



Eco-evolutionary dynamics of cooperation in the presence of policing

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ABSTRACT

Ecology and evolution are inherently linked, and studying a mathematical model that considers both holds promise of insightful discoveries related to the dynamics of cooperation. In the present article, we use the prisoner's dilemma (PD) game as a basis for long-term apprehension of the essential social dilemma related to cooperation among unrelated individuals. We upgrade the contemporary PD game with an inclusion of evolution-induced act of punishment as a third competing strategy in addition to the traditional cooperators and defectors. In a population structure, the abundance of ecologically-viable free space often regulates the reproductive opportunities of the constituents. Hence, additionally, we consider the availability of free space as an ecological footprint, thus arriving at a simple eco-evolutionary model, which displays fascinating complex dynamics. As possible outcomes, we report the individual dominance of cooperators and defectors as well as a plethora of mixed states, where different strategies coexist followed by maintaining the diversity in a socio-ecological framework. These states can either be steady or oscillating, whereby oscillations are sustained by cyclic dominance among different combinations of cooperators, defectors, and punishers. We also observe a novel route to cyclic dominance where cooperators, punishers, and defectors enter a coexistence via an inverse Hopf bifurcation that is followed by an inverse period doubling route.

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1. Introduction

Competition, within and between species for their existence and survivability (Murray, 2007; Banerjee et al., 2019a; Kundu et al., 2017), is one of the fundamental attributes under the realm of Darwinian theory of evolution (Darwin, 1909). The possible persistence and rapid emergence of non-cooperative strategy (Smith and Szathmari, 1997) challenge the cooperative contribution in the presence of defectors and it leads to the “tragedy of the commons” (Hardin, 1968) as only the fittest are most likely to overcome the fierce struggles of life. This mechanism of survival of the fittest generates an act of selfishness among the individuals (Sigmund, 2010), which hinders the evolution and maintenance of cooperation. Surprisingly, contradictory to the famous Darwinian evolutionary theory, cooperation among self-interested individuals is found in diverse circumstances ranging from micro-

bial populations to social systems (Axelrod, 1984; Perc et al., 2017; Fotouhi et al., 2019; Tanimoto, 2007; Axelrod and Hamilton, 1981; Tanimoto, 2007; Fotouhi et al., 2018). Cooperation is often observed in the community of birds in the form of taking care of other's offsprings (Skutch, 1961). Large-scale cooperative behavior is very common even in simple organisms like bee and ant (Wilson, 1971; Wang et al., 2008), which can form captivating things, such as shaft systems to ventilate their nests. A series of publications (Nowak, 2006a; Perc and Szolnoki, 2010; Javarone et al., 2015; Szabó and Fath, 2007; Wakano et al., 2009; Nag Chowdhury et al., 2020; Perc et al., 2013; Pennisi, 2005; Wang et al., 2015; Santos and Pacheco, 2005; Gómez-Gardenes et al., 2007; Fu et al., 2008; Wakano and Hauert, 2011; Wu et al., 2011; Zhang et al., 2013) have been produced by the scientific communities across various disciplines for understanding the mechanisms behind the initiation, emergence and promotion of cooperation.

Evolutionary game theory (Weibull, 1995; Nowak, 2006b; Smith and Smith, 1982; Hofbauer and Sigmund, 1998), one of the powerful competent theoretical frameworks for analyzing the long-standing puzzle on the evolution of cooperation in public goods games, applies the mathematical theory of games in the

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contexts of biological and social systems. Two-player games have become the general relevant metaphor, which help to shed light on the paradigm for studying the emergence of widespread coordination under the paradox between collective and individual rationality. In these simultaneous pair-wise interaction games, the outcome of an individual depends solely on the chosen strategies of the opponent and the player itself. One of the general examples of such 2×2 games is prisoner's dilemma (PD) game (Axelrod and Hamilton, 1981). The pairwise mutual interaction between the players generates a strategy space containing four possible payoff values. Two players may simultaneously decide either to cooperate or to defect without any prior knowledge of other player's choices. A defector exploiting a cooperator gets a temptation amount T and the exploited cooperator receives the sucker's payoff S . They will both receive the reward R and punishment P for mutual cooperation and mutual defection, respectively. Generally, the payoffs in the PD game satisfy the inequalities $T > R > P > S$ and $2R > T + S$ (Szabó and Fath, 2007). Clearly, these inequalities suggest that players need to defect, irrespective of opponent's strategy, for guaranteed highest income in terms of their own payoff. Naturally, if both defect, they will get P , that is comparatively lower than R , which they would have obtained when they both cooperate. This scenario leads to the emergent dilemma, and as a result of that, widespread defection is the natural unfortunate outcome failing to sustain cooperation in the classical well-mixed PD game. The PD game is capable of capturing the notions of several other social dilemma games (Liebrand, 1983; Poundstone, 1992). Recent progress in evolutionary game theory identified various mechanisms that support the evolution of cooperation (Nowak, 2006a).

Punishment (Policing) (Brandt et al., 2006; Cong et al., 2017; Wang et al., 2013; Banerjee et al., 2019b; Yang et al., 2015; Helbing et al., 2010a; Perc, 2012; Dreber et al., 2008; Yang and Wang, 2015) is one of the effective mechanisms, which helps to achieve global and individual optima (evolutionary stable equilibrium) of cooperation under suitable circumstances. Besides two distinct strategies, cooperation and defection, an additional strategy punishment is introduced, which challenges the free-riding behavior of the defectors and entertains the maintenance of cooperation (Fehr and Gächter, 2002). Punishers are also cooperators, but they differ from traditional cooperators ("second-order free riders" Ozono et al., 2016; Szolnoki and Perc, 2017) by imposing a cost in terms of payoff towards restricting the unimpeded exploitation of cooperative goods by the free-riders. The evidence of punishment is ubiquitous in not only human society but also unicellular bacterial community (Banerjee et al., 2019b). The cooperative producers secrete toxins (i.e., hydrogen cyanide) to mitigate the unrestricted usage of public goods, such as elastase, by toxin-sensitive non-productive defective mutants. The act of policing leaves two distinct alternatives to the defectors on how to proceed. Defectors may still continue to defect with the hope that natural selection ultimately favors defection as compared to cooperation, or they may decide to cooperate leading to a situation which is the best for the group. However, a recent study (Jiang et al., 2013) reveals that mild punishment may be more effective in improving selfless cooperative behaviors. It should be noted that punishment is not a mechanism for the evolution of cooperation Nowak, 2006a. In fact, most of these earlier investigations (Helbing et al., 2010b; Fowler, 2005; Szolnoki et al., 2011) are confined to public goods game, and little is known regarding the possible evolutionary impact of punishment on the dynamics of PD game. Various aspects of punishment are already scrutinized by means of different experiments (Egas and Riedl, 2008; Sasaki et al., 2007) and mathematical models (Henrich and Boyd, 2001; Bowles and Gintis, 2004; Ohtsuki et al., 2009; Hauert et al., 2002; Brandt and Sigmund, 2006).

Ecologists and evolutionary biologists typically assume that evolutionary processes are much slower than ecological processes (Slobodkin, 1980). However, recent studies show that ecological changes and species evolution can occur on the same time scale, i.e., ecological and evolutionary dynamics are intertwined (Hendry, 2020). Ecological changes can significantly impact evolutionary dynamics, and the resulting evolutionary changes can feed-back on the ecological dynamics (Colombo et al., 2019). We are at a stage, where the consideration of intimate interlinking between ecology and evolution is a necessary step for the understanding of the processes that regulate biodiversity (Pelletier et al., 2009).

In the present article, we explore the interplay between the punishment and the virtual 'optional discriminatory' altruistic behavior of the free space from a somewhat different perspective. Altruism (De Silva et al., 2010; Bell, 2008) refers to the selflessness of individual, who increases the fitness of another individual, either directly or indirectly, without the expectation of reciprocity for that action. Evolutionary social behaviors are omnipresent in nature, and the impact of ecological free space may be a crucial factor in the context of eco-evolutionary dynamics (Pelletier et al., 2009; Wang and Fu, 2020; Fussmann et al., 2007; Wang et al., 2020). We consider free space as an ecological variable, which can be occupied by an offspring of any subpopulation of cooperators, defectors and punishers. So, by losing its own identity, free space provides benefit to all other individuals and most importantly, it does not take any form of advantages from others. The role of free space (Nag Chowdhury et al., 2020; Armano and Javarone, 2017; Helbing and Yu, 2009; Aktipis, 2004; Smaldino and Schank, 2012; Meloni et al., 2009; Vainstein et al., 2007) receives a great deal of attention under the framework of evolutionary game theory. But, the interdependency between altruist free space and the social punishment has been largely unexplored in the existing literature. We adopt a modeling approach by describing the temporal evolution of the densities of the different subpopulations. Our finding suggests that the selfless one-sided contribution of altruist free space leads to various emergent attractors (Perko, 2013; Nag Chowdhury and Ghosh, 2020).

We add another layer of complexity by introducing a natural per capita mortality rate (Finch, 2010; Burger et al., 2012; Wachter et al., 1997). Many studies have extensively demonstrated the impact of several factors like social, economic, and health implications on the reductions in mortality (Brayne, 2007; Oeppen, 1820). An elementary discussion, concerning the implication of mortality change for evolutionary theories of PD game, is yet to gain its well-deserved attention. We formulate a general mathematical model in the presence of evolutionary social behavior, punishment, to address the combined effect of altruistic free space and mortality change on the evolution of population. We also hope that our research exhibits a better understanding of eco-evolutionary dynamics in social dilemmas. Consideration of all these aspects unveils the coexistence of three competing strategies under favorable conditions, and prompts the emergence of cyclic dominance (Szolnoki et al., 2014), where the population system displays a periodic attractor. Emergence of such periodic attractor through Hopf bifurcation has been studied earlier in eco-evolutionary models (Gokhale and Hauert, 2016; Cortez, 2016). We, hereafter, proceed by investigating the evolutionary dynamics among cooperators, defectors, and punishers in an infinite population and provide a rigorous stability analysis of the system. The presented theoretical investigations are well agreed with our numerical studies. The system experiences two clearly separated time scales consisting of fast jumps followed by a slow manifold (Nag Chowdhury and Ghosh, 2020; Arnold, 1998). The stability properties of the proposed mathematical model are further numerically analyzed by bifurcation theory and Lyapunov exponents of the system.

2. Mathematical Model: Eco-evolutionary dynamics

We consider our model based on the repeated prisoner's dilemma game. The basic game consists of two possible behaviors, cooperation, **C**, and defection, **D**; but, we include punishment to extend the set of strategies to three distinct behaviors, **C**, **D**, and punishment **P**. Instead of the traditional PD game, the weak version of the prisoner's dilemma game (Nowak and May, 1992) is contemplated, where the rank of the payoffs between **C** and **D** are characterized by $T > R > P \geq S$. Without any loss of generality, we set $R = 1$, $S = 0$, $T = \beta$ with $\beta > 1$, and $P = 0$, which helps to preserve the dilemma of the weakly PD game. The punishers (**Ps**) impose a fine on defectors at a personal cost. At the time of interaction with a punisher, defectors have to bear a punishment fine δ , and punishers also endure the same cost of policing, δ . Thus, $\delta > 0$. Since punishers (**Ps**) are cooperative in nature, a punisher (**P**) and a cooperators (**C**) both receive the reward $R = 1$ due to the mutual interaction between them.

In order to combine the game dynamics with the population dynamics, we consider free space as an ecological variable, which interacts with all other subpopulations **C**, **P** and **D**. Free space does not take any advantage from others, but any subpopulation can use free space for their replication, i.e., free space is providing benefit to all **C**, **P** and **D**. Moreover, when free space is occupied by an offspring of **C**, **P** or **D**, then it loses its identity. Therefore, we can assume that the free space is such a behavior, which selflessly increases the fitness of other subpopulations and eliminates its own identity. It needs to be mentioned that free space can be surrounded by cooperators or cooperative-punishers or defectors. Hence, our initial assumption that the free space is also interacting with other subpopulations, such as **C**, **P** and **D**, allows us to depict the selfless act of free space as virtual 'optional discriminatory' altruistic behavior. The altruistic act of free space **F** allows it to contribute positive payoff σ_1 , σ_2 and σ_3 to **C**, **P** and **D**, respectively. Therefore, $\sigma_i > 0$ for $i = 1, 2$, and 3 . The payoff matrix is therefore represented by.

	C	P	D	F
C	1	1	0	σ_1
P	1	1	$-\delta$	σ_2
D	β	$\beta - \delta$	0	σ_3
F	0	0	0	0

in which the entries portray the payoff accumulated by the players in the left.

Let x, y, z and w be the fraction of **C**, **P**, **D** and **F**, respectively. It is assumed that the community is only comprised of **C**, **P**, **D** and **F**, therefore, $x + y + z + w = 1$. As w is a virtual 'optional discriminatory' altruist, the normalized population density becomes $x + y + z$. The overall population density, $x + y + z$, can grow from 0 to an absolute maximum 1. If $x + y + z = 0$, i.e., $w = 1$, then only free space will be available and population extinction will occur. If $x + y + z = 1$, i.e., $w = 0$, then there will be no free space and the maximum normalized population density exists. Therefore, $0 \leq x + y + z \leq 1$, i.e., we consider the varying normalized population density. Using the payoff matrix, the average fitness of each subpopulation can be calculated.

The average fitness of **C** is given by

$$f_C = x + y + \sigma_1 w = (1 - \sigma_1)x + (1 - \sigma_1)y - \sigma_1 z + \sigma_1, \quad (1)$$

where the relation $w = 1 - x - y - z$ is used to eliminate the dependent variable w , i.e., the fraction of available free space, which explicitly depends on the abundances of constituent subpopulations, **C**, **P**, and **D**.

Similarly, the respective average fitness of **P** and **D** are

$$f_P = (1 - \sigma_2)x + (1 - \sigma_2)y - (\delta + \sigma_2)z + \sigma_2, \quad (2)$$

and

$$f_D = (\beta - \sigma_3)x + (\beta - \delta - \sigma_3)y - \sigma_3 z + \sigma_3. \quad (3)$$

Thus, the fractions x, y and z determine the average payoffs f_C , f_P and f_D of cooperators, punishers and defectors, respectively, at any given point of time. As we have assumed that free space is not taking any advantage from others (notion of altruistic behavior), the average fitness of **F** can be denoted by

$$f_F = 0. \quad (4)$$

The average payoff of the entire population is

$$\bar{f} = \frac{x f_C + y f_P + z f_D}{x + y + z} = \frac{x f_C + y f_P + z f_D}{1 - w}. \quad (5)$$

To determine the dynamics of x, y and z , we assume that all individuals die at an equal and common rate ξ and, to reduce the complexity of the system, we assume that the reproduction rate is fully controlled by f_C, f_P and f_D . Thus, the eco-evolutionary dynamics of **C**, **P**, **D** and **F** can be expressed as

$$\begin{aligned} \dot{x} &= x(f_C - \xi), \\ \dot{y} &= y(f_P - \xi), \\ \dot{z} &= z(f_D - \xi), \\ \dot{w} &= -\dot{x} - \dot{y} - \dot{z}. \end{aligned} \quad (6)$$

Clearly, the changes in frequencies of all subpopulations over time, governed by the Eq. (6), can be thought of as an extension of replicator dynamics (Hofbauer and Sigmund, 1998), as by setting $\xi = \bar{f}$ (where \bar{f} , the mean fitness, is given by the Eq. (5)), one can easily recover the traditional replicator system. It needs to be mentioned that in general free space gives a positive feedback to the growth-induced reproduction of a population; hence, in the proposed approach, we consider the per-capita growth rate of each of the subpopulations **C**, **P**, and **D** is dependent on the availability of accessible free space. It is clear from the model formation that we have already considered the fraction of free space w and respective benefits $\sigma_1, \sigma_2, \sigma_3$, in the fitnesses of subpopulations, which signify their reproduction rate. That is why, we have omitted the redundant multiplication of w with f_C, f_P and f_D , which is often observed in the previous studies (Gokhale and Hauert, 2016; Hauert et al., 2006).

After substituting f_C (Eq. (1)), f_P (Eq. (2)) and f_D (Eq. (3)) in dynamics (6), we obtain the following eco-evolutionary dynamics

$$\begin{aligned} \dot{x} &= x[(1 - \sigma_1)x + (1 - \sigma_1)y - \sigma_1 z + (\sigma_1 - \xi)], \\ \dot{y} &= y[(1 - \sigma_2)x + (1 - \sigma_2)y - (\sigma_2 + \delta)z + (\sigma_2 - \xi)], \\ \dot{z} &= z[(\beta - \sigma_3)x + (\beta - \sigma_3 - \delta)y - \sigma_3 z + (\sigma_3 - \xi)], \end{aligned} \quad (7)$$

where, $\sigma_1, \sigma_2, \sigma_3, \delta, \xi > 0$ and $\beta > 1$.

3. Results

3.1. Model calibration and analysis

To explore the dynamics of the system (7), rigorous numerical experiments have been performed for a wide range of six parameters $\sigma_1, \sigma_2, \sigma_3, \xi, \beta$ and δ . The fifth-order Runge-Kutta-Fehlberg method is used to integrate the system (7) with a fixed time step 0.01. To avoid computational error due to sensitive initial data, we observe the evolution of trajectories after sufficient initial transient of 1.3×10^7 iteration steps. Detailed theoretical analysis is shown in Appendix A, ensuring the positive invariance and uniqueness of the solutions of the model (7). The analytical conditions for existence and stability of various equilibria of the system (7) are also analyzed in Appendix B using standard methods of linear stability analysis.

3.2. Temporal behavior of the densities of three subpopulations

The initial fraction of free space \mathbf{F} is kept fixed at $w_0 = 0.1$ ². Thus, the initial individual densities of different subpopulations can be varied within the interval $[0, 0.9]$ maintaining the relation $x_0 + y_0 + z_0 = 0.9$. To investigate the evolutionary dynamics, without loss of any generality, we fix the values of all the parameters at $\sigma_1 = 0.52$, $\sigma_2 = 0.72$, $\sigma_3 = 0.41$, $\xi = 0.5$, $\delta = 1.39$, and $\beta = 2.6$. Interestingly, we observe different emergent dynamical behavior of the attractor solely based on the choices of initial conditions. A glimpse of this scenario is portrayed in Fig. 1. For example, the initial choice of $(x_0, y_0, z_0) = (0.7, 0, 0.2)$ leads to the extinction of punishers \mathbf{P} even in the presence of moderate punishment ($\delta = 1.39$). The temporal evolution of the trajectories (See Fig. 1(a)) depicts that the system (7) converges to the punisher-free stationary point (E_5). In the absence of punishers, the dominance of defectors over the cooperators ($z > x$) is well expressed at the steady-state of coexistence even though the initial fraction of cooperators, x_0 , is higher than the initial fraction of defectors, z_0 . For the same set of parameter values, the initial fraction $(0.7, 0.2, 0)$ of all subpopulation gives rise to unbounded solution of the system (7) (Figure not shown here). Due to non-uniformity in the altruistic reproductive benefit of free space to the cooperators and punishers ($\sigma_1 \neq \sigma_2$), the defector-free stationary steady state (E_4) can not be obtained in this case (for a detailed discussion, please see Appendix B). For interior initial conditions, i.e., initial conditions with non-zero components, the system exhibits a periodic attractor. For instance, equal probabilities of initial fraction $(x_0, y_0, z_0) = (0.3, 0.3, 0.3)$ generate such periodic trajectories, shown in Fig. 1(b). Similar state-space diagram, projected onto the two-dimensional space, is contemplated for the initial condition $(x_0, y_0, z_0) = (0.4, 0.2, 0.3)$ in the Fig. 1(f)–(h). Although the punishers are given less favorable platform as $x_0 > z_0 > y_0$, the post-transient eco-evolutionary dynamics depict these subpopulations indeed cyclically dominate one another in the irregular mixing pattern of trajectories. Note that, even though the temptation to defect is high ($\beta = 2.6$), cooperation is still effectively sustained under adverse conditions while strategy abundances keep oscillating. This prompts the emergence of cyclic dominance, whereby defectors dominate punishers who dominate cooperators who in turn, dominate defectors. Besides cyclic dominance, two clearly disjoint time scales consisting of fast jumps followed by a slow manifold are evidenced in these Fig. 1(b) and (f)–(h). The trajectories slowly approach the origin when in its neighborhood, but, when in close vicinity of the origin, the trajectories are leaving comparatively fast generating a distinct slow-fast time scale.

Focusing on a different scenario, we choose another initial condition $(x_0, y_0, z_0) = (0.0, 0.2, 0.7)$. Clearly, here the initial fraction of defectors are sufficiently high, giving the defectors initial advantage. As $x_0 = 0$, the density of cooperators will remain zero ($x = 0$) as shown in Fig. 1(c). The relation between punishers and defectors in the absence of cooperators provides an emergent oscillatory coexistence between punishers and defectors, where interestingly punishers dominate the defectors, as $y > z$, in spite of the given initial preferences towards defectors. The trade-off between temptation ($\beta = 2.6$) and punishment ($\delta = 1.39$) might be a cause towards the domination of punishers over defectors in the absence of unrestricted defective exploitation of cooperation. A small amplitude oscillations of y and z are visible through Fig. 1(d) and (e).

² The initial fraction of free space, w_0 , does not qualitatively affect the numerical findings obtained. w_0 can be varied within the closed interval $[0, 1]$ obeying the relation $x_0 + y_0 + z_0 + w_0 = 1$. If $w_0 = 1$, then the initial fraction of subpopulations is reduced to a singleton choice $(x_0, y_0, z_0) = (0, 0, 0)$ and hence all the species will die out giving rise to the stationary point E_0 . As $w_0 \rightarrow 0^+$, then the region of initial basin consisting x_0 , y_0 and z_0 is expanded, and $x_0 + y_0 + z_0 \rightarrow 1^-$.

3.3. Interplay of different parameters

We observe different dynamical characteristics in our model depending on initial fraction of species and different parameters. In order to further understand the role of parameters behind the results as presented in Fig. 1, we analyze the frequency of sum of all three subpopulations as a function of free space induced reproductive benefit to the cooperators, σ_1 , with fixed initial condition $(0.3, 0.3, 0.3)$. It is highly anticipated that higher values of σ_1 help to sustain cooperation; however, it additionally depends on the values of other parameters. As soon as σ_1 exceeds σ_2 and σ_3 , i.e., $\sigma_1 > \sigma_2$ and $\sigma_1 > \sigma_3$; the free space is providing greater benefits to the cooperators compared to the punishers and defectors. This feature is well manifested in Fig. 2(a) keeping the parameter values fixed at $\sigma_2 = 1.0$, $\sigma_3 = 0.7$, $\beta = 1.2$, $\delta = 0.3$, and $\xi = 0.7$. The black bifurcation curve reflects an inverse Hopf route corresponding to the destruction of the periodic orbit. Depending on the values of the normalized population density $x + y + z$, we are able to partition the entire bifurcation diagram into three distinct sub-regions. Region I of Fig. 2(a) contemplates the oscillatory coexistence of all three subpopulations. The temporal dynamics (not shown here) at a particular time snapshot suggests that frequencies of three strategies oscillate with $y > z > x$ and thus, punishment strategy can be dominant. In spite of achieving such delightful persistence of all subpopulations, we have to ignore this regime, as $x + y + z > 1$ signifying overcrowded population within this regime. Note that, individual population density still remains within $[0, 1]$ in region I.

Region II of Fig. 2(a) reveals periodic oscillatory coexistence of \mathbf{C} , \mathbf{P} and \mathbf{D} simultaneously up to the dotted vertical line. This periodic attractor demolishes through the inverse Hopf bifurcation and gives rise to stable coexisting stationary point. Here, also $y > z > x$ which establishes the dominance of punishers over other subpopulations. There are two precise differences between the region I and region II. In region I, the normalized population density $x + y + z$ is over crowded being greater than 1. Whereas, in region II, the normalized population density lies within $(0, 1)$. Secondly, region I only contains oscillatory coexistence of x, y, z , but region II portrays collection of periodic attractor and stable stationary points up to $\sigma_1 = 0.775$. At the particular value of $\sigma_1 = 0.775$, we find all fraction of subpopulations are equal after the post-transient dynamics. That is, at $\sigma_1 = 0.775$, we have $x = y = z$. To distinguish this behavior with other observed phenomenon, a red dashed line is drawn in the Fig. 2(a).

Region III only consists stationary states. In this regime, the cooperators are dominant over other subpopulations. Till the branch point (bifurcation point) $\sigma_1 = 0.844$, the fraction of \mathbf{C} is always dominating the fraction of \mathbf{D} , which again dominates the fraction of \mathbf{P} . This behavior $x > z > y$ is also maintained for $\sigma_1 > 0.844$, however, the fraction of punishers vanishes as $y = 0$. In comparison to region II where $y > z > x$, the densities of \mathbf{C} and \mathbf{P} are switched in region III, where $x > z > y$ is sustained.

To further validate our numerical findings, largest Lyapunov exponent of the system (7) (blue curve) is plotted by varying σ_1 in Fig. 2(a) using the Wolf algorithm (Wolf et al., 1985). The sign of maximal Lyapunov exponent λ_{max} changes from 0 to $-ve$ value, which assures the transformation of the attractor from periodic nature to stationary state of the system (7). Clearly, the plotted maximum Lyapunov exponent agrees well with the observed bifurcation diagram in the Fig. 2(a).

The complex dynamics exhibited due to the interplay between different parameters are summarized using bifurcation diagrams in Fig. 2(b)–(d). In the context of PD game dynamics, higher values of temptation parameter β always helps to provide additional benefits to the defectors and destroys the act of cooperation. This understanding is well portrayed through the Fig. 2(b). With

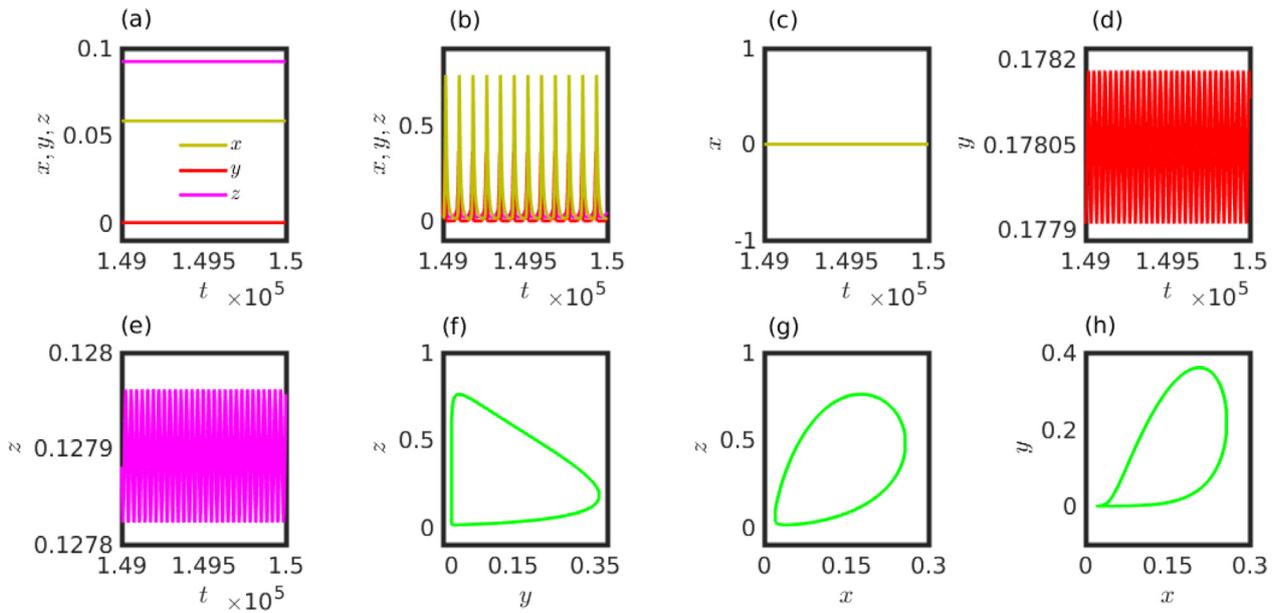


Fig. 1. Example of Eco-evolutionary dynamics of the system (7) for different initial conditions: The system (7) possesses at most three types of multistability for our chosen parameter values of $\sigma_1 = 0.52$, $\sigma_2 = 0.72$, $\sigma_3 = 0.41$, $\zeta = 0.5$, $\delta = 1.39$, and $\beta = 2.6$. The initial condition (x_0, y_0, z_0) is set at (a) (0.7, 0, 0.2), (b) (0.3, 0.3, 0.3), (c)–(e) (0, 0.2, 0.7), and (f)–(h) (0.4, 0.2, 0.3), respectively. (a) The punisher-free ($y = 0$) stationary state E_5 even in the presence of moderate punishment ($\delta = 1.39$). The dominance of defectors over the cooperators is observed, as $z > x$, even though the initial fraction of cooperators, x_0 , is higher than the initial fraction of defectors, z_0 . (b), (f)–(h) Periodic oscillation of the frequencies of **C**, **P** and **D** for initial conditions with non-zero components. Even when the punishers are given less favorable platform as $x_0 > z_0 > y_0$ ((f)–(h)) and the temptation to defect is high ($\beta = 2.6$), cooperation is still effectively sustained under adverse conditions while strategy abundances keep oscillating which prompts the emergence of cyclic dominance. (c)–(e) Extinction of cooperation ($x = 0$) with small amplitude oscillation of y and z . The relation between punishers and defectors in the absence of cooperators provides an emergent oscillatory dynamics, where interestingly punishers dominate the defectors, as $y > z$, in spite of the given initial preferences towards defectors. For further simulation details, please see the text.

increasing values of β , the fraction of **C** is always decreasing up to a critical value of this parameter, and beyond that critical value, x completely diminishes to 0 leading to extinction of cooperators. At the same critical value of β , the initial increment of punisher's population is challenged, and becomes monotonically decreasing as shown in the Fig. 2 (b). This phenomenon can be well interpreted as punishers are also cooperators, and the impact of punishment is neutralized due to high temptation to the defectors. So it is natural that population density of punishers reduces with increasing β . However, punishers do not go extinct in the observed regime for $\beta \in (1, 3]$, as punishment has social security in the form of reduction in the expected payoff of defectors, who need to pay an extra fine. We expect the defector population z to increase with the temptation parameter β and, therefore, find it interesting that z remains constant throughout the interval $(1, 3]$ of β . This may be due to the chosen values of the other parameters, which play a significant role in survivability of each subpopulation. The obtained results can also be verified using linear stability analysis (See Appendix B) at the chosen values of parameters for Fig. 2(b).

Similarly, the role of death rate ζ is inspected in Fig. 2(c). For the particular choice of the other parameters' values, Fig. 2(c) depicts that up to a certain value of ζ , say, $\zeta_{critical} \approx 0.3605$, both the fraction of cooperators, x , and punishers, y , stay at zero, and beyond $\zeta_{critical}$, both x and y are increasing. On the other hand, even though z decreases as ζ increases, $z > 0$ throughout the interval $[0, 0.7]$ of ζ . Hence, up to $\zeta_{critical}$, the cooperator-free and punisher-free stationary point $E_3 = (0, 0, 1 - \frac{\zeta}{\sigma_3})$ is found, which is marginally stable for our particular choice of parameter values (for a detailed analysis, please see Appendix B). Clearly, the z -component of E_3 suggests the growth of ζ ultimately decreases z , the fraction of **D**. This investigation perfectly fits with our numerical findings in Fig. 2(c). Whenever ζ is greater than $\zeta_{critical}$, the stationary point E_3 loses its

stability, and the interior stationary point E_7 gains its stability as shown in Fig. 2(c). Thus, increment of mortality rate surprisingly encourages the coexistence of all subpopulations. The moderate decrement in the population fraction of defectors with increasing ζ substantially suppresses the defective exploitation of cooperative benefit, which may introduce a positive catalytic effect towards the concurrence of **C**, **P**, and **D**. Even when ζ is approximately close to 0.65, the punishers dominate both **C** and **D**. Note that, the initial condition for the numerical simulation is (0.3, 0.3, 0.3), thus we do not give any additional preference, in terms of initial abundance, to the individual subpopulations. The decisive contribution of initial condition will be scrutinized in the next section.

Fig. 2(d) unveils the fundamental role of policing parameter, δ . It is clearly visible that policing of appropriate strength can fight the free-rider's defection and promote cooperation in the long run. Falling off of z is evident in Fig. 2(d) throughout the interval $(0, 0.32]$ of δ . Up to $\delta \approx 0.2$, cooperator-free stationary point E_6 is found and at $\delta \approx 0.2$, the system (7) bifurcates and switches from E_6 to the interior equilibrium E_7 generating stable coexistence of all subpopulations. The enhancement of punishment to the defectors marginally decreases its abundance, which in turn promotes cooperative contribution to the population via stable coexistence of all three subpopulations. The punishers are initially enjoying the initial enhancement with the increment of δ , but for $\delta > 0.2$, the growth of **P** diminishes gradually. This points out the fact that when **P**s are playing against defectors **D**, to penalize them with a fine δ , **P** also tolerates the cost of policing δ . Thus, higher values of δ restricts the monotonically increasing nature of **P** for our chosen parameter values and initial condition. Even though the punishers are reducing in numbers with large values of δ as per this specific numerical simulation, punishment is the dominant strategy in the entire interval $(0, 0.32]$ of δ . It should be noted that punishment is also the dominant strategy in the Region II of Fig. 2(a),

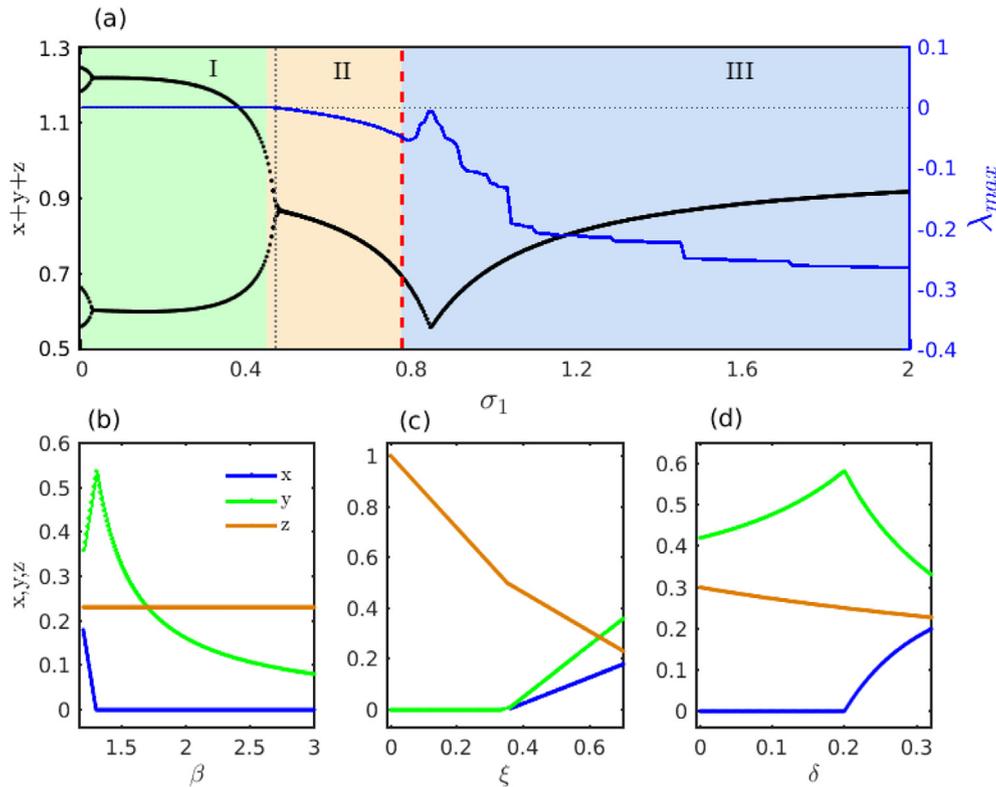


Fig. 2. (a) The largest Lyapunov exponent λ_{max} and bifurcation diagram: The frequency of sum of all three subpopulations is depicted as a function of σ_1 through the black bifurcation curve that reflects an inverse Hopf route corresponding to the destruction of the periodic orbit. Depending on the values of the normalized population density $x + y + z$, the entire bifurcation diagram is partitioned into three distinct sub-regions. Region I: oscillatory coexistence of $x, y, z < 1$ but $x + y + z > 1$ and $y > z > x$. Region II: Oscillatory + stable coexistence of x, y, z and $y > z > x$ until $\sigma_1 = 0.775$. Red dashed curve: $x = y = z$ at $\sigma_1 = 0.775$ (stable coexistence). Region III: $x > z > y$, stable coexistence of x, y, z till $\sigma_1 = 0.844$ (bifurcation point), after that coexistence of x, z ($y = 0, x > z > y$). Higher values of σ_1 help to sustain cooperation depending on values of the other parameters. As soon as σ_1 crosses beyond σ_2 and σ_3 , i.e., $\sigma_1 > \sigma_2$ and $\sigma_1 > \sigma_3$, the free space is providing greater benefits to the cooperators compared to the punishers and defectors. To further validate the appearance of oscillatory or stable coexistence of the populations, the largest Lyapunov exponent λ_{max} is plotted in blue curve by varying σ_1 . The sign of λ_{max} changes from 0 to -ve value, assuring the transformation of the attractor from periodic nature to stationary state. (b)–(d) Individual effect of the parameters β, ξ and δ on x, y, z : Fraction of cooperators, punishers, and defectors as a function of temptation parameter β , per capita mortality rate ξ and policing parameter δ for fixed $\sigma_1 = 0.7$. (b) Higher values of temptation parameter β always helps to provide additional benefits to the defectors and destroys the act of cooperation, (c) increment of mortality rate ξ surprisingly encourages the coexistence of all subpopulations, (d) policing δ of appropriate strength can fight the free-rider's defection and promote cooperation in the long run. All the results are carried out with fixed initial fraction of population (0.3,0.3,0.3) and the parameter values are fixed at: $\sigma_2 = 1.0, \sigma_3 = 0.7, \beta = 1.2, \delta = 0.3$, and $\xi = 0.7$.

from where we choose the value of $\sigma_1 (= 0.7)$. For $\beta = 1.2$ in Fig. 2 (b) and $\xi = 0.7$ in Fig. 2(c), punishment is the dominant strategy in our model (7).

We now emphasize on the investigation of the joint impact of two parameters on the eco-evolutionary dynamics at the same time. Transitions between different stationary states are recognized due to the interplay between several physical parameters, which are used to model the system (7). In Fig. 3(a), the system dynamics under the influence of varying σ_1 and σ_3 is explored, while the other parameters are fixed at $\sigma_2 = 0.8, \beta = 1.2, \delta = 0.3$ and $\xi = 1.1$. It should be noted that the benefits given by the free space to the punishers in the terms of positive payoff $\sigma_2 = 0.8$ is less than the mortality rate $\xi = 1.1$ as per our chosen parameter values for this figure. Till the free space induced reproductive benefit to the cooperators and defectors is less than their common mortality rate ($\sigma_1, \sigma_3 < \xi$), Fig. 3(a) reveals extinction of all population. When free space gives better opportunity to any subpopulation to overcome the death rate, then that subpopulation is emerging as a dominant strategy. For instance, when $\sigma_1 < \xi$ and $\sigma_3 > \xi$, we notice a wide region of defector dominant regime in two-dimensional $\sigma_1 - \sigma_3$ parameter space. In fact, in this regime, defectors are the only surviving population. A reverse storyline is perceived, when $\sigma_1 > \xi$ and $\sigma_3 < \xi$. These extra incentives towards cooperators from F help to sustain cooperation and entertains a

defector-punisher free, cooperator dominant region in the Fig. 3 (a). As $\sigma_2 < \xi$, our choice favors a punisher-free environment throughout the Fig. 3(a). Thus, suitable choice of all parameter values reflects a mechanism for coexistence of C and D as well.

The important role of death rate ξ in the complex dynamics of the system (7) is now reviewed under the influence of σ_1 . The equilibria E_0, E_1, E_3 and E_5 are all occurring in Fig. 3(b), similar to Fig. 3 (a). A fresh captivating feature is observed over a modest region (yellow zone) in Fig. 3(b), where ξ and σ_1 are both comparatively low. In this region, the variables x, y and z are leaving the phase space and tend to infinity after the initial transient dynamics. These types of unbounded solution are also noticed in Fig. 3(c) and (d) too. All simulations of Fig. 3 are performed with fixed initial condition (0.3, 0.3, 0.3). To understand the complicated reciprocity between the death rate and advantages given by the free spaces towards different population densities, Fig. 3(b)–(d) are delineated. If the altruist F is biased towards the defectors by paying them more advantages in terms of payoff $\sigma_3 > \sigma_1$ and that biased favor σ_3 exceeds the mortality rate ξ , then only defector-sustaining population persists (E_3 in Fig. 3(b)). But, the role of other parameters like σ_2 and δ is also important. Depending on other parameters, cooperators are only surviving species, when $\sigma_1 > \xi > 1$ and $\sigma_1 > \sigma_2$ in Fig. 3(b). Even, a moderate zone is noticed in Fig. 3(b), where cooperators are able to survive along with defectors. All

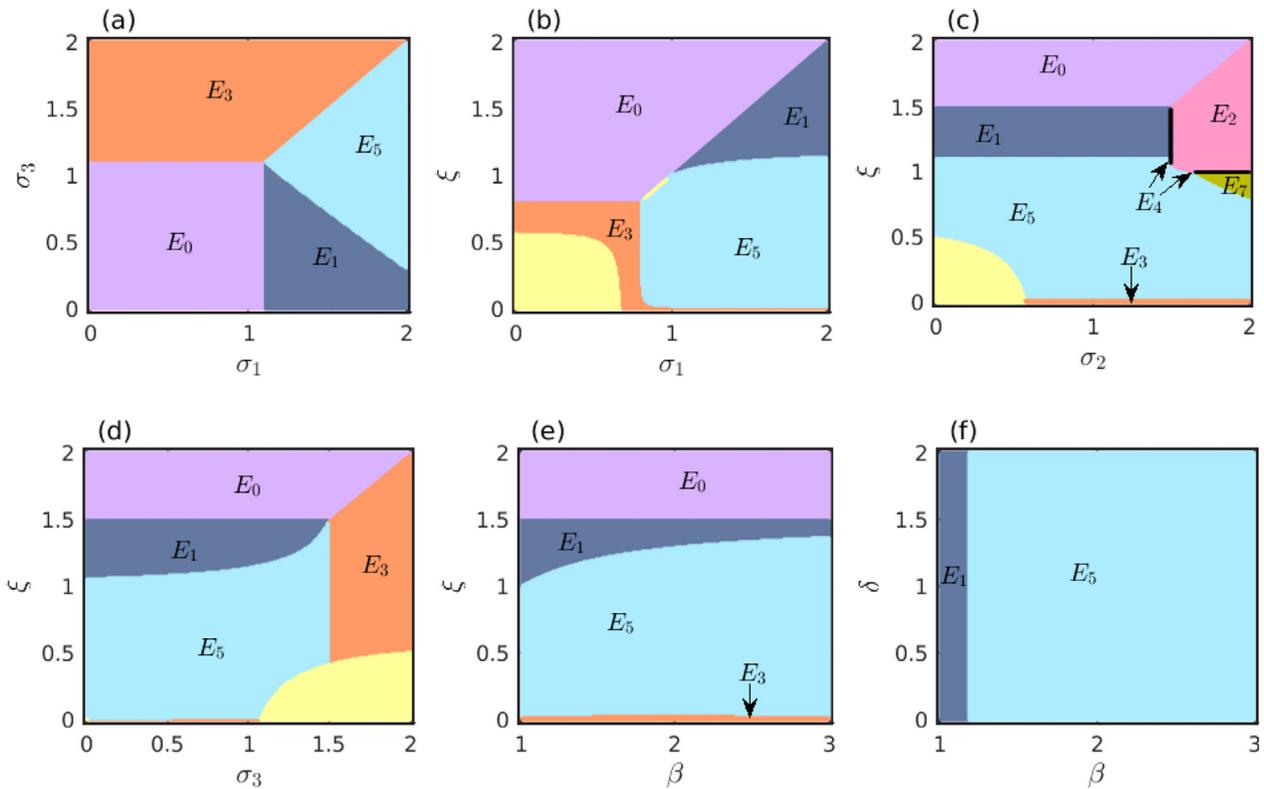


Fig. 3. Comparative plots of two-dimensional parameter phase diagrams: Transition between different population dependent stationary states E_i s for $i = 0, 1, 2, \dots, 5, 7$ (thoroughly addressed in Sec. Appendix B) due to the interplay between the physical parameters. (a) The system dynamics under the influence of varying σ_1 and σ_3 is explored. $\sigma_1, \sigma_3 < \xi$ reveals extinction (E_0) of all population, $\sigma_1 < \xi$ and $\sigma_3 > \xi$ results in a defector dominant regime (E_3), whereas a cooperator dominant region (E_1) is found when $\sigma_3 < \xi$ and $\sigma_1 > \xi$. Also the choice of $\sigma_2 < \xi$ favors a punisher-free environment E_5 . (b)–(d) Complicated reciprocity between the death rate ξ and advantages given by the free spaces ($\sigma_1, \sigma_2, \sigma_3$) towards different population densities are delineated. Various combinations of population steady states emerge depending on the choice of other parameter values. (e) The simultaneous contribution of β and ξ is presented. For very small (close to zero) values of ξ , only defectors (E_3) survive irrespective to the choices of β . As the death rate ξ is increased gradually, the following steady states emerge in the parameter space, respectively: coexistence of cooperators and defectors E_5 , only cooperators E_1 , and extinction E_0 . (f) The role of policing term δ is found to be completely independent of β for the set of chosen parametric values. For lower values of β only cooperators are present, but a wide range of parameter space is observed where **Ds** are coexisting with **Cs** with moderately high values of β . Yellow region reflects unbounded solution of the system (7). For easier comparison, whenever a pair of parameters are varied, others are fixed at these values of parameters: $\sigma_1 = 1.5$, $\sigma_2 = 0.8$, $\sigma_3 = 0.8$, $\beta = 1.2$, $\delta = 0.3$ and $\xi = 1.1$. The initial fraction of subpopulation is $(x_0, y_0, z_0) = (0.3, 0.3, 0.3)$ for all the figures. Lavender, cool grey, pink, coral, black, sky blue and mustard color indicate the stationary points E_i s for $i = 0, 1, 2, \dots, 5, 7$ respectively.

subpopulations go extinct, when per capita death rate ξ exceeds σ_1 , σ_2 and σ_3 .

A fascinating result is shown in Fig. 3(c), where we are able to capture distinct equilibria along with the unbounded trajectories in the 2D-parameter space of free space induced reproductive opportunity to the punishers, σ_2 and common mortality rate, ξ . For sufficiently high values of mortality rate ξ , all population die out. For comparatively lower values of ξ , the cooperators can only survive until $\sigma_1 > \sigma_2$. For $\sigma_1 < \sigma_2$, punishers can only survive. This transition takes place through the emergence of a small region of coexistence of **C** and **P**, whenever $\sigma_1 = \sigma_2$, or $\xi = 1$ is satisfied. Further, lowering the values of ξ , defectors are found along with **C**. Even, a tiny regime for large σ_2 is found, where coexistence of all subpopulations (the stationary state E_7) occur. For too small values of ξ and beyond a certain threshold of σ_2 , a defector dominant solution space is obtained.

The important role of death rate is also demonstrated in Fig. 3 (d) over the parameter free space mediated reproductive benefit to the defectors, σ_3 . For large values of σ_3 , either population extincts or only defectors can survive or the unbounded trajectories are found. Whereas for $\xi > \sigma_1, \sigma_2, \sigma_3$, extinction scenario of all species is again detected. For lower values of σ_3 depending on ξ and other parameter values, either cooperation is the only surviving strategy, or coexistence of cooperation and defection is discovered. The simultaneous contribution of temptation parameter, β

and common death rate, ξ is presented in the Fig. 3(e). Here, the parameter values are set at $\sigma_1 = 1.5$, $\sigma_2 = 0.8$, $\sigma_3 = 0.8$, and $\delta = 0.3$. For very small (close to zero) values of ξ , cooperator-free and punisher-free population can only be noticed irrespective to the choices of β . With increment of death rate, cooperators are coexisting with defectors, and further increment of ξ demolishes the defector population. We observe an interval in the $\beta - \xi$ parameter space, where cooperators are only surviving. If ξ is too high and beyond a critical threshold ($\xi > \sigma_i$ for $i = 1, 2, 3$), then extinction of all species is detected.

Interestingly, it is expected that moderate value of the policing parameter δ always helps in persistence of punishers. But, for our chosen parameter values, Fig. 3(f) depicts a punisher-free society. With enhancing values of temptation parameter β , the defectors are getting extra aid. Thus, although initially only cooperators are present in the 2D parameter space (See Fig. 3(f)), but a wide range of parameter space is observed with moderately high values of β , where **Ds** are coexisting with **C**. Fig. 3(f) suggests the role of policing term δ is completely independent of β at least for these set of chosen parametric values.

3.4. Basin of attraction

Initially with the help of Fig. 1, we have discussed that multistability is observed in our model. Depending on the initial condition,

the state converges either to different Nash equilibria consisting of cooperators, defectors and punishers, or to periodic orbits, where the frequencies of punishers, defectors, and cooperators oscillate endlessly. To illustrate this feature, basin of attraction for three discrete sets of parameters is shown in Fig. 4. We set $w_0 = 0.1$ for all of these subfigures, so that each of the variables x_0, y_0, z_0 varies within the interval $[0, 0.9]$ maintaining the relation $x_0 + y_0 + z_0 = 0.9$. Each subfigure in Fig. 4 depicts that the system (7) converges to various attractors, or grows without any bound solely depending upon the initial abundance of each subpopulation with fixed parameter values. In Fig. 4(a), two distinct cooperator-free stationary states are obtained. In this particular figure, we set the values of the parameters at $\sigma_1 = 1.2, \sigma_2 = 1.5, \sigma_3 = 1.4, \beta = 1.5, \delta = 0.5$ and $\zeta = 1.1$. These values satisfy local stability criterion for both stationary points E_2 (cyan) and E_3 (magenta) respectively (See Appendix B). The chosen parameter set establishes that the free space induced benefit to the cooperators is the least as compared to the free space mediated benefits to the punishers and defectors ($\sigma_1 < \sigma_2, \sigma_3$). The Fig. 4(a) reveals that with suitable choice of initial fraction of each subpopulation, one can reach any one of these cooperator-free stable nodes E_2 and E_3 .

Similarly, three different stationary points are obtained in Fig. 4 (b). Surprisingly, the boundaries of the basin of attraction lead to different stationary points, compared to the interior of the basin. The interior region of the basin of attraction helps the system (7) to reach the punisher-free stable steady state E_5 . We even find a single initial condition $(x_0, y_0, z_0) = (0, 0, 0.9)$ located at the top vertex of the triangle, for which the system (7) converges to the extinction stationary point E_0 (black). The general solution (flow) with real-valued expansion coefficients for the system (7) is given by

$$d_1 e^{\lambda_1 t} \mathbf{u}_1 + d_2 e^{\lambda_2 t} \mathbf{u}_2 + d_3 e^{\lambda_3 t} \mathbf{u}_3, \tag{8}$$

where \mathbf{u}_i 's are the eigen vectors corresponding to the eigen values λ_i of Jacobian J of the linearized system for the chosen fixed set of parameter values for $i = 1, 2, 3$. The λ_i 's are explicitly calculated at the $J(E_0)$ in Appendix B. The initial conditions with $x_0 = 0$ and $y_0 = 0$ yield the constants $d_1 = 0 = d_2$ and hence, the solutions tend to the stationary point at the origin as $\lambda_3 < 0$. An elaborate discussion regarding the role of these boundary initial conditions with at least one zero-component is rigorously addressed in Appendix B.3. There is a line of initial conditions (blue) on the lower boundary of basin of attraction, which yields diverging orbits. Along these initial conditions, the constant d_3 is zero. As for our chosen parameter values $\sigma_1 = 1.2, \sigma_2 = 1.0, \sigma_3 = 0.41, \beta = 2.6$ and $\delta = 1.39, \lambda_1, \lambda_2 > 0$

of the Jacobian J at E_0 and thus, Eq. (8) tends to infinity in the long run (as $t \rightarrow \infty$). Another line of initial conditions on the left boundary (red) converges to cooperator extinction equilibrium E_6 .

Stable coexistence of all subpopulations is observed in Fig. 4(c) for the chosen fixed values of parameters $\sigma_1 = 0.51, \sigma_2 = 1.0, \sigma_3 = 0.41, \beta = 1.1, \delta = 0.1$ and $\zeta = 0.7$. The boundary of the set of initial conditions converges to either of two different stable stationary points; the extinction of population, E_0 (black) and the stable concurrence between punishers and defectors, E_6 (red). The interior of the basin helps to obtain the stable coexistence of all three subpopulations, E_7 (gray). There exists a few initial conditions for which unbounded trajectories (blue) are the only possible solutions. Initial conditions with $y_0 = 0$ lead to $d_2 = 0$ in Eq. (8) and λ_1, λ_3 of $J(E_0)$ will be negative for our chosen parameter values. Thus the general solution converges to the stationary point E_0 for the initial conditions on the right boundary $y_0 = 0$ of the basin of attraction.

4. Conclusion: Summary and final comments

The influence of ecology on the evolution of population (eco-to-evo) and inversely, the impact of population's evolution on ecology (evo-to-eco) encourage a lot of young researchers to focus on how change in one process affects the change on the other. On the other hand, the evolution of rational behavior among population is ideally described using evolutionary game dynamics. This primarily inspects how cooperation emerges inside a population community by overcoming the social dilemma of what is the best for own and what is the best for the society. We look over this Darwinian puzzle by integrating ecologically-accessible free space with the evolution of population in the framework of evolutionary game theory. For this purpose, we consider PD game, in particular, as a paradigm for tackling the problem of cooperation. The game promises that defection always results in a better payoff than cooperation, and thus, two independent rational individuals might defect each other, even if cooperation is the best choice for the group.

A defecting individual always receives the highest fitness if facing a cooperator. To solve this riddle from the evolutionary viewpoint, a new strategy punishment is adopted. Punishers pay a cost to punish the defectors. Punishment has been found as one of the emergent spontaneous behaviors of the human society as a way of treating the defectors for their free-riding mentality. Many previous theoretical works (Brandt et al., 2006; Wang et al., 2013; Banerjee et al., 2019b; Helbing et al., 2010a; Perc, 2012; Dreber et al., 2008; Egas and Riedl, 2008; Sasaki et al.,

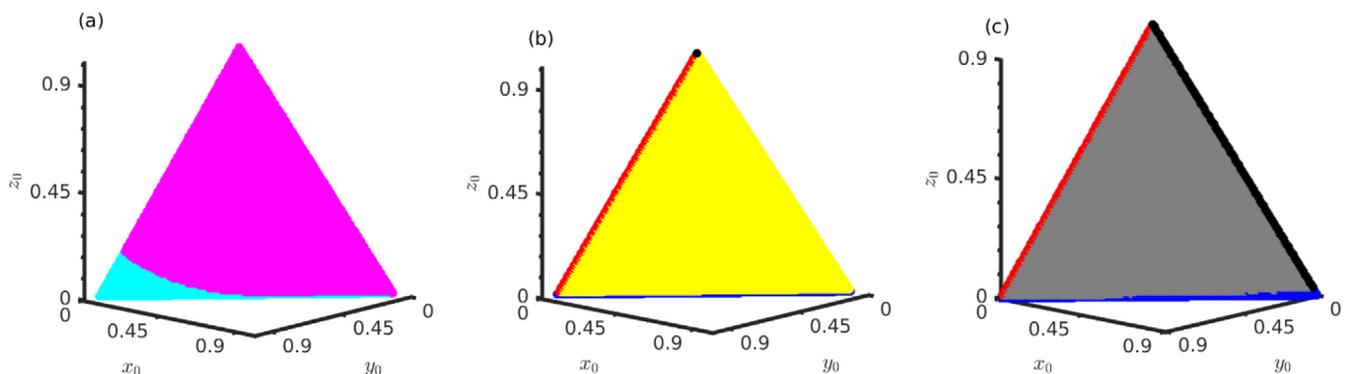


Fig. 4. Basin of attraction of system (7) in 3D xyz-plane: Three distinct sets of parameter values are chosen to demonstrate the effect of initial conditions (x_0, y_0, z_0) . x_0, y_0 and z_0 are varying within $[0, 0.9]$, while the relation $x_0 + y_0 + z_0 = 0.9$ is always kept intact. The system converges to various attractors, or grows without any bound solely depending upon the initial abundance of each population with fixed parameter values. (a) Two distinct cooperator-free stationary states E_2 and E_3 are obtained. (b)-(c) Three different kinds of stationary points are found where the boundaries of the basin of attraction lead to different stationary points, compared to the interior of the basin. Colors: Cyan $\rightarrow E_2$, Magenta $\rightarrow E_3$, Blue \rightarrow Unbounded trajectory, Red $\rightarrow E_6$, Yellow $\rightarrow E_5$, Black $\rightarrow E_0$, Gray $\rightarrow E_7$. The meaning of these stationary points $E_i, i = 0, 1, 2, \dots, 6$ are addressed in Appendix B. Parameter values: (a) $\sigma_1 = 1.2, \sigma_2 = 1.5, \sigma_3 = 1.4, \beta = 1.5, \delta = 0.5$ and $\zeta = 1.1$; (b) $\sigma_1 = 1.2, \sigma_2 = 1.0, \sigma_3 = 0.41, \beta = 2.6, \delta = 1.39$ and $\zeta = 0.5$; and (c) $\sigma_1 = 0.51, \sigma_2 = 1.0, \sigma_3 = 0.41, \beta = 1.1, \delta = 0.1$ and $\zeta = 0.7$.

2007; Henrich and Boyd, 2001; Bowles and Gintis, 2004; Ohtsuki et al., 2009; Hauert et al., 2002; Brandt and Sigmund, 2006; Liu et al., 2018) have revealed the role of punishment for the better understanding of cooperation. However, studies related to the combined effect of altruistic act of free space towards providing the reproductive benefit to the constituents and the punishment are relatively missing in the existing literature to the best of our knowledge. In this paper, we have introduced four distinct competing strategies, viz. cooperation, punishment, defection and free spaces. The interplay of these strategies are particularly common and relevant in our real society. The strategy free space does not take any advantages for providing the benefits to other subpopulations. In fact, any individual from the subpopulation **C**, **P** and **D** can use free space for their replication. In order to shed some light on this one-sided contribution of free space, we have constructed a general mathematical model by combining game and ecological dynamics, where the interaction pattern between cooperators and defectors follows the contemporary PD game. This type of selfless, altruistic act (Axelrod, 1984) can commonly be observed in ants, bacteria, birds, bees, and many other higher mammals. Our eco-evolutionary model captures this remarkable aspect of biological and behavioral sciences (Nowak, 2006a) using the selfless act of free space, which makes an effort to improve the welfare of others by sacrificing personal benefits.

The model developed in this study consists three variables and six parameters. These parameters have important implications in many settings of ecological network, infectious disease dynamics, animal behavior and social interactions of humans. The different choices of these parameter values lead to several emergent dynamics, and our numerical investigations are restricted to only finite possible alternatives of this uncountable parameter space. However, we are able to capture the essence of the multistable replicator dynamics for various possible values of different physical parameters. The model studied here corresponds to scenarios in which cyclic dominance can be maintained through the occurrence of periodic attractor. Such kind of cyclical interaction (Szolnoki et al., 2014) is capable of capturing the beauty of the governing eco-evolutionary dynamics, and similar behavior is found to occur in many real-life instances including the mating strategy of side-blotched lizards, the genetic regulation in the repressilator, the overgrowth of marine sessile organisms, competition in microbial populations, and many more. Few snapshots of such periodic attractor and their temporal evolution are shown for several parameter values. Even, for a particular set of parameter values, we are able to demonstrate the inverse Hopf route for destruction of these periodic attractors. The result is also validated using the largest Lyapunov exponent of the system (7). This Hopf bifurcation, yielding periodic oscillations through destabilization of the steady state behavior, is ubiquitous in many biological and physical systems including Lotka-Volterra model of predator-prey interaction, the Lorenz attractor, the Selkov model of glycolysis, the Hodgkin-Huxley model for nerve membranes, to name but a few examples. Interestingly, slow-fast time scales are noticed for our model (7) during the manifestation of such periodic attractor. This periodic orbit gives all species a fair chance to dominate one another in a cyclic fashion.

We have also been able to map the different potential dynamical states in the two-dimensional parameter plane by keeping fixed the other four parameter values. Various stationary states are obtained during numerical investigation reflecting five different possibilities: (i) extinction of all subpopulations, (ii) existence of only one outcompeting subpopulation, (iii) survival of any two subpopulations, (iv) coexistence of all subpopulations, and (v) unbounded diverging orbits. The reasoning behind these results are thoroughly addressed using physical interpretations of all

parameters. The understanding is further explicated using linear stability analysis of the eco-evolutionary dynamics.

From our analytical findings and associated numerical simulation results, it is clear that if the mortality rate is higher than the benefits provided by the free space, then it is almost impossible for the species to survive. Our results unveil the influence of the death rate, which proves to be quite significant in maintaining biodiversity. With suitable contribution of other parameters, increment of mortality rate as well as the policing parameter is found to encourage the coexistence of all subpopulations (Fig. 2(c) and (d)). The contribution of the temptation parameter in PD game, that disrupts the evolution of cooperative nature of individuals by providing greater benefit to defectors, is well established in the literature. Consistently, if the temptation to defect is sufficiently large, our approach may fail to sustain cooperation, as illustrated in Fig. 2(b). Even, this figure contemplates the decreasing fraction of punishers with increment of temptation parameter β . In addition, potential evolutionary advantage of punishment is presented in Fig. 2(d). Suitable choice of policing parameter δ helps to maintain the survivability of both the traditional cooperators as well as the punishers (that are also cooperative in nature), thereby restricting the total extinction of cooperators. Fig. 2(c) reveals the fascinating twist that the increment of mortality rate ξ ultimately leads to the collapse of defector's population, and consequently, coexistence of all subpopulations under favourable conditions is observed. In fact, if free space is biased towards a particular subpopulation and that free space induced advantage is higher than the common mortality rate, then our eco-evolutionary model may help to promote that particular subpopulation. This behavior is demonstrated in Fig. 3. For instance, if cooperation is favoured by the free space compared to other strategies (i.e., $\sigma_1 > \sigma_2, \sigma_3$) and this favouritism σ_1 is higher than the death rate ξ , then only cooperators survive and other subpopulations become extinct (See the cool grey region of Fig. 3(a)). Moreover, the observed phenomenon of multistability that reveals coexistence of more than one attractors is also emphasized in detail throughout the article. Figs. 1 and 4 ensuring the multistable dynamics exhibited by our model points out the vulnerability of the system to small perturbations. The presence of multistability and multiple operating regimes are essential for biology such as in prey-predator communities, biochemical responses and generation of cell cycle oscillation (Angeli et al., 2004; Banerjee et al., 2020). To clarify the understanding behind the multistability, particularly at the boundaries of the basin of attraction, mathematical analysis is found to be effective.

In conclusion, our constructed model provides certain features with several significant feasible inferences. Our study supports a deeper understanding of the impact of free space induced reproductive benefit on the evolution of population, where the act of punishment improves the emergence and promotion of population-wide cooperation. It comes up with an effective yet simple way for the promotion of the stable coexistence of different strategies including cooperation, which may lead to an interesting direction for future research and for better understanding of the ecological balance in nature.

CRediT authorship contribution statement

Sayantana Nag Chowdhury: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Visualization. **Srilena Kundu:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Visualization. **Jeet Banerjee:** Conceptualization, Validation, Methodology, Visualization, Writing - review

& editing. **Matjaž Perc:** Validation, Visualization, Writing - review & editing. **Dibakar Ghosh:** Supervision, Validation, Visualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Existence, uniqueness and positive invariance of solutions

Positivity of a model guarantees that the model is biologically well behaved. It is easy to notice that the functions on the right side of each of the equations of system (7) are continuously differentiable in $\mathbb{R} \times \mathbb{R} \times \mathbb{R}$. Thus, the solution of Eqs. (7) with a positive initial condition always exists. Also, the uniqueness of solutions for the system (7) in \mathbb{R}_+^3 is assured, as the right-hand side of each of the equations in system (7) is locally Lipschitz in the first quadrant. The solution of system (7) in terms of time $t \geq 0$ can be written in the form

$$\begin{aligned} x(t) &= x(0) \exp \left[\int_0^t \phi_1(x, y, z, \sigma_1, \xi) ds \right], \\ y(t) &= y(0) \exp \left[\int_0^t \phi_2(x, y, z, \sigma_2, \delta, \xi) ds \right], \\ z(t) &= z(0) \exp \left[\int_0^t \phi_3(x, y, z, \sigma_3, \delta, \xi, \beta) ds \right], \end{aligned} \tag{A.1}$$

where,

$$\begin{aligned} \phi_1(x, y, z, \sigma_1, \xi) &= (1 - \sigma_1)x + (1 - \sigma_1)y - \sigma_1 z \\ &\quad + (\sigma_1 - \xi), \\ \phi_2(x, y, z, \sigma_2, \delta, \xi) &= (1 - \sigma_2)x + (1 - \sigma_2)y - (\sigma_2 + \delta)z \\ &\quad + (\sigma_2 - \xi), \\ \phi_3(x, y, z, \sigma_3, \delta, \xi, \beta) &= (\beta - \sigma_3)x + (\beta - \sigma_3 - \delta)y - \sigma_3 z \\ &\quad + (\sigma_3 - \xi). \end{aligned} \tag{A.2}$$

The system of integral equations (A.1) asserts all the solutions of the system (7) that start in \mathbb{R}_+^3 remain positive for all the time.

Appendix B. Existence and stability analysis of the stationary state

B.1. Stationary states and their existence

Setting $\frac{dx}{dt} = 0$, $\frac{dy}{dt} = 0$, and $\frac{dz}{dt} = 0$, the system (7) has at most eight non-negative equilibria, viz.

1. The trivial extinction stationary point $E_0 = (0, 0, 0)$.

2. The punisher-free and defector-free stationary point $E_1 = \left(\frac{\sigma_1 - \xi}{\sigma_1 - 1}, 0, 0\right)$. This stationary point exists, i.e., only cooperators are present if $\sigma_1 > \xi \geq 1$, or $0 < \sigma_1 < \xi \leq 1$.
3. The cooperator-free and defector-free stationary point $E_2 = \left(0, \frac{\sigma_2 - \xi}{\sigma_2 - 1}, 0\right)$, which exists if $\sigma_2 > \xi \geq 1$, or $0 < \sigma_2 < \xi \leq 1$.
4. The cooperator-free and punisher-free stationary point $E_3 = \left(0, 0, 1 - \frac{\xi}{\sigma_3}\right)$. In this case, only defector exists, if $\sigma_3 > \xi$.
5. The defector-free stationary point $E_4 = (\alpha_1, \alpha_2, 0)$, where $\alpha_1 + \alpha_2 = \frac{\sigma_1 - \xi}{\sigma_1 - 1}$. This stationary point exists, if $\sigma_1 > \xi > 1$ or $0 < \sigma_1 < \xi < 1$ and $\sigma_1 = \sigma_2$. If $\xi = 1$, then $\sigma_1 (\neq 1)$ need not be equal to $\sigma_2 (\neq 1)$ for existence of E_4 , where $\alpha_1 + \alpha_2 = 1$.
6. The punisher-free stationary point $E_5 = (\eta_1, 0, 1 - \eta_1 + \eta_2)$, where $\eta_1 = \frac{\xi(\sigma_1 - \sigma_3)}{\beta\sigma_1 - \sigma_3}$ and $\eta_2 = \frac{\xi(1 - \beta)}{\beta\sigma_1 - \sigma_3}$. Clearly, η_1 lies within $(0, 1)$, if $(\xi - \beta)\sigma_1 < (\xi - 1)\sigma_3$ for $\beta\sigma_1 - \sigma_3 > 0$ or, $(\xi - \beta)\sigma_1 > (\xi - 1)\sigma_3$ when $\beta\sigma_1 - \sigma_3 < 0$. Similarly, $1 - \eta_1 + \eta_2 < 1$, if $(1 - \beta) < (\sigma_1 - \sigma_3)$ for $\beta\sigma_1 - \sigma_3 > 0$ and $\xi > 0$ or, $(1 - \beta) > (\sigma_1 - \sigma_3)$ for $\beta\sigma_1 - \sigma_3 < 0$ and $\xi > 0$. The z-component will be positive, if $\beta\sigma_1 - \sigma_3 < \xi(\sigma_1 - \sigma_3 - 1 + \beta)$ for $\beta\sigma_1 - \sigma_3 < 0$, or, $\beta\sigma_1 - \sigma_3 > \xi(\sigma_1 - \sigma_3 - 1 + \beta)$ for $\beta\sigma_1 - \sigma_3 > 0$. Also, $-1 < \eta_2 \leq 0$, as the sum of x and z components should be bounded above by 1 and bounded below by 0.
7. The cooperator-free stationary point $E_6 = (0, \gamma_1, 1 - \gamma_1 + \gamma_2)$, where $\gamma_1 = \frac{\xi(\sigma_2 - \sigma_3) + \delta(\xi - \sigma_3)}{\Delta}$, $\gamma_2 = \frac{\xi(1 - \beta + 2\delta) - \delta(\beta - \delta)}{\Delta}$ and $\Delta = (\beta\sigma_2 - \sigma_3) + \delta(\beta - \delta - \sigma_2 - \sigma_3) \neq 0$. This stationary point exists, if

$$\begin{cases} \delta\sigma_3 < \xi(\sigma_2 - \sigma_3 + \delta) < (\beta - \delta)(\delta + \sigma_2) - \sigma_3 \\ \text{and} \\ \delta(\delta + \sigma_3 - \beta) < \xi(\sigma_2 - \sigma_3 - \delta - 1 + \beta) \\ < \beta\sigma_2 - \sigma_2\delta - \sigma_3 \\ \text{for } \Delta > 0 \end{cases}$$

or,

$$\begin{cases} \delta\sigma_3 > \xi(\sigma_2 - \sigma_3 + \delta) > (\beta - \delta)(\delta + \sigma_2) - \sigma_3 \\ \text{and} \\ \delta(\delta + \sigma_3 - \beta) > \xi(\sigma_2 - \sigma_3 - \delta - 1 + \beta) \\ > \beta\sigma_2 - \sigma_2\delta - \sigma_3 \\ \text{for } \Delta < 0. \end{cases}$$

Also, $-1 < \gamma_2 \leq 0$ should be hold.

8. The interior stationary point $E_7 = (\zeta_1, \zeta_2, \zeta_3)$, where

$$\begin{cases} \zeta_1 = -\gamma - \alpha - \zeta_3 + \Delta_1, \\ \zeta_2 = \alpha + \gamma, \\ \zeta_3 = \frac{(\xi - 1)(\sigma_2 - \sigma_1)}{\sigma_1 - \sigma_2 - \delta + \sigma_1\delta}, \\ \alpha = \frac{(1 - \xi)(\sigma_1 - \sigma_3)}{\sigma_1 - \sigma_2 - \delta + \sigma_1\delta}, \\ \gamma = \frac{(\beta - 1)[\xi(\sigma_1 - \sigma_2 - \delta) + \sigma_1\delta]}{\sigma_1 - \sigma_2 - \delta + \sigma_1\delta}, \\ \Delta_1 = 1 + \frac{\delta(1 - \xi)}{\sigma_1 - \sigma_2 - \delta + \sigma_1\delta}, \\ \text{and } \sigma_1 - \sigma_2 - \delta + \sigma_1\delta \neq 0. \end{cases}$$

This stationary point exists, if $0 < \zeta_1, \zeta_2, \zeta_3 < 1, 0 < \zeta_1 + \zeta_2 + \zeta_3 \leq 1$ and

$$\begin{cases} \xi(\sigma_2 - \sigma_1) < \delta(\sigma_1 - 1) \\ (\xi - 1)(\sigma_2 - \sigma_1) > 0 \\ \text{for } \sigma_1 - \sigma_2 - \delta + \sigma_1\delta > 0, \end{cases}$$

or,

$$\begin{cases} \xi(\sigma_2 - \sigma_1) > \delta(\sigma_1 - 1) \\ (\xi - 1)(\sigma_2 - \sigma_1) < 0 \\ \text{for } \sigma_1 - \sigma_2 - \delta + \sigma_1\delta < 0. \end{cases}$$

B.2. Stationary states and their local stability

The Jacobian matrix of the system (7) at any stationary point (x_*, y_*, z_*) can be expressed as.

$$J(x_*, y_*, z_*) = \begin{pmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{pmatrix},$$

where

$$\begin{cases} J_{11} = 2(1 - \sigma_1)x_* + (1 - \sigma_1)y_* - \sigma_1z_* + (\sigma_1 - \xi), \\ J_{12} = (1 - \sigma_1)x_*, \\ J_{13} = -\sigma_1x_*, \\ J_{21} = (1 - \sigma_2)y_*, \\ J_{22} = (1 - \sigma_2)x_* + 2(1 - \sigma_2)y_* - (\sigma_2 + \delta)z_* + (\sigma_2 - \xi), \\ J_{23} = -(\sigma_2 + \delta)y_*, \\ J_{31} = (\beta - \sigma_3)z_*, \\ J_{32} = (\beta - \sigma_3 - \delta)z_*, \\ J_{33} = (\beta - \sigma_3)x_* + (\beta - \sigma_3 - \delta)y_* - 2\sigma_3z_* + (\sigma_3 - \xi). \end{cases}$$

The different equilibria of the system and their stability properties are described below:

1. The trivial equilibrium E_0 is asymptotically stable node, if $\sigma_1, \sigma_2, \sigma_3 < \xi$ with $\xi > 0$. The eigenvalues λ_i of the Jacobian matrix J , evaluated at E_0 are given by $\lambda_i = \sigma_i - \xi, i = 1, 2, 3$.
2. The eigenvalues of $J(E_1)$ are

$$\begin{cases} \lambda_1 = \xi - \sigma_1, \\ \lambda_2 = \frac{(\sigma_1 - \sigma_2)(1 - \xi)}{\sigma_1 - 1}, \\ \lambda_3 = \frac{\beta\sigma_1 - \sigma_3 + \xi(1 - \beta + \sigma_3 - \sigma_1)}{\sigma_1 - 1}. \end{cases}$$

Thus, the stability criteria of the node E_1 reduces to $\sigma_1 > \sigma_2, \sigma_1 > \xi > 1$ and $\beta\sigma_1 - \sigma_3 + \xi(1 - \beta + \sigma_3 - \sigma_1) < 0$.

3. The eigenvalues of the Jacobian J at the stationary point E_2 are

$$\begin{cases} \lambda_1 = \frac{(1 - \xi)(\sigma_2 - \sigma_1)}{\sigma_2 - 1}, \\ \lambda_2 = \xi - \sigma_2, \\ \lambda_3 = \frac{\xi(1 - \sigma_2 + \sigma_3 - \beta + \delta) + \sigma_2(\beta - \delta) - \sigma_3}{\sigma_2 - 1}. \end{cases}$$

The negative values of these set of eigenvalues suggest E_2 is a stable node. Thus, the solution of system (7) containing only punishers (y) is stable, if $\sigma_2 > \sigma_1, \sigma_2 > \xi > 1$ and $\xi(1 - \sigma_2 + \sigma_3 - \beta + \delta) + \sigma_2(\beta - \delta) - \sigma_3 < 0$.

4. The eigenvalues of $J(E_3)$ are

$$\begin{cases} \lambda_1 = \xi\left(\frac{\sigma_1}{\sigma_3} - 1\right), \\ \lambda_2 = \frac{\xi(\sigma_2 + \delta - \sigma_3) - \delta\sigma_3}{\sigma_3}, \\ \lambda_3 = \xi - \sigma_3. \end{cases}$$

Hence, E_3 will be a stable node, if $0 < \xi < \sigma_3, \sigma_3 > \sigma_1$ and $\delta\sigma_3 > \xi(\sigma_2 + \delta - \sigma_3)$.

5. The eigenvalues of the Jacobian J at the stationary point $E_4 = (\alpha_1, \alpha_2, 0)$ are

$$\begin{cases} \lambda_1 = (\beta - \sigma_3)\frac{\xi - \sigma_1}{1 - \sigma_1} - \delta\alpha_2 + (\sigma_3 - \xi), \\ \lambda_2 = 0, \\ \lambda_3 = \xi - \sigma_1. \end{cases}$$

Note that, α_1 and α_2 are related by the relation $\alpha_1 + \alpha_2 = \frac{\xi - \sigma_1}{1 - \sigma_1}$ with $\sigma_1 \neq 1$. Therefore, the stationary point E_4 is marginally stable, if $\xi < \sigma_1$ and $\lambda_1 < 0$.

Till now, using the existential criterion and the negativity of the eigenvalues, the stability of the autonomous system (7) is investigated. But, the eigenvalues of the Jacobian matrix J at the remaining stationary points E_5, E_6 and E_7 are very complicated to work out. Depending on the stationary points E_5, E_6 and E_7 and the various parameters, the roots of the complex polynomials possess at least one real eigenvalue and the remaining two characteristic roots may be complex conjugate or real, solely depending on the different values of parameters and stationary points E_5, E_6 and E_7 .

6. Using Routh-Hurwitz stability criterion, $E_5 = (\eta_1, 0, 1 - \eta_1 + \eta_2)$ is stable, if

$$\begin{cases} \eta_1 - \sigma_2\eta_2 - \xi - \delta(1 + \eta_2 - \eta_1) < 0, \\ \eta_1(\beta + \sigma_3 + 2 - \sigma_1) - \sigma_3(1 + 2\eta_2) - \sigma_1\eta_2 - 2\xi < 0, \text{ and} \\ [2\eta_1 - \sigma_1(\eta_1 + \eta_2) - \xi][\beta\eta_1 - \xi + \sigma_3(\eta_1 - 1 - 2\eta_2)] \\ + \sigma_1\eta_1(\beta - \sigma_3)(1 + \eta_2 - \eta_1) > 0, \end{cases}$$

7. The cooperator-free stationary point $E_6 = (0, \gamma_1, 1 - \gamma_1 + \gamma_2)$ is stable, if

$$\begin{cases} \gamma_1 - \sigma_1\gamma_2 - \xi < 0, \\ \gamma_1(\beta + \sigma_3 + 2 - \sigma_2) - \sigma_3(1 + 2\gamma_2) \\ - \gamma_2(\sigma_2 + \delta) - 2\xi - \delta < 0, \\ \text{and } [2(1 - \sigma_2)\gamma_1 + (\sigma_2 - \xi)][(\beta - \sigma_3 - \delta)\gamma_1 \\ - 2\sigma_3(1 - \gamma_1 + \gamma_2) + (\sigma_3 - \xi)] \\ + (\sigma_2 + \delta)(1 - \gamma_1 + \gamma_2)[2\sigma_3(1 - \gamma_1 + \gamma_2) \\ - (\sigma_3 - \xi)] > 0, \end{cases}$$

8. Routh-Hurwitz stability criterion yields that E_7 is stable, if

$$\begin{cases} a_{11} + a_{22} + a_{33} < 0, \\ a_{11}a_{23}a_{32} - a_{11}a_{22}a_{33} + a_{12}a_{21}a_{33} \\ - a_{12}a_{23}a_{31} - a_{13}a_{32}a_{21} + a_{13}a_{31}a_{22} > 0, \\ -(a_{11} + a_{22} + a_{33})(a_{11}a_{22} + a_{11}a_{33} + a_{22}a_{33} \\ - a_{23}a_{32} - a_{12}a_{21} - a_{13}a_{31}) > (-a_{11}a_{22}a_{33} \\ + a_{11}a_{23}a_{32} + a_{12}a_{21}a_{33} - a_{12}a_{23}a_{31} \\ - a_{13}a_{32}a_{21} + a_{13}a_{31}a_{22}), \end{cases}$$

where,

$$\begin{cases} a_{11} = 2(1 - \sigma_1)(\Delta_1 - \alpha - \gamma - \xi_3) + (1 - \sigma_1)(\alpha + \gamma) - \sigma_1\xi_3 + (\sigma_1 - \xi), \\ a_{12} = (1 - \sigma_1)(\Delta_1 - \alpha - \gamma - \xi_3), \\ a_{13} = -\sigma_1(\Delta_1 - \alpha - \gamma - \xi_3), \\ a_{21} = (1 - \sigma_2)(\alpha + \gamma), \\ a_{22} = (1 - \sigma_2)(\Delta_1 - \alpha - \gamma - \xi_3) + 2(1 - \sigma_2)(\alpha + \gamma) - (\sigma_2 + \delta)\xi_3 \\ + (\sigma_2 - \xi), \\ a_{23} = -(\sigma_2 + \delta)(\alpha + \gamma), \\ a_{31} = (\beta - \sigma_3)\xi_3, \\ a_{32} = (\beta - \sigma_3 - \delta)\xi_3, \text{ and} \\ a_{33} = (\beta - \sigma_3)(\Delta_1 - \alpha - \gamma - \xi_3) + (\beta - \sigma_3 - \delta)(\alpha + \gamma) - 2\sigma_3\xi_3 + (\sigma_3 - \xi). \end{cases}$$

B.3. Analysis of the system (7), when at least one initial component of (x_0, y_0, z_0) is zero

1. If $(x_0, y_0, z_0) = (0, 0, 0)$, then the system (7) will always converge to E_0 irrespective choice of any parameters, since $(0, 0, 0)$ is a fixed point of the functions on the right-hand side of each of the Eqs. (7). Physically this result will be meaningful in the sense that there will be no entertainment of replication, if there are no species available in the society initially.

2. If $x_0 = 0$ and $y_0 = 0$, then the system (7) is exactly solvable and the component of x, y will be 0 for all remaining time t , and $z = \frac{(\sigma_3 - \xi)[1 + \tanh(c_1 + t)(\frac{\sigma_2 - \xi}{2})]}{2\sigma_3}$ with $\sigma_3 \neq 0$, where c_1 is a constant depending on initial condition z_0 . This kind of initial condition may prefer defector dominated alliance within the system depending on the values of ξ and σ_3 .
3. If $x_0 = 0$ and $z_0 = 0$, then the system will be free from cooperators and defectors ($x = 0$ and $z = 0$) for all the remaining time t . The fraction of punisher y will be $\frac{(\sigma_2 - \xi)[1 + \tanh(c_2 + t)(\frac{\sigma_2 - \xi}{2})]}{2\sigma_2 - 2}$ with $\sigma_2 \neq 1$, where c_2 is an initial condition dependent constant. Note that, proceeding to the limit as $t \rightarrow \infty, y$ will be tending to $\frac{\sigma_2 - \xi}{\sigma_2 - 1}$ with $\sigma_2 \neq 1$ if $\sigma_2 > \xi$.
4. If $y_0 = 0$ and $z_0 = 0$, then the punishers and defectors ($y = 0$ and $z = 0$) will die out. The empty initial state with respect to the punishers and defectors actually do not give them opportunity to replicate in future. However, the fraction of cooperator x will be $\frac{(\sigma_1 - \xi)[1 + \tanh(c_3 + t)(\frac{\sigma_1 - \xi}{2})]}{2\sigma_1 - 2}$ with $\sigma_1 \neq 1$, where c_3 is x_0 dependent constant.
5. If only $z_0 = 0$, then extinction of defectors will happen. Now, if $\sigma_1 = \sigma_2$ and $(1 - \sigma_1)(x + y) + (\sigma_1 - \xi) \neq 0$, then $y = c_4 x$, where c_4 is a constant. Also, if $\sigma_1 = \sigma_2$ and $(1 - \sigma_1)(x + y) + (\sigma_1 - \xi) = 0$, then $x = y = 0$, and thus all species will die out.
6. If only $y_0 = 0$, then $y = 0$ and generates a punisher-free society. Under this circumstance, E_5 will be stable, if

$$\begin{cases} \eta_1(\beta + \sigma_3 + 2 - \sigma_1) - \sigma_3(1 + 2\eta_2) \\ -\sigma_1\eta_2 - 2\xi < 0, \text{ and} \\ [2\eta_1 - \sigma_1(\eta_1 + \eta_2) - \xi][\beta\eta_1 - \xi + \sigma_3(\eta_1 - 1 - 2\eta_2)] \\ + \sigma_1\eta_1(\beta - \sigma_3)(1 + \eta_2 - \eta_1) > 0. \end{cases}$$

7. If only $x_0 = 0$, then all cooperators will be vanished ($x = 0$). Other non-zero components of initial condition $y_0, z_0 \neq 0$ leads to stable stationary point E_6 , if

$$\begin{cases} \gamma_1(\beta + \sigma_3 + 2 - \sigma_2) - \sigma_3(1 + 2\gamma_2) \\ -\gamma_2(\sigma_2 + \delta) - 2\xi - \delta < 0, \\ \text{and } [2(1 - \sigma_2)\gamma_1 + (\sigma_2 - \xi)][(\beta - \sigma_3 - \delta)\gamma_1 \\ - 2\sigma_3(1 - \gamma_1 + \gamma_2) + (\sigma_3 - \xi)] + (\sigma_2 + \delta)(1 - \gamma_1 + \gamma_2) \\ [2\sigma_3(1 - \gamma_1 + \gamma_2) - (\sigma_3 - \xi)] > 0. \end{cases}$$

References

Aktipis, C.A., 2004. Know when to walk away: contingent movement and the evolution of cooperation. *Journal of Theoretical Biology* 231 (2), 249–260.

Angeli, D., Ferrell, J.E., Sontag, E.D., 2004. Detection of multistability, bifurcations, and hysteresis in a large class of biological positive-feedback systems. *Proceedings of the National Academy of Sciences* 101 (7), 1822–1827.

Armano, G., Javarone, M.A., 2017. The beneficial role of mobility for the emergence of innovation. *Scientific Reports* 7, 1781.

Arnold, L., 1998. *Random Dynamical Systems*. Springer, Berlin, Heidelberg.

Axelrod, R., 1984. *The Evolution of Cooperation*. Basic Books, New York.

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211 (4489), 1390–1396.

Banerjee, J., Sasmal, S.K., Layek, R.K., 2019a. Supercritical and subcritical Hopf-bifurcations in a two-delayed prey–predator system with density-dependent mortality of predator and strong Allee effect in prey. *BioSystems* 180, 19–37.

Banerjee, J., Layek, R.K., Sasmal, S.K., Ghosh, D., 2019. Delayed evolutionary model for public goods competition with policing in phenotypically variant bacterial biofilms. *EPL (Europhysics Letters)* 126 (1), 18002.

Banerjee, S., Sha, A., Chattopadhyay, J., 2020. Cooperative predation on mutualistic prey communities. *Journal of Theoretical Biology* 490, 110156.

Bell, G., 2008. *Selection: The Mechanism of Evolution*. Oxford University Press.

Bowles, S., Gintis, H., 2004. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theoretical Population Biology* 65 (1), 17–28.

Brandt, H., Sigmund, K., 2006. The good, the bad and the discriminator—Errors in direct and indirect reciprocity. *Journal of Theoretical Biology* 239 (2), 183–194.

Brandt, H., Hauert, C., Sigmund, K., 2006. Punishing and abstaining for public goods. *Proceedings of the National Academy of Sciences* 103 (2), 495–497.

Brayne, C., 2007. The elephant in the room—healthy brains in later life, epidemiology and public health. *Nature Reviews Neuroscience* 8 (3), 233–239.

Burger, O., Baudisch, A., Vaupel, J.W., 2012. Human mortality improvement in evolutionary context. *Proceedings of the National Academy of Sciences* 109 (44), 18210–18214.

Colombo, E.H., Martínez-García, R., López, C., Hernández-García, E., 2019. Spatial eco-evolutionary feedbacks mediate coexistence in prey-predator systems. *Scientific Reports* 9, 18161.

Cong, R., Zhao, Q., Li, K., Wang, L., 2017. Individual mobility promotes punishment in evolutionary public goods games. *Scientific Reports* 7, 14015.

Cortez, M.H., 2016. How the magnitude of prey genetic variation alters predator-prey eco-evolutionary dynamics. *The American Naturalist* 188 (3), 329–341.

Darwin, C., 1909. *The Origin of Species*. PF Collier & Son New York.

De Silva, H., Hauert, C., Traulsen, A., Sigmund, K., 2010. Freedom, enforcement, and the social dilemma of strong altruism. *Journal of Evolutionary Economics* 20 (2), 203–217.

Dreber, A., Rand, D.G., Fudenberg, D., Nowak, M.A., 2008. Winners don't punish. *Nature* 452 (7185), 348–351.

Egas, M., Riedl, A., 2008. The economics of altruistic punishment and the maintenance of cooperation. *Proceedings of the Royal Society B: Biological Sciences* 275 (1637), 871–878.

Fehr, E., Gächter, S., 2002. Altruistic punishment in humans. *Nature* 415 (6868), 137–140.

Finch, C.E., 2010. Evolution of the human lifespan and diseases of aging: roles of infection, inflammation, and nutrition. *Proceedings of the National Academy of Sciences* 107 (Suppl 1), 1718–1724.

Fotouhi, B., Momeni, N., Allen, B., Nowak, M.A., 2018. Conjoining uncooperative societies facilitates evolution of cooperation. *Nature Human Behaviour* 2 (7), 492–499.

Fotouhi, B., Momeni, N., Allen, B., Nowak, M.A., 2019. Evolution of cooperation on large networks with community structure. *Journal of the Royal Society Interface* 16 (152), 20180677.

Fowler, J.H., 2005. Altruistic punishment and the origin of cooperation. *Proceedings of the National Academy of Sciences* 102 (19), 7047–7049.

Fu, F., Hauert, C., Nowak, M.A., Wang, L., 2008. Reputation-based partner choice promotes cooperation in social networks. *Physical Review E* 78, (2) 026117.

Fussmann, G.F., Loreau, M., Abrams, P.A., 2007. Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* 21, 465–477.

Gokhale, C.S., Hauert, C., 2016. Eco-evolutionary dynamics of social dilemmas. *Theoretical Population Biology* 111, 28–42.

Gómez-Gardenes, J., Campillo, M., Floría, L.M., Moreno, Y., 2007. Dynamical organization of cooperation in complex topologies. *Physical Review Letters* 98, (10) 108103.

Hardin, G., 1968. The tragedy of the commons. *Science* 162 (3859), 1243–1248.

Hauert, C., De Monte, S., Hofbauer, J., Sigmund, K., 2002. Replicator dynamics for optional public good games. *Journal of Theoretical Biology* 218 (2), 187–194.

Hauert, C., Holmes, M., Doebeli, M., 2006. Evolutionary games and population dynamics: maintenance of cooperation in public goods games. *Proceedings of the Royal Society B: Biological Sciences* 273 (1600), 2565–2571.

Helbing, D., Yu, W., 2009. The outbreak of cooperation among success-driven individuals under noisy conditions. *Proceedings of the National Academy of Sciences* 106 (10), 3680–3685.

Helbing, D., Szolnoki, A., Perc, M., Szabó, G., 2010a. Defector-accelerated cooperativeness and punishment in public goods games with mutations. *Physical Review E* 81, (5) 057104.

Helbing, D., Szolnoki, A., Perc, M., Szabó, G., 2010b. Evolutionary establishment of moral and double moral standards through spatial interactions. *PLoS Computational Biology* 6, (4) e1000758.

Hendry, A.P., 2020. *Eco-evolutionary Dynamics*. Princeton University Press.

Henrich, J., Boyd, R., 2001. Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology* 208 (1), 79–89.

Hofbauer, J., Sigmund, K., 1998. *Evolutionary Games and Population Dynamics*. Cambridge University Press.

Javarone, M.A., Atzeni, A.E., Galam, S., 2015. Emergence of cooperation in the prisoner's dilemma driven by conformity. In: *European Conference on the Applications of Evolutionary Computation*. Springer, pp. 155–163.

Jiang, L.-L., Perc, M., Szolnoki, A., 2013. If cooperation is likely punish mildly: insights from economic experiments based on the snowdrift game. *PLoS One* 8, (5) e64677.

Kundu, S., Majhi, S., Sasmal, S.K., Ghosh, D., Rakshit, B., 2017. Survivability of a metapopulation under local extinctions. *Physical Review E* 96, (6) 062212.

Liebrand, W.B., 1983. A classification of social dilemma games. *Simulation & Games* 14 (2), 123–138.

Liu, L., Wang, S., Chen, X., Perc, M., 2018. Evolutionary dynamics in the public goods games with switching between punishment and exclusion. *Chaos: An Interdisciplinary Journal of Nonlinear Science* 28 (10), 103105.

Meloni, S., Buscarino, A., Fortuna, L., Frasca, M., Gómez-Gardeñes, J., Latora, V., Moreno, Y., 2009. Effects of mobility in a population of prisoner's dilemma players. *Physical Review E* 79, (6) 067101.

- Murray, J.D., 2007. *Mathematical Biology: I. An Introduction*, vol. 17, Springer Science & Business Media.
- Nag Chowdhury, S., Ghosh, D., 2020. Hidden attractors: a new chaotic system without equilibria. *The European Physical Journal Special Topics* 229, 1299–1308.
- Nag Chowdhury, S., Kundu, S., Duh, M., Perc, M., Ghosh, D., 2020. Cooperation on interdependent networks by means of migration and stochastic imitation. *Entropy* 22 (4), 485..
- Nowak, M.A., 2006a. Five rules for the evolution of cooperation. *Science* 314 (5805), 1560–1563.
- Nowak, M.A., 2006b. *Evolutionary Dynamics: Exploring the Equations of Life*. Harvard University Press.
- Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. *Nature* 359 (6398), 826–829.
- Oeppen, J., 1820. Life expectancy convergence among nations since 1820: separating the effects of technology and income. *Old and New Perspectives on Mortality Forecasting 2019*, 197–219.
- Ohtsuki, H., Iwasa, Y., Nowak, M.A., 2009. Indirect reciprocity provides only a narrow margin of efficiency for costly punishment. *Nature* 457 (7225), 79–82.
- Ozono, H., Jin, N., Watabe, M., Shimizu, K., 2016. Solving the second-order free rider problem in a public goods game: An experiment using a leader support system. *Scientific Reports* 6, 38349.
- Pelletier, F., Garant, D., Hendry, A., 2009. Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, 1483–1489.
- Pennisi, E., 2005. How did cooperative behavior evolve? *Science* 309 (5731), 93.
- Perc, M., 2012. Sustainable institutionalized punishment requires elimination of second-order free-riders. *Scientific Reports* 2, 344.
- Perc, M., Szolnoki, A., 2010. Coevolutionary games—A mini review. *BioSystems* 99 (2), 109–125.
- Perc, M., Gómez-Gardeñes, J., Szolnoki, A., Floría, L.M., Moreno, Y., 2013. Evolutionary dynamics of group interactions on structured populations: a review. *Journal of the Royal Society Interface* 10 (80), 20120997.
- Perc, M., Jordan, J.J., Rand, D.G., Wang, Z., Boccaletti, S., Szolnoki, A., 2017. Statistical physics of human cooperation. *Physics Reports* 687, 1–51.
- Perko, L., 2013. *Differential Equations and Dynamical Systems*, vol. 7. Springer, New York.
- Poundstone, W., 1992. *Prisoner's Dilemma*. Doubleday, New York.
- Santos, F.C., Pacheco, J.M., 2005. Scale-free networks provide a unifying framework for the emergence of cooperation. *Physical Review Letters* 95, (9) 098104.
- Sasaki, T., Okada, I., Unemi, T., 2007. Probabilistic participation in public goods games. *Proceedings of the Royal Society B: Biological Sciences* 274 (1625), 2639–2642.
- Sigmund, K., 2010. *The calculus of selfishness*, vol. 6. Princeton University Press.
- Skutch, A.F., 1961. Helpers among birds. *The Condor* 63 (3), 198–226.
- Slobodkin, L.B., 1980. *Growth and Regulation of Animal Populations*. Dover Publications.
- Smaldino, P.E., Schank, J.C., 2012. Movement patterns, social dynamics, and the evolution of cooperation. *Theoretical Population Biology* 82 (1), 48–58.
- Smith, J.M., Smith, J.M.M., 1982. *Evolution and the Theory of Games*. Cambridge University Press.
- Smith, J.M., Szathmari, E., 1997. *The Major Transitions in Evolution*. Oxford University Press.
- Szabó, G., Fath, G., 2007. Evolutionary games on graphs. *Physics Reports* 446 (4–6), 97–216.
- Szolnoki, A., Perc, M., 2017. Second-order free-riding on antisocial punishment restores the effectiveness of prosocial punishment. *Physical Review X* 7, (4) 041027.
- Szolnoki, A., Szabó, G., Perc, M., 2011. Phase diagrams for the spatial public goods game with pool punishment. *Physical Review E* 83, (3) 036101.
- Szolnoki, A., Mobilia, M., Jiang, L.-L., Szczesny, B., Rucklidge, A.M., Perc, M., 2014. Cyclic dominance in evolutionary games: a review. *Journal of the Royal Society Interface* 11 (100), 20140735.
- Tanimoto, J., 2007. Emergence of cooperation supported by communication in a one-shot 2×2 game. In: *IEEE Congress on Evolutionary Computation*. IEEE, pp. 1374–1381.
- Tanimoto, J., 2007. Does a tag system effectively support emerging cooperation? *Journal of Theoretical Biology* 247 (4), 756–764.
- Vainstein, M.H., Silva, A.T., Arenzon, J.J., 2007. Does mobility decrease cooperation? *Journal of Theoretical Biology* 244 (4), 722–728.
- Wachter, K.W., Finch, C.E., N.R.C.U.C. on Population, editors, *Evolutionary biology and age-related mortality*, in: *Between Zeus and the Salmon: The Biodemography of Longevity*, vol. 5, Washington (DC): National Academies Press (US), 1997..
- Wakano, J.Y., Hauert, C., 2011. Pattern formation and chaos in spatial ecological public goods games. *Journal of Theoretical Biology* 268 (1), 30–38.
- Wakano, J.Y., Nowak, M.A., Hauert, C., 2009. Spatial dynamics of ecological public goods. *Proceedings of the National Academy of Sciences* 106 (19), 7910–7914.
- Wang, X., Fu, F., 2020. Eco-evolutionary dynamics with environmental feedback: cooperation in a changing world. *EPL (Europhysics Letters)* 132 (1), 10001..
- Wang, R.W., Shi, L., Ai, S.M., Zheng, Q., 2008. Trade-off between reciprocal mutualists: local resource availability-oriented interaction in fig/fig wasp mutualism. *Journal of Animal Ecology* 77 (3), 616–623.
- Wang, Z., Xia, C.-Y., Meloni, S., Zhou, C.-S., Moreno, Y., 2013. Impact of social punishment on cooperative behavior in complex networks. *Scientific Reports* 3, 3055.
- Wang, Z., Wang, L., Szolnoki, A., Perc, M., 2015. Evolutionary games on multilayer networks: a colloquium. *The European Physical Journal B* 88 (5), 124.
- Wang, X., Zheng, Z., Fu, F., 2020. Steering eco-evolutionary game dynamics with manifold control. *Proceedings of the Royal Society A* 476 (2233), 20190643.
- Weibull, J.W., 1995. *Evolutionary Game Theory*. MIT Press, Cambridge, MA.
- Wilson, E.O., 1971. *The Insect Societies*. Harvard University Press.
- Wolf, A., Swift, J.B., Swinney, H.L., Vastano, J.A., 1985. Determining Lyapunov exponents from a time series. *Physica D: Nonlinear Phenomena* 16 (3), 285–317.
- Wu, T., Fu, F., Wang, L., 2011. Moving away from nasty encounters enhances cooperation in ecological prisoner's dilemma game. *PLoS One* 6, (11) e27669.
- Yang, H.-X., Wang, Z., 2015. Role of mutual punishment in the snowdrift game. *EPL (Europhysics Letters)* 111 (6), 60003..
- Yang, H.-X., Wu, Z.-X., Rong, Z., Lai, Y.-C., 2015. Peer pressure: enhancement of cooperation through mutual punishment. *Physical Review E* 91, (2) 022121.
- Zhang, Y., Fu, F., Wu, T., Xie, G., Wang, L., 2013. A tale of two contribution mechanisms for nonlinear public goods. *Scientific Reports* 3 (1), 1–5.