Species diversity in rock–paper–scissors game coupling with Levy flight*

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The rock–paper–scissors (RPS) game is a nice model to study the biodiversity in an ecosystem. However, in the previous studies only the nearest-neighbor interaction among the species was considered. In this paper, taking the long-range migration into account, the effects of the interplay between nearest-neighbor-interaction and long-range-interaction given by Levy flight with distance distribution l^h $(-3 \leq h < -1)$ in the spatial RPS game are investigated. Taking the probability, exchange rate, and power-law exponent of Levy flight as parameters, the coexistence conditions of three species are given. The critical curves for stable coexistence of three species in the parameter space are presented. It is also found that Levy flight has interesting effects on the final spatiotemporal pattern of the system. The results reveal that the long-range-interaction given by Levy flight exhibits pronounced effects on biodiversity of the ecosystem.

Keywords: RPS game, Levy flight, biodiversity, spatial pattern

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1. Introduction

The rock–paper–scissors (RPS) game describes a basic kind of cyclic, non-transitive interaction among competing populations.[1–4] Experimental and theoretical investigations have shown that the diversity of the species in some ecosystems is maintained by this type of mechanism.

Together with the other biological models to study the spatial-temporal pattern formation, the previous theoretical investigations were mainly based on the nearest-neighbor interaction (NNI).[5–11] Recently, the RPS game was studied, with the interplay between the interaction range and mobility taken into consideration.[12–15] In reality, individuals in a population may go a long distance from one place to another before predation or reproduction. For example, birds fly to places apart from their habitat and prey. In special seasons, some kinds of birds migrate over very long distances. Some other animals also migrate in different territories in some seasons. Bacteria swim and tumble in the air or water and so on. So long-range interaction (LRI) is the general case in the process of biological evolution.

Empirical studies on the pattern of mobility of many living organisms have revealed the existence of Levy flight. Now observations of Levy flight have been extended to many species.[16–24] Levy flight is characterized by many small steps connected by longer re-locations, with the same sites rarely revisited. The probability density function for the traveling distance has a power-law tail in the long-distance regime as follows:

$$P(l_i) \sim l_i^h, \quad (-3 \leq h < -1),$$

where l_i is the flight length of step i, and h is the power-law exponent. Levy-flight foraging hypothesis[19,25,26] predicts that Levy flight has a higher search efficiency in the environments where prey is scarce, nevertheless a Brownian walk takes place more likely where prey is abundant. Hence there exist NNI and LRI with Levy flight among species, such as selection, reproduction, and migration. Based on the above ideas, we explore the effects of Levy flight on species diversity in the framework of the RPS game in a spatially extended ecological system in this paper.

The model is described in Section 2. Section 3 gives some simulation results. Firstly, taking the probability and the exchange rate as parameters, the coexistence conditions of three species are found. The critical curves for stable coexistence of three species in the parameter space are presented. The results display that the higher the probability of Levy flight, the smaller the exchange rate on the critical curve in order to maintain the coexistence of three species is. Secondly, taking the probability and the power-law exponent as parameters, the coexistence conditions of three species are also given. They show that the higher the probability of Levy flight, the smaller

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the exponent h on the critical curve to preserve the coexistence of three species is. More interestingly, comparing with the only NNI, just a small probability of Levy flight can generate more fragments in the patterns, leading to spatial heterogeneity and patchiness which are common in an ecosystem. Larger probability of Levy flight can bring about patches or spiral waves of larger size in the patterns. When there is only LRI of Levy flight, the final steady patterns form a larger dense spiral wave than when only NNI exists. The results reveal that the LRI of Levy flight exhibits pronounced effects on biodiversity of the ecosystem.

2. Spatial RPS game with Levy flight

Consider a spatial and stochastic model of cyclically competing populations. Three species A, B, and C populate in a square lattice of $N \times N$ sites with periodic boundary condition. Each site is occupied by one individual or left empty, ϕ denotes empty site. Agents can interact with each other by cyclic competition, following the rules

$$AB \xrightarrow{\mu} A\phi, \quad BC \xrightarrow{\mu} B\phi, \quad CA \xrightarrow{\mu} C\phi, \tag{1}$$

$$A\phi \xrightarrow{\delta} AA, \quad B\phi \xrightarrow{\delta} BB, \quad C\phi \xrightarrow{\delta} CC, \tag{2}$$

$$XY \xrightarrow{e} YX, \quad (X,Y \in \{A,B,C,\phi\}). \tag{3}$$

Equation (1) reflects a cyclic selection: A can kill or prey B, yielding an empty site. In the same way, B outperforms C, and C in turn defeats A. Selection occurs at rate μ. Equation (2) describes the reproduction of individuals at rate δ, which is only allowed on an empty site. In Eq. (3), individuals are able to swap position with each other at exchange rate e, including empty sites.

Our interest is focused on the interplay between NNI and LRI of Levy flight in the spatial RPS game. In stochastic lattice simulations with periodic boundary conditions, the initial densities of three species and empty sites are always fixed to be 25% equally. At each Monte Carlo simulation process, the steps are as follows.

(i) An individual is chosen randomly.

(ii) The interaction pattern is determined randomly. NNI is chosen with probability p_0, and LRI of Levy flight is chosen with probability $1 - p_0$.

(ii)-1 When the interaction is NNI, the individual previously chosen will interact with one of its four nearest neighbors, which is also randomly determined.

(ii)-2 When the interaction is LRI of Levy flight, the individual previously chosen will interact with another site which is determined by Levy flight using the algorithm of Monte Carlo simulation. We first choose a distance l (Manhattan distance in this paper) from the power law distribution $P(l_i) \sim l_i^h$, and then randomly choose a site from all the sites with the same distance.

(iii) Given the previously chosen individual and the selected site, according to the algorithm of Gillespie,[27,28] the probabilities of the three possible reactions in Eqs. (1)–(3), are computed by the corresponding reaction rates. Selection occurs with the probability $\mu/(\mu+\delta+e)$, reproduction occurs with the probability $\delta/(\mu+\delta+e)$, and exchange occurs with the probability $e/(\mu+\delta+e)$.

(iv) When each individual has reacted once on average, one generation is set as the unit of time.

3. Simulation results

3.1. Critical curve of p_0 versus e

For the species in a realistic situation, an individual usually walks or flies under the constraints of its bioenergy and territory. So we propose that the step for Levy flight has a maximal length (denoted by $l_{\max}$) on average. Thus in the following discussion, the Levy flight gives long-range mobility with a distance that obeys power law $P(l_i) \sim l_i^h$ but under the constraint of maximal length $l_{\max}$. For simplicity and without losing any generality, selection rate μ and reproduction rate δ are set to be 1 in the whole article. In our stochastic lattice simulations, according to the definition of stability in previous work,[5] we employ 10^4 generations for each realization. We define the condition of species extinction as the condition under which one of the three species is extinct in the simulations. We mainly study the coexistence condition of the three species, such as, relation between probability parameter p_0 and exchange rate e on condition that the maximal step length $l_{\max}$ and power-law exponent h of Levy flight are given. Figures 1(a)–1(f) show the relations. Each curve means critical and stable coexistence of three species.

The critical curves show us various effects of long range interactions. Firstly, as the parameter p_0 is reduced (which means that the probability of choosing Levy flight increases), exchange rate e must decrease (which means that the local mobility must be lowered) to maintain the coexistence of three species. The reason for those results is that Levy flight results in super-diffusion.[16] Thus increasing the probability of choosing Levy flight is equivalent to amplifying the mobility. Hence the exchange rate e must decrease. The relation between probability parameter p_0 and exchange rate e shows an exponential rise, indicating that the influence is remarkable when we introduce the probability of choosing Levy flight.

Secondly, when the power-law exponent h decreases from -1.0 to -3.0 (which means that the probability of choosing long steps of Levy flight decreases and the mobility is lowered), the area which represents stable coexistence of three species on the graph enlarges obviously. Thirdly, for a given h, with the increasing of maximal step length $l_{\max}$, the area of stable coexistence of three species on the graph diminishes gradually when $-2.6 < h < -1.0$ and $1 \leq l_{\max} \leq 100$ in Figs. 1(a), 1(b), and 1(d). However, when $-3.0 \leq h \leq -2.6$ and $l_{\max} \geq 50$ in Figs. 1(c), 1(e), and 1(f), the area enlarges a little with the increase of $l_{\max}$. It seems that the maximal step length $l_{\max} = 50$ is the turning point which corresponds to the limiting case of stable coexistence of three species on the graph. These results are different from results in previous studies of the effects of NNI or LRI.[5–15] They give us a deeper insight into the effects of Levy flight.

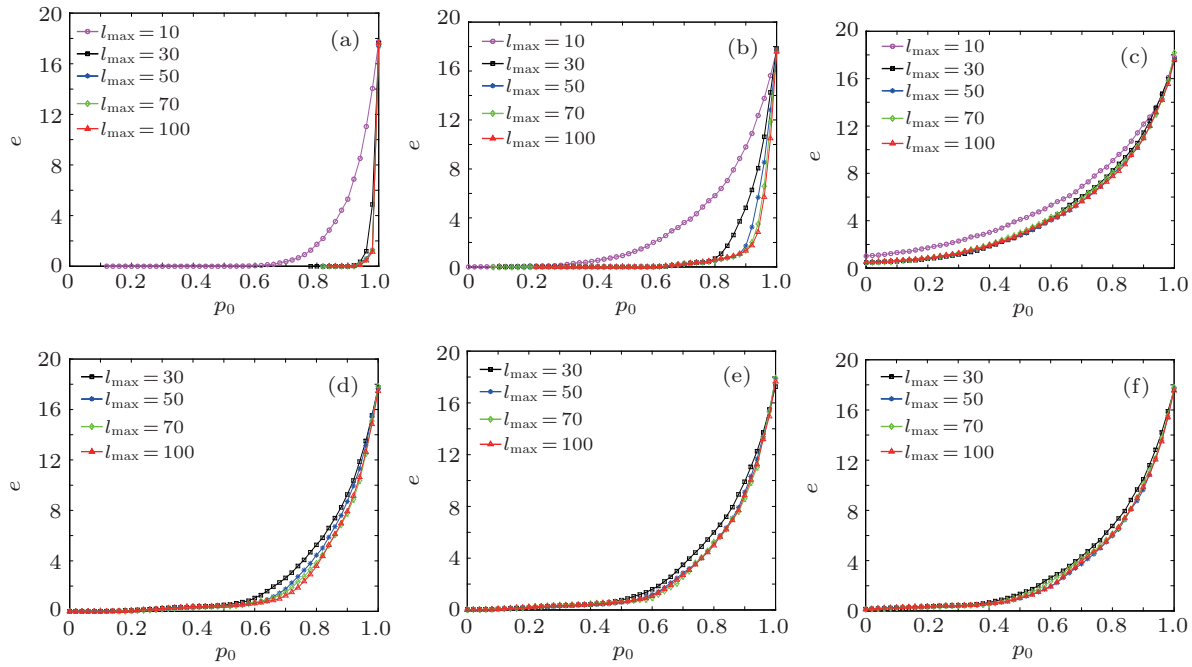


Fig. 1. (color online) Critical curves given by parameter p_0 (horizontal axes) and exchange rate e (vertical axes) in the cases of different values of maximal step length $l_{\max}$ and power-law exponent h of Levy flight: (a) $h = -1.0$, (b) $h = -2.0$, (c) $h = -3.0$, (d) $h = -2.5$, (e) $h = -2.6$, and (f) $h = -2.7$. Each point is averaged over 100 random realizations of stochastic simulations under the same initial densities on a 100×100 square lattice. Each realization consists of 10^4 generations. Each curve above is the extinction region of three species, correspondingly (and including) each curve below is the stable coexistence region of three species.

3.2. Critical curves of p_0 versus h

In order to investigate the influence of Levy flight in depth, we further set the exchange rate $e = 0.2$, then study the critical curves of parameter p_0 and power-law exponent h for different values of maximal step length $l_{\max}$ of Levy flight.

In order to let the system reach the final steady state, in the following stochastic lattice simulations, we employ 10^5 generations for each realization. Figures 2(a) and 2(b) show the results on the lattice of 100×100 sites. Each curve means critical and stable coexistence of three species in Figs. 2(a) and 2(b).

The LRI effects of Levy flight are obvious with the change of power-law exponent h. As parameter p_0 is reduced (which means that the probability of choosing Levy flight increases), power-law exponent h must decrease for maintaining the stable coexistence of three species. The reason is that decreasing h means the reduction of the probability of large steps of Levy flight. It is equivalent to the reduction of mobility caused by super-diffusion. Therefore the coexistence of three species is maintained through reducing h when the probability of choosing Levy flight increases. In Fig. 2(a), when maximal step length $l_{\max}$ increases from 10 to 50, the area which represents stable coexistence of three species on the graph diminishes gradually. But the further increase of $l_{\max}$ has less effects on the critical curves. With maximal step length $l_{\max}$ increasing from 50 to 100 in Fig. 2(b), we could find that the area of stable coexistence of three species varies a little. Furthermore the area of stable coexistence state tends to a minimal limit with the increase of the maximal step length $l_{\max}$ in Figs. 2(a) and 2(b). The limited size of the lattice and periodic boundary conditions lead to the minimal limit of the stable coexistence area jointly. These results are interesting and have not been found in previous research.[5–15] They also show that the LRI of Levy flight affects the stability of coexistence state of three species strikingly.

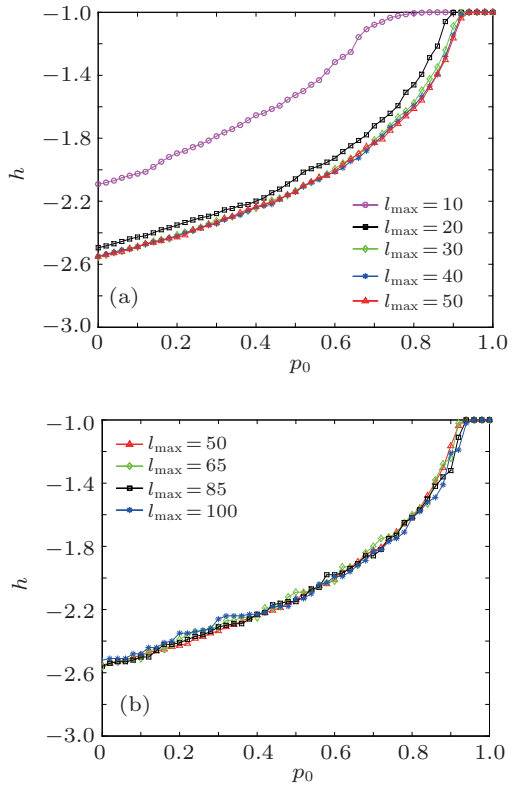


Fig. 2. (color online) Critical curves given by parameter p_0 (horizontal axes) and power-law exponent h (vertical axes) in the context of different values of maximal step length $l_{\max}$ of Levy flight. Each point is averaged over 10 random realizations of stochastic simulations employing the same initial densities on a 100×100 square lattice. Each realization consists of 10^5 generations. The area below (and including) each curve is the stable coexistence region of three species.

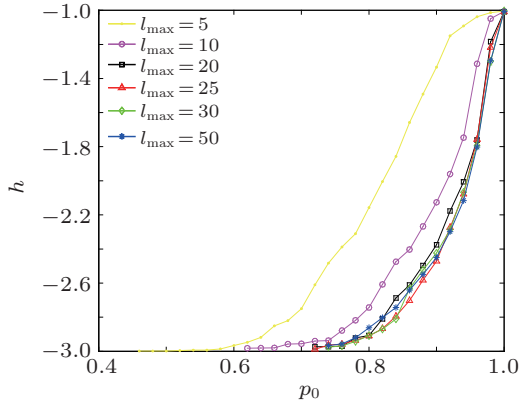


Fig. 3. (color online) Critical curves of parameter p_0 and power-law exponent h with different values of maximal step length $l_{\max}$ of Levy flight. The square lattice is 50×50. The horizontal and vertical coordinates represent the same parameters as in Fig. 2. Each point is averaged over 10 random realizations of stochastic simulations of the same initial densities. Each realization contains 10^5 generations.

In order to investigate whether the lattice scale has any effect on stable coexistence conditions of three species, we reduce the square lattice into 50×50 for further simulations. The results are shown in Fig. 3. Each curve represents critical and stable coexistence of three species. As in the above simulations, each realization is the result of 10^5 generations. It could be found that the areas of stable coexistence of three species change in the same trend as that of the 100×100 square lattice. Similarly the effects of Levy flight are displayed obviously. When parameter p_0 is reduced, power-law exponent h must decrease for maintaining the stable coexistence of three species. With maximal step length $l_{\max}$ increasing from 5 to 25, the area representing stable coexistence of three species on the graph shrinks gradually. Furthermore, in Fig. 3, with maximal step length $l_{\max}$ further increasing from 25 to 50, the area of stable coexistence of three species only changes a little. It also appears that the area of stable coexistence has a minimal limit with the increase of maximal step length $l_{\max}$. Comparing with the results in the last subsection, we can see that the size of the system just affects the area size of stable coexistence of three species. All the results are the same qualitatively.

3.3. Spatiotemporal pattern under Levy flight

In stochastic lattice simulations, we find that the LRI of Levy flight also changes the spatial pattern in the RPS game. Figures 4 and 5 show snapshots of the patterns for different values of parameters, the lattice sizes are 100×100 and 500×500 respectively. Individuals of three competing species A (dark gray), B (light gray), C (gray), and empty site (black) occupy the sites of the lattice.

The patterns in Figs. 4 and 5 display some characteristics different from those in previous work.[5–15] For example, there always heterogeneously emerge small or very small patches of a certain species in larger patches of another species which is defeated by the aforementioned species. The reason may lie in the fact that some individuals of three species move with Levy flight behavior clearly. Firstly, as $p_0 = 1.0 \to 0.0$ (which means that the probability of Levy flight increases), the number of species patches abruptly increases and then decreases gradually. Secondly, when $h = -1.0 \to -3.0$ (which means that the probability of long steps of Levy flight decreases), the number of species patches increases gradually. Comparing with NNI, the introduction of LRI of Levy flight generates more fragments in the spatial patterns initially, leading to spatial heterogeneity and patchiness. Those results are similar to the characteristics of species patches in ecosystem. As maximal step length $l_{\max}$ increases, the number of species patches decrease, and larger patches grow in size gradually. On condition that $p_0 = 1.0 \to 0.0$, $h = -3.0 \to -1.0$, and e is unchanged, the patterns vary from a spiral wave of small size to fragmentized patches with smaller size, and then to patches or spiral waves of larger sizes again. In order to see the change of spatiotemporal patterns clearly, we conduct the stochastic lattice simulations in the lattice with 500×500 sites. The results are shown in Fig. 5 and demonstrate the same phenomena. The effects of Levy flight on the final spatiotemporal pattern are interesting and need further investigating.

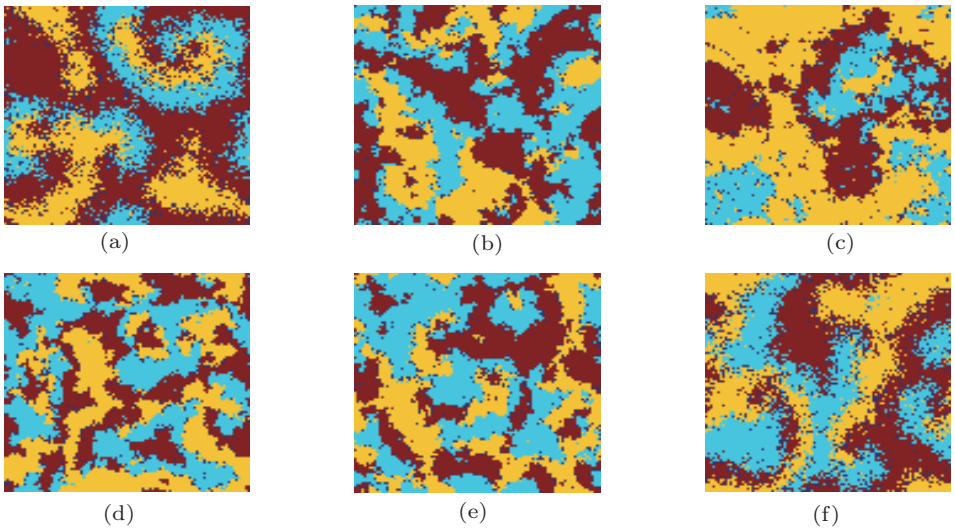


Fig. 4. (color online) Snapshots of patterns. The size of square lattice is 100×100. For each realization, the simulation consists of 10^4 time steps. The maximal step length $l_{\max}$ of Levy flight equals 50. (a) $e = 0.1$, $p_0 = 1.0$; (b) $h = -2.0$, $e = 0.1$, $p_0 = 0.9$; (c) $h = -2.0$, $e = 0.1$, $p_0 = 0.5$; (d) $h = -3.0$, $e = 0.1$, $p_0 = 0.9$; (e) $h = -3.0$, $e = 0.1$, $p_0 = 0.5$; (f) $h = -3.0$, $e = 0.1$, $p_0 = 0.0$.

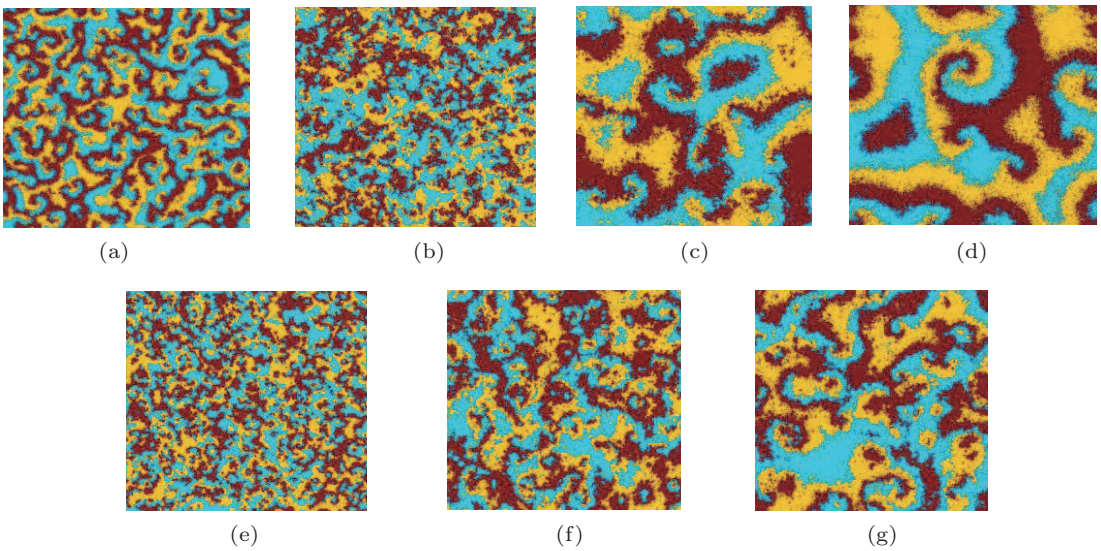


Fig. 5. (color online) Snapshots of patterns. The size of square lattice is 500×500. For each realization, the simulation consists of 10^4 time steps. The maximal step length $l_{\max}$ of Levy flight equals 50. (a) $e = 0.2$, $p_0 = 1.0$; (b) $h = -1.5$, $e = 0.2$, $p_0 = 0.9$; (c) $h = -1.5$, $e = 0.2$, $p_0 = 0.5$; (d) $h = -1.5$, $e = 0.2$, $p_0 = 0.0$; (e) $h = -2.0$, $e = 0.2$, $p_0 = 0.9$; (f) $h = -2.0$, $e = 0.2$, $p_0 = 0.5$; (g) $h = -2.0$, $e = 0.2$, $p_0 = 0.0$.

4. Concluding remarks

In this paper, we mainly study the interplay between NNI and LRI of Levy flight in the spatial rock–paper–scissors game. Our aim is to find the effects of the Levy flight on the biodiversity in the ecosystem. The coexistence conditions of three species, such as the critical curve with the change of parameter p_0, exchange rate e, power-law exponent h, and maximal step length $l_{\max}$ of Levy flight are presented. The curves also show the change of the area representing stable coexistence of three species in the parameter space. It is interesting to find that when the maximal step length $l_{\max}$ approaches to half the lattice length, the area of stable coexistence of three species tends to a minimal limit. The reason is that the limited size of the lattice and periodic boundary conditions lead to the minimal limit of the stable coexistence area jointly. All the simulation results show that probability p_0, exchange rate e, maximal step length $l_{\max}$, and power-law exponent h of Levy flight exert distinct influence on the stability and the forms of the spatiotemporal patterns. Further investigations are needed to reveal the effects and the corresponding mechanisms of Levy flight on the biodiversity.

References

[1] Jackson J B C and Buss L 1975 *Proc. Natl. Acad. Sci. USA* **72** 5160

[2] Paquin C E and Adams J 1983 *Nature* **306** 368
[3] Sinervo B and Lively C M 1996 *Nature* **380** 240
[4] Kerr B, Riley M A, eldman M W and Bohannan B J M 2002 *Nature* **418** 171
[5] Reichenbach T, Mobilia M and Frey E 2007 *Nature* **448** 1046
[6] Reichenbach T, Mobilia M and Frey E 2007 *Phys. Rev. Lett.* **99** 238105
[7] Reichenbach T, Mobilia M and Frey E 2008 *J. Theor. Biol.* **254** 368
[8] Reichenbach T and Frey E 2008 *Phys. Rev. Lett.* **101** 058102
[9] Wang W M, Wang W J, Lin Y Z and Tan Y J 2011 *Chin. Phys. B* **20** 034702
[10] Shi H J, Wang W X, Yang R and Lai Y C 2010 *Phys. Rev. E* **81** 030901
[11] Quan J and Wang X J 2011 *Chin. Phys. B* **20** 030203
[12] Szabo G and Fath G 2007 *Phys. Rep.* **446** 97
[13] Zhang G Y, Chen Y, Qi W K and Qing S M 2009 *Phys. Rev. E* **79** 062901
[14] Ni X, Wang W X, Lai Y C and Grebogi C 2010 *Phys. Rev. E* **82** 066211
[15] Wang W X, Ni X, Lai Y C and Grebogi C 2011 *Phys. Rev. E* **83** 11917
[16] Metzler R and Klafter J 2000 *Phys. Rep.* **339** 1
[17] Metzler R and Klafter J 2004 *J. Phys. A: Math. Gen.* **37** R161
[18] Dieterich P, Klages R, Preuss R and Schwab A 2008 *Proc. Natl. Acad. Sci. USA* **105** 459
[19] Viswanathan G M, Raposo E P and da Luz M G E 2008 *Phys. Life Rev.* **5** 133
[20] Nossal R 1983 *J. Stat. Phys.* **30** 391
[21] Levandowsky M, White B S and Schuster F L 1997 *Acta Protozool.* **36** 237
[22] Ramos F G, Mateos J L, Miramontes O, Cocho G, Larralde H and Ayala O B 2004 *Behav. Ecol. Sociobiol.* **55** 223
[23] Sims D W, Southall E J, Humphries N E, Hays G C, Bradshaw C J A, Pitchford J W, James A, Ahmed M Z, Brierley A S, Hindell M A, Morritt D, Musyl M K, Righton D, Shepard E L C, Wearmouth V J, Wilson R P, Witt M J and Metcalfe J D 2008 *Nature* **451** 1098
[24] Humphries N E, Queiroz N, Dyer J R M, Pade N G, Musyl M K, Schaefer K M, Fuller D W, Brunnschweiler J M, Doyle T K, Houghton J D R, Hays G C, Jones C S, Noble L R, Wearmouth V J, Southall E J and Sims D W 2010 *Nature* **465** 1066
[25] Bartumeus F, Peters F, Pueyo S, Marrase C and Catalan J 2003 *Proc. Natl. Acad. Sci. USA* **100** 12771
[26] Bartumeus F 2007 *Fractals* **15** 151
[27] Gillespie D T 1976 *J. Comput. Phys.* **22** 403
[28] Gillespie D T 1977 *J. Phys. Chem.* **81** 2340