





The Unification of Evolutionary Dynamics through the Bayesian Decay Factor in a Game on a Graph

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Received: 7 March 2024 / Accepted: 18 April 2024 / Published online: 7 May 2024 © The Author(s), under exclusive licence to the Society for Mathematical Biology 2024

Abstract

We unify evolutionary dynamics on graphs in strategic uncertainty through a decaying Bayesian update. Our analysis focuses on the Price theorem of selection, which governs replicator(-mutator) dynamics, based on a stratified interaction mechanism and a composite strategy update rule. Our findings suggest that the replication of a certain mutation in a strategy, leading to a shift from competition to cooperation in a well-mixed population, is equivalent to the replication of a strategy in a Bayesianstructured population without any mutation. Likewise, the replication of a strategy in a Bayesian-structured population with a certain mutation, resulting in a move from competition to cooperation, is equivalent to the replication of a strategy in a well-mixed population without any mutation. This equivalence holds when the transition rate from competition to cooperation is equal to the relative strength of selection acting on either competition or cooperation in relation to the selection differential between cooperators and competitors. Our research allows us to identify situations where cooperation is more likely, irrespective of the specific payoff levels. This approach provides new perspectives into the intended purpose of Price's equation, which was initially not designed for this type of analysis.

Keywords Bioeconomics \cdot Evolutionary game theory \cdot Games on graphs \cdot Price equation \cdot Strategic uncertainty \cdot Structured population \cdot Bayesian updating

1 Introduction

Non-cooperative games (Harsanyi 1973) involve individual players making decisions that affect the game outcome, with each player's action corresponding to a payoff that determines their success in the game. In contrast, cooperative games, as introduced by Shapley (1971), involve joint actions taken by groups of players, and the game

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outcome is described by the collective actions of the coalition, along with the associated payoff distribution. However, in reality, economic and institutional players often alternate between cooperation and competition in cycles, even in situations where public goods provision is required. Studies have found that such cyclical-type interactions can emerge in various games, including public goods games with correlated reward and punishment (Szolnoki and Perc 2013), ultimatum games (Szolnoki et al. 2012), and social dilemma games with coevolution (Perc and Szolnoki 2010). To better understand the complex dynamics of real-world situations where cooperation and competition alternate, game theory has embraced interdisciplinary approaches that draw on knowledge from biology, economics, sociology, psychology, and statistical physics (Wang et al. 2015). These interdisciplinary approaches provide valuable insights into the factors that drive the emergence and persistence of cooperation and competition over time. By exploring the evolutionary dynamics of such games, researchers can gain a deeper understanding of the strategic behavior of individuals and groups in real-world settings, and identify ways to promote cooperative behavior even in situations where the incentives for defection may be high.

The problem of agents having the incentive to free-ride on the contributions of others creates social dilemmas that have been extensively studied in game theory (Bach et al. 2006; Hauert et al. 2006; Santos et al. 2008; Wang et al. 2009; Dragicevic 2017). In these dilemmas, individual defectors may benefit more than cooperators, despite the higher collective payoff obtainable through mutual cooperation (Perc 2006). However, various mechanisms have been proposed to promote cooperation in different types of games. For example, spatial patterns (Nowak and May 1992), moral behavior (Capraro and Perc 2018), indirect reciprocity (Nowak and Sigmund 1998), voluntary interactions (Hauert et al. 2002), stochastic processes (Yoshimura and Jansen 1996), and adaptive learning (Traulsen et al. 2004) have all been shown to facilitate cooperative behavior. Stochastic processes, in particular, have been found to play a significant role in promoting cooperation, especially when the payoff functions are endowed with white Gaussian noise, leading to coherence resonance (Perc 2006; Perc and Marhl 2006; Perc, 2007). In situations where game-theoretic strategies and the environment are both time-evolving, coevolutionary rules can help maintain cooperative behaviors (Perc and Szolnoki 2010). Evolutionary dynamics (Hofbauer and Sigmund 1998) is a powerful tool for studying global issues, as it considers the whole population of agents and can be formalized using the law of mass action (De Roos and Persson 2005). Statistical physics has also proven to be useful in studying large populations undergoing stochastic phase transitions (Perc 2016; Capraro and Perc 2018).

The literature emphasizes the importance of population structure in evolutionary games. Models in population ecology commonly fall into two categories: well-mixed and structured populations (Odenbaugh 2005). Well-mixed or unstructured populations consist of identical agents, whereas structured populations group agents into homogeneous classes. Structured populations are considered to provide a more accurate reflection of reality than models based on a well-mixed sampling of players (Perc et al. 2017). While Nowak and May (1992) demonstrated that evolutionary games in structured populations can enable cooperators to avoid being exploited by defectors, the emergence of cooperation and its outcomes may depend on various other factors, including the structure of the interaction network and the type of interactions (Perc

et al. 2017). The number of cooperators in a group, for example, can influence conditional cooperation (Szolnoki and Perc 2012; Perc et al. 2013). Strategic uncertainty is also an important consideration in evolutionary game theory, particularly when players are unaware of whether the game plan is cooperative or non-cooperative (Perc 2006). Random payoff variations are more representative of long-term contexts, and thus, population dynamics should be considered under strategic uncertainty (Dragicevic 2019a, b). Overall, population structure and the nature of interactions are critical factors in determining the emergence and persistence of cooperative behavior in evolutionary games. While structured populations have been shown to facilitate cooperation, other factors can also influence game outcomes. Therefore, a deeper understanding of population structure dynamics is essential for studying the evolution of cooperation.

Our investigation of cooperation dynamics employs tools from evolutionary game theory (Maynard and Price 1973) and takes advantage of the unified framework that encompasses various evolutionary dynamics (Page and Nowak 2002; Dragicevic 2019a, b).¹ We utilize the Price version of replicator(-mutator) dynamics in a mixed population setting consisting of model-players sampled from both well- and poorly-mixed population settings. The Price theorem (Price 1970; Frank 1995; Kerr and Godfrey-Smith 2008) was initially designed to understand how the frequency of a particular character state changes over time (Dragicevic 2016, 2019b). It provides a model of selection that considers how character states co-vary with fitness or the outcomes they produce (Page and Nowak 2002; Knudsen 2004; Fox 2006; Collins and Gardner 2009; Helanterä and Uller 2010). The original Price equation, $\dot{E}(p) = cov(\pi, p) + E(\dot{p})$, describes the change in the value of an arbitrary character state over time (p), where π is the subsequent outcome, and $cov(\cdot)$ represents selection. In this context, selection refers to the differential survival of individuals due to variations in their character-state values. $E(\dot{p})$ describes the environmental pressure on the evolution of the character-state value. We define p as the probability of playing against a cooperator, and π as the payoff from playing a certain strategy. By combining the two, we can study the expected payoff associated with a given strategy available to the players. We translate selection $cov(\pi, p)$ into the difference between the expected payoff of a model-player and the average payoff in the population. Meanwhile, $E(\dot{p})$ represents the evolution of the payoff with respect to the probability update. The expanded Price equation (Page and Nowak 2002; Page 2003) yields $\dot{E}(p) = cov(\pi, p) + E(\dot{p}) + E(\pi\Delta)$, where the additional term describes random mutations from one type of model-player to another.

In this study, we endeavor to unify evolutionary dynamics on graphs through the implementation of a decaying Bayesian update mechanism. The study focuses on the dynamics of evolutionary games in populations structured on graphs (Nowak et al. 2010). Individuals are situated on the vertices of a graph, where the edges of the graph determine which individuals interact with each other (Lieberman et al. 2005; Ohtsuki et al. 2006). In games on graphs, an individual's fitness is determined by interactions with their neighbors. The traditional replicator equation applies to a complete graph, where all individuals are adjacent to one another. In contrast to updating rules such as

¹ Chatterjee and Chakrabartty (2018) demonstrated that various types of evolutionary game dynamics can be considered as specific instances of a dynamical system model derived from a framework of generalized growth transforms.

birth-death (BD), death-birth (DB), imitation (IM), or pairwise comparison (PC), we adopt a composite updating rule that integrates birth, death, and neighbor selection, which collectively determine the transition rate (Lieberman et al. 2005; Okushima et al. 2018).² The transition rate represents the degree to which selection favors or disfavors a particular trait and can be influenced by factors such as mutation rates, genetic drift, and environmental pressures. It can be calculated in various ways depending on the specific model and context being used. When studying the expected frequency of strategies on an infinitely large graph, the pair-approximation calculation in the limit of weak selection leads to a surprisingly simple equation (Nowak et al. 2010). ³ The replicator equation on graphs describes how the expected frequencies of strategies on a graph change over time. It provides insight into the evolutionary outcomes of structured populations and how different factors can influence the evolution of traits in these populations. The study of evolutionary game dynamics on graphs has applications in a variety of fields, including population biology, ecology, and social sciences.

In the study by Zhang and Perc (2016), the conflict between contributors and defectors was addressed using the Price equation. The authors assumed that the size of a group increases proportionally to its relative payoff, and individuals selectively migrate to groups with higher average payoffs. Their results showed that cooperation emerges when inter-group selection outweighs intra-group selection. In contrast, our study, based on a stratified interaction mechanism and a composite strategy update rule, demonstrates a conditional equivalence between well-mixed population replicator dynamics and Bayesian-structured population replicator dynamics in a population of model-players organized on a graph, subject to strategic uncertainty and mutation towards cooperation. This equivalence is based on the proportion of cooperators being equivalent to the relative payoff advantage of a competitor over a cooperator, rather than a relative payoff. The equivalence holds when the transition rate from competition to cooperation is equal to the relative strength of selection acting on cooperation or competition in relation to the selection differential between the competitors and cooperators. Our approach differs from that of Zhang and Perc but addresses a similar issue. Our study demonstrates that the replicator-mutator dynamics, whether in a well-mixed or structured population, can only lead to complete cooperation when the density of competitors is near one. This unexpected finding underscores that the presence of a mutation towards cooperation causes a transient full density of cooperators that emerges through free-riders. The sucker's payoff, which guarantees meeting a cooperator, serves as an incentive for individuals to engage in free-riding behavior. However, these cooperators ultimately revert to defection before transitioning back to cooperators again.

 $^{^2}$ Previous research by Zhang et al. (2021) has demonstrated that alternative updating rules, such as the delayed group-based sequential myopic best response adjustment rule (MBRAR), have been verified to ensure convergence of the evolutionary game and enhance convergence efficiency.

³ Weak selection on graphs refers to the situation in which the evolution of a trait on a graph is influenced by weak selective forces. In this context, the fitness of a particular node or edge is determined by its ability to contribute to the spread of the trait through the graph. Even if evolution can be quick, it requires strong selection pressure, which is seldom demonstrated (Kun 2022). This aspect gains particular significance for our investigation as the influence of weak selection escalates when other evolutionary drivers, such as mutation, exert a comparatively substantial impact on the population dynamics (Ueda et al. 2017).

Following this introduction, we introduce the static game plan under strategic uncertainty in Sect. 2. In Sect. 3, we describe the population dynamics using the Price identity. Section 4 presents simulation examples to illustrate our findings. Finally, we conclude in Sect. 5.

2 Static Model

The standard game-theoretic model is characterized by a simultaneous interaction between two players, with each player having the option to select either the cooperative or competitive strategy, and their types are not predetermined. The player endowment, or initial amount of wealth, is denoted by w > 0. The willingness of players to contribute to cooperation at the expense of personal gain is represented by c, where $c \le w$. If both players choose to cooperate, they each receive a reward of $\epsilon w > 0$, where $\epsilon \in [0, 1]$ is a reward coefficient.⁴

In this game, players operate under strategic uncertainty, which is characterized by a lack of knowledge regarding each other's strategies.⁵ While pure strategies involve deterministic choices without probabilities, strategic uncertainty introduces an element of expected outcomes associated with encountering specific types of players. Consequently, there exists a probability p of playing against a cooperator, and its complementary probability of playing against a competitor. If both players choose to adopt the cooperative strategy, they can receive an expected reward of $p(w(1 + \epsilon) - c)$. However, if both players adopt the competitive strategy and mutually defect, they both receive an expected punishment payoff of (1 - p)w. In the scenario where one player adopts the competitive strategy while the other player adopts the cooperative strategy, the former receives an expected temptation payoff of pw, while the latter receives an expected sucker's payoff of (1 - p)(w - c). These expected payoffs reflect the trade-offs involved in the players' decision-making process, as they balance the potential benefits of cooperation against the costs of personal sacrifice and the risk of exploitation by the other player.

2.1 Two-Player Game

The following table depicts the game payoff matrix derived from the classic scenario known as the prisoner's dilemma.

⁴ Whenever we discuss defection as an alternative term for competition, it is considered in the context of defecting to cooperate, as described by Nowak and Sigmund (2000). In other words, when players choose to defect, they are essentially engaging in competition.

⁵ Considering the variety of terms used in the literature, it is imperative to elucidate that the concept of strategic uncertainty encompasses two distinct components: strategic risk, which pertains to uncertainty about the realization of the opponent's mixed strategy, and strategic ambiguity, referring to the uncertainty surrounding the selection of a mixed strategy by the opponent (Calford 2020; Dragicevic 2024).

	Cooperation	Competition
Cooperation	$w(1+\epsilon) - c$; $w(1+\epsilon) - c$	w - c; w
Competition	w; $w - c$	w; w

The expected payoffs associated with a model-cooperator and a model-competitor, operating in a scenario involving strategic uncertainty, are as follows:

$$\Pi(p) := \begin{cases} \pi_i = p \left(w(1+\epsilon) - c \right) + (1-p) \left(w - c \right) \\ \pi_j = p w + (1-p) w. \end{cases}$$
(1)

Given $p \in [0, 1]$, it holds that $\pi_i \ge \pi_j \Leftrightarrow p \in w \ge c$. Specifically, if the expected value of the payoff from mutually cooperative actions exceeds the cost of engaging in such behavior, denoted by *c*, i.e., $p \in w > c$, then cooperative strategies will prevail over competitive strategies in the game-theoretic context.

Proposition 1 In the context of strategic uncertainty, a mixed-strategy Nash equilibrium entails a model-player choosing cooperative behavior if the probability of encountering a cooperator is sufficiently high, i.e. when $p > \frac{c}{\epsilon w}$.

Proof The proof can be found in "Appendix A".

2.2 N-Player Game

To analyze cooperation in a population-wide context, the standard game setting is extended to encompass *N* players. This approach has been commonly employed in the literature, such as in the works by Santos et al. (2008) and Perc et al. 2013. We consider a well-mixed population of infinite size, which is composed of fractions of cooperators denoted by x_i . The complement of x_i represents the proportion of competitors, which we denote by $x_j = 1 - x_i$. The proportions represent the distribution of strategies within the population (Lampert and Tlusty 2011). We assume that $x_i + (1 - x_i) = 1$ represents the normalized population density, where 0 denotes extinction and 1 full density.⁶

We designate a specific player as *i*, who represents a cooperator randomly selected from the population. Alongside this model-player *i*, a subgroup of N - 1 individuals, who compete with *i*, is also randomly chosen from the population. Together, they form a cluster of N players who then participate in an N-player game characterized by pairwise interactions, as described by Dyer and Mohanaraj (2011). Concurrently,

⁶ Utilizing the concept of prevalence proportion, it is understood that the probability of selecting an agent at risk from the population corresponds to the population's at-risk proportion (Dragicevic 2017). From this standpoint, the probability p of engaging with a cooperator in gameplay can be deemed proportional to the cooperator fraction x_i within the entire population. Nevertheless, a critical distinction emerges between the two: p originates from the context of an N-player game, wherein players are selected from a population characterized by a specific cooperator density x_i . Therefore, although p and x_i are interrelated, they originate from distinct dimensions of the model's framework.

another model-player, *j*, representing a competitor, is randomly selected from a different stochastic sample of *N* entities within the population. The resulting payoffs for both *i* and *j* model-players conform to the defined payoff structure $\Pi(p, x_i)$.⁷

Let $\Sigma_i x_i$ and $\Sigma_j x_j$, with i, j = 1, ..., N, denote the sizes of the subpopulations that play the cooperative and competitive strategies, respectively. We assume that $\Sigma_i p = \Sigma_j p = 1$ represents the normalized probability of strategy occurrence among the model-players. We then define $\overline{p} = \Sigma_i x_i p$ for i = 1, ..., N and note that $\Sigma_i x_i p \pi_i = \overline{p} \pi_i$ represents the average expected payoff for cooperative behavior across the entire population. Model-players are sampled from the binomial distribution, where the probability of having *n* cooperators among N - 1 players is given by

$$\binom{N-1}{n} x_i^n (1-x_i)^{N-1-n}.$$
 (2)

The players evaluate their own payoffs in comparison to a model-player, who is selected at random from the population. The likelihood of adopting the model-player's strategy is proportional to the difference between their own payoff and that of the model-player. Given that $\sum_{n=0}^{N-1} {N-1 \choose n} x_i^n (1-x_i)^{N-1-n} = 1$, the expected payoffs associated with a model-cooperator and a model-competitor are as follows

$$\Pi(p, x_i) := \begin{cases} \pi_i = p \left(w(1+\epsilon) - c \right) x_i^{N-1} + (1-p) \left(w - c \right) \\ \pi_j = p w + (1-p) w \left(1 - x_i^{N-1} \right). \end{cases}$$
(3)

By incorporating x_i^{N-1} and $1 - x_i^{N-1}$ into the payoff functions, we introduce strategic uncertainty for the model-players, as both cooperative and competitive outcomes are possible.

Given $p \in [0, 1]$, it follows that $\pi_i \geq \pi_j \Leftrightarrow x_i \geq [(c + p(w - c))/(w + p(\epsilon w - c))]^{\frac{1}{N-1}}$. Therefore, to determine whether cooperative or competitive behavior is dominant, we must compare the proportion of cooperators in a well-mixed population with the cost-benefit ratio augmented by the anticipated net gain from cooperation.

If the likelihood of encountering a cooperator in the game is uncertain, the cooperative strategy will dominate in mixed strategies as the fraction of cooperators approaches full density. In contrast, competition will prevail when the fraction of cooperators is low. Specifically, when $c \rightarrow w$, competition will always be the dominant strategy. When the cost of engaging in cooperation approaches zero ($c \rightarrow 0$), a critical mass of cooperators in the population can foster the spread of cooperative behavior among

⁷ Recent advancements in the field of evolutionary dynamics have expanded the scope of inquiry to include not merely pairwise interactions within networks but also those entailing higher-order connectivity. These higher-order interactions, characteristic of evolutionary games, facilitate group-based play rather than the traditional dyadic exchanges. A hallmark of such interactions is the capacity of a single connection, or a hyperlink in this context, to encompass multiple individuals simultaneously, diverging from the conventional network models limited to pairwise links. This architecture permits the modeling of complex group interactions through hyperlinks, effectively capturing the essence of collective play among interconnected participants (Alvarez-Rodriguez et al. 2021).

competitors. Overall, while the probability of encountering a particular type of modelplayer may influence the game's outcome, its impact significantly diminishes as the population fraction adopting a specific strategy increases.⁸

Proposition 2 In the context of strategic uncertainty within a population of N players, a mixed-strategy Nash equilibrium entails a model-player choosing cooperative behavior if the proportion of cooperative agents is sufficiently high, i.e. when $x_i > [(c + p(w - c))/(w + p(\epsilon w - c))]^{\frac{1}{N-1}}$.

Proof The proof can be found in "Appendix B".

It is important to underline that the use of indices *i* and *j* serves a multifaceted purpose, reflecting both strategic roles (π_i and π_j) and subpopulation types (x_i and x_j). This dual use is fundamental, particularly in the context of an *N*-player game where players are randomly drawn to participate. In such a setup, contrasting *i* and *j* effectively pits two distinct strategies—cooperation or competition—against each other. However, it is critical to understand that this opposition is not just between two strategies but also represents a player adopting one of these strategies against another player randomly selected from a population that consists of both cooperators and competitors. Thus, the distinction between *i* and *j* evolves throughout our analysis, initially denoting strategic choices and later embodying the individuals who adopt these strategies during gameplay. Consequently, this notation serves as a bridge between the micro-level individual strategies and the macro-level population strategy profiles.

3 Price Identity Dynamic Model

Our study enhances traditional evolutionary game theory by incorporating analyses of both well-mixed and structured populations (Su et al. 2019) and delves into the dynamics of evolutionary games on graphs (Ohtsuki and Nowak 2006). At the core of our model is an N-player game initiation phase, characterized by a selection process that recruits players from either a well-mixed pool (Sect. 3.1) or a structurally defined population (Sect. 3.2). This selection sets the stage for analyzing interactions between a focal player and their immediate neighbors within the N-player framework, with population structure precisely mapped onto a graph. The introduction of this stratified interaction mechanism (Dragicevic 2024) signifies a methodological advancement. It enables a dual-level analysis, capturing both broad evolutionary dynamics at the population level and localized interactions that stem from the population's structure.

In the game-theoretic framework, players are situated at nodes within a network and engage exclusively with their adjacent neighbors. We thus have a game on a graph. The network may manifest as either a lattice or a regular graph—where each vertex has the same number of neighbors—devoid of cycles (Allen and Nowak 2014). Interactions between neighboring pairs occur at a consistent rate, contingent upon both

⁸ It is worth noting that at the mixed strategy Nash equilibrium, both players have the same expected payoffs from their respective strategies.

players being available for engagement (Broom and Křivan 2020). The interaction graph is considered to be unweighted and undirected (Su et al. 2019). To maintain a broad applicability, we refrain from imposing supplementary assumptions on the structural characteristics of the graph. Regardless of the specific graph configuration, it is represented by an adjacency matrix, the elements of which are hidden in the probability of interaction among players (Chen et al. 2016).

3.1 The Price Identity of Replicator Dynamics Within an Unstructured Population

We now shift our focus to the context of an infinitely large population, wherein an *N*-player game is being played. In this scenario, the constituent agents, termed replicators, are assumed to co-evolve within existing types. A well-mixed population on a graph corresponds to the absence of clusters (Kim et al. 2015). According to the replicator dynamics framework (Hofbauer and Sigmund 1998), the evolution of the replicators is described by the following system of differential equations

$$\dot{X} := \begin{cases} \dot{x}_i &= x_i \left(\pi_i - \bar{\pi} \right) \\ \dot{x}_j &= \left(1 - x_i \right) \left(\pi_j - \bar{\pi} \right). \end{cases}$$
(4)

Within this system, x_i and x_j or $1 - x_i$ represent the densities of the payoffs associated with the model-cooperator and model-competitor, respectively, at any given point in time. The rate at which the model-players modify their strategies is determined by a per capita rate, which is equivalent to the difference between the expected payoff of a model-player and the average payoff observed within the population (Cressman and Tao 2014). These payoffs arise from interactions occurring in randomly formed groups of individuals. The expression $\bar{\pi} = x_i \pi_i + x_j \pi_j = x_i \pi_i + (1 - x_i) \pi_j$ denotes the average payoff within the population.

Building on the work of Ohtsuki and Nowak (2006), we introduce the replicator equation on graphs, which incorporates an additional parameter δ that reflects the local competition among different strategies. We can thus talk about a spatial prisoner's dilemma (Cardinot et al. 2018). In the spatial prisoner's dilemma game, players are situated on a network and engage only with their nearby neighbors. This parameter, also known as the transition rate, represents the probability of transitioning from one state to another within a birth-death process.⁹ Within our framework, the network serves as a representation of the individual dynamics in which a competing neighbor could potentially be supplanted by a cooperator should the local population structure favor efficient outcomes.¹⁰

⁹ The transition rate, also known as selection intensity or selection strength, represents the rate at which a strategy is replaced by another strategy due to selection pressure in the population. This means that a higher transition rate implies a higher rate of selection, and strategies that are less fit will be replaced more quickly. On the other hand, the mutation probability represents the probability that a strategy will mutate into a different strategy due to a copying error during reproduction. This means that even if a strategy is fit and successful, it can still be replaced by another strategy due to a random mutation event.

¹⁰ It has been established that, in the absence of correlations between hyperdegrees, the dynamics of higher-order-interaction networks align with the replicator dynamics observed in homogeneously mixed populations (Alvarez-Rodriguez et al. 2021).

The mechanisms of strategy update rules in evolutionary games have been extensively documented in the literature (Ohtsuki and Nowak 2006; McAvoy and Hauert 2015; Su et al. 2019). For instance, under a birth-death update rule, a player is selected for reproduction based on their fitness relative to the population. Subsequently, a neighboring player is randomly chosen to be replaced by the offspring, who inherits the strategy of the reproducing parent. Conversely, in a death-birth update rule, a player is randomly selected for death, and the neighboring players vie to occupy the vacated spot through reproduction. Both of the aforementioned rules involve modifying a single strategy during each iteration. However, our study introduces a unique rule characterized by the simultaneous revision of all strategies, representing a global update. This can be described as a composite strategy update rule. This approach allows for a holistic view of the evolutionary dynamics on graphs. Following Yagoobi et al. (2023) and Dragicevic (2024), we have

$$\delta = \underbrace{\frac{rp}{rp + (1-p)}}_{\text{birth probability}} \cdot \underbrace{\frac{\alpha_{ij}(1-p)}{s\alpha_{ik}p + \alpha_{ik}(1-p)}}_{\text{death probability}} \cdot \underbrace{\frac{N-n}{N}}_{\text{selection}}.$$
(5)

The first ratio captures the probability of a cooperator being born, while the second ratio captures the probability of a cooperator dying. The third ratio pertains to neighbor selection through local competition between strategies, which involves the stochastic selection of a node for transformation into a cooperator.

The probability of encountering a cooperator during play is denoted by p. This parameter characterizes the probability that a player interacts with a cooperative neighbor; higher values of p indicate that a player is more likely to play with cooperative neighbors, whereas lower values indicate a higher likelihood of playing with defecting neighbors. The selection parameter r pertains to the birth of a cooperator and denotes the likelihood of a new cooperator being born into the population. In the spatial prisoner's dilemma game, this parameter reflects the tendency of a player to adopt a cooperative strategy when their neighbors are also cooperative. The selection parameter s corresponds to the death of a cooperator and determines the probability that a cooperator will perish and be replaced by a defector. In the spatial prisoner's dilemma game, this parameter reflects the propensity of a player to abandon cooperation when most of their neighbors are defectors. The weight of a link between neighboring players is represented by α_{ii} and the weight of a link between individuals in different subpopulations i and k is α_{ik} . When the graph is regular, we have $\alpha_{ii} = \alpha_{ik} = \alpha$. This parameter influences the extent to which a neighbor's strategy affects a player's decision to cooperate or defect. Higher values of α_{ii} indicate that the neighbor's strategy has a stronger influence on the player's decision. Finally, N denotes the total population size, while *n* represents the number of neighbors in a player's local group of cooperators. The (N - n)/N ratio represents the relative probability that a node's offspring will belong to the same group or neighborhood of cooperators as the parent node, given the spatial structure of the network. This probability influences the likelihood that a node will adopt a cooperative strategy, as cooperation may be favored if there is a high probability of interacting with other cooperators in the local neighborhood.

By multiplying these ratios with the probability of playing against a cooperator, the resulting transition rate includes p^2 and provides an estimate of the expected rate of phase transition toward cooperation. In the spatial prisoner's dilemma game, the probability of a player adopting a cooperative strategy depends on the payoff values and the local environment, which includes the strategy of the neighboring players. Multiplying the transition rate by p incorporates the effect of cooperative neighbors on the probability of a player adopting a cooperative strategy. Overall, it captures the influence of both the payoff values and the local environment on the emergence of cooperative clusters.

We can express the system in the form of a Price equation, as follows

$$\begin{split} \dot{E}(p) &= cov(\pi_i, p) + E(\dot{p}) \quad (6) \\ &= \sum_i x_i \pi_i p + \sum_i x_i \pi_i \delta p - \bar{\pi} \, \bar{p} + \sum_i x_i \dot{p} \\ &= \sum_i x_i \pi_i p (1+\delta) - \left(x_i \pi_i + (1-x_i)\pi_j\right) \sum_i p x_i + \sum_i x_i \dot{p} \\ &= \sum_i p x_i \left((1+\delta)\pi_i - x_i \pi_i - (1-x_i)\pi_j\right) + \sum_i x_i \dot{p} \\ &= \sum_i p x_i \left((1+\delta-x_i)\pi_i - (1-x_i)\pi_j\right) + \sum_i x_i \dot{p} \\ &= \sum_i p x_i (1+\delta-x_i)\pi_i - \sum_i p x_i (1-x_i)\pi_j + \sum_i x_i \dot{p} \\ &= \sum_i p x_i (1+\delta-x_i) \left[p \left(w(1+\epsilon) - c\right) x_i^{N-1} + (1-p) \left(w-c\right) \right] \\ &- \sum_i p x_i (1-x_i) \left[p w + (1-p) w \left(1-x_i^{N-1}\right) \right] + \sum_i x_i \dot{p}, \end{split}$$

where i = 1, ..., n, ..., N.

The equation $\dot{p} = n\bar{p}\left(N + 10^{-3}\frac{n}{N}\right) \frac{\pi_i(n) - \pi_j(n)}{\pi_i(n-1) - \pi_j(n-1)}$ describes the time derivative of the probability p that a player adopts a cooperative strategy in a population with N players, where n players currently adopt the cooperative strategy and (N - n)players adopt the competitive strategy. Here are the definitions of the variables used in the equation: \bar{p} is the average probability that a randomly selected player adopts the cooperative strategy in the current population, 10^{-3} is a small increment rate added to ensure that the denominator of the expression is non-zero,¹¹ and $\pi_i(n)$ and $\pi_i(n)$ are the payoffs obtained by players adopting the cooperative and competitive strategies, respectively, when n players in the population adopt a strategy. The denominator of the expression, $\pi_i(n-1) - \pi_i(n-1)$, represents the difference in payoffs obtained by the cooperative and competitive strategies when n-1 players adopt the cooperative strategy. This represents the change in payoffs resulting from a small increase in the number of players adopting the cooperative strategy.

The properties of the differential equation lead to the following proposition

Proposition 3 In unstructured population replicator dynamics under strategic uncertainty, the system of differential equations exhibits a corner equilibrium at (0, 0) and

¹¹ The value of 10^{-3} is chosen to be small enough to have a negligible impact on the overall result, but large enough to ensure that the denominator is non-zero.

an interior equilibrium that fulfills the constraint of x_i^* being equal to $1 - x_j^*$. All equilibria in the system are classified as saddle points, meaning they are neither stable nor unstable. Furthermore, the behavior of the system is contingent on the initial density of cooperators. If the initial density is below the attraction coordinates, the cooperation goes extinct. Conversely, if the initial density is higher than the coordinates of the attraction, then cooperation thrives fully.

The observed outcome dependence on the initial conditions emphasizes the system's sensitivity to small variations in the starting state. This underscores the crucial significance of considering the influence of strategic uncertainty when analyzing population dynamics.

Proof The proof can be found in "Appendix C".

3.2 The Price Identity of Replicator Dynamics Within a Bayesian-Structured Population

The critical question raised by Hilbe (2011) is whether replication can be an accurate approximation of how humans update their strategies, particularly given that individuals may blindly copy the strategies of co-players with higher payoffs. By implementing an update decay mechanism in the comparison of payoffs with randomly selected model-players, we transition from an unstructured population to a structured one (Sato and Crutchfield 2003). We differ from the approach in which the average payoff is adjusted based on the proportion of players adopting an adverse strategy, resulting in binomial sampling from a poorly-mixed population of model-players (Dragicevic 2019a, b).

We integrate Bayesian updating to assess payoff comparisons, introducing decay parameters for both cooperative ($\lambda(x_i|1-x_i)$) and competitive ($\lambda(1-x_i|x_i)$) strategies. This approach results in binomial sampling from a heterogeneously mixed population of model players, reflecting the replication's aftermath in unbalanced population fractions. Consequently, this could diminish the propagation rate of specific strategies among model players. Within the framework of replicator dynamics on a regular graph, we utilize the Bayesian decay factor to modulate the frequency at which players revise their strategies in response to neighboring strategies. Adjusting the Bayesian decay factor allows us to examine the effects of strategic uncertainty on the progression of cooperation within structured populations. Bayes' theorem provides a quantitative mechanism for evaluating the likelihood of a given hypothesis, considering prior information. To further elucidate the application of Bayesian updating within evolutionary game theory, we analyze the expression through the lens of complementary fractions, x_i and $1 - x_i$,

$$\lambda(x_i|1 - x_i) = \frac{x_i\lambda(1 - x_i|x_i)}{1 - x_i} = \frac{x_i(1 - x_i)}{1 - x_i},$$
(7)

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where λ is the decay parameter in the context of Bayesian updating; $\lambda(x_i|1 - x_i)$ represents the likelihood of adopting the cooperative strategy x_i , given the current prevalence of the competing strategy $1 - x_i$, and reflects a player's tendency to adopt a cooperative strategy based on the observed distribution of strategies within the population; $\lambda(1-x_i|x_i)$ quantifies the probability of transitioning from a competitive strategy $1-x_i$ to a cooperative strategy x_i , based on the current proportion of cooperators within the population x_i . In essence, the expression $\frac{x_i(1-x_i)}{1-x_i}$ describes a scenario where the likelihood of transitioning from one state to another, as dictated by the probability of the alternate state, is solely dependent on the proportion of players adopting that strategy. It highlights the self-adjusting nature of Bayesian updating, illustrating that the probability of a strategy shift is directly related to the number of players utilizing that strategy within the population.

The system evolution across the time is equivalent to

$$\dot{X}(\lambda) := \begin{cases} \dot{x}_i(\lambda(x_i|1-x_i)) &= x_i (\pi_i - \lambda(x_i|1-x_i)\bar{\pi}) \\ \dot{x}_j(\lambda(1-x_i|x_i)) &= (1-x_i) (\pi_j - \lambda(1-x_i|x_i)\bar{\pi}). \end{cases}$$
(8)

The differential equations yield a single Price formulation in form of

$$\begin{split} \dot{E}(\lambda, p) &= cov(\pi_{i}, p) + E(\dot{p}) \end{split} \tag{9} \\ &= \Sigma_{i}x_{i}\pi_{i}p + \Sigma_{i}x_{i}\pi_{\delta}p - \lambda\bar{\pi}\,\bar{p} + \Sigma_{i}x_{i}\dot{p} \\ &= \Sigma_{i}x_{i}\pi_{i}p(1+\delta) - \frac{x_{i}(1-x_{i})}{1-x_{i}}\left(x_{i}\pi_{i} + (1-x_{i})\pi_{j}\right)\Sigma_{i}px_{i} + \Sigma_{i}x_{i}\dot{p} \\ &= \Sigma_{i}x_{i}\pi_{i}p(1+\delta) - \Sigma_{i}px_{i}\left(\frac{x_{i}(1-x_{i})}{1-x_{i}}x_{i}\pi_{i} + \frac{x_{i}(1-x_{i})}{1-x_{i}}(1-x_{i})\pi_{j}\right) + \Sigma_{i}x_{i}\dot{p} \\ &= \Sigma_{i}x_{i}\pi_{i}p(1+\delta) - \Sigma_{i}px_{i}\left(x_{i}^{2}\pi_{i} + x_{i}(1-x_{i})\pi_{j}\right) + \Sigma_{i}x_{i}\dot{p} \\ &= \Sigma_{i}x_{i}\pi_{i}p(1+\delta) - \Sigma_{i}px_{i}^{2}\left(x_{i}\pi_{i} + (1-x_{i})\pi_{j}\right) + \Sigma_{i}x_{i}\dot{p} \\ &= \Sigma_{i}px_{i}\left((1+\delta) - x_{i}^{2}\right)\left[p\left(w(1+\epsilon) - c\right)x_{i}^{N-1} + (1-p)\left(w-c\right)\right] \\ &- \Sigma_{i}px_{i}^{2}(1-x_{i})\left[pw + (1-p)w\left(1-x_{i}^{N-1}\right)\right] + \Sigma_{i}x_{i}\dot{p}, \end{split}$$

where i, j = 1, ..., n, ..., N and $\dot{p} = n\bar{p}\left(N + 10^{-3}\frac{n}{N}\right) \frac{\pi_i(n) - \pi_j(n)}{\pi_i(n-1) - \pi_j(n-1)}$. The following proposition ensues.

Proposition 4 In Bayesian-structured population replicator dynamics under strategic uncertainty, the system of differential equations exhibits a corner equilibrium at (0, 0)and an interior equilibrium that fulfills the constraint of x_i^* being equal to $1 - x_j^*$. All equilibria in the system but one are classified as saddle points, meaning they are neither stable nor unstable. The sole stable equilibrium corresponds to the attractor. Furthermore, the behavior of the system is contingent on the initial density of cooperators. If the initial density is below the attraction coordinates, the cooperation heads toward the system attraction point. Conversely, if the initial density is higher than the coordinates of the attraction, cooperation decreases until it reaches the attraction point. The sensitivity of the system to minor changes in the initial state is highlighted by the observed dependency of outcomes on initial conditions. This underscores the critical importance of considering the impact of strategic uncertainty when analyzing population dynamics, even when Bayesian updating is present.

Proof The proof can be found in "Appendix D".

3.3 The Price Identity of Replicator-Mutator Dynamics Within an Unstructured Population

The probability of a change in strategy between two points in time echoes the happening of mutation (Chatterjee et al. 2012), the rate of which is given by $q_{ji} \in [0, 1]$. The mutation rate is the probability that a player with strategy *j* will mutate to strategy *i*. This brings to the fore a differential equation, which describes the adaptive dynamics of the population distribution (Levin 2002), termed replicator-mutator dynamics with a frequency-dependent fitness (Bürger 1998). Mutation mostly arises when groups of players form alliances in order to increase their payoffs (Nolte 2015). When it comes to the topic addressed in this paper, a competitive strategist then replicates into a cooperative one (Dercole and Rinaldi 2008). Recent findings indicate that the introduction of mutation in dynamical systems has been found to result in increased behavioral diversity (Duong and Han 2020; Ariful Kabir et al. 2023).

The population evolution, as defined in the Price equation with mutational events (Page and Nowak 2002), takes the form of

$$\begin{split} \dot{E}(\Delta, p) &= cov(\pi_j, p) + E(\dot{p}) + E(\pi_i \Delta) \end{split} \tag{10} \\ &= \Sigma_j x_j \pi_j p + \Sigma_j x_j \pi_j \delta p - \bar{\pi} \, \bar{p} + \Sigma_i x_i \dot{p} + \Sigma_i x_i \pi_i \Sigma_j q_{ji} p \\ &= \Sigma_j x_j \pi_j p(1+\delta) - \left(x_i \pi_i + (1-x_i)\pi_j\right) \Sigma_i p x_i + \Sigma_i x_i \dot{p} + \Sigma_i x_i \pi_i \Sigma_j q_{ji} p \\ &= \Sigma_j \pi_j x_j p(1+\delta) - \Sigma_i x_i^2 \pi_i p - \Sigma_i x_i (1-x_i) \pi_j p + \Sigma_i x_i \dot{p} + \Sigma_i x_i \pi_i \Sigma_j q_{ji} p \\ &= -\Sigma_i x_i^2 \pi_i p + \Sigma_i x_i \pi_i \Sigma_j q_{ji} p + \Sigma_j \pi_j x_j p(1+\delta) - \Sigma_i x_i (1-x_i) \pi_j p + \Sigma_i x_i \dot{p} \\ &= \Sigma_i x_i p(\Sigma_j q_{ji} - x_i) \pi_i + p(\Sigma_j x_j (1+\delta) - \Sigma_i x_i (1-x_i)) \pi_j + \Sigma_i x_i \dot{p} \\ &= \Sigma_i x_i p(\Sigma_j q_{ji} - x_i) \left[p \left(w(1+\epsilon) - c \right) x_i^{N-1} + (1-p) \left(w - c \right) \right] \\ &+ p(\Sigma_j x_j (1+\delta) - \Sigma_i x_i (1-x_i)) \left[p w + (1-p) w \left(1 - x_i^{N-1} \right) \right] + \Sigma_i x_i \dot{p}, \end{split}$$

where i, j = 1, ..., n, ..., N, $\Delta = 1^{12}$ and $\dot{p} = n\bar{p}\left(N + 10^{-3}\frac{n}{N}\right) \frac{\pi_i(n) - \pi_j(n)}{\pi_i(n-1) - \pi_j(n-1)}$.

Proposition 5 In unstructured population replicator-mutator dynamics under strategic uncertainty, the system of differential equations exhibits a corner equilibrium at (0, 0) and an interior equilibrium that fulfills the constraint of x_i^* being equal to

¹² Based on the prevalence proportion principle (Dragicevic 2017), we can determine that the mutation probability of a player chosen at random from the population is equal to the proportion of cooperators in the population. In the case of a population-level mutation from type *j* to type *i*, $E(\pi_i \Delta)$ represents the expected surplus from cooperating. This is assuming that the probability of mutation is certain, or in other words, $E(\Delta) = 1$.

 $1 - x_j^{\star}$. All equilibria in the system but one are classified as saddle points, meaning they are neither stable nor unstable. The sole unstable equilibrium corresponds to the source. Furthermore, the behavior of the system is non-contingent on the initial density of cooperators. Whatever the initial density, the system converges toward the system attraction point. However, the certainty of mutation towards cooperation, which encourages free-riding, results in the system being consistently drawn towards a transient full population density.

Proof The proof can be found in "Appendix E".

3.4 The Price Identity of Replicator-Mutator Dynamics Within a Bayesian-Structured Population

In the lookout for the Bayesian population structure version of the differential equation, the replicator-mutator dynamics takes place in the form of

$$\begin{split} \dot{E}(\lambda, \Delta, p) &= cov(\pi_j, p) + E(\dot{p}) + E(\pi_i \Delta) \end{split}$$
(11)

$$&= \sum_j x_j \pi_j p + \sum_j x_j \pi_j \delta p - \lambda \bar{\pi} \, \bar{p} + \sum_i x_i \dot{p} + \sum_i x_i \pi_i \sum_j q_{ji} p \\ &= \sum_j x_j \pi_j p (1 + \delta) - \frac{x_i (1 - x_i)}{1 - x_i} \left(x_i \pi_i + (1 - x_i) \pi_j \right) \sum_i p x_i \\ &+ \sum_i x_i \dot{p} + \sum_i x_i \pi_i \sum_j q_{ji} p \\ &= \sum_j x_j \pi_j p (1 + \delta) - (x_i^2 \pi_i + x_i (1 - x_i) \pi_j) \sum_i p x_i + \sum_i x_i \dot{p} + \sum_i x_i \pi_i \sum_j q_{ji} p \\ &= \sum_i x_i \pi_i \sum_j q_{ji} p - \sum_i x_i^3 \pi_i p - \sum_i x_i^2 (1 - x_i) \pi_j p + \sum_i x_i \dot{p} + \sum_i x_i \pi_i \sum_j q_{ji} p \\ &= \sum_i x_i n_i \sum_j q_{ji} p - \sum_i x_i^3 \pi_i p + \sum_j x_j \pi_j p (1 + \delta) - \sum_i x_i^2 (1 - x_i) \pi_j p + \sum_i x_i \dot{p} \\ &= \sum_i x_i p (\sum_j q_{ji} - x_i^2) \pi_i + p (\sum_j x_j (1 + \delta) - \sum_i x_i^2 (1 - x_i)) \pi_j + \sum_i x_i \dot{p} \\ &= \sum_i x_i p (\sum_j q_{ji} - x_i^2) \left[p \left(w (1 + \epsilon) - c \right) x_i^{N-1} + (1 - p) \left(w - c \right) \right] \\ &+ p (\sum_j x_j (1 + \delta) - \sum_i x_i^2 (1 - x_i)) \left[pw + (1 - p)w \left(1 - x_i^{N-1} \right) \right] + \sum_i x_i \dot{p}, \end{split}$$

where i, j = 1, ..., n, ..., N and $\dot{p} = n\bar{p} \left(N + 10^{-3} \frac{n}{N} \right) \frac{\pi_i(n) - \pi_j(n)}{\pi_i(n-1) - \pi_j(n-1)}$.

Proposition 6 In unstructured population replicator-mutator dynamics under strategic uncertainty, the system of differential equations exhibits a corner equilibrium at (0, 0) and an interior equilibrium that fulfills the constraint of x_i^* being equal to $1 - x_j^*$. All equilibria in the system but one are classified as saddle points, meaning they are neither stable nor unstable. The sole unstable equilibrium corresponds to the source. Furthermore, the behavior of the system is non-contingent on the initial density of cooperators. Whatever the initial density, the system converges toward the system attraction point. However, the certainty of mutation towards cooperation, which encourages free-riding, results in the system being consistently drawn towards a transient full population density.

Proof The proof can be found in "Appendix F".

3.5 Unified Evolutionary Dynamics Through the Price Identity

By combining the aforementioned result with the findings from a previous subsection, and assuming a certainty of mutation by setting $E(\Delta) = 1$,¹³ we can derive the following conditional equivalence

$$\begin{split} & \Sigma_i x_i \pi_i p(1+\delta) - \Sigma_i p x_i^2 \left(x_i \pi_i + (1-x_i) \pi_j \right) + \Sigma_i x_i \dot{p} \\ &= \Sigma_i x_i p (\Sigma_j q_{ji} - x_i) \pi_i + p (\Sigma_j x_j (1+\delta) - \Sigma_i x_i (1-x_i)) \pi_j + \Sigma_i x_i \dot{p} \\ &\Leftrightarrow \Sigma_i x_i \pi_i p (1+\delta) - \Sigma_i p x_i^2 \left(x_i \pi_i + (1-x_i) \pi_j \right) \\ &= \Sigma_i x_i p (\Sigma_j q_{ji} - x_i) \pi_i + p (\Sigma_j x_j (1+\delta) - \Sigma_i x_i (1-x_i)) \pi_j \\ &\Leftrightarrow (cov(\pi_i, p) + \bar{\pi} \bar{p}) (1+\delta) - (cov(\pi_i, p) + \bar{\pi} \bar{p}) x_i^2 - (cov(\pi_i, p) \\ &+ \bar{\pi} \bar{p}) (\Sigma_j q_{ji} - x_i) \\ &= \Sigma_i x_i (1-x_i) \pi_j (x_i - p) + (cov(\pi_j, p) + \bar{\pi} \bar{p}) (1+\delta), \end{split}$$

where i, j = 1, ..., n, ..., N. Allen and Rosenbloom (2012) observed that high mutation rates are commonly found in cyclical frequency-dependent dynamics and fluctuating environments. When the proportion of cooperators is small,¹⁴ i.e., $x_i \rightarrow 0$ and $\bar{\pi} \bar{p} \rightarrow 0$, the following situation arises

$$\delta = \frac{cov(\pi_j, p)}{cov(\pi_i - \pi_j, p)}$$
(13)

The next proposition ensues.

Proposition 7 In replicator-mutator dynamics under strategic uncertainty, as outlined in the Price theorem of selection, the replication of an unstructured population strategy with certain mutation, from competition to cooperation, is conditionally equivalent to the replication of a Bayesian-structured population strategy without mutation. This equivalence holds when the transition rate from competition to cooperation is equal to the relative strength of selection acting on competition in relation to the selection differential between the cooperators and competitors.

Proof The proof can be found in "Appendix G".

Calculations have previously shown that, in the context of replicator-mutator dynamics, the replication of a strategy with a certain mutation in an unstructured population is equivalent to the negative replication of the same strategy in a structured population without mutation, as demonstrated by Dragicevic (2019a). Although the Price equation is part of a unified evolutionary framework, the outcomes obtained in terms of reflective evolution are no longer observed. Furthermore, it must be highlighted that the newest result is also different from the one in Dragicevic (2019b). Indeed, it has been previously found that in the context of replicator-mutator dynamics

 $^{^{13}} E(\Delta) = 1$ implies $E(\dot{p}) \rightarrow 0$, such that the expected change in p tends toward zero as the player population shifts toward cooperation on a particular basis.

¹⁴ Conversely, if there is a preponderance of cooperators, the mutation is less significant.

with strategic uncertainty, which can be traced back to the Price theorem of selection, the replication of an unstructured-population strategy, subject to certain mutation, from competition to cooperation, is conditionally interchangeable with the replication of a structured-population strategy that is free from mutation. This equivalence arises when the fraction of competitors, weighted by the payoff of a cooperative model-player and inversely proportional to the expected payoff from cooperation, is less than or equal to the joint selection of cooperators and competitors, which is augmented by the double average population payoff. In our latest result, what comes out is that the equivalence is valid if and only if the rate of transition from competition to cooperation equals the ratio of the strength of selection acting on competition relative to the selection differential between the cooperators and competitors.

In evolutionary dynamics, the selection differential is a measure of the fitness difference between individuals with certain traits and those without. The selection differential between cooperators and competitors refers to the difference in payoff between individuals who cooperate and those who compete in a given population. This difference in payoffs is due to various factors, such as the rewards and costs associated with each strategy, and how well each strategy performs in the environment.

The selection differential between cooperators and competitors plays a crucial role in determining the evolutionary outcomes of social dilemmas. If the selection differential favors cooperators, meaning that cooperators have a higher payoff than competitors, then cooperation is likely to spread in the population over time. On the other hand, if the selection differential favors competitors, then cooperative strategy. A positive covariance between the selection differential and the probability of meeting a cooperator suggests that individuals with higher payoff—due to a higher selection differential—are more likely to encounter other cooperators, which would further increase their payoff.

Once again, the implication of the value of δ is as follows. If δ approaches 0, it suggests a lack of correlation or assortment between payoffs and the probability of encountering a cooperator, which implies that the population is more randomly mixed and that there is no clear relationship between payoffs and the likelihood of encountering a cooperator. Conversely, a value of δ near 1 indicates a strong correlation or a high degree of assortment between payoffs and the probability of encountering a cooperator, suggesting that individuals are more likely to interact with those who have similar payoffs.

Remark 1 The equivalence between Bayesian-structured population replicator dynamics and unstructured population replicator-mutator dynamics, in the context of the Price theorem of selection under strategic uncertainty, can be indirectly established by calibrating replicator dynamics in a poorly-mixed population setting.

Combining the assumption of a certain mutation with the results obtained previously, we can establish the following conditional equivalence

$$\Sigma_i p x_i (1+\delta - x_i) \pi_i - \Sigma_i p x_i (1-x_i) \pi_j + \Sigma_i x_i \dot{p}$$

$$= \Sigma_i x_i p (\Sigma_j q_{ji} - x_i^2) \pi_i + p (\Sigma_j x_j (1+\delta) - \Sigma_i x_i^2 (1-x_i)) \pi_j + \Sigma_i x_i \dot{p}$$
(14)

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$$\Leftrightarrow (1+\delta)(\Sigma_i x_i \pi_i p - \Sigma_j q_{ji} - x_i^2) - \Sigma_i x_i \pi_j p(1-x_i)(1+x_i)$$

$$= \Sigma_i x_i p(\Sigma_j q_{ji} - x_i)\pi_i + p(\Sigma_j x_j(1+\delta) - \Sigma_i x_i(1-x_i))\pi_j$$

$$\Leftrightarrow (cov(\pi_i, p))(1+\delta) - (cov(\pi_i, p) + \bar{\pi} \bar{p})x_i$$

$$= (cov(\pi_j, p)(1+\delta) - (cov(\pi_j, p) + \bar{\pi} \bar{p})(1-x_i)(1+x_i) + \Sigma_i x_i \pi_i (\Sigma_j q_{ji} - x_i^2),$$

where i, j = 1, ..., n, ..., N. In the presence of a small proportion of cooperators, such that $x_i \to 0$ and $\bar{\pi} \bar{p} \to 0$, we fall on

$$\delta = \frac{cov(\pi_i, p)}{cov(\pi_i - \pi_i, p)} \tag{15}$$

We summarize the result in the following proposition.

Proposition 8 In replicator-mutator dynamics under strategic uncertainty, as outlined in the Price theorem of selection, the replication of a Bayesian-structured population strategy with certain mutation, from competition to cooperation, is conditionally equivalent to the replication of an unstructured population strategy without mutation. This equivalence holds when the transition rate from competition to cooperation is equal to the relative strength of selection acting on cooperation in relation to the selection differential between the competitors and cooperators.

Proof The proof can be found in "Appendix H".

This outcome is contingent on $x_i^* = 1$, which is only possible when the payoff for cooperation is zero. This counterintuitive finding arises when the population is large, a mixed strategy including cooperation is present, and mutual cooperation yields benefits that outweigh the costs of exploitation. A structured population graph is a requisite for this occurrence.

Calculations have previously shown that, in the context of replicator-mutator dynamics, the replication of a strategy in an unstructured population without mutation is equivalent to the negative replication of the strategy in a structured population with mutation, as demonstrated by Dragicevic (2019a). Moreover, Dragicevic (2019b) demonstrated that the replication of a structured-population strategy, subject to certain mutation from competition to cooperation, is conditionally equivalent to the replication of an unstructured-population strategy free from mutation, in the context of replicator-mutator dynamics under strategic uncertainty, as outlined in the Price theorem of selection. This equivalence occurs when the fraction of cooperators, weighted by the payoff of a cooperative model-player and inversely proportional to the expected payoff from cooperation, is less than or equal to the joint selection of cooperators and competitors increased by the double average population payoff. Our latest finding indicates that the equivalence is only valid if the rate of transition from cooperation is equal to the ratio of the strength of selection acting on cooperation in relation to the selection differential between competitors and cooperators.

Remark 2 The equivalence between Bayesian-structured population replicator dynamics and unstructured population replicator-mutator dynamics, in the context of the

Price theorem of selection under strategic uncertainty, can be indirectly established by calibrating replicator dynamics in a well-mixed population setting.

Equations (13) and (15) provide a means for determining the proportion of cooperators required for the convergence of evolutionary dynamics. As such, we can derive the following result

$$\frac{cov(\pi_i, p)}{cov(\pi_j - \pi_i, p)} = \frac{cov(\pi_j, p)}{cov(\pi_i - \pi_j, p)}$$

$$\Leftrightarrow -\Sigma_i x_i \pi_i = \Sigma_j x_j \pi_j$$

$$\Leftrightarrow -x_i \pi_i = (1 - x_i) \pi_j$$

$$\Leftrightarrow x_i^{\star} = \frac{\pi_j}{\pi_j - \pi_i},$$
(16)

where i, j = 1, ..., n, ..., N. The final examination of the game-theoretic scenario leads to the following corollary.

Corollary 1 The Price theorem of selection establishes a conditional equivalence between unstructured population replicator dynamics and Bayesian-structured population replicator dynamics within a population of model-players organized on a graph and subjected to strategic uncertainty and mutation towards cooperation. This equivalence is contingent upon the proportion of cooperators being equivalent to the relative payoff advantage of a competitor over a cooperator.

Proof The proof can be found in "Appendix I".

4 Simulations

Starting from the propositions obtained in the modeling section, we shall now illustrate, by means of numerical simulations performed on stream diagrams, the various evolutionary dynamics.¹⁵ Four examples are presented, each of which covers the properties and the conditions exposed hereinabove. The purpose of the incremental fifth subsection is to bring to light the unified evolutionary dynamics through the Price identity.

In what follows, consider the initial numerical values of the modeling items to be fixed at w = 10, $\epsilon = 0.5$, c = 5, N = 100, $q_{ji} = 1$ and $\delta = 0.5$. As we now launch the simulations, the dynamic mappings yield the following outputs.

4.1 The Price Identity of Replicator Dynamics Within an Unstructured Population

Figure 1 depicts an example of replicator dynamics in an unstructured population context.

Analyzing a stream plot of the basins of attraction in the context of Price-wise unstructured population replicator dynamics involves examining the patterns and

¹⁵ The Python codes for the numerical simulations are available upon request for interested readers.



Fig. 1 A stream plot is produced to visualize the basins of attraction of the Price-wise unstructured population replicator dynamics, represented by the derivative $\dot{E}(p)$, for a constant transition rate ($\delta = 0.5$). We consider four probability levels defining the likelihood of cooperation ($p = \{0.25, 0.50, 0.75, 1\}$). The *x*-axes represent the differential equation of the time-varying fraction of cooperators (\dot{x}_i). The *y*-axes represent the differential equation governing the time evolution of the proportion of competitors (\dot{x}_i). We observe saddle attractors in the system. At p = 0.25, { x_i, x_j } = (0.38, 0.38). At p = 0.50, { x_i, x_j } = (0.3, 0.3). At p = 0.75, { x_i, x_j } = (0.13, 0.13). At p = 1, { x_i, x_j } = (0,0) (Color figure online)

directional flow of the streamlines. These streamlines depict the evolution of the frequency of various strategies over time, while the basins of attraction indicate the steady-state frequencies of strategies within the population.¹⁶

¹⁶ The Python code uses NumPy's np.linspace and np.meshgrid functions to define the *x* and *y* coordinates of the plot. The ax.streamplot function from Matplotlib is used to create a plot of the vector field for the replicator dynamics model. Contour lines are added to the plot using the contourf function to color the regions of the basins of attraction. The set_xlim, set_ylim, set_xmargin, and set_ymargin functions are used to set the axis limits and margins. Finally, the plot is displayed using the plt.show function from Matplotlib.

We analyzed the stability conditions of the system under consideration by examining its fixed points, with a fixed value of δ equal to 0.5. This was accomplished by solving the system of differential equations represented by the time derivative of the strategy frequencies, given by $\dot{E}(p) = \{x_i, x_j\}$. This yielded the fixed point values for x_i^* and x_j^* , given by $x_i^* = \{0, \frac{-2+15p-15p^2-10px_j+10p^2x_j+30p^2x_j^{99}-20p^2x_j^{100}}{20p(1-x_j^{99}+px_j^{99})}\}$ and $x_j^* = \{0, \frac{-2+15p-15p^2-10px_i+10p^2x_i+30p^2x_j^{99}-20p^2x_i^{100}}{20p(1-x_j^{99}+px_j^{99})}\}$. These fixed point values represent the equilibrium points of the system.

Our analysis revealed that the system under consideration has both a corner equilibrium and an interior equilibrium. However, all fixed points are identified as saddle points, given that the eigenvalues of the Jacobian matrix show opposite signs. At a saddle point, the system displays both stable and unstable behavior in different directions, resulting in trajectories near the point to either converge or diverge. Since certain equilibria may only be stable within a specific range of parameter values, we conducted a sensitivity analysis to examine the impact of the probability of cooperating on the equilibria. Notably, fixed points can serve as attraction points in a dynamic system.

At a specific value of p equal to 0.25, we observe an attractor with coordinates $\{x_i, x_j\} = (0.38, 0.38)$. As p increases, the coordinates of the attractor approach zero, indicating a faster transition from competition to cooperation with increasing probability of meeting a cooperator. We observe attractors with coordinates $\{x_i, x_j\} = (0.3, 0.3)$ at p = 0.50, and $\{x_i, x_j\} = (0.13, 0.13)$ at p = 0.75. At p = 1, the system converges towards $\{x_i, x_j\} = (0, 0)$. Additionally, below the attractor point, the dynamics lead to the attractor bifurcating towards the extinction of one subpopulation for the benefit of the other, while beyond the attraction point, the arrows bifurcate and lead to the hegemony of either subpopulation. These findings verify $x_i + (1 - x_i) = 1$ and indicate that the bifurcation from cooperation to cooperation to cooperation of the entire population.

The colors in the basins of attraction indicate regions where a strategy frequency will converge over time. Blue regions are lower stable frequencies, and red regions are higher stable frequencies, with a gradient of colors in between representing intermediate stable frequencies. Higher stable frequencies are resistant to invasion and attract nearby strategy frequencies over time, while lower stable frequencies are stable against small perturbations in the strategy frequencies. The difference between the two is the frequency relative to the population average. Red regions favor cooperation above the attraction coordinates and competition below them, as the cooperative strategy is more successful in those areas. Blue regions mostly appear near the corner equilibrium where either strategy prevails, indicating the presence of both strategies in those areas.

4.2 The Price Identity of Replicator Dynamics Within a Bayesian-Structured Population

Figure 2, which displays structured population replicator dynamics, exhibits patterns that diverge notably from those detected in conventional replicator dynamics.



Fig. 2 A stream plot is produced to visualize the basins of attraction of the Price-wise Bayesian-structured population replicator dynamics, represented by the derivative $\dot{E}(p)$, for a constant transition rate ($\delta = 0.5$). We consider four probability levels defining the likelihood of cooperation ($p = \{0.25, 0.50, 0.75, 1\}$). The *x*-axes represent the differential equation of the time-varying fraction of cooperators (\dot{x}_i). The *y*-axes represent the differential equation governing the time evolution of the proportion of competitors (\dot{x}_j). We observe stable attractors in the system. At p = 0.25, { x_i, x_j } = (0.62, 0.62). At p = 0.50, { x_i, x_j } = (0.55, 0.55). At p = 0.75, { x_i, x_j } = (0.37, 0.37). At p = 1, { x_i, x_j } = (0.03, 0.03) (Color figure online)

The stream plot of the basins of attraction in Price-wise structured population replicator dynamics involves examining the streamlines' patterns and directional flow, depicting the frequency of various strategies' evolution over time. The basins of attraction indicate the steady-state frequencies of strategies within the population.

The stability conditions of the system were investigated by analyzing its fixed points, while assuming a value of $\delta = 0.5$. The Jacobian matrix was utilized for this purpose. We solved the differential equations $\dot{E}(p) = \{x_i, x_j\}$ and obtained the values of the fixed points as $x_i^{\star} = \{0, \frac{-2x_j + 15px_j - 15p^2x_j - 10px_j^3 + 10p^2x_j^3 + 30p^2x_j^{100} - 20px_j^{2102}}{20px_j^2(1-x_j^{99} + px_j^{99})}\}$

and $x_j^{\star} = \{0, \frac{-2x_i + 15px_i - 15p^2x_i - 10px_i^3 + 10p^2x_i^3 + 30p^2x_i^{100} - 20p^2x_i^{102}}{20px_i^2(1 - x_i^{99} + px_i^{99})}\}$. These fixed point values represent the equilibrium points of the system

values represent the equilibrium points of the system.

Our analysis revealed the presence of both a corner and an interior equilibrium within the system. Except for the attractor coordinates, all other fixed points were classified as saddle points based on the opposite signs of the eigenvalues of the Jacobian matrix. A saddle point displays both stable and unstable behavior in different directions, leading trajectories near the point to either converge or diverge. To investigate the impact of the probability of cooperation on equilibria, we conducted a sensitivity analysis since some equilibria may only be stable within a certain range of parameter values. Notably, fixed points can act as attraction points in dynamic systems.

Our analysis of the system's fixed points led us to investigate the presence of attractors, which are sets of trajectories or states that a system converges towards over time regardless of initial conditions. Attractors can also include fixed points. We observed an attractor with coordinates $\{x_i, x_j\} = (0.62, 0.62)$ at p = 0.25, while p = 0.50and p = 0.75 had attractors at $\{x_i, x_j\} = (0.55, 0.55)$ and $\{x_i, x_j\} = (0.37, 0.37)$, respectively. At p = 1, the system converged towards $\{x_i, x_j\} = (0.03, 0.03)$.

In scenarios where the probability of encountering cooperators is uncertain, the population dynamics system generally exhibits convergence towards the interior equilibrium. As the probability of meeting a cooperator approaches one, the interior equilibrium tends towards zero. The system displays attraction towards a stable attractor point as a whole. However, in cases where players are guaranteed to interact with cooperators and free-riding behavior is incentivized by means of the sucker's payoff, the corner equilibrium is the only attractor. This leads to competition between player populations, eventually resulting in the extinction of one or both populations.

The system exhibits convergence towards the attractor point without any subpopulation domination, occurring both below and above the attractor point. This indicates the absence of bifurcation from competition to cooperation in the system. Furthermore, the attractor point displays the stable property of attracting nearby strategy frequencies over time, which makes it resistant to invasion. However, an intriguing finding is that the probability of cooperation increasing causes both subpopulations to approach zero, suggesting a mutual push towards extinction. As a result, a more in-depth examination of the basins of attraction is required to understand the underlying mechanisms of this phenomenon.

The basins of attraction depict the regions of strategy frequency convergence over time, with blue regions representing lower stable frequencies and red regions representing higher stable frequencies. The gradient of colors in between indicates intermediate stable frequencies. Higher stable frequencies are resistant to invasion and attract nearby strategy frequencies over time, while lower stable frequencies are stable against small perturbations in the strategy frequencies. Red regions favor competition when the cooperation density is low, while blue regions mostly appear around a density of 0.5 of cooperators. Near the attraction coordinates, red regions favor competition above the attractor and cooperation below it. When encountering a cooperator is certain, red regions favor full density of competition and the extinction of cooperators. Therefore, Bayesian updating favors competition in all cases except when the initial level



Fig. 3 A stream plot is produced to visualize the basins of attraction of the Price-wise unstructured population replicator-mutator dynamics, represented by the derivative $\dot{E}(p)$, for a constant transition rate ($\delta = 0.5$). We consider four probability levels defining the likelihood of cooperation ($p = \{0.25, 0.50, 0.75, 1\}$). The *x*-axes represent the differential equation of the time-varying fraction of cooperators (\dot{x}_i). The *y*-axes represent the differential equation governing the time evolution of the proportion of competitors (\dot{x}_j). We observe unstable attractors in the system. At p = 0.25, { x_i, x_j } = (1, 1). At p = 0.50, { x_i, x_j } = (1, 1). At p = 0.75, { x_i, x_j } = (1, 1). At p = 1, { x_i, x_j } = (1, 1) (Color figure online)

of cooperators is already high. The prevalence of cooperators in the entire population would not occur unless this condition is met.

4.3 The Price Identity of Replicator-Mutator Dynamics Within an Unstructured Population

The patterns observed in Fig. 3, which illustrates replicator-mutator dynamics in an unstructured population, significantly deviate from those observed in the previous cases.

The stream plot of the basins of attraction in Price-wise unstructured population replicator-mutator dynamics involves analyzing the streamlines' patterns and directional flow, which depicts the evolution of various strategies' frequency over time. The basins of attraction signify the steady-state frequencies of strategies within the population.

After assuming a value of $\delta = 0.5$, the stability of the system was investigated by analyzing its fixed points using the Jacobian matrix. The fixed points were obtained by solving the differential equations $E(p) = \{x_i, x_j\}$. The resulting fixed points are $x_i^{\star} = \{0, \frac{-x_i + 5px_i - 5p^2x_j - 5px_j^2 + 5p^2x_j^2 + 10p^2x_j^{100} - 10p^2x_j^{101}}{5p(2x_j - 3)(1 - x_j^{99} + px_j^{99})}\}$ and $x_j^{\star} = \{0, \frac{-x_i + 5px_i - 5p^2x_i - 5px_i^2 + 5p^2x_i^2 + 10p^2x_i^{100} - 10p^2x_i^{101}}{5p(2x_i - 3)(1 - x_j^{99} + px_j^{99})}\}$. The eigenvalues of the Jacobian matrix indicate at the second sec

matrix indicated the existence of an unstable corner equilibrium.

In the context of dynamical systems, an unstable fixed point refers to a state where small perturbations result in the system moving away from the fixed point rather than converging towards it. Our analysis revealed that the unstable fixed point acts as a source, with trajectories diverging away from it in all directions, similar to the behavior of a repeller. To assess the influence of the probability of cooperation on equilibria, we performed a sensitivity analysis concerning the probability of cooperating.

Following our analysis of the stability of fixed points in the system, the fixed points do not serve as attractors in this system. We thus shift our focus to the presence of attractors. In a system of differential equations, an attractor is defined as a set of states or trajectories that the system tends to converge towards over time, regardless of its initial conditions. At p = 0.25, we observe an attractor with coordinates $\{x_i, x_i\} = (1, 1)$. Similarly, at p = 0.50 and p = 0.75, we have attractors with coordinates $\{x_i, x_j\} = (1, 1)$ and $\{x_i, x_j\} = (1, 1)$, respectively. At p = 1, we observe $\{x_i, x_i\} = (1, 1)$. The study found that the population dynamics system converges towards an unstable attractor, regardless of the probability of encountering a cooperator. An unstable attractor attracts nearby trajectories, but slight perturbations can cause trajectories to diverge. Assuming that there is a certain probability of mutation towards cooperation occurring, the system eliminates competitors who return as free-riders due to certain encounters with cooperators, driving the system towards a transient full population density. However, guaranteed interaction with cooperators incentivizes free-riding through the sucker's payoff, and only mutation can restore cooperation.

The basins of attraction are colored regions indicating the convergence of a strategy frequency over time. They include lower stable frequencies shown in blue, higher stable frequencies shown in red, and a gradient of colors in between representing intermediate stable frequencies. Higher stable frequencies attract nearby strategy frequencies over time and are resistant to invasion, while lower stable frequencies are stable against small perturbations in the strategy frequencies. This difference between the two is the frequency relative to the population average. Our study of the basins of attraction confirms the aforementioned observation. Red regions favor cooperation asymptotically. When the density of competitors is low, cooperation prevails. When the density of cooperators is full, they turn into free-riders due to certain encounters with cooperators before mutating into cooperators. Blue regions appear along



Fig. 4 A stream plot is produced to visualize the basins of attraction of the Price-wise Bayesianstructured population replicator-mutator dynamics, represented by the derivative $\dot{E}(p)$, for a constant transition rate ($\delta = 0.5$). We consider four probability levels defining the likelihood of cooperation ($p = \{0.25, 0.50, 0.75, 1\}$). The *x*-axes represent the differential equation of the time-varying fraction of cooperators (\dot{x}_i). The *y*-axes represent the differential equation governing the time evolution of the proportion of competitors (\dot{x}_i). We observe unstable attractors in the system. At p = 0.25, $\{x_i, x_j\} = (1, 1)$. At p = 0.50, $\{x_i, x_j\} = (1, 1)$. At p = 0.75, $\{x_i, x_j\} = (1, 1)$. At p = 1, $\{x_i, x_j\} = (1, 1)$ (Color figure online)

the bisector, illustrating the continuous mutation towards cooperation driven by the free-riding problem.

4.4 The Price Identity of Replicator-Mutator Dynamics Within a Bayesian-Structured Population

Figure 4 provides an overview of replicator-mutator dynamics within a structured population structure. There is a high degree of similarity between this scenario and the previous one.

The stream plot of the basins of attraction in Price-wise structured population replicator-mutator dynamics involves visualizing the direction of flow of the streamlines, which represent the frequency of various strategies' evolution over time. The basins of attraction reveal the stable steady-state frequencies of strategies within the population.

We examined the stability of the system by analyzing its fixed points, assuming a constant value of $\delta = 0.5$ and a certain probability of mutation towards cooperation. Using the Jacobian matrix, we determined the stability conditions by solving the differential equations $\dot{E}(p) = \{x_i, x_j\}$. The fixed points were computed as $x_i^{\star} = \{0, \frac{-x_j + 5px_j - 5p^2x_j - 5px_j^3 + 5p^2x_j^3 + 10p^2x_j^{100} - 10p^2x_j^{102}}{5p(2x_j^2 - 3)(1 - x_j^{99} + px_j^{99})}\}$ and $x_j^{\star} = \{0, \frac{-x_i + 5px_i - 5p^2x_i - 5px_i^3 + 5p^2x_i^3 + 10p^2x_j^{100} - 10p^2x_j^{102}}{5p(2x_i^2 - 3)(1 - x_j^{99} + px_j^{99})}\}$. Our analysis revealed the presence of an unstable correspondible to a stability as the air experimentation of the Lapohian matrix.

of an unstable corner equilibrium, as the eigenvalues of the Jacobian matrix were found to be positive.

In a system with an unstable fixed point, even small perturbations can cause the system to move away from the point rather than converge towards it. In our case, the unstable fixed point behaves like a source and produces a repeller-like behavior where trajectories diverge in all directions away from the fixed point. To investigate the impact of cooperation probability on equilibria, we conducted a sensitivity analysis by varying the probability of cooperating.

Upon analyzing the stability of fixed points in the system, our next task was to investigate the presence of attractors. An attractor is a set of states or trajectories to which a system of differential equations converges over time, regardless of its initial conditions. Although fixed points can also serve as attractors in a system, this is not the case in our scenario. We observe an attractor at coordinates $\{x_i, x_j\} = (1, 1)$ when p = 0.25. Similarly, at p = 0.50 and p = 0.75, we find attractors at $\{x_i, x_j\} = (1, 1)$. When p = 1, the attractor is located at $\{x_i, x_j\} = (1, 1)$.

The findings of the study indicate that the population dynamics system converges towards an unstable attractor, regardless of the probability of encountering cooperators. An unstable attractor is a point that attracts nearby trajectories but any slight perturbation can cause them to diverge and move away from it. Assuming that mutation towards cooperation is a certain event that will occur during the game, the system continuously eliminates competitors who persist as free-riders due to their certain encounters with cooperators, driving the system towards a transient full population density. When players are guaranteed to interact with cooperators, incentivizing free-riding behavior, only mutation can prompt them to revert to cooperation. Interestingly, Bayesian updating has no impact on population dynamics in the case of a certain mutation.

The basins of attraction, depicted as colored regions, represent the convergence of a strategy frequency over time. These regions include lower stable frequencies (blue), higher stable frequencies (red), and a gradient of colors in between representing intermediate stable frequencies. Higher stable frequencies attract nearby strategy frequencies over time and are resistant to invasion, while lower stable frequencies are stable against small perturbations in the strategy frequencies. The difference between the two is the frequency relative to the population average. Our study of the basins of attraction confirms that red regions favor cooperation asymptotically. When the density **Fig. 5** A colormap is produced to illustrate the levels of transition rate δ that equate the rates of change of $\dot{E}(\lambda, p)$ and $\dot{E}(\Delta, p)$. The *x*-axis represents the payoff attained from competing, $\pi_j \in [0, 10]$. The *y*-axis represents the payoff from cooperating, $\pi_i \in [0, 10]$. The *z*-axis illustrates the values of $\delta = \frac{cov(\pi_j, p)}{cov(\pi_i - \pi_j, p)}$. It is noteworthy that δ has an upper bound of 0.1 (Color figure online)



of competitors is low, cooperation prevails. However, when the density of cooperators is full, they turn into free-riders due to certain encounters with cooperators before mutating back to cooperators. Blue regions appear along the bisector, illustrating the continuous mutation towards cooperation driven by the free-riding problem. Furthermore, our study reveals that Bayesian updating has no effect on population dynamics in the case of a certain mutation.

4.5 Unified Evolutionary Dynamics Through the Price Identity

We have conducted an additional analysis of the unified evolutionary dynamics in relation to the Price identity. Our findings, as shown in Fig. 5, indicate that coupling unstructured population replicator dynamics with Bayesian-structured population replicator dynamics results in a distinct definition of the transition rate.¹⁷ The visual representation in the figure provides clear evidence of a contradiction to the commonly observed patterns in evolutionary game theory, where players typically take into account the payoffs or rewards associated with different strategic choices (Sandholm 2012).

The given results imply a relationship between the payoffs, the probability of cooperating, and the selection differential between cooperators and competitors. Specifically, the transition rate, which is the probability of a cooperator replacing their neighbor in the birth-death process, is independent of the levels of payoffs of either type of player and is always approximately 0.1. By replacing $cov(\pi_j, p)$ with $0.1 \cdot cov(\pi_i - \pi_j, p)$, we can derive that $cov(\pi_j, p) = \frac{1}{11}cov(\pi_i, p)$ and $cov(\pi_i - \pi_j, p) = \frac{10}{11}cov(\pi_i, p)$. This indicates that the covariance between the probability of cooperating and the payoff from defecting is reduced to $\frac{1}{11}$ of the covariance between the selection differential and the probability of cooperating, while the covariance between the selection differential and the probability of cooperating

¹⁷ The colorplan surface plot has been obtained on Python by defining ranges for π_i , π_j , and p using NumPy functions, creating a meshgrid, calculating covariance and δ values, and then plotting the result using matplotlib.pyplot functions.

is increased to $\frac{10}{11}$ of the covariance between the probability of cooperating and the payoff from cooperating.

Based on the analysis conducted, it appears that the selection differential between cooperators and competitors has a stronger influence on the probability of cooperation compared to the difference in payoffs between cooperating and defecting. This finding has important implications for our understanding of how cooperation evolves in social dilemmas. Specifically, it suggests that the transition rate, which represents the probability of a cooperator replacing its neighbor in the birth-death process, is more dependent on the covariance between payoffs and the probability of cooperation rather than the specific values of the payoffs themselves. This means that even small changes in the probability of cooperation can have a significant impact on the evolution of cooperation within the population.

Studying the covariance between payoffs and the probability of cooperation can provide a useful framework for understanding the evolution of cooperation in social dilemmas and developing interventions to promote cooperation. In various social and economic settings, promoting cooperation is crucial, and a possible strategy to achieve this is by examining the covariance between cooperation and selection. The relationship between cooperation can be favored by selection in some contexts (Traulsen and Nowak, 2006; Kurokawa, 2019; Madgwick and Wolf, 2020), it can also be subject to selective pressures that can limit its evolution (Fehl et al., 2011; Powers et al., 2012; Waite et al., 2015). Our results enable us to recognize scenarios in which cooperation is more probable, regardless of the particular payoff levels. Such a perspective sheds new light on Price's equation, which was not initially intended for this purpose.

4.6 Sensitivity Analysis

Sensitivity analysis in a dynamic system refers to the study of how changes in the input parameters of the system affect the output or the behavior of the system. It involves examining how small perturbations or variations in the initial conditions or model parameters impact the system's response or stability. Sensitivity analysis can help identify critical parameters that significantly influence the system's behavior.

4.6.1 Different Values of the Cooperation Probability

Initially, we performed a sensitivity analysis by keeping the transition rate ($\delta = 0.5$) and reward coefficient ($\epsilon = 0.5$) fixed. We then varied the values of p and examined the equilibrium densities of cooperators (x_i^*), in the four evolutionary dynamics under study. Each subfigure of Fig. 6 represents a different scenario.¹⁸

In the context of replicator dynamics, we observe that when the probability of encountering a cooperator (p) falls within the range of [0.2, 0.8] and the density of competitor strategies (x_i^*) approaches zero, the density of cooperators steadily

¹⁸ The Python code plots a 3D surface of a math function using the func (p, x) function, with p and x values generated by numpy.meshgrid. The imshow function from the matplotlib.pyplot library creates the plot with color scheme set by cmap and a colorbar added using colorbar.



Fig. 6 A colormap is produced to illustrate the equilibrium densities of cooperators (x_i^*) in the four evolutionary dynamics under consideration, as represented by $\dot{E}(p)$, for a fixed transition rate ($\delta = 0.5$) and a constant reward coefficient ($\epsilon = 0.5$). The *x*-axes correspond to the probability level defining the likelihood of cooperation (*p*). The *y*-axes denote the equilibrium density of competitors (x_i^*) (Color figure online)

increases up to 0.6 in the unstructured population condition. However, in the Bayesianstructured population scenario, the density of cooperators reaches full capacity. The maximum density is achieved at approximately p = 0.4. This result may seem unexpected, as one would anticipate full cooperation to emerge at high levels of p. However, it is important to remember that in the presence of certainty of cooperation, free-riding behavior is incentivized, leading to the corner equilibrium being the sole attractor. This can result in the extinction of one or both populations.

In the replicator-mutator dynamics, it is noteworthy that $x_i^* = 1$ is observed when $x_j^* \ge 0.80$, regardless of the level of p. This observation may seem surprising, but it once again underscores that the presence of a certain mutation towards cooperation leads to a transient full density of cooperators generated by free-riders, which ultimately return to defection before mutating to cooperators again. In contrast, it is important to note that in the Bayesian-structured replicator-mutator dynamics, a full density of cooperators is only encountered when $p \to 0$ for a high density of competitors, since a low probability of encountering a cooperator creates a weak incentive to free-ride, leading to a full density of cooperation.



Fig. 7 A colormap is produced to illustrate the equilibrium densities of cooperators (x_i^*) in the four evolutionary dynamics under consideration, as represented by $\dot{E}(p)$, for a fixed probability of cooperation (p = 0.5) and a constant reward coefficient ($\epsilon = 0.5$). The *x*-axes correspond to the transition rate defining the local competition among different strategies (δ). The *y*-axes denote the equilibrium density of competitors (x_i^*) (Color figure online)

4.6.2 Different Values of the Transition Rate

We then conducted a sensitivity analysis by fixing the probability of cooperation (p = 0.5) and the reward coefficient ($\epsilon = 0.5$) and varying the values of δ . Subsequently, we examined the equilibrium densities of cooperators (x_i^*) in the four evolutionary dynamics under consideration. Each subfigure of Fig. 7 corresponds to a different scenario.

The transition rate is a measure of the probability of transitioning from competition to cooperation in a birth-death process. In the case of replicator dynamics with an unstructured population, the equilibrium level of cooperation remains low regardless of the transition rate. This indicates that the effect of the transition rate on the equilibrium level of cooperation is minimal. The transition rate primarily reflects the local competition between different strategies, indicating that neighbor selection has little impact on the final outcome. In the Bayesian-structured population setting, a full density of cooperators is only observed for low levels of both δ and x_j^* . The occurrence of a cluster of cooperators is due to the high prevalence of cooperators with a low neighbor replacement rate, leading to full cooperation.



Fig. 8 A colormap is produced to illustrate the equilibrium densities of cooperators (x_i^*) in the four evolutionary dynamics under consideration, as represented by $\dot{E}(p)$, for a constant probability of cooperation (p = 0.5) and a fixed transition rate ($\delta = 0.5$). The *x*-axes correspond to the coefficient of reward obtained by engaging in cooperative behavior (ϵ). The *y*-axes denote the equilibrium density of competitors (x_j^*) (Color figure online)

In the replicator-mutator dynamics, an interesting observation is that $x_i^* = 1$ is only observed when $x_j^* \ge 0.80$ for $\delta \le 0.2$. These results are further amplified in the Bayesian-structured population setting, where full density of cooperators is observed for a probability of cooperation up to 0.5. Such findings can be attributed to the high density of competitors in combination with weak selection towards cooperation among neighbors. Those factors ultimately lead to cooperation spreading throughout the population due to the weak incentive to free-ride and the automatic mutation towards cooperation in case of defection.

4.6.3 Different Values of the Reward Coefficient

At last, a sensitivity analysis was performed by keeping the probability of cooperation (p = 0.5) and the transition rate $(\delta = 0.5)$ constant and varying the reward coefficient (ϵ) . The equilibrium densities of cooperators (x_i^*) were then analyzed in the four evolutionary dynamics. Figure 8 presents the results of this analysis, with each subfigure representing a different scenario.

In the case of the original replicator dynamics, where the population is well-mixed, the level of reward does not affect the equilibrium level of cooperators. However, the Bayesian-structured population setting exhibits a full density of cooperators regardless of the reward level, given that the density of competitors is low. This occurs because the Bayesian decay factor influences the equilibrium density of cooperation through the reward scheme. As the density of cooperators increases, the Bayesian decay factor also increases, leading to an increase in the reward amplifying effect. This rise in the reward coefficient reduces the incentives for free-riding and can result in a higher equilibrium density of cooperation.

In the replicator-mutator dynamics, both in the unstructured and structured population settings, full cooperation can only be achieved when the density of competitors is close to one. This can be explained by the fact that, in the presence of a certain mutation rate of competitors, the switch from the full density of cooperators to the full density of competitors is guaranteed. However, in order for the full density of cooperators to persist, a reward for cooperation must be present. Without such a reward, the incentive to free-ride in the face of a cooperator is too strong and leads to cooperators returning to defection.

5 Conclusion

The equivalence between replicator-mutator dynamics and the Price equation, which was first highlighted by Page and Nowak (2002), is a fundamental concept in the field of unified evolutionary dynamics. We use a modeling framework that demonstrates a different equivalence. Specifically, we show that an aggregated version of the Price formula can connect replicator dynamics and replicator-mutator dynamics by taking into account the population structure. As in Dragicevic (2019b), our study represents the second paper to successfully accomplish this objective. It extends previous findings on the interlocking relationship between evolutionary dynamics. It was previously mentioned that the scope of the unifying approach was restricted by a peculiar form of decay factor that only considered the portion of homogeneous individuals in a group that employed the opposite strategy (Dragicevic 2019a). This led us to ask whether a different structuring of the population would lead to different conclusions, and we found that the answer is both yes and no. On the one hand, the equivalence obtained in our study is different from the reflective evolution and the joint selection of competitors and cooperators. On the other hand, by choosing an appropriate decay factor and imposing the certainty of mutation, we can once again achieve a balance between mutation and selection, resulting in a straightforward relationship between the two types of dynamics. Our results validate that this approach gives populationwide cooperation a transient status, which is consistent with previous research (Perc 2016; Dragicevic 2019b). In summary, our study offers a unique viewpoint in the field of evolutionary game theory, and we anticipate that our findings will pave the way for further advancements in this area of research.

Bayes' rule is a powerful tool for understanding the dynamics of social behavior in various settings, including biological populations, social networks, and economic systems. In evolutionary dynamics, Bayes' rule is used to calculate the posterior fraction of strategy players, which is represented as a function of the prior fraction of players (Dragicevic 2015). By updating using Bayes' rule, agents can incorporate new information into their comparisons of payoffs, which can in turn influence their own strategic choices. This updating process can lead to the emergence of cooperative behavior in structured populations, as agents become more likely to cooperate on graphs when they encounter cooperators within a cluster. However, outside the limits of a cluster of cooperators, encountering a cooperator can lead to free-riding as a player relies on their counterpart to make a personal sacrifice for the sake of all. Although the use of Bayes' rule in evolutionary dynamics is a valuable tool, it raises the question of what other decay factors could be considered. Our study has focused on relatively simple spatially-structured populations, where individuals are located in physical space and interact with their neighbors. However, in ecological communities, multiple species interact with each other, often through complex networks of predator– prey or mutualistic interactions. Modeling decay factors on such complex networks is necessary to understand the population dynamics that arise and to determine how well these models reflect real-world situations.

Hilbert (2017) demonstrated that cooperation outperforms selection when there is complementary variety between different population types. Dragicevic (2019b) suggested that the presence of both cooperators and competitors in the Price identity can be seen as a complementary selection of different population types. This means that cooperation and selection are not necessarily in contradiction. In our present work, the selection is presented as the difference between the expected payoff of a model-player and the average payoff within the population. This implies that the more successful individuals within the population are more likely to be selected and reproduce, passing on their strategies to the next generation. We have obtained an equivalence that is valid when the transition rate from competition to cooperation corresponds to the relative strength of selection acting on either cooperation or competition relative to the selection differential between competitors and cooperators. Put simply, this means that the rate at which individuals switch from competing to cooperating is related to how strongly selection is acting on either cooperative or competitive behaviors, compared to the difference in success between cooperators and competitors. Utilizing this model, researchers can enhance their comprehension of how these factors interact and influence the development of populations throughout time. For instance, they can employ simulations to investigate how a population may evolve given a specific level of selection strength or relative payoff advantage, or how to overcome a low rate of transition from competition to cooperation.

6 Appendix A

Proof of Proposition 1 We observe that

$$\pi_i \stackrel{\geq}{\geq} \pi_j$$

$$\Leftrightarrow p(w(1+\epsilon) - c) + (1-p)(w-c) \stackrel{\geq}{\geq} pw + (1-p)w$$

$$\Leftrightarrow pw(1+\epsilon) - pc + w - c - pw + pc \stackrel{\geq}{\leq} pw + w - pw$$

$$\Leftrightarrow pw\epsilon - c \stackrel{\geq}{\geq} 0$$

7 Appendix B

Proof of Proposition 2 We observe that

$$\pi_i \stackrel{\geq}{\leq} \pi_j$$

$$\Leftrightarrow p(w(1+\epsilon)-c) x_i^{N-1} + (1-p)(w-c) \stackrel{\geq}{\leq} pw + (1-p)w\left(1-x_i^{N-1}\right)$$

$$\Leftrightarrow p(w(1+\epsilon)-c) x_i^{N-1} + (1-p)w x_i^{N-1} \stackrel{\geq}{\leq} pw + (1-p)w$$

$$-(1-p)w + (1-p)c$$

$$\Leftrightarrow x_i^{N-1} (p(w(1+\epsilon)-c) + (1-p)w) \stackrel{\geq}{\leq} pw + (1-p)c$$

$$\Leftrightarrow x_i^{N-1} \stackrel{\geq}{\leq} \frac{c+p(w-c)}{w+p(\epsilon w-c)}$$

$$\Leftrightarrow x_i \stackrel{\geq}{\leq} \left(\frac{c+p(w-c)}{w+p(\epsilon w-c)}\right)^{\frac{1}{N-1}}$$

8 Appendix C

Proof of Proposition 3 We analyzed the stability conditions of the system by examining its fixed points, ¹⁹ assuming $\delta = 0.5$.²⁰ To accomplish this, we utilized the Jacobian matrix. We solved the system of differential equations $\dot{E}(p) = \{x_i, x_j\}$, which yielded the fixed point values $x_i^{\star} = \{0, \frac{-2+15p-15p^2-10px_j+10p^2x_j+30p^2x_j^{99}-20p^2x_i^{100}}{20p(1-x_j^{99}+px_j^{99})}\}$ and $x_j^{\star} = \{0, \frac{-2+15p-15p^2-10px_i+10p^2x_i+30p^2x_i^{99}-20p^2x_i^{100}}{20p(1-x_i^{99}+px_j^{99})}\}$. Our analysis revealed that the system possesses both a corner equilibrium and an interior equilibrium. However, we found that all fixed points are classified as saddle points due to the eigenvalues of the Jacobian matrix exhibiting opposite signs. At a saddle point, the system displays both stable and unstable behavior in different directions, causing trajectories near the point to either converge or diverge. It is worth noting that saddle points can lead to complex and unpredictable system behavior.

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¹⁹ An investigation of fixed points and attractors has been carried out using Python with the aid of two tools: (1) fsolve from the scipy.optimize package and (2) the solve_ivp function from the scipy.integrate module. The analysis was performed using the numpy library, which enabled numerical calculations.

²⁰ When the transition rate of switching from a competitor to a cooperation is 0.5 in a birth-death process on networks, it indicates that the probability of a neighboring competitor being replaced by a cooperator is equal to the probability of staying in the competition state. This lack of preference or bias towards either state suggests that the system is equally likely to transition to either state.

After analyzing the stability of fixed points in the system, we now turn our attention to the presence of attractors. In a system of differential equations, an attractor is a set of states or trajectories that the system tends to converge towards over time, regardless of its initial conditions. Fixed points can also act as attractors in a system. At p = 0.25, we observe an attractor with coordinates $\{x_i, x_j\} = (0.38, 0.38)$. Similarly, at p = 0.50 and p = 0.75, we have attractors with coordinates $\{x_i, x_j\} = (0.3, 0.3)$ and $\{x_i, x_j\} = (0.13, 0.13)$, respectively. At p = 1, we observe $\{x_i, x_j\} = (0, 0)$.

A noteworthy finding is that as the probability of encountering a cooperator increases, the population dynamics system tends to converge towards the interior equilibrium, which approaches zero as p approaches one. The system exhibits a bifurcation around the system attractor point. However, when players are guaranteed to encounter a cooperator, incentivizing free-riding behavior, only the corner equilibrium attracts the system. This results in both populations of players competing against each other, ultimately leading to the extinction of one or both populations.

9 Appendix D

Proof of Proposition 4 The stability conditions of the system were investigated by analyzing its fixed points, while assuming a value of δ = 0.5. The Jacobian matrix was utilized for this purpose. We solved the differential $\{x_i, x_i\}$ and obtained the values of the fixed points equations $\tilde{E}(p)$ = $\{0, \frac{-2x_j+15px_j-15p^2x_j-10px_j^3+10p^2x_j^3+30p^2x_j^{100}-20p^2x_j^{102}}{2p^2x_j^2}\}$ and x_i^* x_{i}^{\star} = as $20px_i^2(1-x_i^{99}+px_i^{99})$ $\frac{-2x_i+15px_i-15p^2x_i-10px_i^3+10p^2x_i^3+30p^2x_i^{100}-20p^2x_i^{100}}{200}\}$. Our analysis indicated that the $20px_i^2(1-x_i^{99}+px_i^{99})$ system possesses both a corner equilibrium and an interior equilibrium. Our analysis indicates that, apart from the coordinates of the attractor, all other fixed points were found to be saddle points, as evidenced by the opposite signs of the eigenvalues of the Jacobian matrix. At a saddle point, the system exhibits both stable and unstable behavior in different directions, leading to trajectories that either converge or diverge near the point. It should be noted that saddle points can result in complex and unpredictable system behavior.

Following our analysis of the stability of fixed points in the system, we now shift our focus to the presence of attractors. In a system of differential equations, an attractor is defined as a set of states or trajectories that the system tends to converge towards over time, regardless of its initial conditions. Fixed points can also serve as attractors in a system. At p = 0.25, we observe an attractor with coordinates $\{x_i, x_j\} = (0.62, 0.62)$. Similarly, at p = 0.50 and p = 0.75, we have attractors with coordinates $\{x_i, x_j\} = (0.55, 0.55)$ and $\{x_i, x_j\} = (0.37, 0.37)$, respectively. At p = 1, we observe $\{x_i, x_j\} = (0.03, 0.03)$.

A key observation is that the population dynamics system typically approaches the interior equilibrium in situations where there is uncertainty about encountering a cooperator. The interior equilibrium approaches zero as p approaches one. The system as a whole exhibits attraction towards a stable attractor point. Nevertheless, when players are guaranteed to interact with cooperators, thereby incentivizing freeriding behavior, only the corner equilibrium attracts the system. This leads to both player populations competing against each other, ultimately resulting in the extinction of one or both populations.

10 Appendix E

Proof of Proposition 5 The stability conditions of the system were investigated by analyzing its fixed points, while assuming a value of $\delta = 0.5$. We recall that the mutation is considered to occur for sure. The Jacobian matrix was utilized for this purpose. We solved the differential equations $\dot{E}(p) = \{x_i, x_j\}$ and obtained the values of the fixed points as $x_i^{\star} = \{0, \frac{-x_j+5px_j-5p^2x_j-5px_j^2+5p^2x_j^2+10p^2x_j^{100}-10p^2x_j^{101}}{5p(2x_j-3)(1-x_j^{99}+px_j^{99})}\}$ and $x_j^{\star} = \{0, \frac{-x_i+5px_i-5p^2x_i-5px_i^2+5p^2x_i^2+10p^2x_i^{100}-10p^2x_i^{101}}{5p(2x_i-3)(1-x_j^{99}+px_j^{99})}\}$. Our analysis indicated that the system possesses an unstable corner equilibrium, for the eigenvalues of the Jacobian matrix were positive. When a fixed point is unstable, it means that small perturbations from the fixed point will cause the system to move away from the fixed point rather than converge to it. In out case, the unstable fixed point is a source, such that the system exhibits a behavior similar to that of a repeller: trajectories diverge away from the fixed point in all directions.

Following our analysis of the stability of fixed points in the system, we now shift our focus to the presence of attractors. In a system of differential equations, an attractor is defined as a set of states or trajectories that the system tends to converge towards over time, regardless of its initial conditions. In this system, the fixed points do not serve as attractors. At p = 0.25, we observe an attractor with coordinates $\{x_i, x_j\} = (1, 1)$. Similarly, at p = 0.50 and p = 0.75, we have attractors with coordinates $\{x_i, x_j\} = (1, 1)$.

The finding of this study indicates that the population dynamics system tends to converge towards an unstable attractor, regardless of the probability of encountering a cooperator. An unstable attractor is a point in a dynamical system that attracts nearby trajectories, but any slight perturbation to the system can cause the trajectories to diverge and move away from it. Assuming a certain probability of mutation towards cooperation during the game, the system continuously eliminates competitors who keep returning as free-riders because they are certain to encounter cooperators, thus driving the system towards a transient full population density. However, when players are guaranteed to interact with cooperation.

11 Appendix F

Proof of Proposition 6 The stability of the system was investigated by examining its fixed points, while assuming a fixed value of $\delta = 0.5$ and assuming that mutation towards cooperation always occurs. The Jacobian matrix was utilized to determine the

stability conditions. The differential equations $\dot{E}(p) = \{x_i, x_j\}$ were solved, and the fixed points were obtained as $x_i^{\star} = \{0, \frac{-x_j + 5px_j - 5p^2x_j - 5px_j^3 + 5p^2x_j^3 + 10p^2x_j^{100} - 10p^2x_j^{102}}{5p(2x_j^2 - 3)(1 - x_j^{99} + px_j^{99})}\}$ and $x_j^{\star} = \{0, \frac{-x_i + 5px_i - 5p^2x_i - 5px_i^3 + 5p^2x_j^3 + 10p^2x_i^{100} - 10p^2x_i^{102}}{5p(2x_i^2 - 3)(1 - x_i^{99} + px_j^{99})}\}$. Our analysis revealed the presence of an unstable corner equilibrium, as the eigenvalues of the Jacobian matrix were found to be positive. An unstable fixed point implies that small perturbations from the fixed point will cause the system to move away from it instead of converging towards it. In our case, the unstable fixed point is a source, resulting in a behavior similar to that of a repeller, whereby trajectories diverge away from the fixed point in all directions.

After analyzing the stability of the fixed points in the system, we proceed to investigate the presence of attractors. An attractor is a set of states or trajectories to which a system of differential equations converges over time, regardless of its initial conditions. Fixed points can also serve as attractors in a system, but such is not the case in this particular instance. At p = 0.25, we observe an attractor located at the coordinates $\{x_i, x_j\} = (1, 1)$. Similarly, at p = 0.50 and p = 0.75, we find attractors at $\{x_i, x_j\} = (1, 1)$ and $\{x_i, x_j\} = (1, 1)$, respectively. When p = 1, the attractor is located at $\{x_i, x_j\} = (1, 1)$.

The research finding suggests that the population dynamics system tends to converge towards an unstable attractor, regardless of the probability of encountering a cooperator. An unstable attractor is a point in a dynamical system that attracts nearby trajectories, but any slight perturbation to the system may cause the trajectories to diverge and move away from it. Assuming a certain probability of mutation toward cooperation during the game, the system continuously eliminates competitors who persist as free-riders due to their certain encounters with cooperators, driving the system towards a transient full population density. When players are guaranteed to interact with cooperators, which incentivizes free-riding behavior, only mutation can prompt them to revert to cooperation. Interestingly, Bayesian updating has no effect on population dynamics in the case of certain mutation.

12 Appendix G

Proof of Proposition 7 Through the combination of Eqs. (9) and (10), a general equality can be obtained. It is known that $\sum_i px_i\pi_i = cov(\pi_i, p) + \bar{\pi}\,\bar{p}$, where covariance is given by the expression $cov(\pi_i, p) = \sum_i px_i\pi_i - \bar{\pi}\,\bar{p}$. The identification of all the covariances that are implicit in the equation allows for the derivation of δ , which is obtained through the solution of $cov(\pi_i, p)\delta = cov(\pi_j, p)(1 + \delta) \Leftrightarrow \delta = \frac{cov(\pi_j, p)}{cov(\pi_i - \pi_j, p)}$. In the context of the Price equation, the covariance term represents the impact of natural selection on the alteration in the trait values. Selection is interpreted as the difference between the expected payoff of a model-player and the average payoff within the population. It can be concluded that the equivalence holds when the rate of transition from competition to cooperation corresponds to the relative strength of selection exerted on competition in proportion to the selection differential between the cooperators and competitors.

13 Appendix H

Proof of Proposition 8 The combination of Eqs. (6) and (11) leads to a general equality. Specifically, it is established that $\sum_i px_i\pi_i = cov(\pi_i, p) + \overline{\pi} \overline{p}$, where covariance is expressed as $cov(\pi_i, p) = \sum_i px_i\pi_i - \overline{\pi} \overline{p}$. By identifying the implicit covariances in the equation, we can solve for δ using $cov(\pi_i, p)(1 + \delta) = cov(\pi_j, p)\delta \Leftrightarrow \delta = \frac{cov(\pi_i, p)}{cov(\pi_j - \pi_i, p)}$. In the context of the Price equation, the covariance term indicates the effect of natural selection on changes in trait values. Selection is represented as the difference between the expected payoff of a model-player and the average payoff within the population. The equivalence is valid when the transition rate from competition to cooperation corresponds to the relative strength of selection acting on cooperation relative to the selection differential between competitors and cooperators.

14 Appendix I

Proof of Corollary 1 In order to determine the range of values for π_i and π_i that satisfy $x_i^{\star} = \frac{\pi_j}{\pi_i - \pi_i} \in [0, 1]$, we must solve the inequalities $0 \le x_i^{\star} \le 1$. Substituting the expression for x_i^{\star} into the inequalities, we obtain $0 \leq \frac{\pi_j}{\pi_i - \pi_i} \leq 1$. If $\pi_i > \pi_j$, the denominator is negative, and x_i^{\star} is undefined. Similarly, if $\pi_i = \pi_j$, the denominator is zero, and x_i^{\star} is undefined. Therefore, we require $\pi_i < \pi_j$ to ensure that $x_i^{\star} \in [0, 1]$. By combining these conditions, we can conclude that $x_i^{\star} \in [0, 1]$ if and only if $\pi_i = 0$. In this case, $x_i^* = 1$, which implies full density of cooperators. While a zero payoff for cooperation might initially discourage cooperative behavior, the full density of cooperators can still emerge under certain conditions in an evolutionary context. This typically requires a sufficiently large population, the ability to adopt a mixed strategy that includes cooperation, and the benefits of mutual cooperation outweighing the costs of being exploited by defectors. This implies that $w(1 + \epsilon) - c = w - c$. This equation leads to the conclusion that the reward for cooperation is zero. Another way to come to this result is by posing $w(1 + \epsilon) - c = 0 \Leftrightarrow \epsilon = \frac{c - w}{w}$. Since ϵ cannot be negative, it follows that w = c or $\epsilon = 0$, which suggests that the benefits of mutual cooperation outweigh the costs of being exploited by competitors. Given the conditions described, cooperators are expected to form clusters within the network where the need for rewards is eliminated, as they will interact primarily with other cooperators, thus avoiding exploitation. This phenomenon can only occur when the game is played on a graph with a structured population. In light of the fact that $x_i^* = 1$, we can infer that the entire network can be viewed as a singular, vast cluster of cooperators.

Funding This project received funding from Chulalongkorn University (Grant n°0325/2566).

Acknowledgements The author would like to express gratitude to Sayan Gupta (Center for Complex Systems and Dynamics, IIT Madras), Georges Zaccour (GERAD, HEC Montréal) and Qi Su (Department of Automation, Shanghai Jiao Tong University) for their comprehensive and insightful recommendations. The author is also grateful to the anonymous referees for their thorough comments and suggestions, which significantly contributed in elevating the overall quality of the paper.

Data availability Data sharing does not apply to this article as no new data were created or analyzed in this study.

Declarations

Conflict of interest The authors have no Conflict of interest to declare.

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