

Article

Temporal mortality-colonization dynamic can influence the coexistence and persistence patterns of cooperators and defectors in an evolutionary game model

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Abstract

In the present report, the coexistence and persistence time patterns of Prisoners' Dilemma game players were explored in 2D spatial grid systems by considering the impacts of the mortality-colonization temporal dynamic specifically. Our results showed that the waiting time for triggering a colonization event could remarkably influence and change the extinction patterns of both cooperators and defectors. Interestingly, a relatively high frequency of stochastic colonization events could promote the persistence of defectors but not cooperators. In contrast, a low frequency of stochastic- or constant-time colonization events could facilitate the persistence of cooperators but not defectors. However, a long waiting time would be detrimental to the survival of both game players and drives them to go extinction in faster rates. At last, it was found that colonization strength played a relatively weak role on influencing the coexistence scenarios of both game players, but should be kept small if the coexistence of game players is needed to maintain. In conclusion, our study provides evidence showing that the temporal trade-off of mortality and colonization activities would influence the evolution of PD game and the persistence of cooperators and defectors.

Keywords species coexistence; game theory; colonization-extinction dynamics; individual-based modeling.

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1 Introduction

The classical Prisoner's Dilemma (PD) game has been broadly studied in evolutionary biology (Hui and McGeoch, 2007; Zhang and Hui, 2011; Zhang et al., 2005; Nowak and May, 1993, 1992; Zhang, 2012). Spatial version of Prisoner's Dilemma could allow the emergence of complex defense-cooperation dynamic patterns and make the cooperation become more possible (Langer et al., 2008; Zhang et al., 2005).

In a previous study, the evolution of cooperation under habitat destruction has been well quantified (Zhang et al., 2005). One important part of the model used by the previous work (Zhang et al., 2005) is to model the dynamic between mortality and colonization. However, the trade-off between the occurrence frequency of colonization and mortality events and the relevant impacts on the coexistence and survival of both game players have not been extensively evaluated yet. Because in the previous study (Zhang et al., 2005), colonization and mortality events are allowed to happen at each simulation time step. A detailed study on the trade-off between colonization and mortality occurrence frequency would allow ones to better understand the real-time habitat degeneration and isolation processes on influencing the coexistence patterns of cooperators and defectors.

In the present report, We quantify the condition of coexistence of both defectors and cooperators by varying the occurrence frequency of colonization and mortality events. In specific, We fix the mortality frequency during the simulation (allowed to occur one time per one time step), and evaluate the influence of waiting time of triggering a colonization event on the persistence of cooperators and defectors.

As a summary, the central objective of the present study is to reveal the impacts of the temporal trade-off of the occurrence frequency of colonization and mortality events on the persistence time of PD game players.

2 Materials and Methods

The payoff matrix of a typical evolutionary PD game is defined as (Zhang et al., 2005),

$$\begin{array}{cc} & \begin{array}{c} C \quad D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} \alpha & -\beta \\ \beta & -\alpha \end{pmatrix} \end{array} \quad (1)$$

where $\beta > 0$ and $\alpha > 0$. C represents the cooperator, while D represents the defector.

Assuming that each patch is only allowed to inhabit one individual, the p_i score for the individual in the patch i , taking into account of the rewards during the evolutionary game interaction, is defined as follows (Zhang et al., 2005),

$$p_i = \frac{x_i(x_i + 1)}{2}(f_{C_i}\alpha - f_{D_i}\beta) + \frac{x_i(x_i - 1)}{2}(f_{C_i}\beta - f_{D_i}\alpha) \quad (2)$$

Here we adopt the same notation used in the previous study (Hui et al., 2005). Where $x_i = 1$ if patch We is occupied by a cooperator; $x_i = -1$ if the patch is occupied by a defector; and $x_i = 0$ if it is empty. f_{C_i} is the fraction of cooperators in the two neighboring patches of the patch We and f_{D_i} is the fraction of defectors. Clearly, $f_{C_i} + f_{D_i} \leq 1$.

Degeneration of habitat quality is thought to be related to mortality rate, while patch isolation is related to colonization rate of species (Zhang et al., 2005). As such, as mentioned above, the trade-off between mortality and colonization frequency actually reflects the dynamic of habitat degeneration and isolation on the persistence of both game players.

The mortality rate of individuals for taking into account of the degeneration of habitat quality is defined as (Zhang et al., 2005),

$$M(p_i) = m \frac{\exp(-\lambda p_i)}{1 + \exp(-\lambda p_i)} \quad (3)$$

and the colonization rate of individuals is (Zhang et al., 2005),

$$C(p_i) = c \frac{1}{1 + \exp(-up_i)} \quad (4)$$

Here, m and c are regarded to be related to habitat degeneration and isolation respectively, being in the range of $[0, 1]$. Higher values of m and/or c indicates higher degrees of degeneration and/or isolation of the habitat. Hereafter, We call m and c as mortality and colonization coefficients (or strengths) respectively.

For modeling the temporal impact of trade-off between mortality and colonization events, We define and use the waiting time of triggering a colonization event. In detail, a mortality event is assumed to happen for each time step, while a colonization event could happen only when the next time for triggering it satisfying the waiting time (WT) setting.

Two strategies are used to configure the waiting time setting for triggering a colonization event during the simulation. The first one is to assume the waiting time of a colonization (WT) event is deterministic and constant, which is fixed to be an integral. As such, the colonization or mortality events could happen at the time steps when they are the integral multiples of the waiting time value. For example, if a waiting time for a colonization event is set to $WT=12$, then the colonization events could happen in the time steps 12, 24, 36 and so on. As such, WT measures how many time steps are required to trigger a colonization event. When the simulation has a total time step of 100, the overall colonization event number should $100/12 \approx 8$.

The second strategy is to assume the waiting time of a colonization event being stochastic. The stochastic waiting time is modeled by an acceptance rate (still use WT to indicate the acceptance rate, being less than 1 and larger than 0) and a variate randomly drawn from the uniform distribution $[0,1]$. Different from the constant WT cases, for stochastic WT, for each time step, a colonization event could be allowed to happen only when the randomly drawn variate is smaller than the acceptance rate WT. Consequently, for stochastic WT cases, an acceptance rate WT indicates how many colonization events could happen during the simulation. For example, if $WT=0.5$, and the simulation time is 100 as a total, then the overall colonization event number for the simulation is $100 \times 0.5 = 50$.

Finally, it is worth noting that, whether stochastic or constant strategies are applied, $WT=1$ always implies a perfect synchrony between colonization and mortality events because both are allowed to happen at each time step.

Based on the above definitions, for each time step, a mortality event has to happen, for which an individual has the probability of $M(p_i)$ to die and the patch becomes vacant again. In contrast for each time step, the colonization of the vacant sites could be allowed only when the WT setting for a colonization event is satisfied. When a colonization event can be allowed to happen, the vacant patch will be colonized by an offspring of another individual from the neighboring patches (four neighboring cells are used in the present study: up, low, left and right). Whether the offspring is a cooperator or defector is determined by following probabilities,

$$PC_i = \frac{1}{2} \sum_{j \in S_i} \frac{x_j(x_j + 1)}{2} C(p_j) \quad (5)$$

And

$$PD_i = \frac{1}{2} \sum_{j \in S_i} \frac{x_j(x_j - 1)}{2} C(p_j) \quad (6)$$

where PC_i and PD_i represent the probability of an offspring of the cooperators and defectors from the neighboring patches of patch i to colonize the vacant patch i . If $PC_i > PD_i$, then the patch is colonized by a cooperator offspring; if $PC_i < PD_i$, the patch is colonized by a defector offspring.

During the simulation, we use the occurrence frequency of species (fraction of grid cells occupied) as the index to quantify the influence of varying colonization waiting time on the coexistence and survival of both game players. In our simulation, a 2D square grid system with periodic boundary conditions is employed with a size of 50×50 . For each simulation, 1000 time step is used.

3 Results

3.1 Coexistence of game players by varying mortality and colonization strengths

When evaluating the coexistence of both players as the function of mortality and colonization coefficients, apparently, as indicated by the 3D surface plot (Fig. 1), lower mortality coefficient could allow the coexistence and survival of both game players. Colonization coefficient c has little effect on the coexistence scenarios of both game players. The coexistence of players is principally determined by mortality strength m .

3.2 Coexistence of game players by varying cooperation and defense rewards

When evaluating the coexistence of both players as the function of cooperation and defense rewards, as indicated by the 3D surface plot (Fig. 2), the linear combination between β and α reward could allow the coexistence of both game players. Interestingly, for all the area with $\alpha < \beta$ and part of the region with $\alpha > \beta$ could maintain the coexistence of both species. The latter could be applicable only when their difference is not too large (Fig. 2). Otherwise, cooperators would dominate the community.

3.3 Coexistence of game players by varying defense reward and colonization strength

As showed in Fig. 3, high colonization coefficient c will lead to the dominance of defectors in the community, while cooperators would die out. In contrast, when the colonization coefficient c is low, coexistence of both game players are possible, regardless of the values of defense reward β .

3.4 Coexistence of game players by varying waiting time and colonization strength

As showed in Fig. 4, varying either waiting time or colonization strength could not change the coexistence pattern of cooperators and defectors. Both game players could coexist throughout the simulation, but cooperators have higher population densities.

3.5 Coexistence of game players by varying waiting time and defense reward

As showed in Fig. 5, only when waiting time is small and stochastic, the coexistence of both players is possible. Otherwise, cooperators would dominate the community and defectors go extinct. Interestingly, the population density of cooperators would become highest for the cases of defense reward $\beta > 10$ when WT is around 13 (Fig. 5). Increasing or decreasing WT from the optimum would reduce the population of cooperators in the community, regardless of the existence of defectors.

Another interesting thing is that the cooperators could not occupy all the vacant sites even when defectors have been removed out of the community for most of parameter space (Fig. 6). An exception is found at the bottom-left area which has the parameter space with small β and long stochastic waiting time of triggering colonization events (small WT approaches zero) (Fig. 6).

3.6 Persistence time of both cooperators and defectors for different waiting time situations of triggering colonization events

For the persistence time of defectors, a unimodal pattern was identified (Figs. 5 and 7). The longest persistence time for the players could be found at WT=0.7 (indicating that for each time step, a 0.7 probability of triggering a colonization event). The overall number of colonization events during a simulation with 800 time step would be around 560. However, when WT becomes larger and the probability of triggering colonization events becomes higher, the persistence time of the defectors in the community is decreased and they could not survive until the end of the simulation.

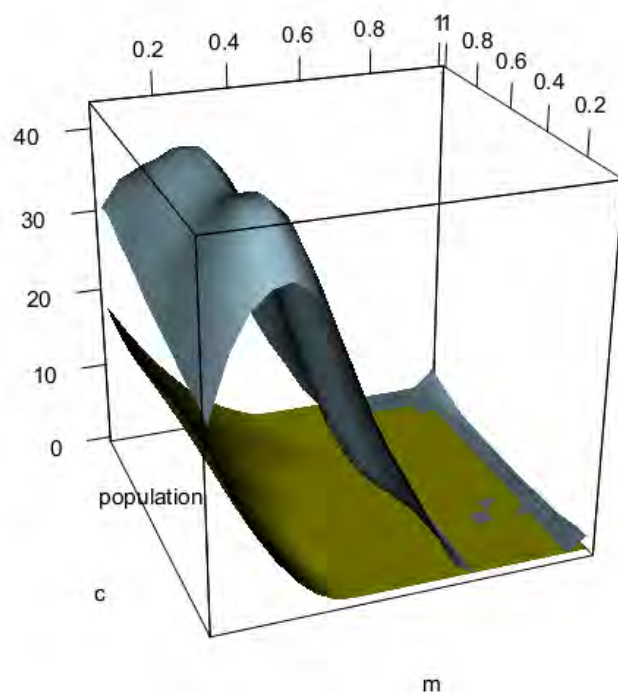


Fig. 1 Coexistence of cooperators and defectors under different combinations of mortality and colonization coefficients m and c . The settings for other parameters: $\alpha = 1$, $\beta = 1.5$, $WT = 0.5$, $\lambda = \mu = 0.9$. The initial populations of both players are set to $1/3$ of the number of total grids (=833).

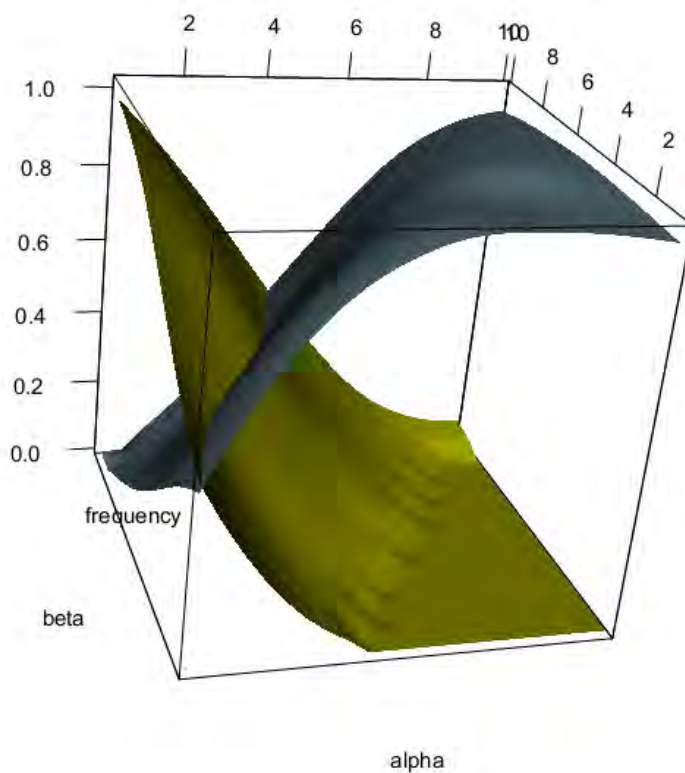


Fig. 2 Coexistence of cooperators and defectors under different combinations of rewards α and β for cooperators and defectors. The settings for other parameters: $m = 0.1$, $c = 0.6$, $WT = 0.5$, $\lambda = \mu = 0.9$. The initial populations of both players are set to $1/3$ of the number of total grids (=833).

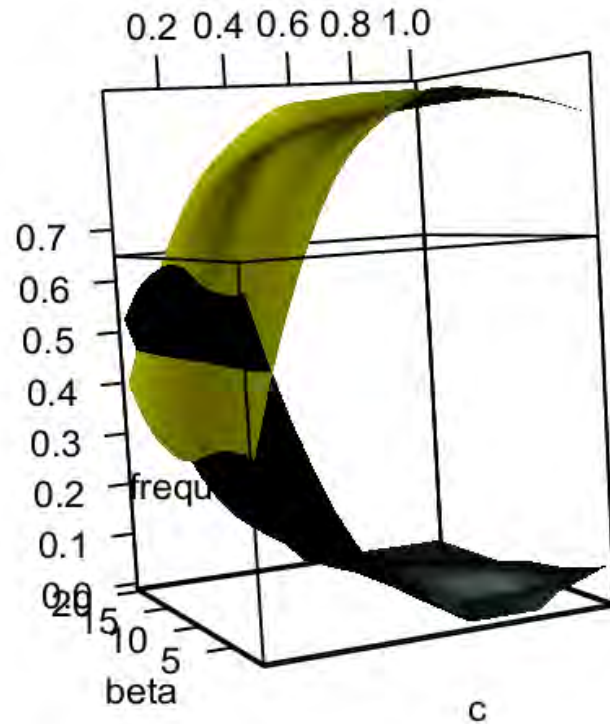


Fig. 3 Coexistence of cooperators and defectors under different combinations of defense reward β and colonization coefficient c . The settings for other parameters: $\alpha = 1, m = 0.1, WT = 0.5, \lambda = \mu = 0.9$. The initial populations of both players are set to $1/3$ of the number of total grids (=833).

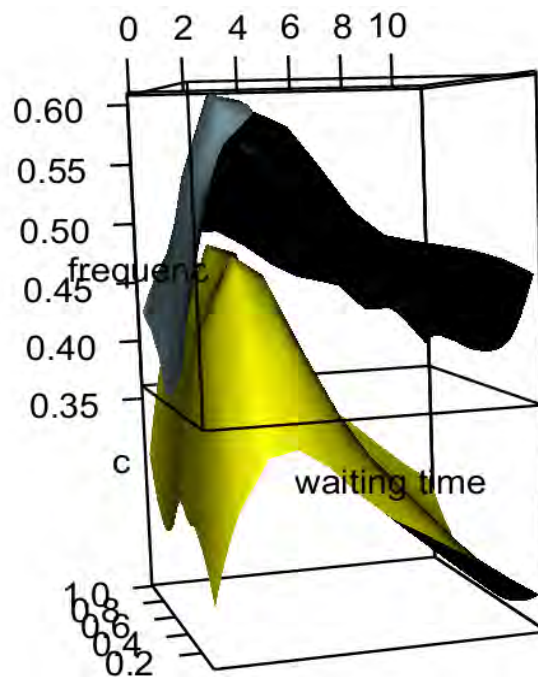


Fig. 4 Coexistence of cooperators and defectors under different combinations of waiting time WT and colonization coefficient c . The settings for other parameters: $\alpha = 1, \beta = 1.5, m = 0.1, \lambda = \mu = 0.9$. The initial populations of both players are set to $1/3$ of the number of total grids (=833).

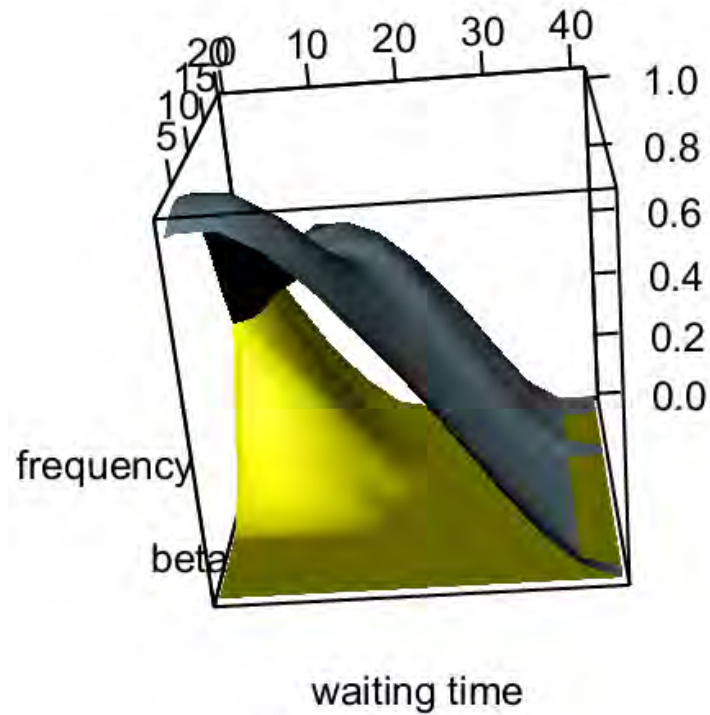


Fig. 5 Coexistence of cooperators and defectors under different combinations of waiting time WT (0.1~40) and defense reward β (1~20). The settings for other parameters: $\alpha = 5$, $m = 0.1$, $c = 0.6$, $\lambda = \mu = 0.9$. The initial populations of both players are set to 1/3 of the number of total grids (=833).

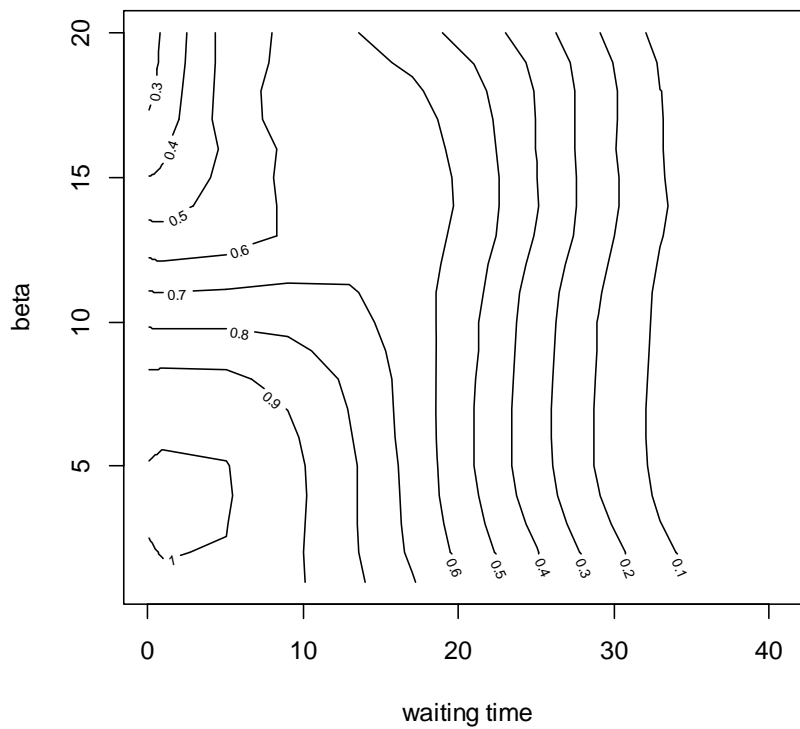


Fig. 6 Contour plot of the frequency of defectors under different combinations of waiting time WT and defense reward β based on Figure 5. The values marked on each contour line indicated the frequency of the defectors in the community.

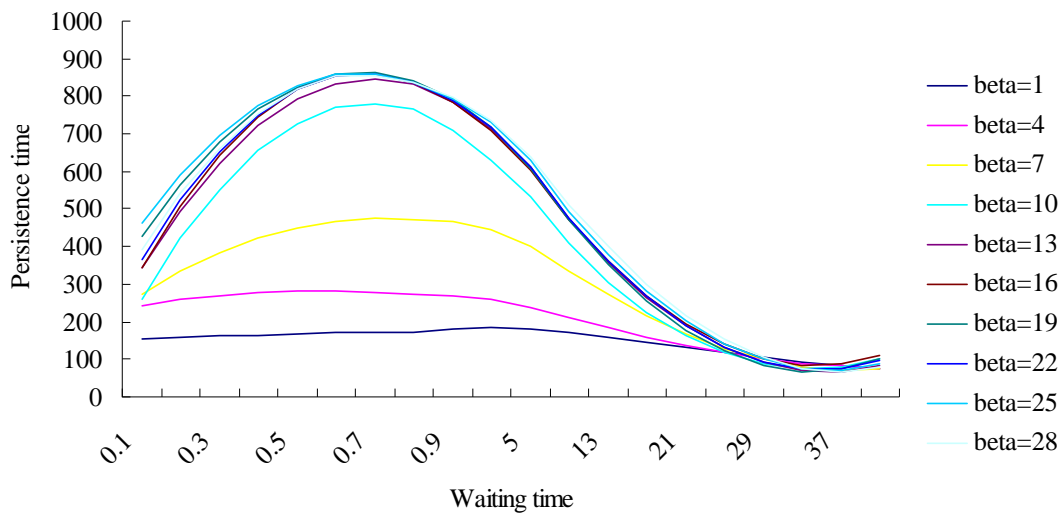


Fig. 7 The influence of different random and constant waiting time of triggering colonization events on the persistence time of defectors. Each curve represented the locally weighted scatterplot smoothing of the mean values of persistence time from 500 replicates of simulation with 800 time step. Values showed in the *x*-axis indicated the waiting time for a colonization event (WT). When $WT < 1$, random waiting time of colonization during the simulation was used. For each time step, the acceptance probability of triggering a colonization event was the corresponding value. When $WT > 1$, constant waiting time of colonization was used. Parameter settings: $\alpha = 5, m = 0.1, c = 0.6, \lambda = \mu = 0.9$.

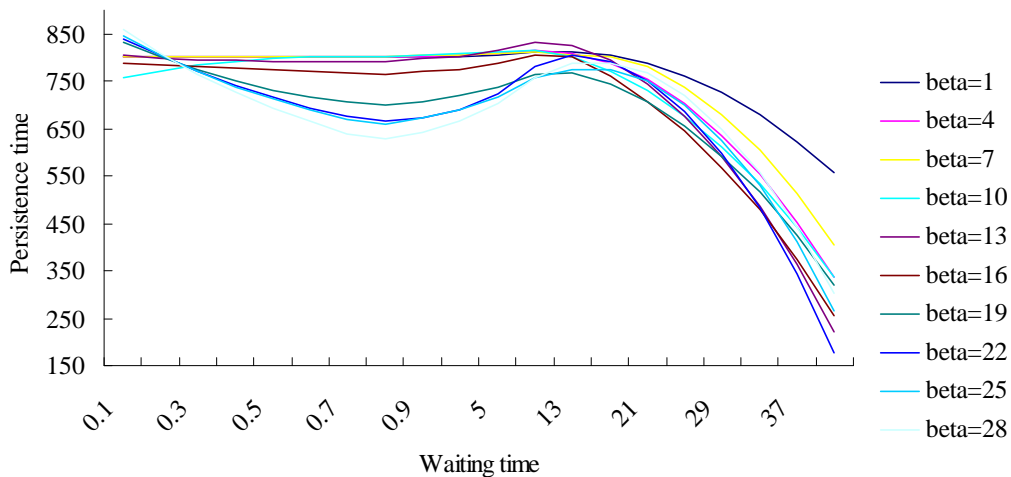


Fig. 8 The influence of different random and constant waiting time of triggering colonization events on the persistence time of cooperators. Each curve represented the locally weighted scatterplot smoothing of the mean values of persistence time from 500 replicates of simulation with 800 time step. Values showed in the *x*-axis indicated the waiting time for a colonization event (WT). When $WT < 1$, random waiting time of colonization during the simulation was used. For each time step, the acceptance probability of triggering a colonization event was the corresponding value. When $WT > 1$, constant waiting time of colonization was used. Parameter settings: $\alpha = 5, m = 0.1, c = 0.6, \lambda = \mu = 0.9$.

For the persistence time of cooperators, the situation is remarkably different (Figs. 5 and 8). For the cases of large defense award β , persistence time of cooperators would have two peaks at low $WT < 0.3$ and $WT = 13-17$ respectively (Fig. 8). For both peaks, the frequency of triggering colonization events is low. When $WT < 0.3$, the overall number of colonization events during a simulation with 800 time step would be less than

240. When $WT=13\sim 17$, the overall number of colonization events during a simulation with 800 time step would be around 47~61.

For both game players, too long constant waiting time of triggering colonization events actually will be detrimental to both species (Figs. 5, 7-8). The persistence time of both players would decline drastically when $WT>20$. Further, too long stochastic waiting time of triggering colonization events is disadvantageous to the survival of defectors as well ($WT<0.3$; Figs. 5 and 7), but not cooperators (Figs. 5 and 8).

4 Discussion

The principal finding of the present study is that waiting time of colonization for the game players during the simulation could considerably affect the survival patterns of cooperators and defectors in the spatial PD game. When comparing the persistence time patterns of both game players by varying different waiting time settings, it is found that stochastic waiting time setting ($0<WT<1$) could allow a longer persistence time of defectors but not cooperators during the evolutionary game. Higher probability of triggering a colonization event ($WT \rightarrow 1$) indicated a lower fluctuation of waiting time, which in turn indicated a high synchrony between mortality and colonization events. Based on the persistence time curve patterns (Fig. 7), a relatively higher synchrony ($WT\sim 0.7$) of the two quantities would allow a longer persistence time of defectors. In contrast, a remarkably temporal asynchrony between colonization and mortality is beneficial to the persistence of cooperators (Fig. 8). That is, a low frequency of triggering colonization events could make cooperators to survive better. As a consequence, a temporal synchrony between colonization and mortality would have opposite influences on the survival of defectors and cooperators. As such, the present study is different from a previous study, which suggested that a strong synchrony of within-population reproduction activity could promote species coexistence (Chen and Hsu, 2011).

A longer waiting time may hinder the survival of both players in the simulation. It should be true because species are very vulnerable for extinction when the mortality events take place too frequent during the simulation in comparison to the colonization events. In the present study, such an assertion could be evidenced by the shorter persistence time of both game players when $WT>40$ (Figs 5, 7-8). However, a stochastic longer waiting time might have a different scenario. As showed in Fig. 8, when $WT<0.3$, the persistence time of cooperators could be facilitated actually (or no worse than the other higher WT cases).

Our present study found that both cooperators and defectors could coexist in the community as long as the mortality coefficient is low enough ($m<0.4$; Fig. 1). Such an observation is contradictory to the previous study (Zhang et al., 2005), which suggested that cooperators would dominate the patches only when the ratio between morality and colonization strengths is moderate. In our study, the coexistence of both game players could be maintained in the small m situations, being irrelevant to the colonization coefficient c (Fig. 1). Interestingly, the weak effect of colonization strength c on the coexistence of game players could be further evidenced by evaluating the influence on players' coexistence for the pair of c and WT . For the combination between c and WT , the role of c could change the frequencies of both game players, but never driving them to go extinct (Fig. 4). Moreover, the colonization strength c plays some important and interesting roles, as evidenced by the combination between c and β : coexistence of cooperators and defectors is possible only when c is controlled to be <0.6 (Fig. 3). Too strong colonization strength actually would lead to the extinction of cooperators.

Acknowledgements

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