversity. Proc. Natl. Acad. Sci. USA 99, 786–790 (2002).
3. Reichenbach, T., Mobilia, M. & Frey, E. Mobility promotes and jeopardizes biodiversity in rock-paper-scissors games. Nature 448, 1046–1049 (2007).
4. Szabo, G. & Fath, G. Evolutionary games on graphs. Phys. Rep. 446, 97–216 (2007).
5. May, R. M. Stability and Complexity in Model Ecosystems (Princeton University Press, Princeton, NJ, 1973).
6. May, R. M. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science 186, 645–647 (1974).
7. Reichenbach, T., Mobilia, M. & Frey, E. Noise and correlations in a spatial population model with cyclic competition. Phys. Rev. Lett. 99, 238105 (2007).
22. Szabo, G. & Szolnoki, A. Phase transitions induced by variation of invasion rates in rock-paper-scissors games. *Phys. Rev. E* **84**, 021912 (2011).

23. Wang, L.-L., Wang, X. & Wang, B.-H. Emergence of target waves in paced populations of cyclically competing species. *New J. Phys.* **11**, 103001 (2009).

24. Juul, J., Sneppen, K. & Mathiesen, J. Clonal selection prevents tragedy of the commons when neighbors compete in a rock-paper-scissors game. *Phys. Rev. E* **85**, 061924 (2012).

25. Juul, J., Sneppen, K. & Mathiesen, J. Labyrinthine clustering in a spatial rock-paper-scissors ecosystem. *Phys. Rev. E* **87**, 042702 (2013).

26. Kang, Y., Pan, Q., Wang, X. & He, M. A golden point rule in rock-paper-scissors-lizard-spock game. *Physica A* **392**, 2652–2659 (2013).

27. Dobrinevski, A., Alava, M., Reichenbach, T. & Frey, E. Mobility-dependent selection of competing strategy associations. *Phys. Rev. E* **89**, 012721 (2014).

28. Wang, W.-X., Lai, Y.-C. & Grebogi, C. Effect of epidemic spreading on species coexistence in spatial rock-paper-scissors games. *Phys. Rev. E* **81**, 046113 (2010).

29. Traulsen, A., Claussen, J. C. & Hauert, C. Coevolutionary dynamics: from finite to infinite populations. *Phys. Rev. Lett.* **95**, 238701 (2005).

30. Lamouroux, D., Eule, S., Geisel, T. & Nagler, J. Discriminating the effects of spatial extent and population size in cyclic competition among species. *Phys. Rev. E* **86**, 021911 (2012).

31. Ni, X., Wang, W.-X., Lai, Y.-C. & Grebogi, C. Cyclic competition of mobile species on continuous space: Pattern formation and coexistence. *Phys. Rev. E* **82**, 066211 (2010).

32. Venkat, S. & Pleimling, M. Mobility and asymmetry effects in one-dimensional rock-paper-scissors games. *Phys. Rev. E* **81**, 021917 (2010).

33. Claudia, C. & Carletti, T. Stochastic patterns in a 1d rock-paper-scissor model with mutation. arXiv preprint arXiv:1401.4302 (2014).

34. Avelino, P., Bazeia, D., Losano, L., Menezes, J. & Oliveira, B. Junctions and spiral patterns in generalized rock-paper-scissors models. *Phys. Rev. E* **86**, 036112 (2012).

35. Avelino, P., Bazeia, D., Losano, L. & Menezes, J. von Neumann’s and related scaling laws in rock-paper-scissors-type games. *Phys. Rev. E* **86**, 031119 (2012).

36. Szolnoki, A. et al. Cyclic dominance in evolutionary games: a review. *J. R. Soc. Interface* **11**, 20140735 (2014).

37. Frey, E. Evolutionary game theory: Theoretical concepts and applications to microbial communities. *Physica A* **389**, 4265–4298 (2010).