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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.

A s 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 interest[1–4]. Earlier models were based on population dynamical equations, which provided a macroscopic picture of species competition[5–7]. 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 interactions[8–10,13–35,37]. In this regard, a paradigm is the three-species cyclic game model (rock-paper-scissor, or RPS game)[3] 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 region[3]. 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 correlation[8], conservation laws[9,10], strength of competition[11], emergence and stability of spatial patterns[12–15], basins of coexistence state[16,17], long-range migration[18,19], local habitat suitability[20], intraspecific competition[21], role of inhomogeneous reaction rates[22–26], multi-strategy competition due to two-toxins bacterial interaction[27], simultaneous epidemic spreading[28], effects of spatial extent and population size[29–31], low dimensional behaviors[32,33], and extension to arbitrary number of species[34,35], 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 ecosystems[38–42] 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 microorganism 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)[43,44], 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[27,35,42,45–50]. 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[51], which is a direct (but nontrivial) extension of the classic three species cyclic-competition game originally proposed by May and Leonard[7], 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 (1) scissors cut paper, (2) paper covers rock, (3) rock crushes lizard, (4) lizard poisons Spock, (5) Spock smashes scissors, (6) scissors decapitate lizard, (7) lizard eats paper, (8) paper disproves Spock, (9) Spock vaporizes rock, and (10) rock crushes scissors. In addition to the cyclic competition rules, each species has a predator-prey relationship with each of its two next nearest neighboring species. The competition rules among five species are illustrated in Fig. 1.

We consider a two-dimensional square lattice of size $N = L \times L$ on which five species interact with one another according to the RPSLS game rules, under the zero flux boundary conditions. Initially, five species are distributed randomly in the spatial domain with equal probabilities. The three distinct actions in the dynamic process, namely prey, reproduction, and migration, occur at the probabilities μ, σ, and ε, respectively. According to Ref. 3, the typical area explored by one mobile individual per unit time is proportional to $M = \varepsilon/2N$, which we refer to as the *mobility*. Without loss of generality, we set $\mu = \sigma = 1$ and normalize the total probability of three actions into unity. The three actions are modeled as follows:
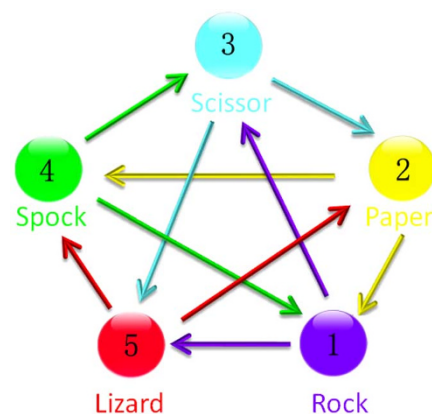

Figure 1 | Schematic illustration of five-species competition. The game is known as Rock-Paper-Scissors-Lizard-Spock (RPSLS), denoted by 1-2-3-4-5 in our paper. Arrows point from predator to prey. The game rules are: scissors cut paper, paper covers rock, rock crushes lizard, Lizard poisons Spock, Spock smashes scissors, Scissors decapitate lizard, Lizard eats paper, Paper disproves Spock, Spock vaporizes rock, and Rock crushes scissors.

$$15 \xrightarrow{\mu} 1\oslash, \ 21 \xrightarrow{\mu} 2\oslash, \ 32 \xrightarrow{\mu} 3\oslash, \ 43 \xrightarrow{\mu} 4\oslash, \ 54 \xrightarrow{\mu} 5\oslash;$$

$$13 \xrightarrow{\mu} 1\oslash, \ 24 \xrightarrow{\mu} 2\oslash, \ 35 \xrightarrow{\mu} 3\oslash, \ 41 \xrightarrow{\mu} 4\oslash, \ 52 \xrightarrow{\mu} 5\oslash;$$

$$1\oslash \xrightarrow{\sigma} 11, \ 2\oslash \xrightarrow{\sigma} 22, \ 3\oslash \xrightarrow{\sigma} 33, \ 4\oslash \xrightarrow{\sigma} 44, \ 5\oslash \xrightarrow{\sigma} 55;$$

$$1\odot \xrightarrow{\varepsilon} \odot 1, \ 2\odot \xrightarrow{\varepsilon} \odot 2, \ 3\odot \xrightarrow{\varepsilon} \odot 3, \ 4\odot \xrightarrow{\varepsilon} \odot 4, \ 5\odot \xrightarrow{\varepsilon} \odot 5;$$

$$(1)$$

where 1, 2, 3, 4, and 5 denote individuals in the five species, respectively, $\oslash$ represents empty sites, and $\odot$ represents any species individual or empty site.

In the dynamical process, at each time step, an individual and one of its neighbor are chosen randomly for possible interaction. Only one action shown in (1) occurs according to the interaction rule and the corresponding probability. Actual realization of the interaction also depends on the species of the two selected individuals. Reproduction can take place only for the case where one site is empty, but migration is always possible. One *generation* is defined to be the period required for N pairwise interactions, during which each individual is selected for interaction once on average.

Species coexistence and mesoscopic interactions. Figure 2(a) 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[3,8], the wavelength λ of the spiral wave tends to increase with the mobility M (in fact proportional to $\sqrt{M}$).

Figure 2(b) shows two kinds of extinction probability P_{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_{c5}), 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_{c3}, two more species become extinct, leading to a uniform state of one species in the system. This signifies
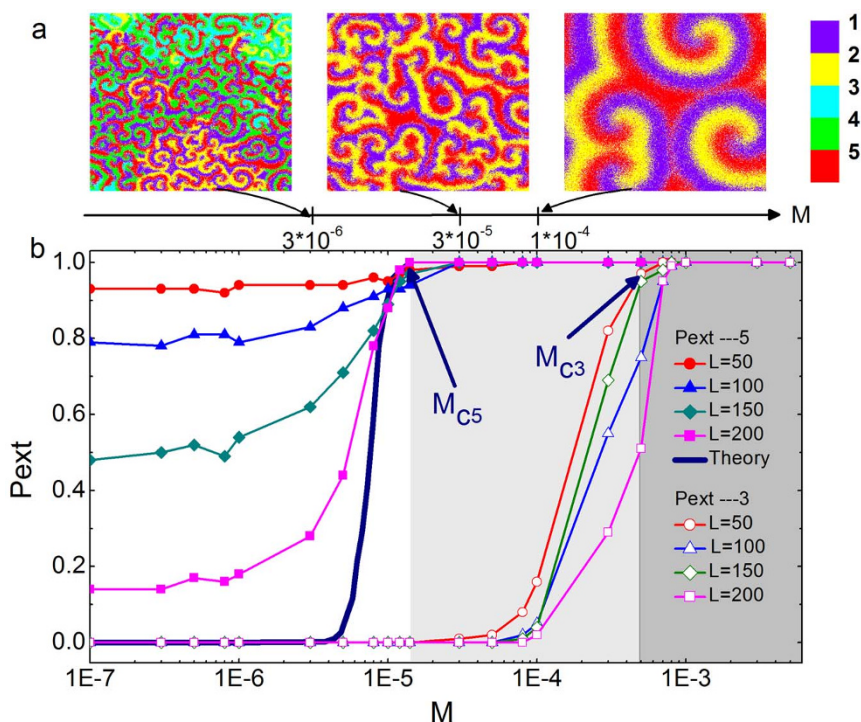
Figure 2 | Effect of mobility on dynamics. (a) Typical snapshots of spatial patterns of five species competition game for different values of the mobility M. Each color represents one of the five species and white denotes empty sites. The system size is $N = 1000 \times 1000$. (b) Extinction probabilities P_{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), 100×100 (blue triangles), 150×150 (green diamonds), and 200×200 (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 event of three-species extinction. In Fig. 2(b), the values of P_{ext} for five- and three-species extinction are obtained from 1000 random realizations for system size $N = 50 \times 50$, 100×100, 150×150, and 200×200. For each statistical realization, the length of the simulation, or the number of generations, is chosen to be $T = N$. We see 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: $M_{c5} \approx 1.5 \times 10^{-5}$, 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[42,50,52]. 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 "*incursion*," 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
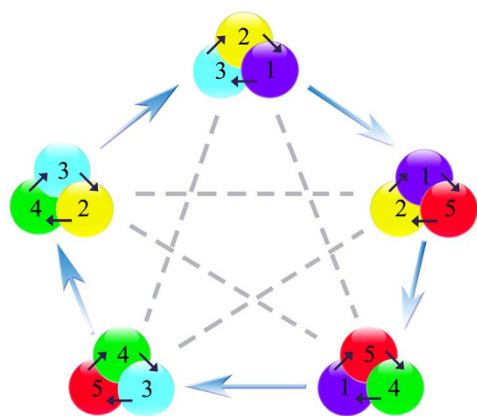
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Figure 3 | Spiral interaction graph (SIG). The SIG lists the interaction rules among the five different kinds of spirals (or groups). The nearest neighbor interaction (blue thick arrows) specifies "incursion" from one to another, and the next-nearest 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.

by others and are destroyed, some new spirals are generated. The detailed process shown in Fig. 5 verifies the spiral interaction rules as specified by SIG in Fig. 3, where incursion and reaction are represented by blue thick arrows and gray dashed lines, respectively. A comparison between the first two snapshots ($t = 14000$ and 20000) indicates incursions from 345 to 234, and from 512 to 451, respectively. As a result, the area of 345 is enlarged but the spiral 451 disappears. 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.

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 the nearest neighbor spiral groups in SIG with the interaction being exclusively the incursion type that leads to destruction of the vulnerable one. Compared with the microscopic level interaction model in Fig. 1, our mesoscopic interaction picture at the group level in Fig. 3 provides a framework to investigate coexistence in ecosystems with more than three species.

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[7]. At the opposite extreme is the relatively recent, microscopic approach based on evolutionary game dynamics, which treats species interactions at the individual level[3]. 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.
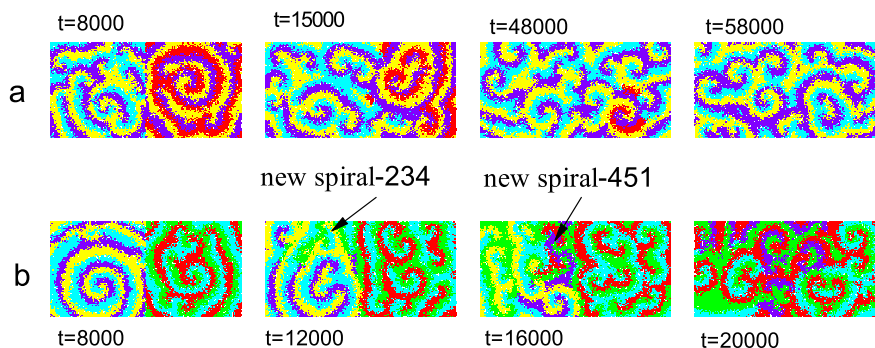

Figure 4 | Pattern evolution due to spiral interactions. (a) Nearest neighbor interaction in SIG (Fig. 3), e.g., the interaction between spirals 123 and 234 with incursion ($234 \rightarrow 123$). (b) Next-nearest neighbor interaction, e.g., between spirals 123 and 345, that generates two products (e.g., 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.
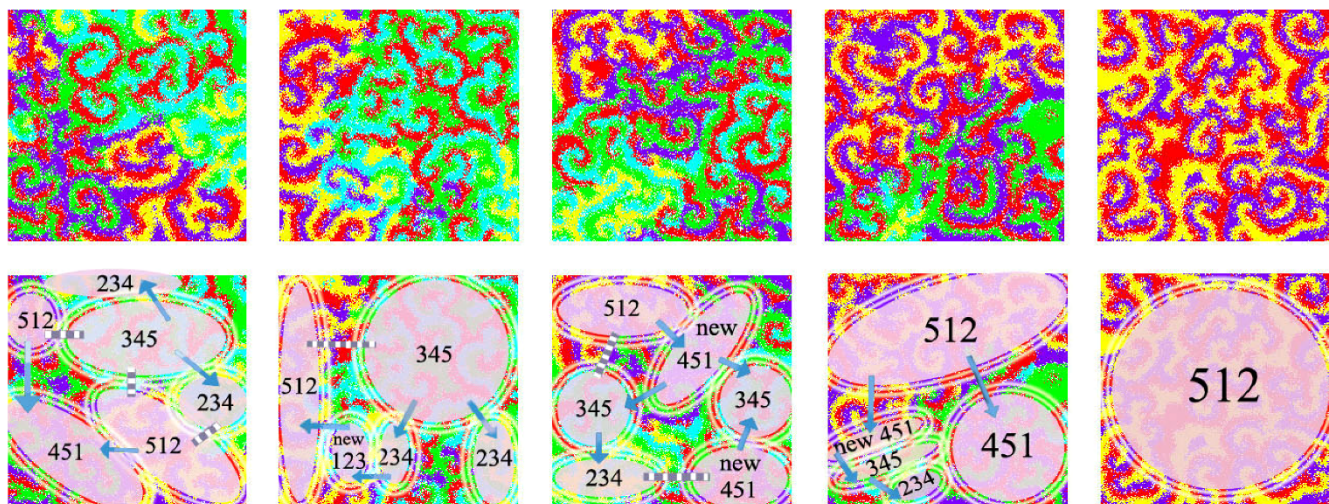
Figure 5 | Pattern evolution of game dynamics. The snapshots are displayed from left to right in chronological order. Different spirals are labeled, where the numbers represent the composition species contained in the spirals and the term "new" means a new spiral being generated from the reaction between two kinds of spirals. The blue thick arrows indicate two spirals' incursion relationship and the gray dashed lines denote the reaction relation between them. The system size is $N = 500 \times 500$.

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 $\xi = 1/7$, while the relative rate of the reaction process for each of the two products to be $\zeta = 1/8$.

For a spatially extended ecosystem self-organized into three-species spiral patterns, the number N_i of certain kind of spirals ($i = 1, 2, \ldots, 5$) changes with time due to the interactions among them. However, the total number of spirals, $N_s = \sum_i N_i$, is approximately invariant. For a system with a large population of spirals (e.g., at the thermodynamic limit $N_s \to \infty$), 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 $n_i = N_i/N_s$ of the five kinds of spirals:

$$\partial_t n_1 = \xi n_1(n_5 - n_2) + \zeta[n_5(n_2 + n_3) - n_1(n_3 + n_4)],$$
$$\partial_t n_2 = \xi n_2(n_1 - n_3) + \zeta[n_1(n_3 + n_4) - n_2(n_4 + n_5)],$$
$$\partial_t n_3 = \xi n_3(n_2 - n_4) + \zeta[n_2(n_4 + n_5) - n_3(n_5 + n_1)], \quad (2)$$
$$\partial_t n_4 = \xi n_4(n_3 - n_5) + \zeta[n_3(n_5 + n_1) - n_4(n_1 + n_2)],$$
$$\partial_t n_5 = \xi n_5(n_4 - n_1) + \zeta[n_4(n_1 + n_2) - n_5(n_2 + n_3)],$$

where, in each equation, the first item with rate ξ represents the incursion processes and the second item with rate ζ represents the reaction processes. The rate equations

are symmetric and the solution denoted by $\mathbf{n} = (n_1, n_2, n_3, n_4, n_5)$ is not sensitive to the values of ξ and ζ. Equation (2) possesses one reactive fixed point $\mathbf{n}^* = \frac{1}{5}(1,1,1,1,1)$ associated with the coexistence of all five spirals, and 6 absorbing fixed points with one kind of spiral persisting, e.g., $\mathbf{n} = (1, 0, 0, 0, 0)$, $(0, 1, 0, 0, 0)$, …, $(0, 0, 0, 0, 1)$, 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 $N_S \to \infty$.

The dynamics in the vicinity of the reactive fixed point $\mathbf{n}^*$ can be studied by linearizing Eq. (2) and then determining the eigenvalues of the corresponding Jacobian matrix. Let $\delta\mathbf{n} = \mathbf{n} - \mathbf{n}^*$ 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 δn_5, leading to the reduced vector $\delta\mathbf{x} = (\delta n_1, \delta n_2, \delta n_3, \delta n_4)$. The linearized Eq. (2) can then be written in the following form:

$$\dot{\delta\mathbf{x}} = \mathcal{A} \cdot \delta\mathbf{x}. \quad (3)$$

The reactive fixed point $\mathbf{n}^*$ turns out to be a *stable focus* as the complex eigenvalues of $\mathcal{A}$ 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 $\mathbf{n}^*$ (*Sidemark*: The envelopes of n_i converge exponentially to 1/5). The behaviors of the system in the two-dimensional subspace defined as $n_1 \sim n_2$ and $n_1 \sim n_5$ are also shown in Fig. 7(a). We see that, the rate equations at the level of spiral interaction predict the existence of $\mathbf{n}^*$, 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 $\mathbf{n}^*$ from rate equations Eq. (2).
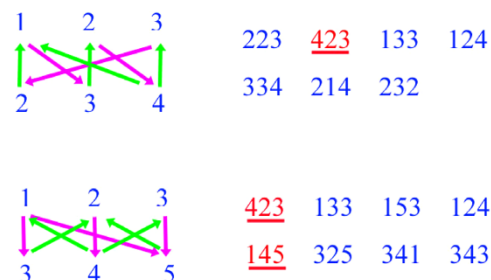

Figure 6 | Illustrations of elementary spiral interactions. Possible elementary interactions and products between a pair of nearest neighbor spirals (upper) and next-nearest neighbor spirals (bottom). The red underlined products are self-sustained through the formation of the spiral patterns.
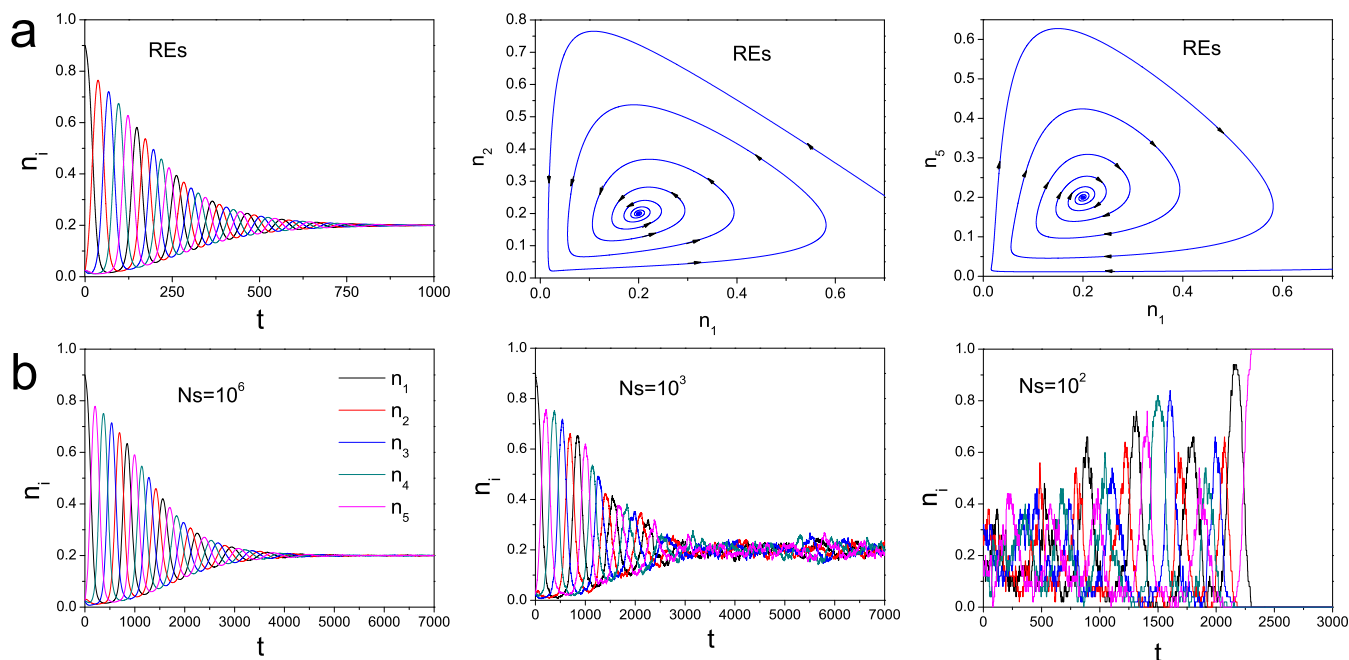
Figure 7 | Spiral density n_i from mesoscopic interaction dynamics. Numerically obtained spiral densities (a) from the rate equations Eq. (2) and (b) from the corresponding stochastic simulations. Simulations are carried out for the systems composed of $N_s = 10^6$, 10^3, and 10^2 spirals, respectively.

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_s, which is characteristically different from the known mechanism responsible for the transition from three-species to uniform states[3]. 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 $N_s = 10^6$, 10^3, and 10^2 spirals. It is worth emphasizing that, the elements in simulation are the N_s 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 $\mathbf{n}^*$ with five coexisting *spirals* (equivalently 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_s, the intrinsic fluctuations may drive the system into an absorbing state, e.g., $\mathbf{n} = (0, 0, 0, 0, 1)$ 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

$$f \equiv \sigma_{n_i}\big/\langle n_i\rangle = \sqrt{5/N_s}, \tag{4}$$

which decreases with N_s, as shown also in Fig. 7(b). Here, σ_{n_i} 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_4 to zero firstly, and as a consequence, n_3 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 competition spiral patterns, the number N_s of spirals can decrease with increasing mobility M. Specifically, the spiral wave length λ increases with M as ref. 8,

$$\lambda = 2\pi a_2 \sqrt{a_1^{-1}M}\left(1 - \sqrt{1 + a_2^2}\right)^{-1}, \tag{5}$$

with

$$a_1 \equiv \frac{\sigma\mu}{2(3\sigma+\mu)}, \quad a_2 \equiv \frac{\sqrt{3}(18\sigma+5\mu)}{48\sigma+11\mu}. \tag{6}$$

The transition from three- to one-species state can be attributed to λ's approaching the linear size of the system around the critical mobility M_{c3}. In addition, the area (number of individuals) occupied by each spiral scales with λ as λ^2. For a system of a given number of individuals, the number of spirals can be estimated as

$$N_s \sim 1/\lambda^2 \sim 1/M. \tag{7}$$

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)]. Firstly, the relationship between the number of spirals N_s and M, as $N_s = N_s(M)$ 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 $P_s(N_s)$ is dependent on the number of spirals N_s and the evolutionary time of the system. Thus, the probability P_s is related to M. The case that satisfies

$$\lim_{M \to M_{c5}} P_s(N_s(M)) = 1.0, \tag{8}$$

can be obtained by setting proper evolutionary time in the spiral interaction dynamics. Then, the value of $P_s(M)$ for $M < M_{c5}$, 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_s 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 $N \to \infty$.

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Author contributions

Devised the research project: Y.C.L. Performed numerical simulations: H.C., N.Y. and Z.G.H. Analyzed the results: Z.G.H., N.Y., H.C. and Y.C.L. Participated in dicussion: J.P. and Y.D. Wrote the paper: Y.C.L., Z.G.H. and H.C.

Additional information