Article

The influence of deterministic and stochastic waiting time for triggering mortality and colonization events on the coexistence of cooperators and defectors in an evolutionary game model

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Abstract

In the present report, the coexistence of Prisoners' Dilemma game players (cooperators and defectors) were explored in an individual-based framework with the consideration of the impacts of deterministic and stochastic waiting time (WT) for triggering mortality and/or colonization events. For the type of deterministic waiting time, the time step for triggering a mortality and/or colonization event is fixed. For the type of stochastic waiting time, whether a mortality and/or colonization event should be triggered for each time step of a simulation is randomly determined by a given acceptance probability (the event takes place when a variate drawn from a uniform distribution [0,1] is smaller than the acceptance probability). The two strategies of modeling waiting time are considered simultaneously and applied to both quantities (mortality: WT_m, colonization: WT_c). As such, when WT (WT_m and/or WT_c) is an integral ≥ 1, it indicated a deterministically triggering strategy. In contrast, when $0<WT<1$, it indicated a stochastically triggering strategy and the WT value itself is used as the acceptance probability. The parameter space between the waiting time for mortality (WT_m~[0.1,40]) and colonization (WT_c~[0.1,40]) was traversed to explore the coexistence and non-coexistence regions. The role of defense award was evaluated. My results showed that, one non-coexistence region is identified consistently, located at the area where $0.3 \leq WT_m \leq 1$ and $0.1 \leq WT_c \leq 40$. As a consequence, it was found that the coexistence of cooperators and defectors in the community is largely dependent on the waiting time of mortality events, regardless of the defense or cooperation rewards. When the mortality events happen in terms of stochastic waiting time ($0.3 \leq WT_m \leq 1$), extinction of either cooperators or defectors or both could be very likely, leading to the emergence of non-coexistence scenarios. However, when the mortality events occur in forms of relatively long deterministic waiting time, both defectors and cooperators could coexist, regardless of the types of waiting time for colonization events. Defense (or cooperation) rewards could determine the persistence time of both game players. When the defense reward is low, cooperators could persist better in the simulation. But when the defense reward becomes sufficiently higher, defectors would persist better. Overall, non-coexistence of cooperators and defectors in the present evolutionary game model is dependent on the stochastic mortality events, but not colonization events. In conclusion, my present study quantifies the influence of the temporally fluctuating motility-colonization dynamic on modeling the coexistence of species in the spatial evolutionary game.

Keywords species coexistence; game theory; mortality-colonization dynamic; deterministic versus stochastic mechanisms.

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1 Introduction

The classical Prisoner's Dilemma (PD) game has been broadly studied in evolutionary biology (Nowak and May, 1993, 1992; Hui and McGeoch, 2007; Zhang et al., 2005; Zhang and Hui, 2011; Zhang, 2012, 2013). Spatial version of Prisoner's Dilemma could allow the emergence of complex defense-cooperation dynamic patterns (Zhang et al., 2005; Langer et al., 2008).

In a previous study, the evolution of cooperation under habitat destruction has been well quantified (Zhang et al., 2005; Chen et al., 2014). 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 colonization and mortality and its impacts on the coexistence and survival of both game players have not been well quantified yet.

One way to quantify the trade-off between colonization and mortality is to model the outbreak frequencies (or waiting time) of both events during the simulation. If one fixes the waiting time of occurrence of one mechanism (for instance, mortality), one could vary and manipulate the waiting time of another mechanism (colonization) so as to reveal the impact of different frequency ratio between colonization and mortality on the persistence of game players (Chen et al., 2014).

In the present report, by adopting and extending a previous 2D individual-based modeling framework (Zhang et al., 2005), I quantify the condition of coexistence of both defectors and cooperators by varying the waiting time of colonization and mortality events. During the *in silico* simulation, I traversed the parameter space between the waiting time for mortality (WT_m~[0.1,40]) and colonization (WT_c~[0.1,40]) to evaluate the coexistence status of both cooperators and defectors (Chen et al., 2014).

As a summary, the central objective of the present study is to reveal the relationship between the persistence time of game players and the temporal stochastic versus deterministic trade-off of the occurrence frequency of colonization and mortality events.

2 Materials and Methods

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

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

Where $\beta>0$ and $\alpha>0$. *C* represents the cooperator, while *D* represents the defector. Usually, $\beta>\alpha$ (Zhang et al., 2005).

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),

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

Here I adopt the same notation used in the previous study (Hui et al., 2005). Where x_i =1 if patch *i* is occupied by a cooperator; x_i =-1 if the patch *i* 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 *i* and f_{D_i} is the fraction of defectors. Clearly, $f_{C_i} + f_{D_i} \leq 1$.

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

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

And the colonization rate of individuals is (Zhang et al., 2005; Chen et al., 2014),

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

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* indicated higher degrees of degeneration and/or isolation of the habitat. Hereafter, I called *m* and *c* as mortality and colonization coefficients respectively.

For modeling the temporal impact of trade-off between mortality and colonization, two strategies are used to configure the waiting time for triggering a colonization and/or mortality event during the simulation. The first one is to assume the waiting time of triggering a colonization (WT_c) or mortality (WT_m) event is deterministic and constant, where the constant waiting time is set to an integral. As such, a colonization and/or mortality event could happen in 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_c=12, then the colonization events could happen in the time steps 12, 24, 36 and so on. Consequently, for determinstic cases, WT values indicated the time step required for triggering an event.

The second strategy is to assume the waiting time of a colonization and/or mortality event being stochastic. The stochastic waiting time is modeled by comparing 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 (WT_c and/or WT_m) cases, for stochastic WT, for each time step, a colonization and/or mortality event could be allowed to happen only when the randomly drawn variate is smaller than the acceptance rate WT. Consequently, for stochastic cases, an acceptance rate WT indicated how likely the emergence of a mortality and/or colonization event is during the simulation. For example, if WT_m=0.5, and the simulation time is 100 in a total, then the overall mortality event number for the simulation is 100×0.5=50.

Based on the above definitions, for each time step, if a mortality event could be triggered when the WT_m setting for a mortality event is satisfied, an individual has the probability of $M(p_i)$ to die and the patch becomes vacant again. For each time step, if the WT_c setting for a colonization event is satisfied, the re-colonization of the vacant sites could be allowed, in which the vacant patch will be re-colonized by an offspring of another individual from the neighboring patches. Whether the offspring is a cooperator or defector is determined by following probabilities (Chen et al., 2014),

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

and

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

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. If $PC_i = PD_i$, the patch is leaved there without occupancy.

During the simulation, the persistence time (or time to extinction) of game players is employed to quantify the influence of different trade-off of colonization and mortality on influencing the coexistence and survival of both game players.

3 Results

Regardless of the defense rewards, one non-coexistence region was identified constantly identified over different treatments, which is located at the area where $0.3 \le WT_m \le 1$ and $0.1 \le WT_c \le 40$ (Figs. 1, 3), indicating that when the waiting time for triggering mortality events of game players is stochastic, the coexistence of both game players is unlikely.

Within the region, when the defense reward is low (=1.5), cooperators are likely to persist until the end of simulation (Fig. 2) in comparison to defectors, especially in the region when the waiting time for colonization events are intermediate (near 1, could be deterministic or stochastic). In contrast, when the defense reward is high (=5), defectors are much likely to survive to the end of the simulation (Fig. 4) in comparison to cooperators.

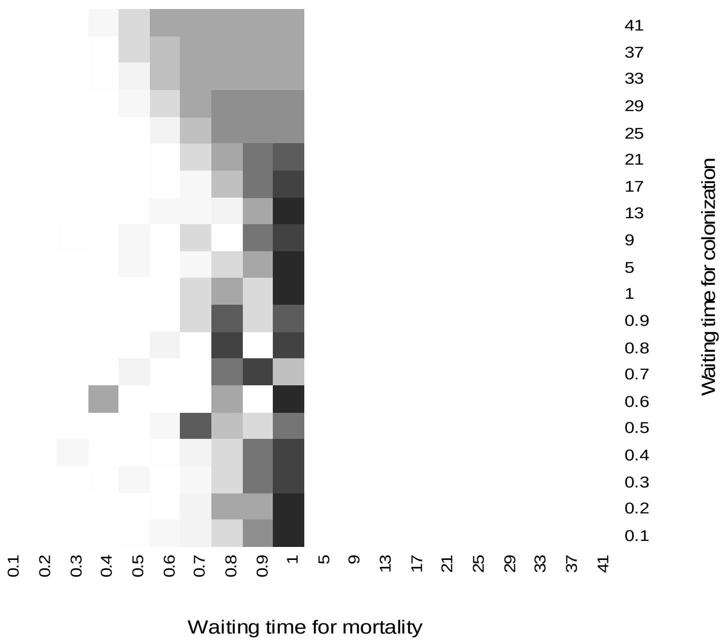

Fig. 1 Heatmap for coexistence outcomes of cooperators and defectors under different combinations of mortality (WT_m) and colonization waiting time (WT_c). The settings for other parameters: α =1, β =1.5, *m*=0.1, *c*=0.6, $\lambda = \mu$ =0.9. The initial populations of both players are set to 1/3 of the number of total grids (=833). Grids with dark colors indicated different levels of non-coexistence probability by checking the 5000 replicates. Other white regions indicated that both cooperators and defectors could coexist always over all the simulations.

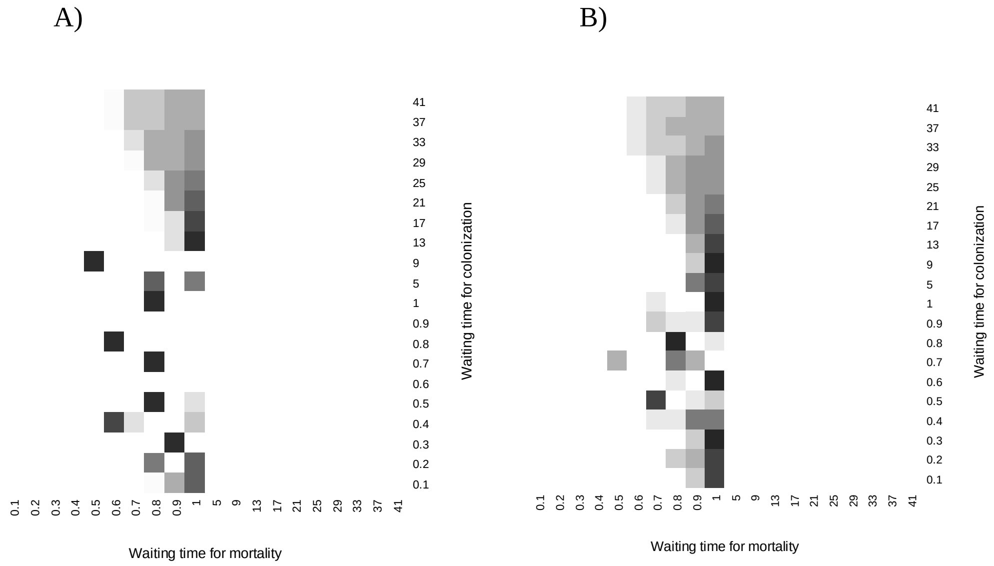

Fig. 2 Persistence heatmaps of cooperators (A) and defectors (B) during the simulation under different combinations of mortality (WT_m) and colonization waiting time (WT_c). The settings for other parameters: α =1, β =1.5, *m*=0.1, *c*=0.6, $\lambda = \mu$ =0.9. The initial populations of both players are set to 1/3 of the number of total grids (=833). Grids with dark colors indicated different levels of persistence time by taking the average of the 5000 replicates. Other white regions indicated that cooperators (for A) or defectors (for B) could always persist until the end of the simulations.

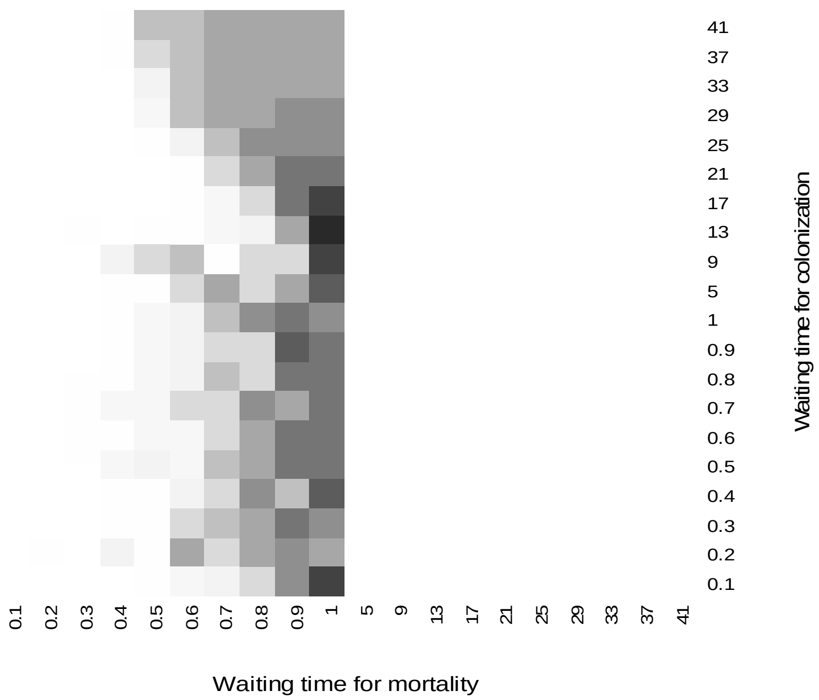

Fig. 3 Heatmap for coexistence outcomes of cooperators and defectors under different combinations of mortality (WT_m) and colonization waiting time (WT_c). The settings for other parameters: α =1, β =5, *m*=0.1, *c*=0.6, $\lambda = \mu$ =0.9. The initial populations of both players are set to 1/3 of the number of total grids (=833). Grids with dark colors indicated different levels of non-coexistence probability by checking the 5000 replicates. Other white regions indicated that both cooperators and defectors could coexist always over all the simulations.

A) B)

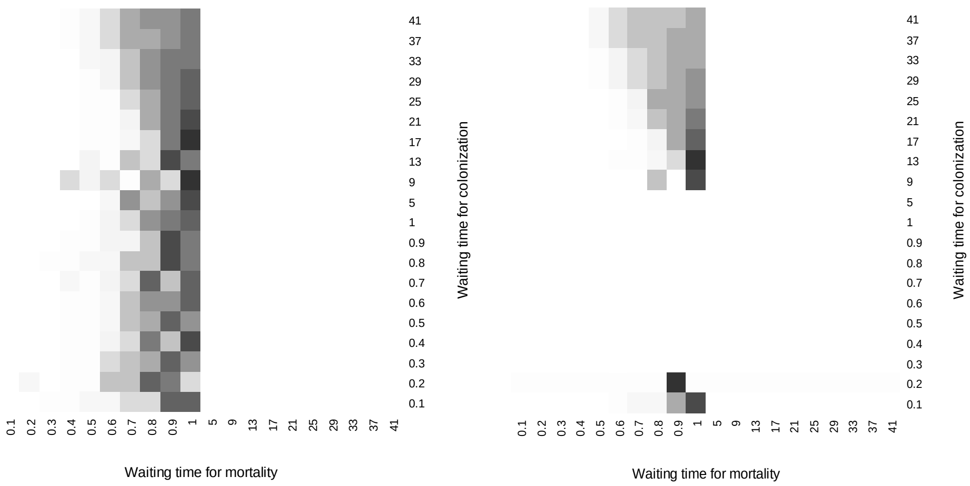

Fig. 4 Persistence heatmaps of cooperators (A) and defectors (B) during the simulation under different combinations of mortality (WT_m) and colonization waiting time (WT_c). The settings for other parameters: α =1, β =5, *m*=0.1, *c*=0.6, $\lambda = \mu$ =0.9. The initial populations of both players are set to 1/3 of the number of total grids (=833). Grids with dark colors indicated different levels of persistence time by taking the average of the 5000 replicates. Other white regions indicated that cooperators (for A) or defectors (for B) could always persist until the end of the simulations.

4 Discussion

Based on the present results, it was found that the coexistence of cooperators and defectors in the community is largely dependent on the behaviors of mortality events. When the mortality events happen in terms of stochastic waiting time ($0.3 \le WT_m \le 1$), extinction of either cooperators or defectors or both could be very likely, leading to the emergence of non-coexistence scenarios. However, when the mortality events occur at deterministic waiting time, both defectors and cooperators could coexist, regardless of the types of waiting time for colonization events.

Intuitively, it might be straightforward to image that when the waiting time for triggering colonization events is high, the probability of extinction of species should be high because the replacement of dead individuals by new ones is very slow. As such, as time goes by, the likelihood of species extinction should be high because no supply of new individuals from colonization events. Based on the above simulation result, such a prediction is proofed. As showed in Figs 1 and 2, for the region where $0.3 \le WT_m \le 1$ and $WT_c \ge 13$, both cooperators and defectors could not persist over the simulation. At that region, on one hand, the morality events come out randomly in high frequency ($WT_m \le 1$), while on the other hand, the time triggering a colonization event is very long ($WT_c \ge 13$). This is the very reason of causing extinction of species for the abovementioned prediction.

The role of waiting time for colonization events has stronger influences on the extinction of defectors than cooperators, only when the defense reward is low (Figs. 1-2), but the extinction of cooperators is much higher when the defense reward is high (Figs. 3-4). When defense reward is 1.5, as showed in the region where $0.3 \le WT_m \le 1$ and $WT_c \le 13$ (Fig. 1), more grids are found to be dark (or grey) for defectors in comparison to those for cooperators. As such, for the parameter condition when α =1, β =1.5, *m*=0.1, *c*=0.6, $\lambda = \mu$ =0.9, high occurrence frequencies of colonization events (could be either deterministic or stochastic) would make defectors to be more vulnerable to extinction. However, the opposite results were found for the case when defense reward is as high as 5 (Figs. 3-4). As seen, for the region where $0.3 \leq WT_m \leq 1$ and $WT_c \leq 13$ (Fig. 1), more grids are found to be dark (or grey) for defectors in comparison to those for cooperators.

5 Conclusions

Non-coexistence of cooperators and defectors in the present evolutionary game model is largely dependent on the waiting time of triggering mortality events, regardless of the defense (or cooperation) rewards. When the waiting time for mortality events is stochastic ($0.3 \leq WT_m \leq 1$), cooperators and defectors could not coexist and persist until the end of the simulations. In contrast, when the waiting time of mortality events is fixed and constant, coexistence is always true, regardless of how the waiting time for colonization events changes during the simulation.

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