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Article

High Cost of Survival Promotes the Evolution of Cooperation

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Abstract: Living organisms expend energy to sustain survival, a process which is reliant on consuming resources—termed here as the “cost of survival”. In the Prisoner’s Dilemma (PD), a classic model of social interaction, individual payoffs depend on choices to either provide benefits to others at a personal cost (cooperate) or exploit others to maximize personal gain (defect). We demonstrate that in an iterated Prisoner’s Dilemma (IPD), a simple “Always Cooperate” (ALLC) strategy evolves and remains evolutionarily stable when the cost of survival is sufficiently high, meaning exploited cooperators have a low probability of survival. We derive a rule for the evolutionary stability of cooperation, $\boldsymbol{x/z} > T/R$, where x represents the duration of mutual cooperation, z the duration of exploitation, T the defector’s free-riding payoff, and R the payoff for mutual cooperation. This finding suggests that higher survival costs can enhance social welfare by selecting for cooperative strategies.

Keywords: evolution of cooperation; prisoner’s dilemma; altruism; survival; reciprocity

1. Introduction

Cooperation, where individuals act to benefit others at a personal cost, lies at the heart of many biological, social, and economic systems. Despite its ubiquity, the evolution of cooperative behavior presents a puzzle for biologists and social scientists. If cooperation imposes a cost on the individual while benefiting others, how does it persist in the face of natural selection, which typically favors selfish behaviors? Foundational theories by Hamilton (1964) and Trivers (1971) frame this dilemma, emphasizing that cooperation provides benefits to the population at the expense of individual self-interest. This tension is commonly captured in the Prisoner’s Dilemma (PD), a widely studied model of social interaction (Axelrod, 1984; Axelrod & Hamilton, 1981; Nowak, 2006).

The PD game pits two players against each other with a choice to either cooperate or defect. Mutual cooperation yields a substantial payoff (R, a “reward” for mutual cooperation) for both players, representing shared benefits. Mutual defection results in a lower payoff (P, a “punishment” for mutual defection) for each player. Temptation to defect (T) occurs when one player defects while the other cooperates, granting the defector the highest payoff in the game at the expense of the cooperator, who receives the game’s lowest payoff (S). The dilemma arises because the payoffs are structured such that $T > R > P > S$. This makes defection the dominant strategy for rational individuals, as defecting always produces a higher personal payoff regardless of the opponent’s choice. However, such behavior leads to a suboptimal outcome of mutual defection (recall that $P < R$).

Several evolutionary mechanisms have been proposed to resolve the tension between individual and group interests in the PD game. Kin selection argues that individuals are more likely to cooperate with genetic relatives, since it promotes the spread of shared genes (Hamilton, 1964). Direct reciprocity states that individuals cooperate with those who have

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cooperated with them in the past (Axelrod & Hamilton, 1981; Trivers, 1971). Multilevel selection approaches suggest that groups of cooperators will outperform groups of defectors, favoring the evolution of cooperative behaviors at the group level (Bowles, 2006; Traulsen & Nowak, 2006). Other theories highlight the role of reputation and indirect reciprocity, where cooperation is rewarded by others based on perceived altruism (Nowak & Sigmund, 2005). These and other frameworks provide various insights by introducing complex strategies (Johnson & Smirnov, 2012; Rabin, 1993), spatial structures (Ohtsuki et al., 2006), decentralized punishment of defectors (Fehr & Gächter, 2002; Smirnov et al., 2010), entrance costs (Salahshour, 2021), and other external mechanisms (Johnson & Smirnov, 2021).

This paper extends the PD framework by introducing metabolic costs of survival in an iterated PD game (IPD), where players engage in repeated interactions over multiple rounds. In this context, survival depends on the payoffs players receive in each round. If a player's payoff in a given round falls below a survival threshold, the player "exits" the game, leaving the other player without a partner in future rounds. This dynamic introduces an endogenous link between a player's strategy and the other player's survival. The survival cost can be interpreted in various ways: for firms, it represents the costs necessary to avoid bankruptcy; for nation-states, it reflects the resources required to maintain sovereignty and territorial integrity; for biological organisms, it corresponds to the energy or resources needed to sustain life. A player's utility, therefore, is determined by the game payoffs weighted by the probability of future interactions, based on both players' payoffs and the cost of survival.

The inclusion of survival costs produces a seemingly counterintuitive result: cooperation can be evolutionarily stable in high-cost environments, where the metabolic threshold is substantial. In such settings, exploited cooperators (those receiving S) are unlikely to survive, reducing opportunities for defectors to free ride. Mutual cooperators (those receiving R), on the other hand, have a higher likelihood of survival, enabling long-lasting cooperative interactions. Conversely, in low-cost environments, where survival is easily achieved, defection becomes dominant, leading to a breakdown of cooperation. These findings reveal that resource scarcity can foster cooperation, aligning with empirical observations that communities facing harsh conditions often develop cooperative social structures (Crespi, 2001; Velicer, 2003).

The model potentially offers an insight into the relationship between cooperation and longevity. Species characterized by cooperative behaviors and group living often exhibit greater longevity and higher survival rates (Clutton-Brock, 2002; Kokko & Johnstone, 1999). Traditional explanations suggest that longevity facilitates cooperation by enabling repeated interactions and the development of social bonds (Hatchwell & Komdeur, 2000; Ridley et al., 2005). However, the current model challenges this view, proposing that longevity may be a consequence, not a cause, of cooperation. In high-cost environments, cooperation enhances survival probabilities, indirectly promoting longer lifespans. Another implication of the model is that greater metabolic costs can improve population fitness by promoting cooperation. While high survival costs decrease individual survival probabilities, they reduce the duration of exploitative interactions, curbing the spread of defection, and select for cooperative strategies, leading to higher overall social welfare.

2. Theoretical Context

The general idea that harsh environments can promote the evolution of cooperation is not novel (Lima, 1989; Salahshour, 2023; Smaldino et al., 2013; Zhang & Lu, 2024). However, the present model has several distinct features. It introduces a simple yet novel mechanism for cooperation and shows that naive unconditional cooperation ("always cooperate") can evolve and remain evolutionary stable among unrelated individuals when the probability of survival is a function of the intermediate game payoffs. The model does not rely on the other theories explaining cooperation that are mentioned above; it assumes no cognitive capacity, memory of past interactions, or spatial/network structure. Cooperation in this framework emerges as a direct consequence of survival pressures rather than through learned behaviors or social institutions.

Theoretically, the addition of mortality to the Prisoner's Dilemma (PD) game may resemble the introduction of the "No-Play option" (Aktipis, 2004; Batali & Kitcher, 1995; Eshel & Cavalli-Sforza, 1982). In such models, individuals can *voluntarily* withdraw from further interactions when cooperation breaks down—often to *secure* a payoff higher than the one they would receive if they continued playing and risked being exploited. Crucially, the withdrawing player preserves utility by exiting. This type of PD game is also known as a Voluntary Prisoner's Dilemma (VPD) game (Adetowubo & Zhang, 2024; Szabó & Hauert, 2002).

In contrast, the exit in our model is not voluntary. When a player's payoff in a round is insufficient to cover the metabolic cost M, the player is forced out of the game (e.g., by dying or going bankrupt) with no payoff preservation. This exit occurs at a payoff strictly lower than even the "punishment" outcome P. Being exploited and exiting the game is the *worst possible outcome* for a player. Unlike standard "No-Play" models, the involuntary exit here does not yield a comparatively better payoff; rather, the individual is effectively removed from the population and gains no further advantage.

Therefore, while both mechanisms reduce opportunities for defectors to free ride, they do so by fundamentally different means. In No-Play models, a player chooses to exit to avoid exploitation. In our model, exiting is compelled by a failure to survive. Because forced mortality involves neither strategic foresight nor voluntary choice, it cannot be equated with a "No-Play" option. Rather, it reflects the real-world notion that insufficient resources (biological, economic, or otherwise) can abruptly end an individual's or organization's ability to continue interacting.

One early model addressed the connection between game payoffs and survival. Lima (1989) proposed that survival in evolutionary games should depend on payoffs, suggesting that such a link fosters mutual dependency and promotes the evolutionary stability of cooperation. Lima's numerical analysis of the two-player PD game demonstrated how this assumption could enhance cooperative stability. The present model advances this concept further. It develops an analytical framework to clarify the mechanism of mutual dependency through a metabolic cost and derives closed-form conditions for the evolutionary stability of cooperation. Our analysis demonstrates how mortality can act as a powerful mechanism to sustain cooperation in harsh environments.

In a similar qualitative argument, Tomasello et al. (2012) introduced the Interdependence Hypothesis, emphasizing mutualistic collaboration as a cornerstone of human cooperation. They argued that humans' unique forms of collaboration emerged from ecological pressures that necessitated interdependence, particularly in small-scale foraging contexts. Their model highlights two evolutionary steps: small-scale collaboration, where survival depends on shared effort, and large-scale cooperation, where cultural norms and institutions maintain group cohesion. While Tomasello et al.'s work focuses on the cognitive and cultural dimensions of cooperation, such as joint intentionality and social norms, our model complements this by showing how forced mortality and metabolic costs—independent of cultural or cognitive mechanisms—can promote cooperation.

Smaldino et al. (2013) further explored the role of environmental adversity in the evolution of cooperation. Using a spatial agent-based model, they demonstrated that harsh environments favor cooperative phenotypes, as only groups with a critical mass of cooperators can survive and reproduce in the long term. However, they also noted that environmental costs temporarily increase defectors' advantages in mixed populations, creating tension between short-term exploitation and long-term survival. This finding aligns with our model's results, where high metabolic costs eliminate exploited cooperators and decrease defectors' evolutionary advantage. Unlike Smaldino et al., who emphasize variable population sizes and socio-spatial dynamics, our model isolates survival thresholds as the primary mechanism, providing a simple explanation of how mortality pressures shape cooperative stability.

Another paper produced a similar argument, albeit through a different analytical approach. Salahshour (2023) examined cooperation through the lens of public goods games in resource-scarce environments, revealing how density fluctuations and population viscosity can bolster cooperation. In such contexts, cooperators achieve higher expected payoffs despite being vulnerable to local exploitation by defectors. While our model does not explicitly incorporate population viscosity, it shares the emphasis on survival as a key driver of cooperation. By focusing on immediate survival thresholds rather than density fluctuations, our approach offers a complementary perspective, establishing the direct link between game payoffs and individual survival.

More recently, Zhang and Lu (2024) introduced a spatial PD model incorporating reward mechanisms as an adaptive strategy for defectors under survival pressure. Their results suggest that defectors can temporarily adopt rewarding behaviors to attract cooperators, indirectly promoting group-level cooperation. However, once defectors secure sufficient cooperators, they revert to exploitation, rendering rewards an intermediate, transient strategy. Our model differs by demonstrating that cooperation can emerge without the need for adaptive strategies like rewards. Instead, the inherent dynamics of survival thresholds and metabolic costs naturally stabilize cooperation.

These studies provide a rich foundation for understanding the evolution of cooperation in the context of challenges to survival, highlighting distinct mechanisms—cognitive and cultural evolution (Tomasello et al., 2012), environmental adversity (Smaldino et al., 2013), density fluctuations (Salahshour, 2023), and adaptive strategies (Zhang & Lu, 2024). The present model advances a minimalistic framework that isolates survival thresholds as the primary mechanism for stabilizing cooperation. While our model can be extended with complex features such as spatial structure, cognitive evolution, social norms, and institutions, we emphasize that a contribution of our model is that the evolution of cooperation is observed precisely, without any such extensions or mechanisms.

3. The Model

We propose an evolutionary game-theoretic model based on the iterated Prisoner's Dilemma (IPD). The IPD is an extension of the classic Prisoner's Dilemma, where the game is played repeatedly over multiple rounds. The central premise of the current model is that players must pay a survival cost after each round, and their survival probability depends on the payoffs they accumulate in the game. The payoff structure follows the classic PD game: R is the payoff for mutual cooperation, T is the payoff for free riding, S is the payoff to the player who cooperates while the other defects, and P is the payoff for mutual defection. According to the standard rules of the game, the payoffs satisfy the following conditions: (1) $T > R > P > S$, and (2) $2R > T + S$.

Each player adopts one of two fixed strategies: (1) Always Cooperate (ALLC), in which the player always chooses to cooperate, providing benefits to the other at a personal cost, and (2) Always Defect (ALLD), in which the player always chooses to defect, attempting to maximize personal gains by exploiting cooperators. The strategies remain unchanged throughout the game. The game is played over t rounds ($t > 1$). The players receive payoffs, U, based on their PD game interactions and then pay the cost of survival, $M > 0$, which represents the energy, resources, or effort required to stay alive. A player's *probability of survival*, therefore, depends on both U and M. In a simple discrete case, if the game payoff exceeds the survival cost ($U > M$), the player survives and proceeds to the next round. Otherwise, the player is eliminated from the game. Exiting can represent death, bankruptcy, or other forms of elimination, depending on the context (e.g., biological, economic, or geopolitical). Thus, the discrete probability of survival can be defined as follows:

$$q(U) = \begin{cases} 1 \text{ if } U \geq M \\ 0 \text{ if } U < M \end{cases} \tag{1}$$

If a player does not survive, their opponent can no longer interact with that player in the subsequent rounds. Notice that for the payoff structure of the Prisoner's Dilemma game ($T > R > P > S$), the probabilities of survival are as follows:

$$q(U = T) \geq q(U = R) \geq q(U = P) \geq q(U = S) \tag{2}$$

To simplify presentation, define $q_k = q(U = k)$, where $k = [T, R, P, S]$. Given these probabilities, we can now specify the modified payoff matrix of the iterated PD game as follows:

$$\begin{pmatrix} R + Rq_R q_R + Rq_R^2 q_R^2 + \ldots + Rq_R^{t-1} q_R^{t-1} & S + Sq_S q_T + Sq_S^2 q_T^2 + \ldots + Sq_S^{t-1} q_T^{t-1} \\ T + Tq_T q_S + Tq_T^2 q_S^2 + \ldots + Tq_T^{t-1} q_S^{t-1} & P + Pq_P q_P + Pq_P^2 q_P^2 + \ldots + Pq_P^{t-1} q_P^{t-1} \end{pmatrix} \tag{3}$$

For example, two cooperators (ALLC vs. ALLC) obtain R in the second round only if both survive after the first round, which occurs with a probability of $q_R q_R$. They obtain R in the third round if both survive the first two rounds, with a probability of $q_R^2 q_R^2$, and so on. Similarly, a free-riding defector (ALLD vs. ALLC) can continue exploiting a cooperator only if both players survive the previous rounds, with the survival probabilities compounding over time.

Notice that the game payoffs accumulate between rounds, and if the game ends prematurely, the payoffs to the players are equal to whatever they managed to accumulate before the interaction stopped. For example, when a defector obtains T in the first round, that payoff is immediately added to the defector's overall fitness or utility. It is not contingent on future rounds. From a biological perspective, even short-lived gains (e.g., acquiring resources in a single feeding event) can increase an organism's short-term reproductive success before it perishes.

The defector's ability to earn additional payoffs may cease if the exploited cooperator does not survive. However, the key point is that the defector's payoff for that round is not reversed or nullified simply because the game ends; the previous round's payoff still contributes to the defector's total fitness. Hence, even a one-round exploitative interaction grants the defector a payoff, T, which can be evolutionarily significant when considering replication over multiple generations.

Part of what makes high metabolic costs M so important is that they limit a defector's ability to enjoy more than one (or a few) rounds of exploitation. In contrast, pairs of cooperators can accumulate repeated mutual-cooperation payoffs R over many rounds, translating into higher overall fitness. This asymmetry, combined with forced exit, drives our central result: cooperation can become evolutionarily stable under sufficiently harsh conditions, even without memory, punishment, or other institutional mechanisms.

In a continuous case ($0 < q_S < 1$), a prospective defector faces a dilemma: they must weigh the higher potential payoff from free riding against the risk of causing their opponent to exit the game prematurely. This trade-off introduces additional strategic complexity, as defectors must balance short-term gains with the potential long-term consequences of exploiting their game partners.

4. Evolutionary Stability of Cooperation in a Two-Player PD Game

A strategy is defined as evolutionarily stable (ESS) if a large incumbent population adopting that strategy cannot be invaded by a rare mutant adopting an alternative strategy (Nowak, 2006). Given the modified payoff matrix (3) above, Always Cooperate (ALLC) is an ESS if

$$R + Rq_Rq_R + Rq_R^2q_R^2 + \ldots + Rq_R^{t-1}q_R^{t-1} > T + Tq_Tq_S + Tq_T^2q_S^2 + \ldots + Tq_T^{t-1}q_S^{t-1} \quad (4)$$

In the discrete case, ALLC is an ESS under three conditions:

(a) Mutual cooperation guarantees survival ($q_R = 1$);
(b) Exploited cooperators do not survive ($q_S = 0$);
(c) The number of rounds is sufficiently large such that $t > T/R$ (notice that if the conditions (1) and (2) are true, then expression 4 above simplifies to $Rt > T$).

Cooperation becomes unstable in two cases: (1) when the cost of survival, M, is so high that no player survives beyond the first round, and (2) when the cost of survival, M, is so low that all players survive regardless of their payoff. *Thus, a relatively high metabolic cost promotes the evolution of cooperation by eliminating exploited cooperators and reducing opportunities for defectors to free ride.*

If the probability of survival is continuous, such that $0 < q_S < 1$, the payoffs in expression (3) can be expressed in the form of geometric series:

$$\begin{pmatrix} R(1-q_R^{2t})/(1-q_R^2) & S\left(1-(q_Sq_T)^t\right)/(1-q_Sq_T) \\ T\left(1-(q_Sq_T)^t\right)/(1-q_Sq_T) & P(1-q_P^{2t})/(1-q_P^2) \end{pmatrix} \quad (5)$$

To simplify presentation, define

$$x \equiv \left(1-q_R^{2t}\right)/\left(1-q_R^2\right) \quad (6)$$

as the expected duration of a mutually cooperative interaction

$$y \equiv \left(1-q_P^{2t}\right)/\left(1-q_P^2\right) \quad (7)$$

as the expected duration of mutual defection, and

$$z \equiv \left(1-(q_Sq_T)^t\right)/(1-q_Sq_T) \quad (8)$$

as the expected duration of an exploitative interaction.

Given the expressions (6)–(8), the modified payoff matrix (expression (3)) becomes

$$\begin{pmatrix} Rx & Sz \\ Tz & Py \end{pmatrix} \quad (9)$$

The duration of mutual cooperation is greater than the duration of mutual defection, $x > y$, since $R > P$. Mutual cooperation also lasts longer than an exploitative interaction, $x > z$, if $q_Rq_R > q_Sq_T$. Given the simplified payoff matrix (9) above, ALLC is an ESS when

$$Rx > Tz \quad (10)$$

or

$$\frac{x}{z} > \frac{T}{R} \tag{11}$$

The left-hand side of the inequality describes the ratio of the expected duration of a cooperative interaction to the expected duration of exploitative interaction. The right-hand side describes the ratio of the free-riding payoff to the payoff for mutual cooperation. Cooperation is evolutionarily stable when the duration ratio is greater than the payoff ratio. Since $T > R$, the only factor than can provide an evolutionary advantage to cooperators is a low probability of survival when exploited, q_S. Similarly to the discrete case, *cooperation is more likely to be evolutionarily stable if exploited cooperators are less likely to survive*.

5. Evolutionary Stability of Cooperation in the *n*-Person PD Game ($n > 2$)

The majority of existing models addressing the evolution of cooperation assume two-player interactions. However, cooperation often involves interactions within groups. The dynamics of cooperation and defection become more complex in the n-Person Prisoner's Dilemma (PD), where $n > 2$. For example, two cooperators in a group may mutually enhance each other's survival, only to be exploited by a third player adopting a free-riding strategy. In such scenarios, defectors benefit not only from their higher individual payoffs but also from the improved survival probabilities of the cooperators they exploit, extending the duration of exploitative interactions.

To assess the evolutionary stability of cooperation in this context, we can generalize the concept of evolutionary stability for symmetric n-player games (Palm, 1984). The key question is whether the "Always Cooperate" (ALLC) strategy remains evolutionarily stable in a population where individuals interact in groups larger than two. Intuitively, in the current framework, ALLC must be an ESS in n-person PD games if the population is on the brink of survival—that is, when the cost of survival is sufficiently high relative to the game payoffs and the probability of survival decreases significantly with *any* instance of defection by any of the players (think about situations where the group's success and survival depend on contributions from all members of the group).

Following the analytical approach of Broom et al. (1997), we can show that ALLC is an ESS if

$$U_{ALLC,0} > U_{ALLD,0} \tag{12}$$

where $U_{ALLC,0}$ and $U_{ALLD,0}$ are the utilities of ALLC and ALLD, respectively, when all other players cooperate (that is, there are no defectors in the *rest of the population* outside of the two-player interaction under consideration).

To simplify, let b represent the benefit received from cooperation, and c represent the cost. Using these parameters, the utilities for ALLC and ALLD can be expressed as follows:

$$U_{ALLC,0} = bA\alpha_0 - c \tag{13}$$

$$U_{ALLD,0} = bA\alpha_1 \tag{14}$$

where A is the total number of cooperators in the population (excluding the focal player) and α_x is the expected duration of mutual cooperation when there are x defectors in the population. Notably, $A\alpha_x$ can be interpreted as the *expected number of surviving cooperators* in a population with *x defectors*.

Using these expressions and assuming $\alpha_0 \neq \alpha_1$, the condition for ALLC to be an ESS becomes

$$\frac{b}{c} > \frac{1}{A(\alpha_0 - \alpha_1)} \tag{15}$$

This inequality, expressed in terms of the b/c ratio, identifies the condition required for cooperation to be evolutionarily stable. The left-hand side represents the benefit-to-cost ratio of cooperation, while the right-hand side is a function of the group size (A) and the difference $\alpha_0 - \alpha_1$. Intuitively, this difference reflects the impact of defection on survival: it represents the reduction in the expected duration or survival of mutual cooperation when a single defector is introduced into a group of cooperators. Since $b/c > 1$ and $A > 1$, the condition of the evolutionary stability of cooperation in the n-Person PD game holds as long as α_0 is sufficiently larger than α_1. This is the case when a single defector has a significant detrimental effect on the probability of survival for the rest of the group (the cooperators). Such an outcome is most likely when the cost of survival is high, meaning that any defection jeopardizes the well-being of the entire group. In this case, evolutionary selection does not favor defection, and cooperation remains evolutionarily stable. Once again, as in the two-player model, we observe that a high cost of survival promotes the evolution of cooperation when future interactions are not guaranteed and are contingent upon players achieving payoffs that exceed an exogenous metabolic cost.

6. Agent-Based Simulation

To provide an intuitive illustration of the theoretical model, we present a computational (agent-based) simulation of the evolution of strategies in a game described above. Each agent adopts one of two fixed strategies: always cooperate (ALLC) or always defect (ALLD). The model introduces survival costs and reproduction based on payoff, providing a framework to explore the evolutionary dynamics of cooperation under different conditions.

The model begins by initializing a population of agents (e.g., $N = 1000$). A proportion of agents are randomly assigned the cooperative strategy (ALLC), while the rest are assigned the defecting strategy (ALLD). Each agent's cumulative payoffs reset at the beginning of each generation. Each agent also starts with "alive" status, which determines whether they can continue interacting within a generation. Generations represent discrete time steps, and the simulation runs for a predefined maximum number of generations or until all agents die, whichever occurs first.

Within each generation, agents are randomly paired to interact. A pair of agents plays the PD game for an exogenous number of rounds. These interactions accumulate payoffs for each agent, and a survival cost is subtracted after every round. If an agent's cumulative payoff falls below zero at any point, the agent "dies" and no further interaction is possible.

At the end of each generation, surviving agents are identified, and reproduction occurs. Reproduction is governed by a selection mechanism, which can either use replicator dynamics or a roulette-wheel selection. Both mechanisms ensure that higher-payoff agents have a greater likelihood of reproducing. Notably, the two selection mechanisms produce substantively identical results. Data are collected throughout the simulation, capturing the proportion of cooperators and defectors, average payoffs for both strategies, and the absolute numbers of agents who survived or died by strategy. These metrics provide an intuitive insight into the evolutionary dynamics.

The computational results replicate the findings from the theoretical model and demonstrate robustness across a wide range of simulation parameters. These parameters include the population size (total number of agents), the initial proportion of cooperators versus defectors, the number of interaction rounds per generation (as long as it exceeds one), the total number of generations, and the payoff parameters of the Prisoner's Dilemma game (which must satisfy the condition $T > R > P > S$).

Consistent with the theoretical predictions, the simulations reveal distinct outcomes depending on the survival cost. Under low costs (e.g., cost = 1), defectors dominate the population (Figure 1). This outcome is driven by their ability to exploit cooperators without facing any consequences, since the cooperators survive and continue to provide resources to defectors. In contrast, when costs are higher (e.g., cost = 2), a qualitatively different evolutionary trajectory emerges. Initially, defectors retain their advantage due to their ability to exploit cooperators. However, as the rounds progress, the high survival cost disproportionately penalizes defectors, since the exploited cooperators do not survive. Without cooperators to exploit and ongoing metabolic demands, defectors begin to die off at a faster rate, allowing mutual cooperators (an ALLC interacting with another ALLC) to gradually increase in numbers. Very quickly, this dynamic stabilizes, leading to the predominance of cooperative strategies in the population. These dynamics demonstrate how environmental adversity can create conditions that allow cooperative behaviors to evolve.

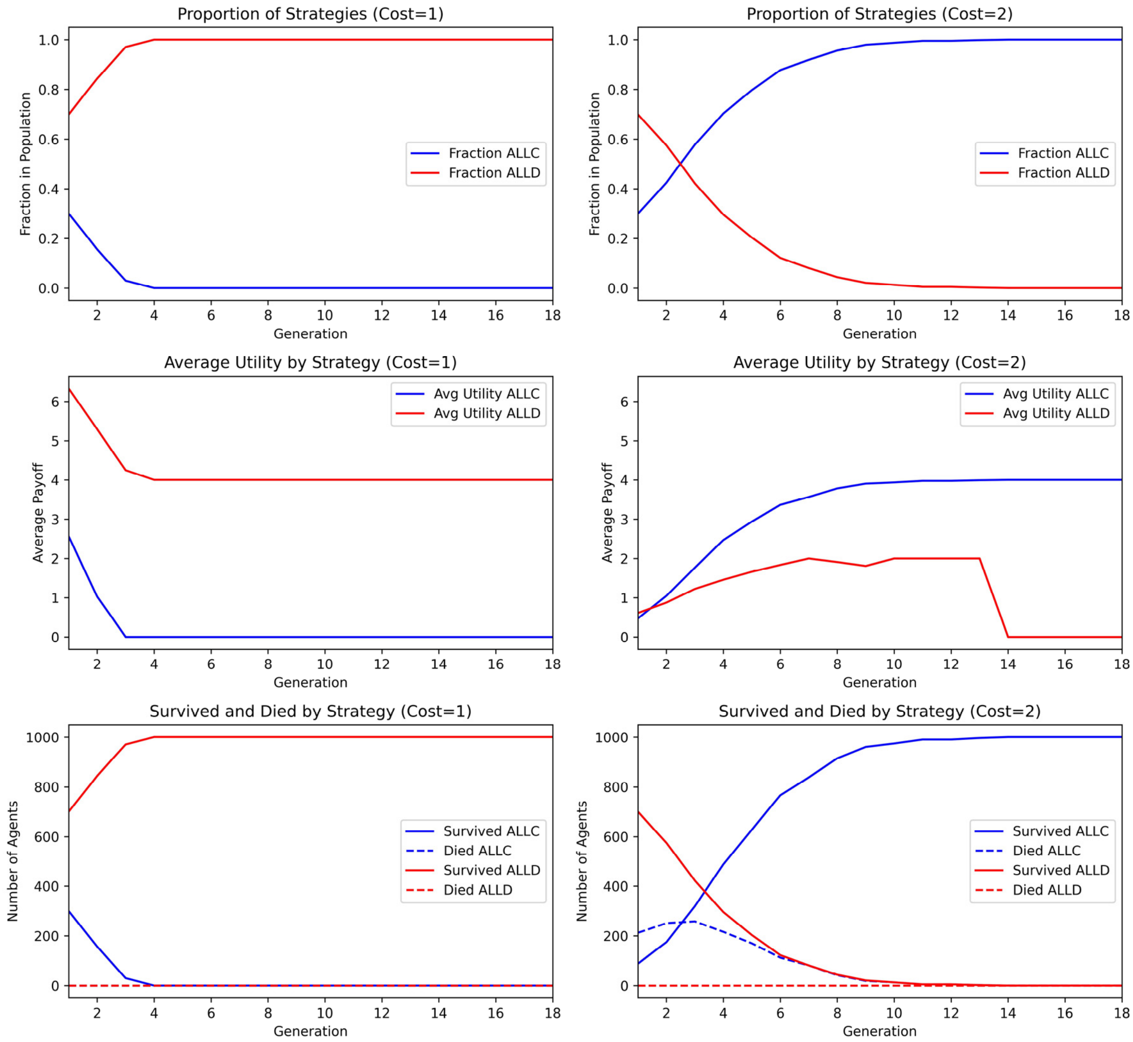

Figure 1. Simulation results illustrating the evolution of ALLC and ALLD strategies in a population of 1000 agents under two survival costs: cost = 1 (left column) and cost = 2 (right column). Parameters used: initial fraction of cooperators = 0.3, maximum number of rounds per pair per generation = 4, number of generations = 18, payoff matrix (T = 4, R = 3, P = 2, S = 1), and replicator dynamics as the selection mechanism.

Overall, these simulation results offer intuitive insights into the mechanisms underlying the evolution of cooperation. They affirm the importance of survival costs as a decisive factor in determining the fate of cooperation, reinforcing the theoretical model's claim that mortality pressures are pivotal in driving the emergence and stability of cooperation in challenging environments.

7. Conclusions

The present model provides new insights into the evolution of cooperation by incorporating mortality and survival dynamics into the classical PD game framework. Importantly, the current approach views survival as endogenous and directly linked to the payoffs players receive during the game. Players with higher payoffs are more likely to survive, while those with lower payoffs face greater risks of exiting. These simple dynamics make the decision to defect more complicated than in the standard PD game. By exploiting cooperators, defectors may undermine the survival of their future game partners. Consequently, higher levels of mortality, rather than hindering cooperation, can promote it by disproportionately reducing the survival of exploited cooperators. As a result, mutual cooperation persists longer than exploitative interactions, leading to an environment where cooperative strategies thrive. Notably, this framework does not rely on complex behaviors, sophisticated cognitive mechanisms, social institutions, or any other common mechanisms traditionally associated with promoting cooperation.

One implication of the model is that longevity may be a consequence, not a cause, of cooperation. Faced with high metabolic costs and survival challenges, cooperative behaviors enhance individual and group survival probabilities, indirectly selecting for longer lifespans. This perspective emphasizes that cooperation evolves as a response to environmental pressures, with longevity emerging as a byproduct of these cooperative dynamics. Another implication is the positive effect of metabolic costs on population fitness. While high survival costs reduce individual survival probabilities, they simultaneously promote cooperation by eliminating exploited cooperators and shortening the duration of exploitative interactions. In this way, higher metabolic costs act as a selective pressure, favoring cooperative strategies and enhancing overall social welfare.

The present model has an intriguing biological parallel (we are thankful to an anonymous reviewer for this idea): a virus that kills its host too rapidly—analogous to exploiting defection—decreases its own reproductive opportunities. In contrast, a virus exhibiting moderate virulence—analogous to “partial” defection—can prolong its host’s survival and enhance its own transmission. Although our model focuses on extreme strategies, such as unconditional defection (ALLD) and unconditional cooperation (ALLC), future work could incorporate more nuanced strategies, such as “moderate” defection. For instance, a strategy that defects only when survival is at immediate risk might reduce the short-term risks of exploitation while preserving future interactions.

While the model offers a simple mechanism by which mortality can stabilize cooperation, several assumptions define its boundary conditions. As discussed, we do not model complex conditional strategies. We also assume that survival depends solely on immediate payoffs relative to a fixed metabolic cost, potentially overlooking environmental randomness and dynamically changing resource availability. Similarly, the assumption of a constant survival cost may not capture the fluctuating pressures faced by agents in ecological or sociopolitical systems. Importantly, the interactions take place in a void, without any spatial structure, kinship, groups, norms, institutions, reputation, or similar social constructs. While this barebones approach is intentional, it must nevertheless be acknowledged that such additional features could drastically affect the dynamics of the model, either reinforcing or undermining the evolution of cooperation.

Our findings have several implications for social contexts. In resource-scarce habitats, cooperative behaviors enhance group survival. Similarly, in sociopolitical environments, existential threats like economic crises or security concerns often foster alliances and collaboration among otherwise competing entities. These parallels suggest that high “maintenance costs” select for cooperation, as long-term exploitation is unsustainable. At the individual level, mutual cooperation may be facilitated by appeals to shared fate and mutual interdependence (Smaldino et al., 2013), regardless of whether the survival imperatives are objectively true or whether they are simply metaphorical tools for promoting mutually beneficial and socially responsible behavior.

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