

Full Length Article



Fixation of cooperation in evolutionary games with environmental feedbacks

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ABSTRACT

The interaction between strategy and environment widely exists in nature and society. Traditionally, evolutionary dynamics in finite populations are described by the Moran process, where the environment is constant. Therefore, we model the Moran process with environmental feedbacks. Our results show that the selection intensity, which is closely related to the population size, exerts varying influences on evolutionary dynamics. In the case of the specific payoff matrix, cooperation cannot be favored by selection in extremely small-sized populations. The medium-sized populations are beneficial for the evolution of cooperation under intermediate selection intensities. For weak or strong selection intensities, the larger the population size, the more favorable it is for the evolution of cooperation. In the case of the generalized payoff matrix, the low incentives for the defector to cooperate in the degraded state cannot promote the emergence of cooperation. As the incentive for the defector to cooperate in the degraded state increases, selection favors cooperation or defection depending on the population size and selection intensity. For large values of the incentive for the defector facing the cooperative opponent to cooperate in the degraded state, selection always favors cooperation. We further investigate the impact of the time-scale on the fixation probability of cooperation.

1. Introduction

The study of how cooperation emerges among selfish individuals has received significant attention [1]. Evolutionary game theory provides a suitable framework for explaining how cooperative behavior can emerge in social dilemma [2–4]. In the classical approach, deterministic replicator dynamics is a frequently used framework to investigate the evolution of cooperation in infinite populations [5, 6]. However, in nature, population size is finite, and the evolutionary dynamics is subject to random effects. Therefore, stochastic dynamics such as the Moran process is proposed to study the evolution of cooperation in finite populations [7–9].

In the classical Moran process, the payoff matrix is fixed in the evolution of strategies. But in many cases, environment changes over time, which affects the game payoff matrix [10]. Ashcroft et al. investigate the fixation in fluctuating environments independently of strategy evolution [11], which neglects the feedback between strategy and environment widely existing in nature and society [12–18]. In ecosystems, for example, the spatial patterns of Balinese rice terraces are influenced by the feedback between paddy ecosystem and

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farmers' decisions, and evolve toward the optimal state where farmers reap the greatest harvests [19]. In fisheries, over-harvesting diminishes the fish stock, which results in a lower yield and lower profits of all fishers. Conversely, fishers decrease the level of exploitation, which improves the state of fish stock and the profits [20,21]. Among microbes, the density of public goods such as the iron-scavenging pyoverdine molecule changes in response to the environment [22]. In human society, the decision whether to vaccinate or not influence the spread of the infectious disease, and the outbreaks of the disease increase incentives for vaccination [23–25].

In evolutionary games, some scholars focus on formation mechanism of cooperation from the perspective of coupled feedback between strategy and environment [26–33]. Hilbe et al. [26] and Su et al. [27] investigate the evolution of cooperative behaviors by means of stochastic games where the environment changes depending on the previous strategy of individuals. Additionally, some scholars model the replicator dynamics with environmental feedbacks where the changes in environment on different timescales arise from the choice of strategy, so as to investigate the impact of the game-environment feedback on the system dynamics [28–33].

In this paper, considering the finite populations with stochastic dynamics [26,27] and the coupled evolution of strategies and environment [28–33], we model the Moran process with the environmental feedback. The feedback between strategy and environment is based on the cooperation level of populations which affects the payoff matrix [34]. We derive the fixation probability of cooperation and the condition that selection favors the evolution of cooperation.

The remaining of the paper is organized as follows. In section 2, we present the Moran process with environmental feedback where the changes of environment depends on the cooperation level of populations. In section 3, we derive the condition that selection favors the evolution of cooperation by theoretical and numerical analysis. Finally, we summarize the main conclusions and discuss the future study direction.

2. The model

In this section, we propose a framework to model and analyze evolutionary games with environmental feedback, as shown in Fig. 1. In Ref [28], Weitz et al. assume that the change of environment is affected by not only the current environmental state but also the current strategy profile of the population. Different from the research by Weitz et al., we assume that the game environment depends solely on the current population state (i/N) [34] and that the game environment and strategy coevolve at the same timescale, which ensures the memoryless property of the Markov process. We investigate a two-player game with two strategies cooperation (C) and defection (D) in a finite population of N players. Initially, we consider the following specific payoff matrix [28] which is influenced by the game environment based on the cooperation level of the population

$$U(i) = (1 - \frac{i}{N}) \begin{bmatrix} T & P \\ R & S \end{bmatrix} + \frac{i}{N} \begin{bmatrix} R & S \\ T & P \end{bmatrix} \quad (1)$$

where $T > R > P > S$. The payoff matrix $U(i)$ is a linear combination of the following two scenarios. When $i = N$, the game environment is in the replete state, both players obtain the payoff R for mutual cooperation. For mutual defection, both players receive the payoff P . If a player cooperates while its opponent defects, the cooperator obtain the S and the defector receive the payoff P . In the replete state, players are inclined to gain larger benefits from the overuse of common resources which results in the environmental degradation. The mutual defection is the only Nash equilibrium in this game. When $i = 0$, the game environment is in the degraded state, both players obtain the payoff T for mutual cooperation. For mutual defection, both players receive the payoff S . When a player cooperator plays against a defector, the cooperator obtain the P and the defector receive the payoff R . In the degraded state, it is better for players to cooperate in order to get higher payoffs. The over-exploitation of common resources motivate players to cooperate so that the environment could recover form the degraded state. The mutual cooperation is the only Nash equilibrium in this game.

The expected payoffs for cooperators and defectors in a finite population of size N with i cooperators are respectively

$$\pi_C(i) = \frac{1}{N-1} \left\{ \left[T + \frac{i}{N}(R-T) \right] (i-1) + \left[P + \frac{i}{N}(S-P) \right] (N-i) \right\} \quad (2)$$

$$\pi_D(i) = \frac{1}{N-1} \left\{ \left[R + \frac{i}{N}(T-R) \right] i + \left[S + \frac{i}{N}(P-S) \right] (N-i-1) \right\} \quad (3)$$

Then, we further extend the model to the generalized payoff matrix [28] as follows

$$U(i) = (1 - \frac{i}{N}) \begin{bmatrix} R_0 & S_0 \\ T_0 & P_0 \end{bmatrix} + \frac{i}{N} \begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix} \quad (4)$$

where i is the number of cooperators in the population. The payoff matrix is linear in the game environment state. When $i = 0$, the game environment is in the degraded state, and the payoffs R_0, S_0, T_0, P_0 are respectively reward for mutual cooperation, sucker's payoff, temptation to defect, and punishment for mutual defection. In this case, $R_0 > T_0$ and $S_0 > P_0$ and cooperation is the dominant strategy, which is the so-called harmony game. When $i = N$, the game environment is in the replete state, and the reward for mutual cooperation, sucker's payoff, temptation to defect, and punishment for mutual defection are R_1, S_1, T_1, P_1 respectively. In this case, the rank of the payoff is $T_1 > R_1 > P_1 > S_1$ and mutual defection is the unique Nash equilibrium, which corresponds to the prisoner's dilemma.

The expected payoffs for cooperators and defectors in a finite population of size N with i cooperators are respectively

$$\pi_C(i) = \frac{1}{N-1} \left\{ \left[R_0 + \frac{i}{N}(R_1-R_0) \right] (i-1) + \left[S_0 + \frac{i}{N}(S_1-S_0) \right] (N-i) \right\} \quad (5)$$

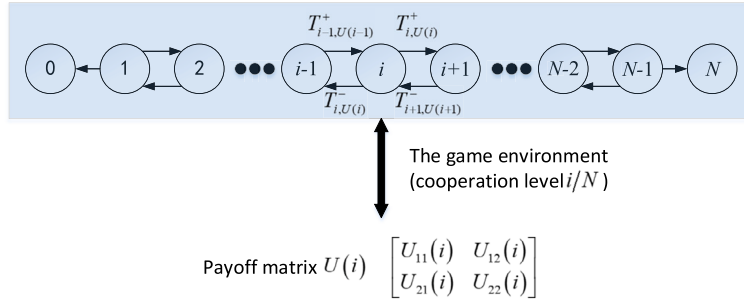


Fig. 1. The evolutionary dynamics with the game environment feedback in a finite population of N players. The game environment varies depending on the cooperation level of the population i/N , which influences the payoff matrix. For any given population state i , the number of cooperators will increase or decrease by one, or stay the same in one time step.

$$\pi_D(i) = \frac{1}{N-1} \left\{ \left[T_0 + \frac{i}{N}(T_1 - T_0) \right] i + \left[P_0 + \frac{i}{N}(P_1 - P_0) \right] (N-i-1) \right\} \quad (6)$$

The reproductive fitness of cooperators and defectors is given by

$$f_C(i) = 1 - \omega + \omega \pi_C(i) \quad (7)$$

$$f_D(i) = 1 - \omega + \omega \pi_D(i) \quad (8)$$

where selection intensity $\omega \in [0, 1]$ specifies the relative contributions of payoff to fitness [4,35,36]. Meanwhile, we assume that each entry of the payoff matrix is non-negative in order to ensure the positive fitness even for strong selection.

In the Moran process, one identical offspring of an individual is produced with the probability proportional to its fitness and replaces one randomly selected individual at every time step. The transition probabilities of the birth-death process are

$$T^+(i) = \frac{if_C(i)}{if_C(i) + (N-i)f_D(i)} \frac{N-i}{N} \quad (9)$$

$$T^-(i) = \frac{(N-i)f_D(i)}{if_C(i) + (N-i)f_D(i)} \frac{i}{N} \quad (10)$$

$$T^0(i) = 1 - T^+(i) - T^-(i) \quad (11)$$

The birth-death process has two absorbing states that $i = 0$ and $i = N$. The fixation probability that a single cooperator takes over the population of defectors is

$$\rho_c = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i)} \quad (12)$$

3. Results and discussion

3.1. Game-environment feedback with the specific payoff matrix

We first investigate the evolutionary game dynamics with the above-mentioned specific payoff matrix in Eq. (1). Under weak selection $\omega \ll 1$, the fixation probability can be approximated as (see the Appendix A for details)

$$\rho_c \approx \frac{1}{N + \left[\frac{2N-1}{6}(T-S) + \frac{N+1}{6}(R-P) - \frac{N(N-2)}{6}(P-S) \right] \omega} \quad (13)$$

When $N(N-2)(P-S) > (2N-1)(T-S) + (N+1)(R-P)$, we have $\rho_c > 1/N$, which means that selection favors cooperation. For $N = 2$, the fixation probability ρ_c is always less than $1/N$ because of $T > R > P > S$, which means that cooperation cannot be favored by selection. For the limit $N \rightarrow \infty$, the condition for selection favoring cooperation is equivalent to $P > S$, which means that cooperation is always favored by selection. When $N > \frac{2T-4S+P+R+\sqrt{4T^2+12S^2-3P^2+R^2-12TS-12RS+6PR+4TR}}{2(P-S)}$, we have $N\rho_c > 1$. As the population size N increases, selection is more favorable for cooperation as shown in Fig. 2.

We further consider the effect of selection intensity ω and population size N on the evolution of cooperation. In Fig. 3(a), for the small population ($N = 10$), the evolutionary rate $N\rho_c$ decreases first and then increases with the increase of ω , and high selection intensity favors cooperation replacing defection. For the medium-sized population ($N = 100$), $N\rho_c$ increases monotonically with the increase of ω , and selection always favors cooperation replacing defection. For the large population ($N = 1000$), selection opposes cooperation replacing defection in the intermediate range of ω where $N\rho_c < 1$. In the remaining range of ω , cooperation can be favored by selection. In Fig. 3(b), our results show that the growing population is more beneficial for the evolution of cooperation

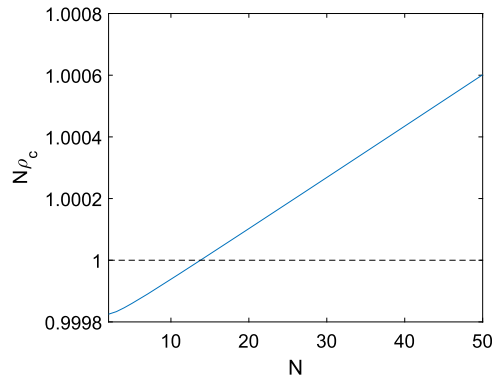


Fig. 2. The evolutionary rate $N\rho_c$ varies as function of population size N under weak selection $\omega = 0.0001$ when payoffs $R = 3$, $S = 0$, $T = 5$ and $P = 1$. For neutral drift, the evolutionary rate $N\rho_c = 1$. When $N\rho_c > 1$, selection favors cooperation replacing defection.

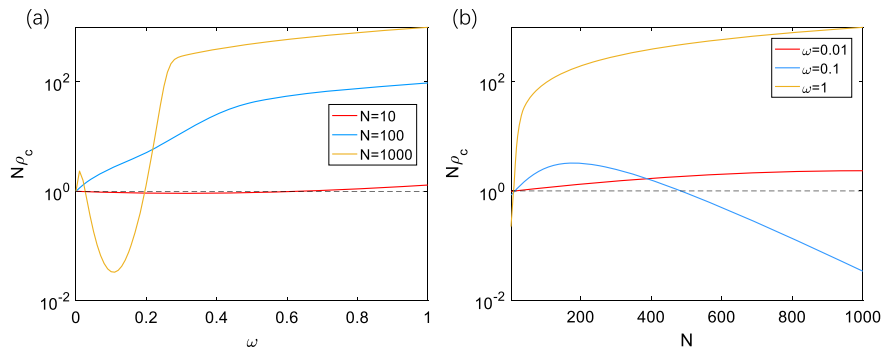


Fig. 3. (a) The evolutionary rate $N\rho_c$ varies as function of selection intensity ω for different population sizes $N = 10, 100$ and 1000 . (b) The evolutionary rate $N\rho_c$ varies as function of population size N under different selection intensity $\omega = 0.01, 0.1$ and 1 . The payoff parameters are $R = 3$, $S = 0$, $T = 5$ and $P = 1$.

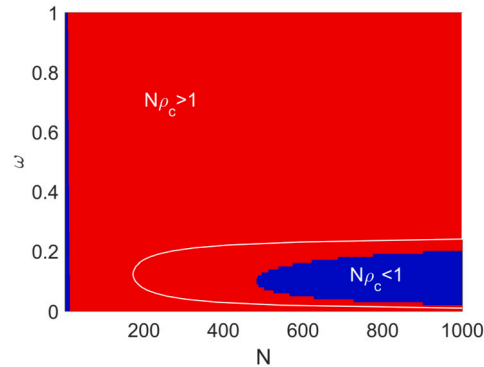


Fig. 4. $N - \omega$ phase diagrams illustrating the impacts of the population size and selection intensity on the condition for selection favoring cooperation. The red and blue regions denote the $N - \omega$ parameter regions where $N\rho_c > 1$ and $N\rho_c < 1$ respectively. The white line indicates the optimum population size for maximizing $N\rho_c > 1$ under different selection intensities. The payoff parameters are $R = 3$, $S = 0$, $T = 5$ and $P = 1$.

under low or high selection intensity ($\omega = 0.01$ or 1). However, for the intermediate selection intensity ($\omega = 0.1$), $N\rho_c$ increases first and then decreases with the increase of N , and medium-sized populations are in favor of the evolution of cooperation.

In Fig. 4, we present $N - \omega$ phase diagrams summarizing the $N - \omega$ parameter regions where selection favors cooperation. For extremely small-sized populations, selection always opposes cooperation replacing defection. On the contrary, selection always favors cooperation replacing defection in medium-sized populations. For large populations, the intermediate range of ω is adverse to the evolution of cooperation, and the ω parameter region where selection opposes cooperation replacing defection expands with the increase of populations. Furthermore, our results show that there exists optimum population sizes in the intermediate range of ω , which is consistent with Fig. 3(b). The optimum population size decreases first and then increases with the increase of ω .

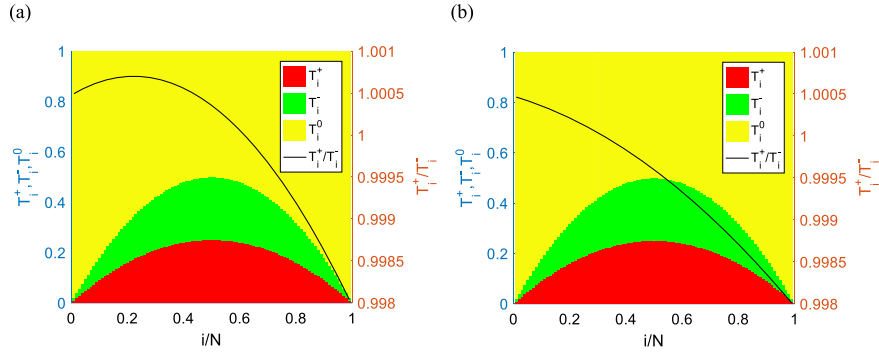


Fig. 5. The transition probabilities T_i^+ , T_i^- and T_i^0 when $N = 100$, $\omega = 0.001$, $R_1 = 3$, $S_1 = 0$, $T_1 = 5$, $P_1 = 1$, $R_0 = 8$, $S_0 = 5.5$, $P_0 = 5$, and $T_0 = 4$ (a) or 7 (b).

3.2. Game-environment feedback with the generalized payoff matrix

We further investigate the evolutionary game dynamics with the generalized payoff matrix in Eq. (4). Under weak selection $\omega \ll 1$, the fixation probability can be approximated as

$$\rho_c \approx \frac{1}{N + \left[\frac{N(N+1)}{12}(\Delta_{TR}^1 - \Delta_{RT}^0 + \Delta_{PS}^1) - \frac{N(N-1)}{4}\Delta_{SP}^0 + \frac{2N-1}{6}\Delta_{RP}^0 + \frac{N+1}{6}\Delta_{RP}^1 \right] \omega} \quad (14)$$

where $\Delta_{TR}^1 = T_1 - R_1$, $\Delta_{RT}^0 = R_0 - T_0$, $\Delta_{PS}^1 = P_1 - S_1$, $\Delta_{SP}^0 = S_0 - P_0$, $\Delta_{RP}^0 = R_0 - P_0$ and $\Delta_{RP}^1 = R_1 - P_1$ (see the Appendix A for the proof). Δ_{TR}^1 quantifies the incentive for the cooperator to defect in the replete state when facing the cooperative opponent. Δ_{RT}^0 implies the incentive for the defector to cooperate in the degraded state when facing the cooperative opponent. Δ_{PS}^1 quantifies the incentive for the cooperator to defect in the replete state when facing the defector opponent. Δ_{SP}^0 implies the incentive for the defector to cooperate in the degraded state when facing the defector opponent. Δ_{RP}^0 and Δ_{RP}^1 is the payoff differences between mutual cooperation and defection in the degraded and replete states respectively.

When $\rho_c > 1/N$, selection favors cooperation replacing defection. Thus, the condition that selection favors cooperation replacing defection is

$$2(2N-1)\Delta_{RP}^0 + 2(N+1)\Delta_{RP}^1 < 3N(N-1)\Delta_{SP}^0 - N(N+1)(\Delta_{TR}^1 - \Delta_{RT}^0 + \Delta_{PS}^1) \quad (15)$$

For the minimum population size $N = 2$, the condition for selection favoring cooperation is equivalent to $\Delta_{RP}^1 + \Delta_{RP}^0 < \Delta_{RT}^0 - \Delta_{TR}^1 + \Delta_{SP}^0 - \Delta_{PS}^1$. For the limit $N \rightarrow \infty$, we obtain $3\Delta_{SP}^0 - \Delta_{PS}^1 > \Delta_{TR}^1 - \Delta_{RT}^0$. Meanwhile, we find that $3\Delta_{SP}^0 - \Delta_{PS}^1 > \Delta_{TR}^1 - \Delta_{RT}^0$ if $\Delta_{RP}^1 + \Delta_{RP}^0 < \Delta_{RT}^0 - \Delta_{TR}^1 + \Delta_{SP}^0 - \Delta_{PS}^1$, which suggests that if selection favors cooperation in the minimum population ($N = 2$) then selection also favors cooperation in the large population ($N \rightarrow \infty$).

In Fig. 5(a), we present the transition probabilities when $2(2N-1)\Delta_{RP}^0 + 2(N+1)\Delta_{RP}^1 < 3N(N-1)\Delta_{SP}^0 - N(N+1)(\Delta_{TR}^1 - \Delta_{RT}^0 + \Delta_{PS}^1)$. The result shows that the transition probabilities T_i^+ and T_i^- firstly increase then decrease. At low frequencies of cooperators, the diminished likelihood of interactions among them hinders cooperation. However, paradoxically, the game itself tends to be more advantageous for cooperators, ultimately causing T_i^+/T_i^- to increase and exceed 1. As the frequency of cooperators increases, the heightened probability of interactions among them fosters cooperation. Nevertheless, the game itself become increasingly disadvantageous for cooperators, leading to a decline in the ratio T_i^+/T_i^- below 1. When $2(2N-1)\Delta_{RP}^0 + 2(N+1)\Delta_{RP}^1 > 3N(N-1)\Delta_{SP}^0 - N(N+1)(\Delta_{TR}^1 - \Delta_{RT}^0 + \Delta_{PS}^1)$, T_i^+/T_i^- decreases monotonically. For low frequencies of cooperators, the detrimental effect of the low likelihood of interactions among cooperators is stronger than the beneficial effect of the game itself. However, as the frequency of cooperators increases, the positive impact of the increased interactions among them is outweighed by the negative impact of the game itself.

For low values of Δ_{RT}^0 and Δ_{SP}^0 , selection always favors defection as shown in the red region of Fig. 6(a). The weak incentive for the defector to cooperate in the degraded state cannot facilitate the evolution of cooperation. However, in the green region, selection always favors cooperation when Δ_{RT}^0 is large enough. In the yellow region, whether selection favors cooperation depends on the population size. Selection opposes cooperation in small populations but favors cooperation with the increase of population, as shown in Fig. 6(b).

In Fig. 7, we show the impact of ω and N on the evolution of cooperation for different values of T_0 . When T_0 is high, cooperation is opposed by selection, and the rise in ω and N is detrimental to the evolution of cooperation. On the contrary, when T_0 is low, cooperation is favored by selection, and the rise in ω and N is beneficial for the evolution of cooperation. For intermediate T_0 , small population sizes are detrimental to the emergence of cooperation. Large population sizes are highly favorable for cooperation under low selection intensity. However, with the increase of selection intensity, intermediate population sizes are highly favorable for cooperation.

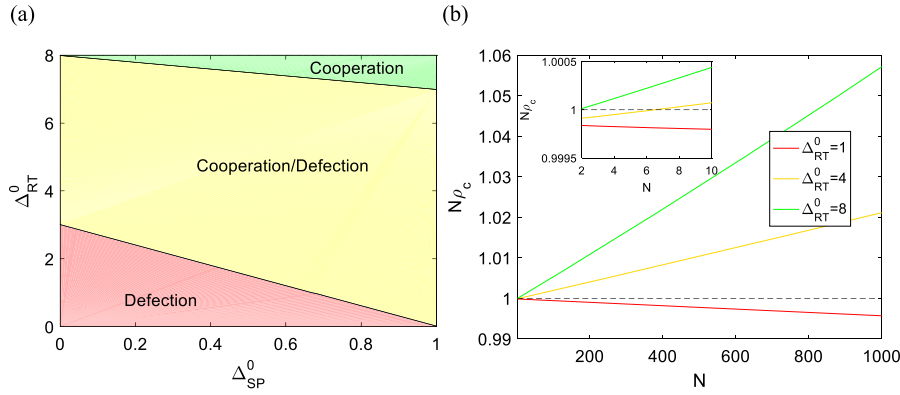


Fig. 6. (a) $\Delta_{SP}^0 - \Delta_{RT}^0$ phase diagrams illustrating the impacts of different combinations of payoffs on the condition for selection favoring cooperation under weak selection. The red and green regions denote the parameter condition that selection favors defection and cooperation respectively. In the yellow region, either defection or cooperation is possible to be favored by selection. (b) The evolutionary rate $N\rho_c$ varies as function of population size N for $\Delta_{RT}^0 = 1, 4$ and 8 when $\Delta_{SP}^0 = 0.5$ and $\omega = 0.0001$. The other parameters are $\Delta_{TR}^1 = 2$, $\Delta_{PS}^1 = 1$, $\Delta_{RP}^1 = 2$ and $\Delta_{RP}^0 = 3$.

Fig. 8 shows the effect of selection intensity ω and population size N on the evolution of cooperation for intermediate T_0 . For extremely small-sized populations, cooperation can never be favored by selection. Under low selection intensity, the larger the population size, the more favorable it is for the evolution of cooperation. As ω increases, intermediate population sizes are highly favorable for cooperation, and the optimum population size decreases monotonically, which is consistent with Fig. 7(c) and (d).

3.3. The time-scale of feedbacks between strategies and environment

In this section, we focus on the role of the time-scale of feedbacks between strategies and environment in the fixation probability of cooperation. We can rewrite payoff matrixes in Eq. (1) and Eq. (4) respectively as

$$U(i) = (1 - \epsilon \frac{i}{N}) \begin{bmatrix} T & P \\ R & S \end{bmatrix} + \epsilon \frac{i}{N} \begin{bmatrix} R & S \\ T & P \end{bmatrix}, U(i) = (1 - \epsilon \frac{i}{N}) \begin{bmatrix} R_0 & S_0 \\ T_0 & P_0 \end{bmatrix} + \epsilon \frac{i}{N} \begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix} \quad (16)$$

where $\epsilon \in (0, 1)$ is the relative speed between strategic and environmental dynamics and the game environment is $\epsilon \frac{i}{N}$. $\epsilon \in (0, 1)$ ensures that the game environment is confined to the domain $[0, 1]$.

In the case of the specific payoff matrix, the fixation probability under weak selection can be approximated as (see the Appendix B for details)

$$\rho_c \approx \frac{1}{N + \left[\frac{3N - (N+1)\epsilon}{6}(T - S) + \frac{\epsilon(N+1)}{6}(R - P) - \frac{N[4N - 2(N+1)\epsilon - 2]}{12}(P - S) - \frac{N(N+1)(1-\epsilon)}{6}(T - R) \right] \omega}. \quad (17)$$

We let $F(\epsilon) = \frac{3N - (N+1)\epsilon}{6}(T - S) + \frac{\epsilon(N+1)}{6}(R - P) - \frac{N[4N - 2(N+1)\epsilon - 2]}{12}(P - S) - \frac{N(N+1)(1-\epsilon)}{6}(T - R)$, then $\frac{\partial F(\epsilon)}{\partial \epsilon} = \frac{(N+1)(N-1)}{6}(T - R + P - S) > 0$ which indicates that $F(\epsilon)$ monotonically increases with ϵ . Therefore, ρ_c monotonically decreases with ϵ . If $N(N+1)(2P - 2S + T - R) \leq 3N(T - 2S + P)$, ρ_c is always smaller than $1/N$. If $3N(T - 2S + P) < N(N+1)(2P - 2S + T - R) \leq 3N(T - 2S + P) + (N+1)(N-1)(P - S + T - R)$, there exists $\epsilon^* = \frac{N(N+1)(2P - 2S + T - R) - 3N(T - 2S + P)}{(N+1)(N-1)(P - S + T - R)}$ such that $\rho_c < 1/N$ for $\epsilon < \epsilon^*$. If $N(N+1)(2P - 2S + T - R) > 3N(T - 2S + P) + (N+1)(N-1)(P - S + T - R)$, ρ_c is always larger than $1/N$.

In the case of the generalized payoff matrix, the fixation probability under weak selection can be approximated as (see the Appendix B for details)

$$\rho_c \approx \frac{1}{N + \left[\frac{\epsilon N(N+1)}{12}(\Delta_{TR}^1 + \Delta_{PS}^1) - \frac{(2-\epsilon)N(N+1)}{12}\Delta_{RT}^0 - \frac{N[4N - 2(N+1)\epsilon - 2]}{12}\Delta_{SP}^0 + \frac{3N - (N+1)\epsilon}{6}\Delta_{RP}^0 + \frac{\epsilon(N+1)}{6}\Delta_{RP}^1 \right] \omega}. \quad (18)$$

We let $G(\epsilon) = \frac{\epsilon N(N+1)}{12}(\Delta_{TR}^1 + \Delta_{PS}^1) - \frac{(2-\epsilon)N(N+1)}{12}\Delta_{RT}^0 - \frac{N[4N - 2(N+1)\epsilon - 2]}{12}\Delta_{SP}^0 + \frac{3N - (N+1)\epsilon}{6}\Delta_{RP}^0 + \frac{\epsilon(N+1)}{6}\Delta_{RP}^1$, then $\frac{\partial G(\epsilon)}{\partial \epsilon} = \frac{N(N+1)}{12}(\Delta_{TR}^1 + \Delta_{PS}^1 + \Delta_{RT}^0 + \Delta_{SP}^0) + \frac{N+1}{6}(\Delta_{RP}^1 - \Delta_{RP}^0)$. When $N(\Delta_{TR}^1 + \Delta_{PS}^1 + \Delta_{RT}^0 + \Delta_{SP}^0) + 2(\Delta_{RP}^1 - \Delta_{RP}^0) > 0$, $G(\epsilon)$ monotonically increases with ϵ , and ρ_c monotonically decreases with ϵ . If $3N\Delta_{RP}^0 - N(N+1)\Delta_{RT}^0 - N(2N-1)\Delta_{SP}^0 > 0$, ρ_c is always smaller than $1/N$. If $3N\Delta_{RP}^0 - N(N+1)\Delta_{RT}^0 - N(2N-1)\Delta_{SP}^0 < 0$ and $N(N+1)\Delta_{RT}^0 + 3N(N-1)\Delta_{SP}^0 - 2(2N-1)\Delta_{RP}^0 > N(N+1)(\Delta_{TR}^1 + \Delta_{PS}^1) + 2(N+1)\Delta_{RP}^1$, there exists $\epsilon^* = \frac{N(N+1)\Delta_{RT}^0 + N(2N-1)\Delta_{SP}^0 - 3N\Delta_{RP}^0}{N(N+1)(\Delta_{TR}^1 + \Delta_{PS}^1 + \Delta_{RT}^0 + \Delta_{SP}^0) + 2(N+1)(\Delta_{RP}^1 - \Delta_{RP}^0)}$ such that $\rho_c < 1/N$ for $\epsilon < \epsilon^*$. If $3N\Delta_{RP}^0 - N(N+1)\Delta_{RT}^0 - N(2N-1)\Delta_{SP}^0 < 0$ and $N(N+1)\Delta_{RT}^0 + 3N(N-1)\Delta_{SP}^0 - 2(2N-1)\Delta_{RP}^0 > N(N+1)(\Delta_{TR}^1 + \Delta_{PS}^1) + 2(N+1)\Delta_{RP}^1$, ρ_c is always larger than $1/N$.

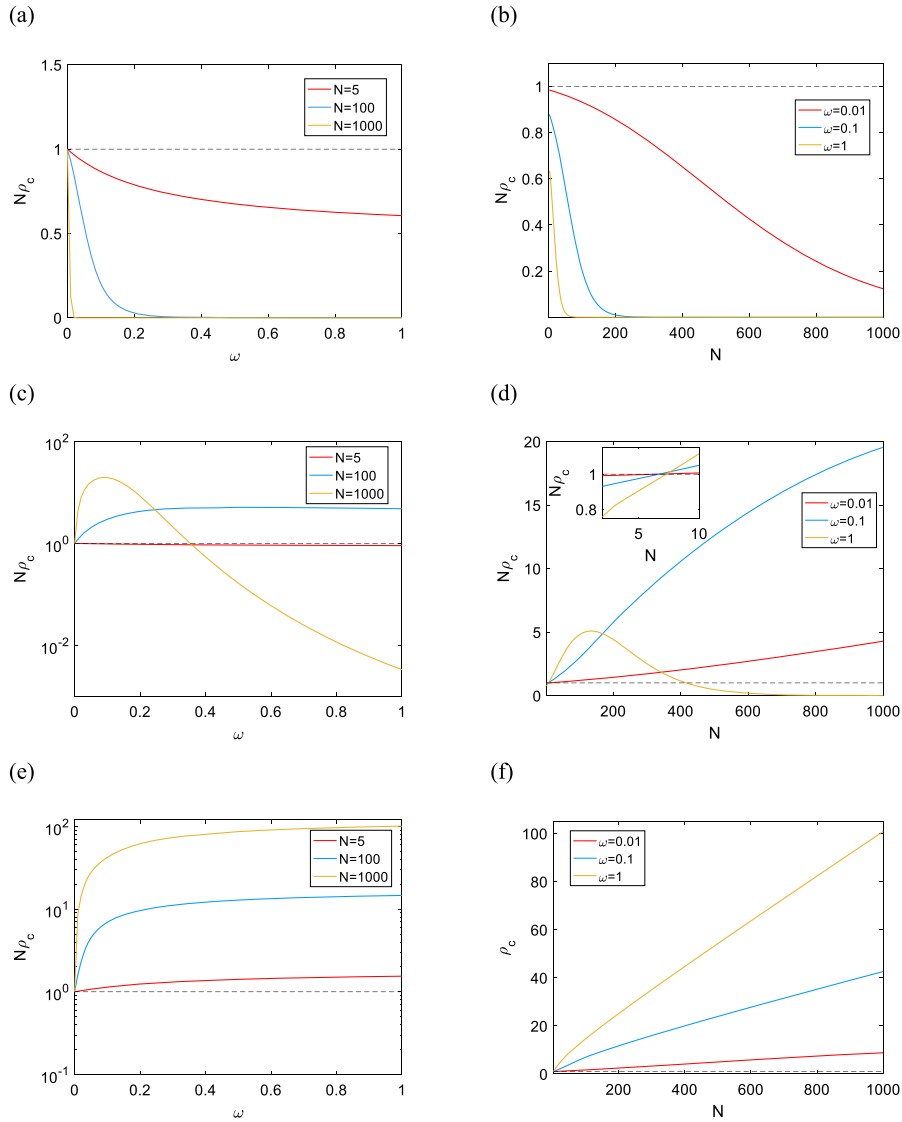


Fig. 7. The evolutionary rate $N\rho_c$ varies as function of selection intensity ω for different population sizes $N = 10, 100$ and 1000 when (a) $T_0 = 7$, (c) $T_0 = 4$ and (e) $T_0 = 0$. The evolutionary rate $N\rho_c$ varies as function of population size N under different selection intensity $\omega = 0.01, 0.1$ and 1 when (b) $T_0 = 7$, (d) $T_0 = 4$ and (f) $T_0 = 0$. The other parameters are $R_1 = 3$, $S_1 = 0$, $T_1 = 5$, $P_1 = 1$, $R_0 = 8$, $S_0 = 5.5$ and $P_0 = 5$.

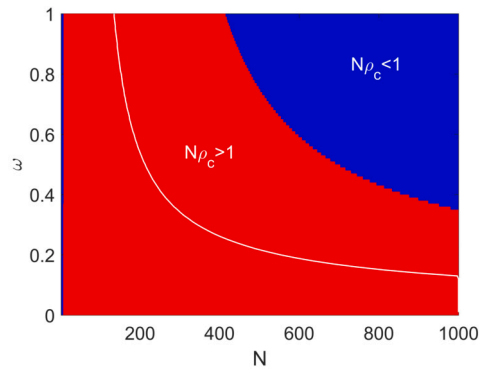


Fig. 8. $N - \omega$ phase diagrams illustrating the impacts of the population size and selection intensity on the condition for selection favoring cooperation when $T_0 = 4$. The red and blue regions denote the $N - \omega$ parameter regions where $N\rho_c > 1$ and $N\rho_c < 1$ respectively. The white line indicates the optimum population size for maximizing $N\rho_c > 1$ under different selection intensities. The other parameters are $R_1 = 3$, $S_1 = 0$, $T_1 = 5$, $P_1 = 1$, $R_0 = 8$, $S_0 = 5.5$ and $P_0 = 5$.

When $N(\Delta_{TR}^1 + \Delta_{PS}^1 + \Delta_{RT}^0 + \Delta_{SP}^0) + 2(\Delta_{RP}^1 - \Delta_{RP}^0) < 0$, $G(\epsilon)$ monotonically decreases with ϵ , and ρ_c monotonically increases with ϵ . If $3N\Delta_{RP}^0 - N(N+1)\Delta_{RT}^0 - N(2N-1)\Delta_{SP}^0 < 0$, ρ_c is always greater than $1/N$. If $3N\Delta_{RP}^0 - N(N+1)\Delta_{RT}^0 - N(2N-1)\Delta_{SP}^0 > 0$ and $N(N+1)\Delta_{RT}^0 + 3N(N-1)\Delta_{SP}^0 - 2(2N-1)\Delta_{RP}^0 > N(N+1)(\Delta_{TR}^1 + \Delta_{PS}^1) + 2(N+1)\Delta_{RP}^1$, there exists $\epsilon^* = \frac{N(N+1)\Delta_{RT}^0 + N(2N-1)\Delta_{SP}^0 - 3N\Delta_{RP}^0}{N(N+1)(\Delta_{TR}^1 + \Delta_{PS}^1) + \Delta_{RT}^0 + \Delta_{SP}^0 + 2(N+1)(\Delta_{RP}^1 - \Delta_{RP}^0)}$ such that $\rho_c < 1/N$ for $\epsilon > \epsilon^*$. If $3N\Delta_{RP}^0 - N(N+1)\Delta_{RT}^0 - N(2N-1)\Delta_{SP}^0 > 0$ and $N(N+1)\Delta_{RT}^0 + 3N(N-1)\Delta_{SP}^0 - 2(2N-1)\Delta_{RP}^0 < N(N+1)(\Delta_{TR}^1 + \Delta_{PS}^1) + 2(N+1)\Delta_{RP}^1$, ρ_c is always smaller than $1/N$.

4. Conclusions

In this paper, we investigate the fixation of cooperation in finite populations under game environment feedback. We model the Moran process with environmental feedback and derive the condition for promoting cooperation in the cases of the specific and generalized payoff matrixes by theoretical and numerical analysis. In the case of the specific payoff matrix, cooperation is never favored by selection in extremely small-sized populations. However, as the population size increases, cooperation can be favored by selection. In the case of the generalized payoff matrix, cooperation cannot emerge irrespective of the selection intensity and population size when the incentives for the defector to cooperate in the degraded state Δ_{SP}^0 and Δ_{RT}^0 are low. When Δ_{RT}^0 is large enough, selection always favor cooperation regardless of the selection intensity and population size. For the intermediate Δ_{RT}^0 , selection cannot favor the emergence of cooperation in extremely small-sized populations, which is the same as the case of the specific payoff matrix.

Our analysis focuses on well-mixed populations of finite size, which neglects the effect of the population structure [37–39]. In the future study, we can further extend the Moran process to structured populations, which will enrich the mechanism of network reciprocity [40] from the perspective of environmental feedback.

Data availability

No data was used for the research described in the article.

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Appendix A

For weak selection, we have

$$\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \approx \sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \Big|_{\omega=0} + \omega \frac{\partial}{\partial \omega} \left[\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \right] \Big|_{\omega=0} \quad (\text{A.1})$$

$$\text{where } \sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \Big|_{\omega=0} = N-1.$$

Meanwhile, we have

$$\frac{\partial}{\partial \omega} \left[\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \right] \Big|_{\omega=0} = \sum_{k=1}^{N-1} \frac{(\prod_{i=1}^k f_D(i))' \prod_{i=1}^k f_C(i) - \prod_{i=1}^k f_D(i) \prod_{i=1}^k f_C(i)'}{(\prod_{i=1}^k f_C(i))^2} \Big|_{\omega=0} \quad (\text{A.2})$$

$$= \sum_{k=1}^{N-1} \sum_{i=1}^k [\pi_D(i) - \pi_C(i)]$$

In the case of the specific payoff matrix, we can obtain

$$\begin{aligned} \frac{\partial}{\partial \omega} \left[\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \right] \Big|_{\omega=0} &= \sum_{k=1}^{N-1} \sum_{i=1}^k [\pi_D(i) - \pi_C(i)] \\ &= \frac{1}{N-1} \sum_{i=1}^{N-1} \left[i(N-i)R + \frac{i^2(N-i)}{N}(T-R) + (N-i-1)(N-i)S + \frac{i(N-i-1)(N-i)}{N}(P-S) \right. \\ &\quad \left. - (i-1)(N-i)T - \frac{i(i-1)(N-i)}{N}(R-T) - (N-i)^2P - \frac{i(N-i)^2}{N}(S-P) \right] \end{aligned}$$

$$\begin{aligned}
&= \frac{N(N+1)}{12}(T+R) + \frac{N-2}{12}[(N+1)P + (3N-1)S] \\
&\quad - \frac{N-2}{12}[(N+1)R + (N-1)T] - \frac{N}{12}[(N+1)S + 3(N-1)P] \\
&= \frac{2N-1}{6}(T-S) + \frac{N+1}{6}(R-P) - \frac{N(N-2)}{6}(P-S)
\end{aligned} \tag{A.3}$$

Therefore, the fixation probability can be approximated as

$$\begin{aligned}
\rho_c &\approx \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \Big|_{\omega=0} + \omega \frac{\partial}{\partial \omega} \left[\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \right] \Big|_{\omega=0}} \\
&= \frac{1}{1 + N - 1 + \left[\frac{2N-1}{6}(T-S) + \frac{N+1}{6}(R-P) - \frac{N(N-2)}{6}(P-S) \right] \omega} \\
&= \frac{1}{N + \left[\frac{2N-1}{6}(T-S) + \frac{N+1}{6}(R-P) - \frac{N(N-2)}{6}(P-S) \right] \omega}
\end{aligned} \tag{A.4}$$

In the case of the generalized payoff matrix, we can obtain

$$\begin{aligned}
&\frac{\partial}{\partial \omega} \left[\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \right] \Big|_{\omega=0} = \sum_{k=1}^{N-1} \sum_{i=1}^k [\pi_D(i) - \pi_C(i)] \\
&= \frac{1}{N-1} \sum_{i=1}^{N-1} \left[i(N-i)T_0 + \frac{i^2(N-i)}{N}(T_1 - T_0) + (N-i-1)(N-i)P_0 + \frac{i(N-i-1)(N-i)}{N}(P_1 - P_0) \right. \\
&\quad \left. - (i-1)(N-i)R_0 - \frac{i(i-1)(N-i)}{N}(R_1 - R_0) - (N-i)^2S_0 - \frac{i(N-i)^2}{N}(S_1 - S_0) \right] \\
&= \frac{N(N+1)}{12}(T_1 + T_0) + \frac{N-2}{12}[(N+1)P_1 + (3N-1)P_0] \\
&\quad - \frac{N-2}{12}[(N+1)R_1 + (N-1)R_0] - \frac{N}{12}[(N+1)S_1 + 3(N-1)S_0] \\
&= \frac{N(N+1)}{12}(\Delta_{TR}^1 - \Delta_{RT}^0 + \Delta_{PS}^1) - \frac{N(N-1)}{4}\Delta_{SP}^0 + \frac{2N-1}{6}\Delta_{RP}^0 + \frac{N+1}{6}\Delta_{RP}^1
\end{aligned} \tag{A.5}$$

where $\Delta_{TR}^1 = T_1 - R_1$, $\Delta_{RT}^0 = R_0 - T_0$, $\Delta_{PS}^1 = P_1 - S_1$, $\Delta_{SP}^0 = S_0 - P_0$, $\Delta_{RP}^0 = R_0 - P_0$ and $\Delta_{RP}^1 = R_1 - P_1$.

Therefore, we have

$$\rho_c \approx \frac{1}{N + \left[\frac{N(N+1)}{12}(\Delta_{TR}^1 - \Delta_{RT}^0 + \Delta_{PS}^1) - \frac{N(N-1)}{4}\Delta_{SP}^0 + \frac{2N-1}{6}\Delta_{RP}^0 + \frac{N+1}{6}\Delta_{RP}^1 \right] \omega} \tag{A.6}$$

Appendix B

We consider the time-scale difference between strategic and environmental dynamics. In the case of the specific payoff matrix, we can obtain

$$\begin{aligned}
&\frac{\partial}{\partial \omega} \left[\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \right] \Big|_{\omega=0} = \sum_{k=1}^{N-1} \sum_{i=1}^k [\pi_D(i) - \pi_C(i)] \\
&= \frac{1}{N-1} \sum_{i=1}^{N-1} \left[i(N-i)R + \epsilon \frac{i^2(N-i)}{N}(T-R) + (N-i-1)(N-i)S + \epsilon \frac{i(N-i-1)(N-i)}{N}(P-S) \right. \\
&\quad \left. - (i-1)(N-i)T - \epsilon \frac{i(i-1)(N-i)}{N}(R-T) - (N-i)^2P - \epsilon \frac{i(N-i)^2}{N}(S-P) \right] \\
&= \frac{3N-(N+1)\epsilon}{6}(T-S) + \frac{\epsilon(N+1)}{6}(R-P) - \frac{N[4N-2(N+1)\epsilon-2]}{12}(P-S) \\
&\quad - \frac{N(N+1)(1-\epsilon)}{6}(T-R)
\end{aligned} \tag{B.1}$$

Therefore, the fixation probability under weak selection for the specific payoff matrix is

$$\rho_c \approx \frac{1}{N + \left[\frac{3N-(N+1)\epsilon}{6}(T-S) + \frac{\epsilon(N+1)}{6}(R-P) - \frac{N[4N-2(N+1)\epsilon-2]}{12}(P-S) - \frac{N(N+1)(1-\epsilon)}{6}(T-R) \right] \omega} \tag{B.2}$$

In the case of the generalized payoff matrix, we can obtain

$$\begin{aligned}
 & \frac{\partial}{\partial \omega} \left[\sum_{k=1}^{N-1} \prod_{i=1}^k f_D(i)/f_C(i) \right] \bigg|_{\omega=0} = \sum_{k=1}^{N-1} \sum_{i=1}^k [\pi_D(i) - \pi_C(i)] \\
 & = \frac{1}{N-1} \sum_{i=1}^{N-1} \left[i(N-i)T_0 + \epsilon \frac{i^2(N-i)}{N} (T_1 - T_0) + (N-i-1)(N-i)P_0 + \epsilon \frac{i(N-i-1)(N-i)}{N} (P_1 - P_0) \right. \\
 & \quad \left. - (i-1)(N-i)R_0 - \epsilon \frac{i(i-1)(N-i)}{N} (R_1 - R_0) - (N-i)^2 S_0 - \epsilon \frac{i(N-i)^2}{N} (S_1 - S_0) \right] \\
 & = \frac{N(N+1)(2-\epsilon)}{12} T_0 + \frac{N(N+1)\epsilon}{12} T_1 + \frac{N-2}{12} [\epsilon(N+1)P_1 + (4N-\epsilon N-\epsilon)P_0] \\
 & \quad - \frac{N-2}{12} [\epsilon(N+1)R_1 + (2N-\epsilon N-\epsilon)R_0] - \frac{N}{12} [\epsilon(N+1)S_1 + (4N-\epsilon N-2-\epsilon)S_0] \\
 & = \frac{\epsilon N(N+1)}{12} (\Delta_{TR}^1 + \Delta_{PS}^1) - \frac{(2-\epsilon)N(N+1)}{12} \Delta_{RT}^0 - \frac{N[4N-(N+1)\epsilon-2]}{12} \Delta_{SP}^0 \\
 & \quad + \frac{3N-(N+1)\epsilon}{6} \Delta_{RP}^0 + \frac{\epsilon(N+1)}{6} \Delta_{RP}^1
 \end{aligned} \tag{B.3}$$

Therefore, we have

$$\rho_c \approx \frac{1}{N + \left[\frac{\epsilon N(N+1)}{12} (\Delta_{TR}^1 + \Delta_{PS}^1) - \frac{(2-\epsilon)N(N+1)}{12} \Delta_{RT}^0 - \frac{N[4N-(N+1)\epsilon-2]}{12} \Delta_{SP}^0 + \frac{3N-(N+1)\epsilon}{6} \Delta_{RP}^0 + \frac{\epsilon(N+1)}{6} \Delta_{RP}^1 \right] \omega} \tag{B.4}$$

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