

RELATIVISTIC INTERPLAY BETWEEN ADAPTIVE MOVEMENT AND MOBILITY ON BIODIVERSITY IN THE ROCK-PAPER-SCISSORS GAME

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ABSTRACT. Adaptive behaviors are one of ubiquitous features in evolutionary dynamics of populations, and certain adaptive behaviors can be witnessed by individuals' movements which are generally affected by local environments. In this paper, by revisiting the previous work, we investigate the sensitivity of species coexistence in the system of cyclic competition where species movement can be affected by local environments. By measuring the extinction probability through Monte-Carlo simulations, we find the relativistic effect of weights of local fitness and exchange rate for adaptive movement on species biodiversity which promotes species coexistence as the relativistic effect is intensified. In addition, by means of basins of initial conditions, we also found that adaptive movement can also affect species biodiversity with respect to the choice of initial conditions. The strong adaptive movement can eventually lead the coexistence as a globally stable state in the spatially extended system regardless of mobility.

1. INTRODUCTION

Evolutionary game dynamics has been employed as useful ways to describe and explain complex behaviors in social and ecological sciences [1, 2, 3, 4, 5, 6, 7]. Especially for nonhierarchically competing structured populations, rock-paper-scissors game, one of famous children's games, is a standard tool to describe dynamical systems and explain evolution of populations [8, 9]. While fields of the metaphor of rock-paper-scissors game have been traditionally implemented to describe interaction among different species or groups in macroscopic levels which are generally investigated by replicator equations, after the importance of an individual's mobility has been reported [10, 11], contemporary evolutionary dynamics of cyclic competition have been explored by both macroscopic and microscopic approaches since describing local interactions between individuals can be well described in microscopic levels.

In ecological frameworks, one of important issues in systems of cyclic competition is how to maintain biodiversity. For systems of cyclic competition, since interspecific competition

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between different species occurs following the cyclic pathway, the broken of coexistence can be lead easily due to the extinction of any one species. In this regard, many works on this field have been performed mathematically to take into account mechanisms to promote coexistence in both microscopic and macroscopic levels such as mobility [10, 11, 12, 13, 14, 15, 16], asymmetric interplay of interactions [17, 18], mutation [19, 20, 21, 22], adaptive behavior based on local fitness [23, 24], sensitiveness depending on initial densities for biodiversity [25, 26, 27], and intraspecific competition [28, 29, 30, 31].

In the perspective of population behaviors, it is a common phenomenon for individuals to behave adaptively to their surroundings [23, 32, 33, 34], and such adaptive behavior is usually manifested by individual movements [24, 35]. In particular for rock-paper-scissors game, an exchange motion between individuals based on local fitness has been introduced [24]. In the work, it has been reported that considering local environments which is defined by local habitat suitability can be a beneficial role to promote species coexistence regardless of mobility. By utilizing the extinction probability, it has been addressed that such persistent coexistence can occur for certain rates of sensitivity parameter α where the parameter β for the weight on prey species is fixed, e.g., $\beta = 2.0$. In addition, it has been uncovered that, even if the extinction occurs finally, coexistence in rock-paper-scissors game can be maintained at larger mobility by local payoff based mutation [23]. In recent studies on evolutionary dynamics of cyclic competition, however, it has been addressed that considering weights on payoff and species abundance at the initial stage which is defined by initial densities of population are highlighted as key roles to affect biodiversity [18, 23, 25, 27]. While the beneficial role of adaptive movement on biodiversity has been reported, the two issues that relativistic interplay of sensitivity weights for adaptive movement and initial densities on biodiversity are still ambiguous and thus should be elucidated.

In this paper, based on the previous result in Ref. [24], we investigate the relativistic interplay of adaptive movement and mobility on biodiversity in a broader aspect by focusing the relativity of sensitivity parameters and the choice of initial conditions by employing the same model and computational conditions used in [24] to make an unbiased comparison. Briefly, the main findings are as follows. By means of adaptive movements, species coexistence can be promoted as the relative strength of sensitivity parameters becomes strong. In this case, strong adaptive movement with high relative strength of sensitivity parameter can lead robust coexistence at high mobility regime. In addition, we also found that adaptive movement can affect on biodiversity which will be sensitive to initial conditions. As an individual's initial mobility increases, while weak adaptive movement exhibit similar basin structures of initial conditions to classic rock-paper-scissors game in the absence of adaptive movement [10, 25], strong adaptive movement leads the robust coexistence regardless of the choice of initial conditions and mobility, and the coexistence can eventually become a globally stable state as M increases through the critical mobility, which is validated by exploiting the basin area as a function M .

This paper is organized as follows. In Section 2, we introduce rock-paper-scissors game with adaptive movement which has been introduced in Ref. [24]. In Section 3, we address the main results. By carrying out Monte-Carlo simulations, we calculate the extinction probability in both relative parameters for local fitness and exchange rate to investigate the robustness of

biodiversity, in particular coexistence of species. In addition, in light of the definition of local fitness, we additionally investigate how same species can affect such local fitness for adaptive movement. Conclusion and further discussions are listed in Sec. 4.

2. MODEL

For nonhierarchically competing populations, one of evolutionary game models, rock-paper-scissors game, has been employed as a useful tool to describe dynamics of the system. In the May-Leonard limit [8], the rock-paper-scissors game among three species (referred to as A , B , and C) on spatially extended systems is generally defined by the following set of rules [10, 11, 21, 23, 25, 28, 29, 30, 31]:

$$AB \xrightarrow{\sigma} A\emptyset, \quad BC \xrightarrow{\sigma} B\emptyset, \quad CA \xrightarrow{\sigma} C\emptyset, \quad (2.1)$$

$$A\emptyset \xrightarrow{\mu} AA, \quad B\emptyset \xrightarrow{\mu} BB, \quad C\emptyset \xrightarrow{\mu} CC, \quad (2.2)$$

$$A\Box \xrightarrow{\varepsilon} \Box A, \quad B\Box \xrightarrow{\varepsilon} \Box B, \quad C\Box \xrightarrow{\varepsilon} \Box C, \quad (2.3)$$

where \emptyset indicates an empty site which will be produced by (2.1), and \Box is one of any species or an empty site. Relation (2.1) presents interspecific competition (or called as predation) which occurs with a rate σ . Relation (2.2) describes the reproduction process with a rate μ , in which can be allowed if empty sites in neighbors are available, and the exchange motion between two selected species (or sites) are defined by relation (2.3), which will occur at a rate $\varepsilon = 2MN$ based on the theory of random walks with an individual's mobility M and a system size N [36].

In the previous work [24], species adaptive behavior, especially on exchange motion, has been considered and its effect on species coexistence was uncovered. To be concrete, the adaptive movement which is defined by local fitness (LoF_i) with respect to the number of predator, prey and same species in a neighborhood of focal species i , where the local fitness of species i is of a form [23, 24]:

$$LoF_i = \frac{-n_{\text{pred}}^i + \beta n_{\text{prey}}^i + w(n_{\text{same}}^i)n_{\text{same}}^i}{4},$$

where n_{pred} and n_{prey} are the numbers of predators and preys of species i , respectively, and β is a relative weight of the prey in neighbors of species i . Here, the coefficient $w(n_{\text{same}}^i)$ is a weight of same species against to species i , and we here use the linear function of n_{same}^i : $w(n_{\text{same}}^i) = (5 - 2n_{\text{same}}^i)/3$ which is employed in Ref. [24].

To apply LoF_i on the exchange motion (2.3), we first focus on local interaction between two neighboring sites. Traditionally, as defined by (2.1)-(2.3), species interactions in rock-paper-scissors games are generally defined by pairwise interactions, i.e., one of randomly selected relations in (2.1)-(2.3) may occur between two neighboring sites if the selected nodes satisfy the reaction. For instance, if species A and B are randomly selected neighboring sites for interactions, then predation and exchange may be allowed. In this case, however, there is no event if the reproduction process is randomly chosen. Based on such rules of pairwise interactions, if we want to apply LoF_i on (2.3), we should consider LoF_i in each species in a pair, i.e., LoF_i and LoF_j for species i and j in a pair, respectively, which will be newly

defined by a pairwise LoF (referred to as $pLoF$). Among various ways to consider $pLoF$, as in Ref. [24], we employ the average of two values LoF_i and LoF_j : $pLoF = (LoF_i + LoF_j)/2$, and the “new local exchange rate” will be given by

$$\varepsilon' = \varepsilon \cdot e^{-\alpha \cdot pLoF},$$

to make an unbiased comparison. The parameter α indicates the sensitivity weight of exchange rate with respect to $pLoF$, and $\varepsilon (= 2MN)$ is the initial exchange rate defined by the initial mobility M . Thus, by asynchronously updated processes, the original rule of exchange (2.3) will occur with a new rate ε' depending on species in a pair.

On spatially extended systems, the evolutionary dynamics, in particular three reactions (2.1)-(2.3), will occur with normalized probabilities based on asynchronous update of exchange with $pLoF$: $\sigma/(\mu + \sigma + \varepsilon')$, $\mu/(\mu + \sigma + \varepsilon')$ and $\varepsilon'/(\mu + \sigma + \varepsilon')$, respectively. An interaction can actually occur only when the states of both sites meet the requirement for the particular interaction. To make an unbiased comparison with previous works [10, 24, 23], we assume $\sigma = \mu = 1$. On a square lattice of size $N = L \times L$ with periodic boundaries, since it is obvious that a small spatial scale can sensitively affect to species biodiversity and can lead extinction even at low mobility regimes, considering large scales are generally considered to avoid the negative effect of size on biodiversity. In this paper, however, we consider a $N = 40 \times 40$ sized square lattice to explore that how such adaptive movement can affect on biodiversity even if small spatial scales are exploited. In all our simulations, we use the total time step $T = 2N$ to obtain more robust features for biodiversity.

3. RESULTS

On spatially extended systems of cyclic competition among mobile population, species biodiversity are usually affected by (a) interplay of local behavior between species [24, 29, 18] and (b) initial densities of species [25, 27]. Even if species biodiversity under adaptive movement has been explored for specific parameter conditions in the previous work [24], such effects on biodiversity in the spatial rock-paper-scissors game are still veiled. In this regard, we investigate dynamics of the system within two frameworks: (a) sensitivity of biodiversity by interplay between sensitivity parameters for $pLoF$ and ε' and (b) the effect of initial densities of three species for biodiversity with respect to an individual’s mobility.

3.1. Sensitivity of biodiversity under adaptive movement. In the previous work [24], we have found that the adaptive movement based rock-paper-scissors game can yield the persistent coexistence by varying the initial mobility for specific parameter conditions, e.g., $\alpha \geq 3$ for fixed $\beta = 2$. In that case, under the specific parameter condition, the species coexistence is persistent regardless of mobility M , i.e., the coexistence occurs even if M is considered at high mobility regime such as $M > M_c = (4.5 \pm 0.5) \times 10^{-4}$ which is identified in Ref. [10]. In general, it has been a well-known finding that species biodiversity is strongly affected by an individual’s mobility M and coexistence is hampered as M exceeds M_c . On the other hand, in our previous work, we found that, under the assumption that species can show adaptive behavior, coexistence of mobile population in rock-paper-scissors games can be promoted even

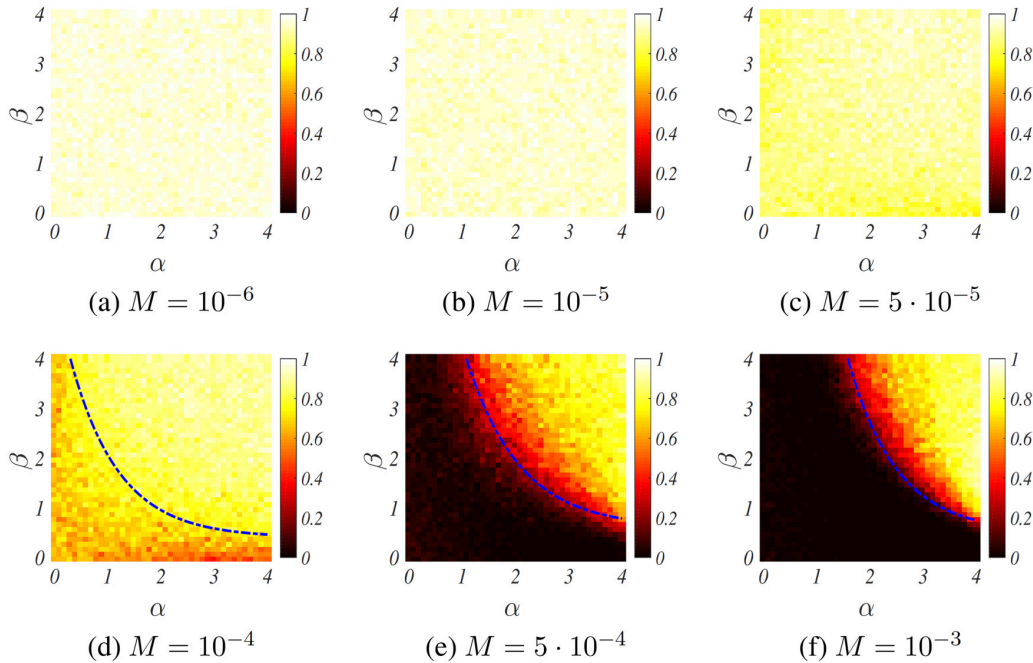


FIGURE 1. Dependence of coexistence P_{coex} in the spatial rock-paper-scissors game on both α and β for adaptive movement with different initial mobility M . (a-c) For low mobility values, the system exhibits coexistence which is robust. (d-f) While extinction can robustly occur for most parameter regimes as M increases, species coexistence can be promoted by the relativity between α and β increases even if $M > M_c$. Blue lines in panels (d-f) indicate thresholds of (α, β) for promoting coexistence which are approximately detected by $\beta \sim K \cdot e^{-\alpha}$, where K can be numerically predicted.

if the mobility exceeds the threshold. Nevertheless, even if the persistent coexistence was revealed out, it is still ambiguous that how such persistent coexistence can appear robustly depending on the interplay of sensitivity parameters α and β in a broader aspect. In this regard, we first investigate the sensitivity of biodiversity, in particular the robustness of coexistence, depending on both α and β . One of common ways to obtain the robustness of the survival state, in particular coexistence, is to measure the coexistence probability P_{coex} , which is calculated by the number of coexistence from 100 independent initial realizations:

$$P_{coex} = \frac{\text{the total number of the occurrence of coexistence after } T}{100 \text{ independent realizations}}.$$

Figure 1 presents the dependence of coexistence in the spatial rock-paper-scissors game with adaptive movement for different initial mobility values. As presented in Figs. 1(a)-1(b), the system can exhibit robust coexistence with $P_{coex} \approx 1$ at low mobility regimes, and such

phenomena can be obtained regardless of choices of α and β , which means the interplay of sensitivity parameters for adaptive movement may have no effect on species biodiversity.

However, as M increases, the effect of adaptive movement on coexistence can be witnessed. To be concrete, for $M = 10^{-4}$ [see Fig. 1(d)], even if the landscape of P_{coex} exhibits a high probability overall, i.e., species coexistence is quite robust, the coexistence probability is gradually lowered in some parameter ranges which indicates the frequent occurrence of extinction. In particular, when β is low such as $\beta < 1$, the strong α can lead the decrease of P_{coex} rather than cases for $\beta > 1$. As shown in Figs. 1(e) and 1(f), similar features are obtained for higher mobility regimes such as $M = 5 \cdot 10^{-4}$ and 10^{-3} .

For adaptive movement with respect to LoF_i , one of control parameters is β . Against to the weight for predator species, the weight β for prey species may play the key role to realize adaptive movement. Based on $\beta = 1$ which may indicate the same weights for predator and prey, a focal individual may be willing to stay or move away from the position if the parameter β is considered either $\beta > 1$ or $\beta < 1$, respectively. In addition, from Figs. 1(d-f), we found that the second sensitivity parameter α also needs to be relatively strong enough even if β is assumed by $\beta > 1$. In these cases, we found a common feature that, at high mobility regime satisfying $M > M_c$, coexistence can be promoted by relativistic effect between α and β . To be concrete, coexistence can be robust if β is relatively stronger than α satisfying the region over the thresholds [blue lines in Figs. 1(d-f)], where the relationship between two parameters can be approximately detected by

$$\beta \sim K \cdot e^{-\alpha}.$$

Here, the coefficient K differs to M which increases with respect to M .

From the investigation of P_{coex} , we found the followings: (a) species coexistence is robust regardless of adaptive movement for low mobility regimes; and (b) the effect of adaptive movement can appear clearly at high mobility regimes according to the relativistic interplay between two sensitivity parameters.

3.2. Basin of initial conditions for biodiversity under adaptive movement. In classic spatial dynamics of rock-paper-scissors games, it has been generally considered that the initial densities of three species are equally given [10, 17, 18, 19, 24, 26, 29, 31], and we also used the same initial condition, i.e., $\rho_A(0) = \rho_B(0) = \rho_C(0) = 1/3$ to carry out numerical calculations for P_{coex} . However, it has been reported that the initial density of species is also one of key factors for biodiversity in spatial cyclic competition systems [25, 26, 27]. As a matter of fact, in the perspective of ecological sciences, species abundance is an important issue to predict evolution and biodiversity of ecosystems. While we have already explored that, at high mobility regimes, species coexistence can be promoted by adaptive movement under the relativistic interplay between two parameters, it is still veiled the effect of initial densities of three species on biodiversity when adaptive movement is working. As investigated in Fig. 1, since it is obvious that biodiversity is sensitively affected by both M and a combination of (α, β) , we explore the role of an initial density by means of basins of attractions: extinction and coexistence, by varying M . Here, to compare and investigate the effect of sensitivity parameters on forming basin structures at the fixed M , we consider two parameter sets: $(\alpha, \beta) = (1, 1)$

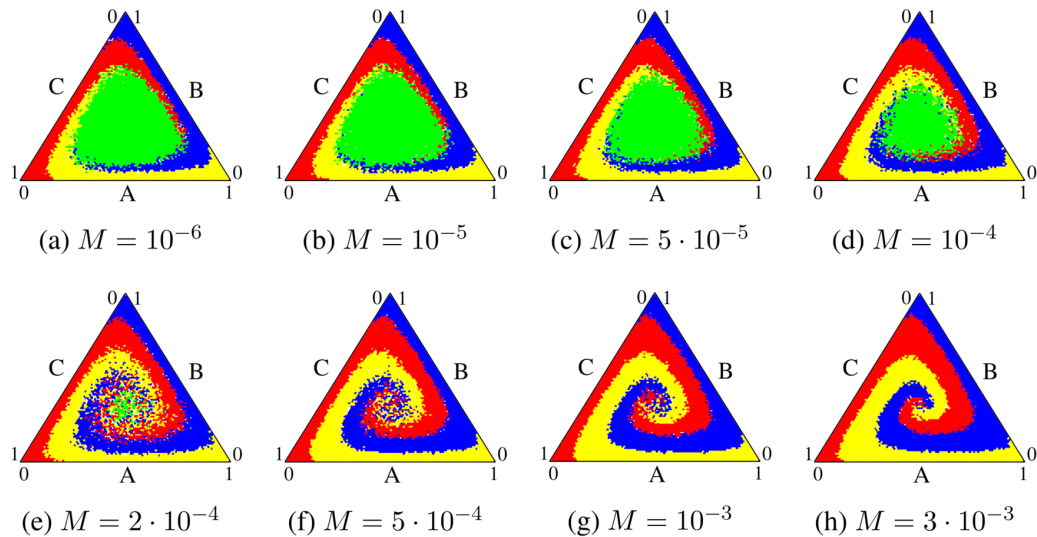


FIGURE 2. Basin of attractions for coexistence and extinction of the rock-paper-scissors game with adaptive movement for $(\alpha, \beta) = (1, 1)$ with different M . Three colors red, blue, and yellow indicate basins of initial densities for extinction which indicate different survival species A , B , and C , respectively, and the green area corresponds to the basin for coexistence. (a-e) For $M < M_c$, the phase space are divided into four distinct basins: three extinctions and one coexistence. While the overall patterns of extinction basins are similarly formed, the area of the coexistence basin is decreasing as M increases. For $M = 2 \cdot 10^{-4}$, the coexistence basin emerges near the center of Δ^2 and all basins are fuzzy which mean the final survival state is very sensitive to the choice of initial conditions near the center point. (f-h) For $M > M_c$, the basin for coexistence is disappeared, and, as M increases, the spirally entangled three basins of extinction are getting robust.

and $(4, 4)$ in each given M , which yield different states either extinction or coexistence at high mobility regimes.

Figures 2(a)-2(h) present basin structures initial densities for different attractions in the phase space 2-simplex (Δ^2) for different values of mobility M with $(\alpha, \beta) = (1, 1)$, where the sum of initial densities of three species is given by 1. For $M < M_c$, the phase space of initial densities are occupied by one of states. To be concrete, a uniform state associated to extinction is divided into three basins (colored by red, blue, and yellow) where each basin consists of initial conditions to lead the survival of only one species A , B , or C . In addition, we have another basin, a green colored basin, where all species coexist. Even if two different basins of attractions coexist for $M < M_c$, the coexistence basin is shrinking as M increases to M_c . Near the center point of Δ^2 , the basin structure is fuzzy and all basins are appeared which

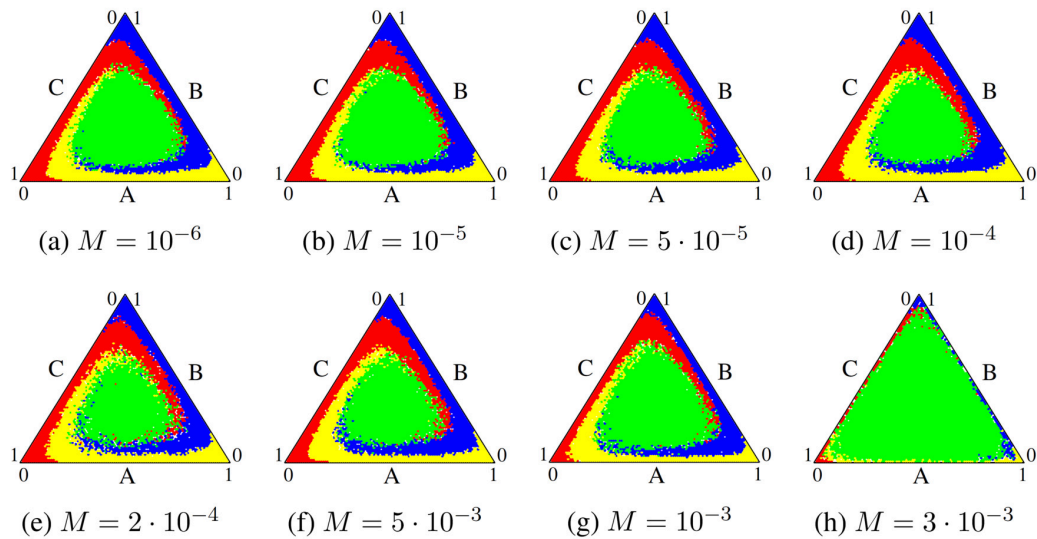


FIGURE 3. Basin of attractions for coexistence and extinction of the rock-paper-scissors game with adaptive movement for $(\alpha, \beta) = (4, 4)$ for different initial individual's mobility M . (a-d) For low mobility values, the overall feature of basins are similarly obtained to Figs. 2(a-d). (e) For $M = 2 \cdot 10^{-4}$ which is close to M_c , the coexistence basin still exists and its area is larger than that of $(\alpha, \beta) = (1, 1)$ as shown in Fig. 2(e). (f-h) For $M > M_c$, on the contrary to the case of $(\alpha, \beta) = (1, 1)$, the coexistence basin is not disappeared. In addition, as M increases, the coexistence basin enlarges and may fully occupy the phase space.

mean the final survival state is very sensitive to the choice of initial conditions. The coexistence basin is eventually disappeared as M exceeds to M_c in the high mobility regime ($M > M_c$) as shown in Figs. 2(f-h). In this mobility regime, the phase space Δ^2 only presents three basins of extinction which are spirally entangled at the center of Δ^2 and become robust. In this case, as shown in Fig. 2, in addition to along the boundary between two different basins of extinction, the final extinction state is still sensitive to small variations in initial densities of three species near the center point, and one of the uniform state will be depicted in the spatial dynamics.

While the parameter set $(\alpha, \beta) = (1, 1)$ with the equally given initial condition can yield two distinct survival states depending on M : either coexistence for $M < M_c$ or extinction for $M > M_c$, the different choice of (α, β) such as $(\alpha, \beta) = (4, 4)$ can yield different phases of basin structures depending on M which are presented in Figs. 3(a)-3(h).

From the basin structure of $(\alpha, \beta) = (4, 4)$ as illustrated in Fig. 3, we found the followings. While the overall feature of basins structures are similarly obtained to those of $(\alpha, \beta) = (1, 1)$ for low mobility values $M < M_c$, the structure, in particular the coexistence basin, exhibits in a different way. To be concrete, when the rate is small such as $(\alpha, \beta) = (1, 1)$, the coexistence

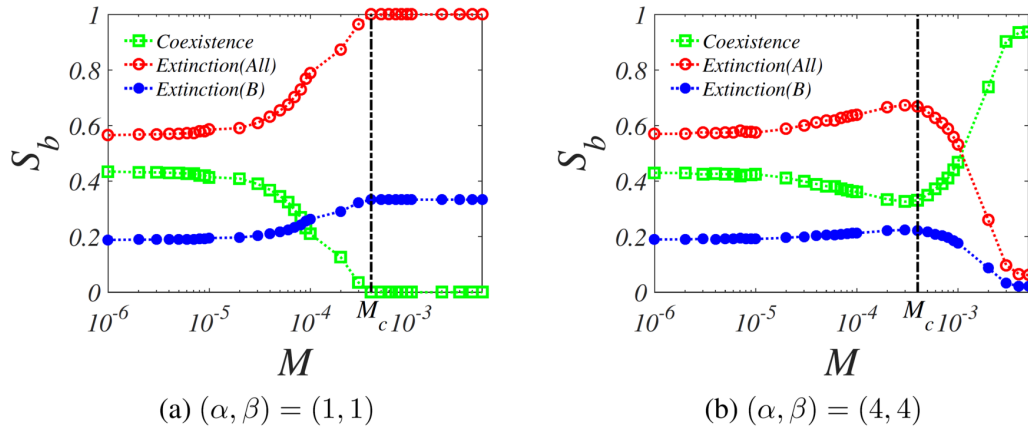


FIGURE 4. Changes of areas S_b of the coexistence (green squared line) and three extinction basins (red circled line) as functions M for two different parameter conditions. (a) The coexistence basin is maintained at low mobility values and decreasing as M approaches to M_c . As M exceeds M_c , S_b converges to 0 and thus only one of extinction states appears at the end of the evolution. Even if adaptive movement is influenced, weak adaptive movement has no effect on species coexistence and the mobility plays a key role to control biodiversity. (b) On the contrary to the weak adaptive movement, strong adaptive movement can promote species coexistence and the coexistence becomes a globally stable state as M increases through M_c .

basin is shrinking as M increases, and the basin is only appeared near the center point as M is close to M_c [see Fig. 2(e)]. However, as illustrated in Fig. 3(e), the parameter condition $(\alpha, \beta) = (4, 4)$ still yields the coexistence basin in a wide range on the phase space where the area of the basin is similar to those for lower mobilities. As M exceeds M_c , the coexistence basin is still appeared which is contrast to the case of $(\alpha, \beta) = (1, 1)$. When the relativity strength of two parameters on adaptive movement is low, the spatial rock-paper-scissors game only exhibits the extinction state at high mobility regime which is similar to the classic model of rock-paper-scissors game [10]. On the other hand, the strong relativity effect on adaptive movement can maintain species coexistence and lead the increase of the area of the coexistence basin. Furthermore, we found that the stability of coexistence in the spatial rock-paper-scissors game is changed. To be concrete, the coexistence on the spatially extended system is locally stable at low mobility regimes which means coexistence occurs at initial conditions of the limited area around the center point of Δ^2 . However, as M increases, the coexistence becomes globally stable, i.e., the almost initial conditions can lead the coexistence. Such a strength (or “degree”) of the stability of coexistence can be characterized by the size of its basin area [25].

Figure 4 shows the area S_b of coexistence and extinction basins as a function of the initial mobility M for two parameter assumptions. For $(\alpha, \beta) = (1, 1)$ as shown in Fig. 4(a), it can be

seen that, when M increases through M_c , S_b of coexistence is decreasing from 0.44 approximately to 0, and the phase space of the initial condition is fully occupied by extinction basins. In this case, any one of extinction basins (blue dot line) approaches to $1/3$ asymptotically for $M > M_c$. However, for $(\alpha, \beta) = (4, 4)$ as illustrated in Fig. 4(b), the phase is changed against to $(\alpha, \beta) = (1, 1)$. To be concrete, the S_b of coexistence is gradually decreasing as M approaches to M_c , and rapidly increasing as M exceeds M_c . In this case, as the coexistence basin enlarges, it can fully occupy the phase space of initial conditions, and hence the coexistence can almost appear regardless of the choice of initial conditions. In the vicinity of M_c , the initial mobility seems to have a relatively strong influence on coexistence compared to adaptive movement. However, eventually, the effect of adaptive movement can be obviously revealed at high mobility regime by promoting coexistence, and the effect of the initial mobility may be ignored when strong adaptive movement is working.

4. CONCLUSION

In this paper, we investigate the effect of relativistic interplay between adaptive movement and mobility on species biodiversity in the spatial rock-paper-scissors game. By focusing the relative relationship between two parameters for local fitness and an exchange rate to describe adaptive movement, we found that, when two sensitivity parameters have sufficiently strong relationships, species coexistence can be promoted even if an individual's mobility is high which exceeds the critical mobility. In addition, we also uncover that the adaptive movement can also affect initial conditions of species. For strong adaptive movement, species coexistence can become a globally stable state as an individual's mobility increases through the critical value, i.e., the coexistence occurs regardless of choices of initial conditions. Furthermore, such phenomena can occur even the mobility is high. In general, high mobility values hamper coexistence and eventually lead extinction that the only one of species survives. However, our findings show that, for sufficiently strong adaptive movement which are relatively high between two sensitivity parameters, species coexistence always occurs regardless of mobility and initial conditions.

Our findings can provide an additional insight on elucidating biodiversity in spatial rock-paper-scissors game that adaptive behavior may strongly affect species biodiversity and such adaptive strategies can neutralize the effect of initial values and mobility which are commonly known as key factors for controlling biodiversity.

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