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Public Goods Games in Disease Evolution and Spread

Christo Morison[1] · Małgorzata Fic[2,3] · Thomas Marcou[4] · Javad Mohamadichamgavi[5] · Javier Redondo Antón[6] · Golsa Sayyar[7] · Alexander Stein[8] · Frank Bastian[9] · Hana Krakovská[10,11] · Nandakishor Krishnan[12,13] · Diogo L. Pires[14] · Mohammadreza Satouri[15] · Frederik J. Thomsen[16] · Kausutua Tjikundi[6,17] · Wajid Ali[18]

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Abstract
Cooperation arises in nature at every scale, from within cells to entire ecosystems. Public goods games (PGGs) are used to represent scenarios characterised by the conflict/dilemma between choosing cooperation as a socially optimal strategy and defection as an individually optimal strategy. Evolutionary game theory is often used to analyse the dynamics of behaviour emergence in this context. Here, we focus on PGGs arising in the disease modelling of cancer evolution and the spread of infectious diseases. We use these two systems as case studies for the development of the theory and applications of PGGs, which we succinctly review. We also posit that applications of evolutionary game theory to decision-making in cancer, such as interactions between a clinician and a tumour, can learn from the PGGs studied in epidemiology, where cooperative behaviours such as quarantine and vaccination compliance have been more thoroughly investigated. Furthermore, instances of cellular-level cooperation observed in cancers point to a corresponding area of potential interest for modellers of other diseases, be they viral, bacterial or otherwise. We aim to demonstrate the breadth of applicability of PGGs in disease modelling while providing a starting point for those interested in quantifying cooperation arising in healthcare.

Keywords Public goods game · Evolutionary game theory · Cancer · Epidemics

1 Introduction

Interactions between individuals amidst an ever-changing environment provide nature with immense complexity. Modelling essential features of evolution, such as selection for advantageous traits, can in part be reduced to interrelations between entities—which can range in scale from subcellular molecules to entire organisms belonging to the same or different species. While game theory is the mathematical discipline of strategic interactions, typically with players seeking to maximise (monetary) payoffs, evolutionary game theory (EGT) studies the evolution of traits within (biological) populations [70]. In this framework, players

C. Morison, M. Fic have contributed equally to this work.

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are not overtly rational, and strategies (types) are inherited according to principles of Darwinian evolution rather than being rationally chosen. Consequently, natural selection leads to changes in the frequency of strategies depending on their relative fitness [98]. Some of these strategies, at first glance, seem to contradict Darwinian selection: for instance, the emergence of behaviours favouring the group over the individual [69].

Despite natural selection being centred on competition, cooperative behaviour and relationships arise across nature. Symbiosis can take many forms, such as services like protection (e.g. plant-ant [99]) or reproductive services (e.g. pollination [118] or seed dispersal [49]), often in exchange for resources like food or nutrients [102]. It can also be found at the microscale: for instance, eukaryotes evolved from primitive unicellular organisms (including the predecessors to mitochondria), once independently living, via a cooperative process called endosymbiosis [90]. Because cooperation is an overarching theme across the scales of organisation, EGT provides a methodological path towards a deeper understanding of evolutionary processes .

While cooperation may arise via many different mechanisms [74], the issues surrounding allocations of resources and distributions of costs are common. This is aptly described by public goods games (PGGs), where individuals can contribute to a public good, from which they then benefit, regardless of whether or not they contributed [30]. The two-player version of a PGG is perhaps the most well-known game: the Prisoner's Dilemma (PD), introduced in an experiment by Dreshner and Flood, named by Tucker [105, 111] and used to study cooperation for decades [13]. Both of these will be more formally introduced in the following section, as this paper surveys their use in a prominent area of mathematical biology: disease modelling.

Two significant applications of mathematical modelling in healthcare are the spread of pathogens and cancer evolution. Both of these have been widely described with a variety of methods. For instance, population dynamics can be explored with differential equations [31, 119], agent-based models [19, 32], or stochastic processes [5, 87], whereas including social structure involves borrowing tools from network science [60]. Notably, PGGs can be applied in many contexts, albeit in different ways: the social aspects of epidemiology lend themselves to the emergence of cooperative behaviour via implementations such as quarantine or vaccination mandates [3]. On the other hand, cells that evolve to be cancerous are both defecting from the healthy population [22] and cooperating with one another in support of the new entity called the tumour [26], whose cells are sometimes even considered a distinct species [112].

2 Public Goods Games

In the context of EGT, PGGs are used to study how cooperative strategies arise or collapse over time. The dynamics that emerge showcase the tension between the benefit of the group and the self-interests of individuals [97]. In the game, a group of N players, each endowed with a resource c, is considered. We focus on the two-strategy version of the game: players can invest in a public pool (a strategy called Cooperate) or not (a strategy called Defect). Notably, in many experimental studies, the game is instead framed as continuous; that is, the players decide on the fraction of endowment they invest in the unit interval [55]. The total investment within the group is then multiplied by a factor r, where $1 < r < N$, and distributed back to all players, regardless of individual contribution (see Fig. 1a). If n_c players

Table 1 The matrix representing the payoffs received by Player 1 depending on its strategies and the strategies of Player 2 in the Prisoner's Dilemma

Player 1 / Player 2	Cooperate	Defect
Cooperate	$b - c$	$-c$
Defect	b	0

cooperate, the payoffs of defectors and cooperators are

$$P_d = rc\frac{n_c}{N} \quad \text{and} \quad P_c = rc\frac{n_c}{N} - c, \tag{1}$$

respectively, since the cooperators incur the additional cost of investing in the public good [45]. Note that in many biological processes, the benefit of growth factors is not linear (that is, r is not a constant in n_c/N). For example, this might arise as a sigmoidal curve:

$$P_d = \frac{\sigma(n_c) - \sigma(0)}{\sigma(N) - \sigma(0)}, \quad \text{for} \quad \sigma(x) = \frac{1}{1 + \mathrm{e}^{-s(x-k)/N}}, \tag{2}$$

where k determines the inflection point's location (so that $k \to N$ gives increasing returns and $k \to 0$ gives diminishing returns) and s determines the steepness at the inflection point (so that the step-function $s \to \infty$ represents a threshold PGG, which will be introduced later, and $s \to 0$ represents an N-player PD).

Though there are incentives for players to invest for the benefit of the group, there also exist incentives to free ride off others' contributions [83, 97] (see Fig. 1b). A rise in the frequency of defectors may lead to a phenomenon commonly known as the tragedy of the commons, where selfish behaviour leads to a depletion of the common good [42]. The idea of the tragedy of the commons stems from an alternative formulation of the PGG, wherein players decide whether or not to refrain from depleting a common good (for example, a pasture or fish in the ocean [54]). The remainder of the good is then multiplied and can be used in the future. The arising dilemma contrasts the needs of an individual in the present with the needs of the group in the future. However, as opposed to the benefit-cost formulation of the PGG (as in Fig. 1a), the player cannot always refrain from using the good (for example, because of needing to sustain itself); this creates a tension between balancing current and future consumption.

When $N = 2$, the PGG can be formulated as the PD [13, 24]. Similarly to the multiplayer game, cooperation involves a cost c (equivalent to the net cost $c - rc/N$ in the PGG) and brings a benefit b (equivalent to rc/N in the PGG), which are symmetric to both players. Assuming that $b > c > 0$, this game can be summarised by the matrix representation of Table 1.

The production of the public good is not always possible by one individual alone; sufficiently many contributors may be necessary for the good to be reaped. When this is the case, the social dilemma can be represented by a threshold PGG, also known as an N-player Snowdrift Game. In this game, if the number of cooperators n_c is greater than a threshold M (where $1 \leq M \leq N$), then the public good is produced. Thus, all players receive a benefit b, while the cooperators incur the cost c/n_c, so that when $n_c \geq M$, $P_d = b$ and $P_c = b - c/n_c$. If, however, the threshold is not met, no benefit is provided (since the public good was not created) but the cooperators still suffer a cost [101].

Historically, the emergence of cooperation was examined with well-mixed population models that assume all-to-all interactions [46], with evolutionary dynamics most commonly described by the replicator equation, wherein strategies providing higher payoffs increase in frequency [108] (as in Fig. 1b). Nevertheless, these models fail to capture the complexity

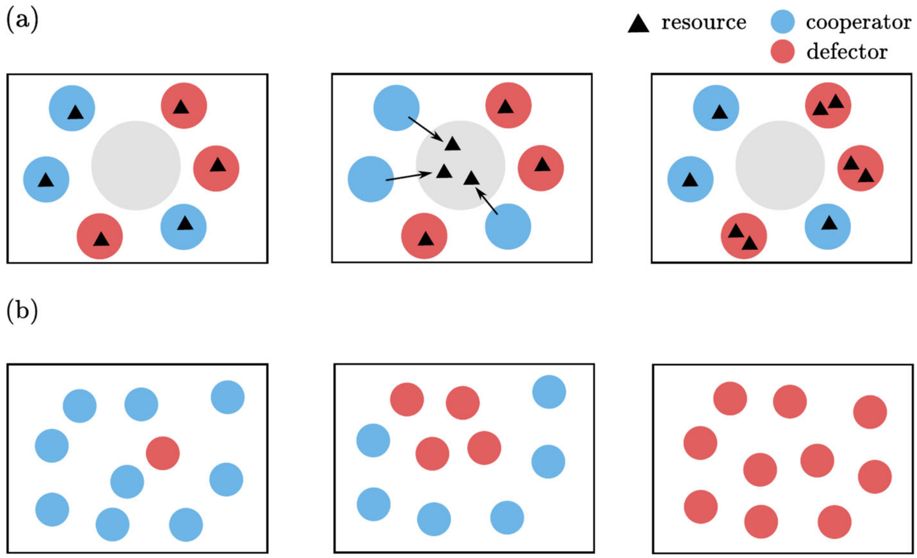

Fig. 1 **a** In public good games, individuals are presented with a choice to either contribute an amount c to a common pot (Cooperate) or not (Defect). All contributions are then multiplied by a factor r (in the example depicted, $r = 2$) and shared equally amongst all players, regardless of their contribution. Hence, a temptation to free ride arises, as defectors still benefit from the public good without incurring the contribution cost. **b** Cooperators sustain a cost to supply the whole population with the public good; however, defectors can take advantage of this public good and not suffer said cost. Thus, defectors have an evolutionary advantage, as their payoff (P_d) is always higher than the cooperators' payoff ($P_c < P_d$). Subsequently, a defector introduced in a population of cooperators would be favoured by selection and reproduce faster, eventually leading to their fixation in the population. However, the emergence of cooperation in real-life suggests that other factors are sometimes at play [74]. (This figure was created with Inkscape 1.1.2, https://inkscape.org/release/inkscape-1.1/?latest=1.)

of real-life interactions [113]. Introducing networks into the framework of EGT allows for the inclusion of some of those complexities, like spatial and temporal structure or social relations [40]. On networks, individuals are then represented as nodes and interactions as edges [79, 80]. Players interact locally with their neighbours, either with one at a time, in two-player games [78], or with all neighbours simultaneously, in N-player games [82, 95]. Strategies are updated according to a specified rule, which typically involves choosing an individual to replicate and a neighbour to be replaced (or vice versa), with selection acting on one of the two events [67]. Successful strategies then spread, and depending on the update rule, different evolutionary outcomes may be achieved: for example, Ohtsuki et al. (2006) observed that network reciprocity alone allowed cooperation to evolve when selection acted on the second event, unlike when it acted on the first [78].

By studying various network structures, it has been shown that the interaction topology impacts strategy evolution [89]. For example, the spread of cooperation in the PD varies across lattice [75, 106], small-world [1], regular [92], and real-world networks [61]. The impact of other topological aspects of networks on cooperation has been studied: some examples include the average degree of the network [107], the degree distribution heterogeneity [93], the presence of hubs on scale-free networks [94], as well as the strategic placement of cooperators [123]. Likewise, when considering PGGs with more than two players, introducing an interaction structure influences the emergence of cooperation. This holds without considering additional features and when incorporating mechanisms such as punishment strategies, reputation, voluntary participation, or social diversity. This has been demonstrated, for instance, on lattice networks [18, 44], as well as on regular graphs and heterogeneous scale-free networks [17, 21, 95].

Additionally, multilayer networks can represent multiple types of interactions and individuals, add temporal and spatial context or depict communities [63, 84]. They are shown to have a significant impact on the evolutionary dynamics and can promote the evolution of cooperation in the PD [39, 115], multiplayer PGGs [117] and when several games are present [29, 96].

The strength of game theory lies in its ability to unify seemingly disparate ideas, offering a common language to researchers in widely varying fields. For instance, PGGs can help us approach current global issues such as the climate emergency, where the planet's resources might be thought of as a public good [72], or the international refugee crisis, wherein governments must navigate providing for citizens versus people seeking shelter and balancing domestic resources with human rights ideals [62]. In light of these examples, it is evident that defection is not inherently morally wrong or selfish in the context of evolutionary PGGs. Instead, game theory demonstrates that these behaviours emerge from payoff perceptions so that the tragedy of the commons can arise without ill intent amongst players. The same holds for populations comprising individuals such as cells or microbes, where rationality is not central to the system at all.

3 Applications

PGG models have found applications in both epidemiology and oncology, two crucial areas of public health. Game theoretic tools have been used for decades to study infectious diseases [16] and cancer [109, 114], and, spurred by the recent COVID-19 pandemic and high incidence rates of cancer worldwide, they have been used even more widely.

3.1 Epidemics

Epidemiology is the study of the distribution and determinants of health-related events in populations [37]. With the help of mathematical models, one can monitor the occurrence of infectious diseases and the course of epidemics, help design public health responses and plan for future incidences. Though Kermack and McKendrick's susceptible-infected-recovered (SIR) model [52] is almost a century old, the first appearance of a game theoretical model in epidemiology was in 2004, when Bauch and Earn (2004) described a vaccination game [16]. In the game, the payoffs were related to the morbidity of vaccination, as well as the infection probability and morbidity of the illness. The authors stress that people have biased perceptions and make decisions with respect to "perceived" morbidity and thus readjust the payoff to a perceived payoff [16]. A SIR model with a vaccination term was used to describe the dynamics of the illness in the population and determine the probability of infection. The study showed that for any perceived relative risk of vaccination, the expected vaccine uptake falls below the threshold needed for disease eradication. Thus, voluntary vaccination alone cannot eradicate a disease when individuals prioritise personal interests. Additionally, if vaccination is considered riskier than the disease itself, no one is expected to choose to vaccinate. Furthermore, the authors analysed the dynamics during and after a vaccine scare

Table 2 Examples of public goods found in epidemiological modelling, with corresponding cooperating and defecting strategies

Public good	Cooperate	Defect
Herd immunity (e.g. [28])	Immunisation	Susceptibility
Pathogen-free environment (e.g. [124])	Following non-pharmaceutical interventions, such as mask mandates or social distancing	Not following non-pharmaceutical interventions
Sensitivity to antibiotics (e.g. [86])	Not overusing antibiotics	Overusing antibiotics

when the perceived vaccine risk becomes high. The results showed that restoring pre-scare vaccination levels is relatively difficult compared to the drop during a scare [16].

In the two decades since Bauch and Earn (2004) [16], many PGGs have been used to model epidemiological phenomena, from herd immunity to antibiotic resistance, as well as non-pharmaceutical interventions like social distancing and mask mandates, as shown in Table 2.

Herd immunity is established within a population when a sufficiently large fraction has undergone immunisation, either naturally or via vaccination, ensuring that the disease cannot persist as an endemic condition [31]. Because it safeguards individuals against the onset of infectious diseases and is both non-excludable and non-rivalrous, herd immunity can be conceptualised as a public good [28]. Through this lens, immune individuals (regardless of whether they acquire immunity through infection or vaccination) are cooperators, and those susceptible (irrespective of the reason) are defectors. If a large enough fraction of the population is immune—that is, if n_c/N is greater than some threshold, typically around 90%, depending on the disease [28]—the potential drawbacks linked to getting vaccinated may surpass the risks posed by the actual infection. As a result, a free riding strategy may be favoured by some individuals (see Fig. 2a), and the vaccination game with herd immunity can be seen as a threshold PGG [38]. The game can be introduced into classical SIR-type models to better understand individual behaviour in the face of voluntary vaccination.

Many PGG models have been used to study problems relating to vaccination; here we highlight a few notable examples. Alam et al. (2020) considered the effects of quarantine and isolation policies, using game theory to model vaccination decisions [3]. They stressed the importance of individual vaccination decisions on government-mandated policy effectiveness and showed that successful implementation of vaccination policies can significantly lower the level of control measures required to manage disease outbreaks [3]. The model can be further enriched by introducing an incubation period between infection and symptom onset. Soltanolkottabi et al. (2020) showed that the inclusion of this time delay can fundamentally change the epidemic dynamics, leading to fewer vaccinated and fewer free riding (non-vaccinated and healthy) individuals and more infections [100]. The model also included a community structure wherein individuals got vaccinated when their (vaccinated) neighbours obtained a higher payoff. Fu et al. (2011) introduced uncertainty into the decision to imitate vaccinated neighbours [33]. Their model showcased the social structure's ability to either promote voluntary vaccinations at low vaccination costs or facilitate disease spread, even stopping vaccination completely at higher cost levels [33]. Chen et al. (2019) explored the importance of vaccine efficacy on individuals' vaccination choices both in well-mixed and structured populations, highlighting the importance of education and providing accurate

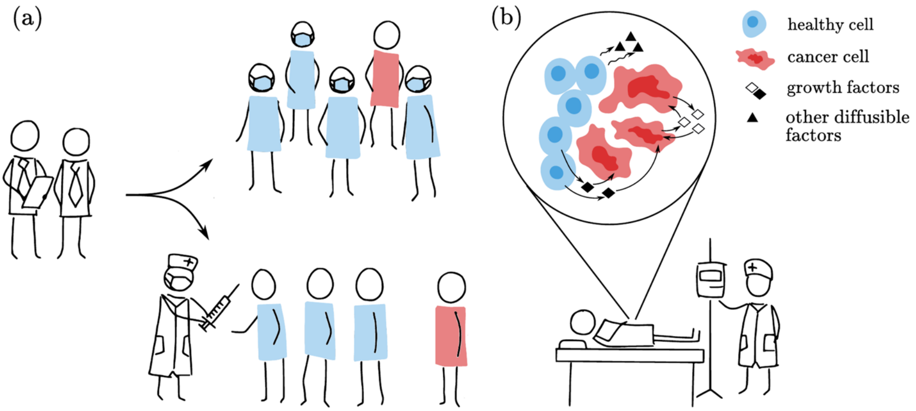

Fig. 2 **a** During an epidemic, policy-makers are faced with implementing intervention policies aiming at disease containment and eradication. These approaches include vaccines as well as non-pharmaceutical interventions such as mask mandates or lockdowns, where defecting individuals are shown in red and cooperating individuals in blue. PGG models can inform policy-makers by providing insights into how both infectious disease and individual behaviours evolve in the population. **b** Within the complex tumour microenvironment, healthy and cancerous cells are constantly exchanging information and resources. While tumour cells may free ride by not producing some diffusible factors, they may also cooperate amongst themselves. Clinicians can use evolutionary insights from these underlying dynamics to inform their therapeutic protocols. (This figure was created with Inkscape 1.1.2, https://inkscape.org/release/inkscape-1.1/?latest=1.)

information to the public [121]. Their model explained the slow recovery of vaccination rates after vaccine scares and showed that vaccine protection in age-structured populations can substantially impact vaccination dynamics [121]. Finally, Wang et al. (2020) further investigated the motivation behind vaccination decisions [116]. Two reasons were considered for getting vaccinated: conforming and increasing one's payoff. A multilayer network approach then decoupled the epidemic dynamics from the vaccination behaviour and captured the multi-levelled nature of human interactions. The results suggested that conformity-driven behaviour can be detrimental to herd immunity, as imitation does not cause individuals to get vaccinated [116]. These results emphasised the criticality of individual motivation and social structure in vaccination campaigns.

PGGs have also been used to model other dilemmas arising in the wake of epidemics, such as wearing masks [10, 88], self-quarantining [6] and social distancing [4]. Here, rather than herd immunity, the pathogen-free environment can be seen as a public good, which is depleted when individuals do not comply with interventions. For example, Yong and Choy (2021) used PGGs to model noncompliance as a free riding problem in public health [124]. They focused on the social dynamics of compliance and underlined that individual decisions are interdependent, influenced by factors like perceived costs, social norms and population behaviour. Their study suggested several approaches to counteract free riding, including social norms and sanctions, incentives and subsidies, and targeted communication [124]. The findings emphasised the importance of tailoring interventions to leverage evolved psychological mechanisms for cooperation, using both top-down (legal enforcement) and bottom-up (social norms) strategies to encourage compliance and maintain public health as a shared good [124].

In models introducing non-pharmaceutical interventions, individuals can change their strategy based on the current situation, as opposed to the vaccination game, where vaccinated individuals cannot become susceptible at will. This leads to a phenomenon known as the oscillatory tragedy of the commons, as introduced by Glaubnitz and Fu (2020): high levels of infection in the population lead to high costs of noncompliance with the intervention, leading in turn to a higher fraction of individuals following them. That, however, decreases the risk of infection, prompting individuals to defect by not following the interventions), subsequently increasing the risk of infections [4]. Moreover, Glaubnitz and Fu (2020) showed that a lower cost of practising social distancing induces a higher number of people practising it, which appears as a good strategy for governments to encourage compliance [4]. This result highlights the importance of individual preference in designing intervention campaigns, a notion also emphasised by Traulsen et al. [110] In their work, authors presented a game-theoretical model capturing the individual costs and societal benefits of both pharmaceutical and non-pharmaceutical interventions. They showed that individuals with higher perceived risks of infection are more likely to adhere to the interventions and provided a simple mathematical framework to determine what fraction of the population is expected to follow them. Real-world dynamics depend greatly on players' perceptions of payoffs and risks associated with becoming infected or vaccinating. It is therefore crucial for accurate modelling to consider payoff calibration depending on players' properties like demographics, location, frequency of interactions and attitude towards vaccination, as well as properties of the disease itself [85].

Although a whole population can enjoy public goods, sometimes the underlying PGGs are played only by a fraction of the individuals. In the case of antibiotic resistance evolution, those individuals are clinicians, and the public good in question is the sensitivity to antibiotics. One such model was introduced by Porco et al. (2012) to study the development of antibiotic resistance [86]. They derived a two-player game between the individual and the population from an equilibrium of the differential equations describing their compartmental model. They observed diverse incentive landscapes, depending on the rates at which the drug-resistant strain is acquired through social transmission and early antibiotic treatment [86]. If both are low, both the individual and society benefit from treatment. If both are high, neither the individual nor society benefits from treatment. However, if transmissibility is high and the probability of acquired resistance during early treatment is low, then a tragedy of the commons is eminent as individuals benefit from high early treatment rates, while society is hindered by them [86]. Colman et al. (2019) also proposed a antibiotic-prescribing game to study the development of antibiotic resistance [27]. Their results showed that it is in medical practitioners' self-interest to prescribe antibiotic use to their patients, as long as the risk of infection is positive. However, this leads to the continuous increase of antibiotic usage above the social optimal state, thus describing a tragedy of the commons [27]. The game theoretical formalisation highlights the conflict of interest between medical practitioners and society, a clash inevitable within the framework proposed, thus showing that systems of regulation, management, and monitoring of antibiotic prescribing are crucial [27].

3.2 Cancer

Cancers are evolutionary diseases initiated in a process termed carcinogenesis, in which normal cells transform into malignant tumour cells [76]. EGT models have been used to study interactions occurring during disease progression and treatment at different scales: between cancer cells and cancer cells [56], cancer cells with the tumour microenvironment [20], and cancer cells with the physician [103]. In particular, frequency-dependent modelling in oncology began with tools from optimal control [65] before being formalised as EGT [109, 114]. One of its most significant applications has been modelling the emergence of resistance to treatment [26, 120]. In particular, PGGs have been used to study the evolution of cooperation

Table 3 Examples of public goods found in cancer modelling, with corresponding cooperating and defecting cell types

Public good	Cooperate	Defect
Growth factors (e.g. [9])	Producing growth factors (cancerous or healthy cells)	Not producing (only cancer cells)
Other diffusible factors, such as those promoting neoangiogenesis or disabling an immune response (e.g. [14])	Producing diffusible factors	Not producing
Adhesion (e.g. [8])	Producing adhesion molecules	Not producing

in cancer, both from the perspective of cancer cells defecting from the healthy population as well as cooperation amongst the cancer cells themselves [8], as depicted in Table 3.

Carcinogenesis can be viewed as cancer cells free riding on a homeostatic (i.e. under regulation to maintain stability), healthy population; this has led to cancer cells being sometimes called "cheater cells" [22]. On the other hand, an established tumour can also be modelled as a collection of cooperating subpopulations [25]. Many cancer processes rely on the production of diffusible factors by the cancer cells to promote growth [41] (see Fig. 2b). However, producing these factors comes with a cost, such that it is often beneficial for an individual to free ride on the resources produced by others, by not producing the factors themselves. Here, the benefit of growth factors is often nonlinear, modelled as sigmoidal in concentration [11], as in equation (2). For example, Archetti et al. (2015) modelled insulin-like growth factor II (IGF-II) as a public good amongst pancreatic cancer cells in mice [9]. The evolutionary dynamics between cooperators (producers of IGF-II) and defectors (non-producers), assuming a nonlinear payoff, is modelled on a Voronoi network to represent the spatial structure of cells. Depending on the cost to produce IGF-II, the model predicted a heterogenetic population and a small bistable region. Both results have been experimentally verified in vitro, providing insights into potential reasons that maintain the heterogeneity of cancer cells within tumours [9]. Here, game theory is necessary to explain why cooperation exists among cancer cells, since we do not observe a tragedy of the commons with all cancer cells defecting by producing no growth factors [8]. By modelling the N-player PD with a sigmoidal payoff, growth signal concentration dynamics are more realistically captured, resulting in a stable coexistence of cooperators and defectors (though there is no polymorphic equilibrium if the cost is too high relative to the yield) [8]. The shape of the sigmoid function also plays a role in how an equilibrium is achieved: cooperation is facilitated if the sigmoid function is close to a step function ($s \to \infty$ in equation (2)), though it is also less robust in this case [8]. It is also worth noting that the pure-defector state is stable (i.e. cannot be invaded by cooperators) while the pure-cooperator is not; this suggests that we may observe a pure-defector state but never a pure-cooperator state [8].

Beyond growth factors shared amongst cancer cells, other diffusible factors such as those promoting neoangiogenesis (the production of new blood vessels to supply the tumour with resources such as oxygen) or those disabling the immune system [51] can be considered public goods. Axelrod et al. (2006) posit that this kind of cellular-level cooperation between partially transformed tumour cells is possible because several hallmarks of cancer—sustaining proliferative signalling, inducing angiogenesis, and activating tissue invasion and metastasis [41]—involve shareable resources [14]. Furthermore, beyond exchanges of resources, they argue that modulation of the microenvironment and avoidance of immune detection are also pathways via which cancer cells may cooperate. By suggesting an evolutionary perspective on cancer, viewing it as a community of cooperating cells, treatments might aim to disrupt cooperative behaviors instead of solely targeting individual cells [14]. For instance, blocking angiogenesis or interfering with metabolic cooperation could make the tumour less viable. This approach reframes cancer not as isolated cell proliferation but as a dynamic system with adaptable, cooperative interactions [14].

Another approach is more explicitly physical: threshold PGGs can be used to model contact between cells and their neighbours, as discussed by Archetti and Pienta (2019). Here, the public good (adhesion between cells) is provided so long as a minimum number of cells contribute adhesion molecules [8]. In particular, for two cells to adhere to each other, it is enough if one of the two has the relevant adhesion molecule. Cooperation in this case is desirable because adhesion limits invasion and metastasis [8].

Moreover, Archetti (2021) has proposed leveraging cooperation amongst cancer cells to improve treatment [7]. Genetically engineering some cancer cells to free ride (by not producing a certain growth factor) led to a decrease in the proliferation rate of the tumour population. The predictions of both experiments and EGT modelling established that only when the ratio between the cost and the benefit of producing the growth factor was large would it be valuable to engineer such defector cells [7]. Additionally, adding growth factors to the system via an external mechanism also decreased the overall tumour growth, since more cells were induced to decrease their own production [7]. Hence, PGGs could join other evolutionary concepts in mathematical oncology that have led to novel treatment strategies such as adaptive [125], double-bind [15] and extinction therapies [36].

4 Discussion

Game theory provides a general framework with which to study problems in wide-ranging fields, from the social sciences and economics [47, 73, 91] to computer science [50] and biology [71]. Importantly, researchers who develop and apply game theory have the opportunity to look to other fields for results that they can then import to their own domain of interest, rather than beginning from scratch. As two examples, we consider the application of PGGs to the evolution of tumours and the spread of pathogens. Mathematical models in epidemiology and oncology can inform public health officials and clinicians in their quest to manage and eradicate infectious diseases and cancers.

Applying game theory to epidemiology provides insight into drivers of individual behaviour in the wake of pandemics: why do some people refuse to comply with governmental sanctions? How detrimental must a vaccine be for someone to avoid it, rather than immunising themselves? Are isolation or self-quarantining measures effective in reducing the spread of an infectious disease? While many questions like these only have clear answers in specific contexts, game theory can provide insight as to why certain decisions are being made by certain fractions of the population. For instance, Alam et al. (2020)'s demonstration that vaccination mandates reduce the criticality of other disease control measures when sufficiently followed exemplifies the interplay between decisions policy-makers can make with those made by the population [3]. Also, Wang et al. (2020)'s assertion that herd immunity may be impeded by imitating behaviour, a result deduced using the underlying game theory in their model, is an example of how game theory can (and should) influence our approaches to containing diseases [116]. This is also shown by Glaubnitz and Fu (2020)'s suggestion that governments consider the costs associated to social distancing when estimating how properly mandates will be followed [4]. In these examples as well as in the case of modelling antibiotic resistance, PGGs help quantify the conflict (or alignment) between personal and societal needs. Subsequently, this approach allows decision-makers to assess societal reactions to preventive measures and adapt future strategies.

As for the cellular interactions central to cancer, the questions PGG models try to answer move from game theory's rationality to EGT's natural selection. Can cancer cells be conceived as defectors amidst a cooperating population of healthy cells? In which ways do cancer cells cooperate with each other and what does this imply for the evolutionary dynamics of the tumour? Can understanding what public goods are relevant in the tumour microenvironment illuminate new treatment options? Here, Archetti (2019)'s argument that inhibiting growth factors secreted by the stroma is more successful than reducing cancer cells relies upon the PGG perspective [8]. That PGGs can help identify scenarios in which it is better to influence game parameters or player populations remains to be seen experimentally, though the promotion of cell-cell competition to improve patient outcomes is a central argument of proponents of adaptive therapy [35]. As applying game theory to cancer modelling is still relatively recent (see Wölfl et al. [120] for a thorough review), using PGGs to understand how heterogeneous cell populations (of competitors, cooperators, or other players) can be sustained is exciting territory to explore. In the following section, three possible directions of future research in PGG modelling in healthcare are discussed.

5 Outlook

Here, we highlight three avenues for further research that are relevant for our two case studies of epidemiology and cancer: treatment resistance, population structure and leader-follower dynamics.

First, the evolution of resistance is a central issue in both fields: cancers not eradicated with a first line of therapy are prone to decreasing treatment sensitivity [34]; likewise, antibiotic resistance threatens one's ability to eliminate pathogenic bacteria [59]. Just as sensitivity to antibiotics is a public good to a population of (possibly infected) individuals (see Table 2), therapeutic sensitivity can be thought of as a public good within a cancer cell population. In both cases, resistance is positively selected for when treatment is applied. For example, Masroni et al. (2023) used EGT modelling in identifying cooperative behaviour in breast cancers [66]. They found resistant cancer cells behaving altruistically and shielding sensitive cells from treatment, leading to lower fitness—though rather than go extinct these altruists would regenerate epigenetically, securing their stability within the population [66]. Likewise, it has been shown that bacteria resistant to antibiotics can help shield their sensitive counterparts, increasing the survival capability of the whole population [57]. With these parallels in mind, recall Archetti (2021)'s engineered defector cells and their role in collapsing intra-tumour cooperation [7]. Such a defecting population will spread in the cancer population under clonal selection. If this subpopulation could be kept sensitive to a certain treatment, then once it subsumes the cooperating population, the tumour might have a better chance of being eradicated by said treatment. Similarly, in epidemiology, one might create a strain of bacteria that does not produce a certain metabolite [58], thus defecting in the PGG though not evolving antibiotic resistance.

Next, introducing network structure in EGT models allows for more accurate representations of real-world dynamics [40]. For instance, knowledge of the underlying social network during an epidemic can help identify the most influential individuals to vaccinate [23, 43, 77, 122]. However, during dynamical processes—such as the evolution and spread of diseases—these structures are rarely static [68] and often co-evolve with the strategies [81] or even independently [2]. Another class of spatial models considers individuals moving through networks, allowing for the inclusion of complex, ever-changing social interaction patterns [64]. As such, tools from evolving network theory can sharpen current EGT models. Much like in mathematical epidemiology, the inclusion of spatial structure in cancer models impacts the evolution of cooperation and could also benefit from dynamical networks. For instance, Coggan and Page (2022) review the impact of spatial structure on cooperation in game theoretic models of cancer [26]. They report that cooperation is favoured in PD-based models of cancer if the benefit-cost ratio b/c is greater than $(\varsigma+1)/(\varsigma-1)$ (for $\varsigma \in [0, 1]$ the structure factor, or level of assortment, where $\varsigma = 1$ for a well-mixed infinite population), though this is both dependent on the game played as well as the update rule considered [26].

Finally, an aspect of game theory that has more recently been coupled to evolutionary games is sequential decision-making, as in leader-follower, or Stackelberg, games [53]. Here, a decision-maker such as a medical professional (the leader) acts to control the evolution of a disease, where the follower is either the person carrying the disease or the disease itself. In the oncological setting, the cancer cells are themselves playing an evolutionary game, which allows the clinician to apply evolutionarily-informed treatments by anticipating the evolution of the disease [104]. This two-layer framework may find parallels with epidemiological modelling: policy-makers involved in infectious disease response can be considered the leader whose knowledge of the evolving epidemic informs their decision-making, recommendations and offered incentives [12]. For example, targeting vaccinations can be optimised in pursuit of the public good of herd immunity [48]. Stackelberg evolutionary game theory may help formalise these optimal control problems in both cancer and epidemic modelling.

PGGs appear in many areas of mathematical biology and point to unexpected connections between disparate fields of research. Though game theoretic models are informative in understanding the key interactions within a system, real-world data is nevertheless crucial to effectively translate theoretical insights into practical applications. As mathematical modelling in healthcare matures, active discourse between theoreticians, experimenters, clinicians and policy-makers is vital to ensure appropriate model predictions and health interventions.

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References

1. Abramson G, Kuperman M (2001) Social games in a social network. Phys Rev E 63(3):030901
2. Ádám Kun and István Scheuring (2009) Evolution of cooperation on dynamical graphs. Biosystems 96(1):65–68
3. Alam M, Kabir KMA (2020) Tanimoto J (2020) "Based on mathematical epidemiology and evolutionary game theory, which is more effective: quarantine or isolation policy?". J Stat Mech Theor Exp 3:033502
4. Alina Glaubitz and Feng Fu (2020) Oscillatory dynamics in the dilemma of social distancing. Proce Royal Soc A 476(2243):20200686
5. Allen Linda JS (2008) An introduction to stochastic epidemic models. Mathematical epidemiology, vol 1945. Springer, Berlin, pp 81–130
6. Amaral MA, de Oliveira MM, Javarone MA (2021) An epidemiological model with voluntary quarantine strategies governed by evolutionary game dynamics. Chaos Solitons Fractals 143:110616
7. Archetti M (2021) Collapse of intra-tumor cooperation induced by engineered defector cells. Cancers 13(15):3674
8. Archetti M, Pienta Kenneth J (2019) Cooperation among cancer cells: applying game theory to cancer. Nat Rev Cancer 19(2):110–117
9. Archetti M, Ferraro DA, Christofori G (2015) Heterogeneity for IGF-II production maintained by public goods dynamics in neuroendocrine pancreatic cancer. Proce Natl Acad Sci 112(6):1833–1838
10. Ariful Kabir KM, Risa T, Tanimoto J (2021) Prosocial behavior of wearing a mask during an epidemic: An evolutionary explanation. Sci Rep 11(1):12621
11. Cornish-Bowden Athel (2013) Fundamentals of enzyme kinetics. John Wiley and Sons, Hoboken
12. Aurell A et al (2022) Optimal incentives to mitigate epidemics: a Stackelberg mean field game approach. SIAM J Control Optim 60(2):S294–S322
13. Axelrod R, Hamilton William D (1981) The evolution of cooperation. Science 211(4489):1390–1396
14. Axelrod R, Axelrod DE, Pienta Kenneth J (2006) Evolution of cooperation among tumor cells. Proce Natl Acad Sci 103(36):13474–13479
15. Basanta D, Gatenby RA, Anderson Alexander RA (2012) Exploiting evolution to treat drug resistance: combination therapy and the double bind. Mol Pharm 9(4):914–921
16. Bauch CT, Earn DJD (2004) Vaccination and the theory of games. Proce Natl Acad Sci 101(36):13391–13394
17. Bramoullé Y, Kranton R (2007) Public goods in networks. J Econ Theo 135(1):478–494
18. Brandt H, Hauert C, Sigmund K (2003) Punishment and reputation in spatial public goods games. Proce Royal Soc London Ser B Biol Sci 270(1519):1099–1104
19. Bravo RR et al (2020) Hybrid automata library: a flexible platform for hybrid modeling with real-time visualization. PLOS Comput Biol 16(3):e1007635
20. Buhler CK et al (2021) Do mechanisms matter? Comparing cancer treatment strategies across mathematical models and outcome objectives. Math Biosci Eng 18(5):6305–6327
21. Cao X-B, Wen-Bo D, Rong Z-H (2010) The evolutionary public goods game on scale-free networks with heterogeneous investment. Phys A Stat Mech Appl 389(6):1273–1280
22. Chris C, David L, Robert A (2012) Physics of cancer propagation A game theory perspective. AIP Adv 2:011202. https://doi.org/10.1063/1.3699043
23. Christley RM et al (2005) Infection in social networks: using network analysis to identify high-risk individuals. Am J Epidemiol 162(10):1024–1031

24. Christoph Hauert and György Szabo (2003) Prisoner's dilemma and public goods games in different geometries: compulsory versus voluntary interactions. Complexity 8(4):31–38
25. Cleary Allison S et al (2014) Tumour cell heterogeneity maintained by cooperating subclones in Wnt-driven mammary cancers. Nature 508(7494):113–117
26. Coggan H, Page KM (2022) The role of evolutionary game theory in spatial and non-spatial models of the survival of cooperation in cancer: a review. J Royal Soc Interface 19(193):20220346
27. Colman AM et al (2019) Medical prescribing and antibiotic resistance: a game-theoretic analysis of a potentially catastrophic social dilemma. PLOS ONE 14(4):e0215480
28. Dees RH (2018) Public health and normative public goods. Public Health Ethics 11(1):20–26
29. Deng Z-H et al (2018) Multigames with voluntary participation on interdependent networks and the evolution of cooperation. Chaos, Solitons Fract 114:151–157
30. Ernst Fehr and Simon Gächter (2002) Altruistic punishment in humans. Nature 415(6868):137–140
31. Fred B, Carlos C-C, Feng Zhilan (2019) Mathematical models in epidemiology, vol 32. Springer, New york
32. Frias-Martinez Enrique, Williamson Graham, Frias-Martinez Vanessa (2011) "An agent-based model of epidemic spread using human mobility and social network information". In: 2011 IEEE third international conference on privacy, security, risk and trust and 2011 IEEE third international conference on social computing. IEEE. pp. 57–64
33. Fu F et al (2011) Imitation dynamics of vaccination behaviour on social networks. Proce Royal Soc B Biol Sci 278(1702):42–49
34. Gatenby Robert A (2009) A change of strategy in the war on cancer. Nature 459(7246):508–509
35. Gatenby Robert A et al (2009) Adaptive Therapy. Cancer Res 69(11):4894–4903
36. Gatenby RA, Zhang J, Brown JS (2019) First strike-second strike strategies in metastatic cancer: lessons from the evolutionary dynamics of extinction. Cancer Res 79(13):3174–3177
37. Johan Giesecke (2017) Modern infectious disease epidemiology. CRC Press
38. Giubilini A (2021) Vaccination ethics. British Med Bull 137(1):4–12
39. Gómez-Gardenes J et al (2012) Evolution of cooperation in multiplex networks. Sci Rep 2(1):620
40. György Szabó and Gábor Fáth (2007) Evolutionary games on graphs. Physics Reports 446(4–6):97–216
41. Hanahan D, Weinberg RA (2000) The hallmarks of cancer. Cell 100(1):57–70
42. Hardin G (1968) The tragedy of the commons. Sci 162(3859):1243–1248
43. Hartnett GS et al (2021) "Modelling the impact of social distancing and targeted vaccination on the spread of COVID-19 through a real city-scale contact network". J Complex Netw 9(6):cnab042
44. Hauert C et al (2002) Volunteering as red queen mechanism for cooperation in public goods games. Science 296(5570):1129–1132
45. Hauert C, Haiden N, Sigmund K (2004) The dynamics of public goods. IIASA Interim Report, IIASA, Laxenburg, Austria
46. Josef Hofbauer, Karl Sigmund (1998) Evolutionary games and population dynamics. Cambridge University Press
47. Hoffman Moshe, Yoeli Erez (2022) Hidden games: the surprising power of game theory to explain irrational human behaviour. Hachette UK
48. Hu Tingwei, Mei Lili, Wang Zhen (2023) "Stackelberg Strategies on Epidemic Containment Games". In: International workshop on frontiers in algorithmics. Springer. pp. 281–294
49. David Iluz (2011) Zoochory: The dispersal of plants by animals. In: Dubinsky Zvy, Seckbach Joseph (eds) All Flesh Is Grass: Plant-Animal Interrelationships. Springer, Netherlands, Dordrecht, pp 199–214
50. Jingzhen W (2023) The state-of-art applications of game theory in computer science. Highlights Sci Eng Technol 49:280–286
51. Joyce JA, Pollard JW (2009) Microenvironmental regulation of metastasis. Nature Rev Cancer 9(4):239–252
52. Kermack William Ogilvy, McKendrick Anderson G (1927) "A contribution to the mathematical theory of epidemics". In: Proceedings of the Royal Society of London. Series A, Containing papers of a mathematical and physical character 115(772):700–721
53. Kleshnina M et al (2023) Game theory for managing evolving systems: challenges and opportunities of including vector-valued strategies and life-history traits. Dyn Games Appl 13(4):1130–1155
54. Kraak SBM (2011) Exploring the public goods game model to overcome the tragedy of the commons in fisheries management. Fish Fish 12(1):18–33
55. Ledyard John O et al (1994) Public goods: A survey of experimental research. Division of the Humanities and Social Sciences, California Inst. of Technology
56. Lee Nathan D, Kaveh Kamran, Bozic Ivana (2023)"Clonal interactions in cancer: Integrating quantitative models with experimental and clinical data". In: Seminars in Cancer Biology. Elsevier
57. Lee HH et al (2010) Bacterial charity work leads to population-wide resistance. Nature 467(7311):82–85

58. Lenski RE, Velicer GJ (2001) Games microbes play. Selection 1(1–3):89–96
59. Levy SB (1998) The challenge of antibiotic resistance. Sci Am 278(3):46–53
60. Loscalzo J, Barabási A (2017) and Edwin K Silverman. Complex systems in human disease and therapeutics. Harvard University Press, Network Medicine
61. Lozano S, Arenas A, Sánchez A (2008) Mesoscopic structure conditions the emergence of cooperation on social networks. PLOS ONE 3(4):1–9
62. Lutz P, Kaufmann D, Stünzi A (2020) "Humanitarian protection as a European public good: the strategic role of states and refugees". JCMS: J Common Market Stud 58(3):757–775
63. Manlio De Domenico (2023) More is different in real-world multilayer networks. Nature Phys 19(9):1247–1262
64. Mark B, Erovenko Igor V, Jan R (2021) Modelling evolution in structured populations involving multiplayer interactions. Dyn Games Appl 11:270–293
65. Martin RB et al (1992) Optimal control of tumor size used to maximize survival time when cells are resistant to chemotherapy. Math Biosci 110(2):201–219
66. Masroni MSB et al (2023) Dynamic altruistic cooperation within breast tumors. Molecular Cancer 22(1):206
67. Masuda N (2009) Directionality of contact networks suppresses selection pressure in evolutionary dynamics. J Theor Biol 258(2):323–334
68. Matjaž Perc and Attila Szolnoki (2010) Coevolutionary games-a mini review. BioSystems 99(2):109–125
69. Maynard Smith J (1974) The theory of games and the evolution of animal conflicts. J Theor Biol 47(1):209–221
70. Maynard Smith J, Price GR (1973) The logic of animal conflict. Nature 246(5427):15–18
71. McNamara John M, Olof Leimar (2020) Game theory in biology: concepts and frontiers. Oxford University Press, USA
72. Milinski M et al (2006) Stabilizing the Earth's climate is not a losing game: supporting evidence from public goods experiments. Proce Natl Acad Sci 103(11):3994–3998
73. Myerson RB (1992) On the value of game theory in social science. Ration Soc 4(1):62–73
74. Nowak Martin A (2006) Five rules for the evolution of cooperation. Science 314(5805):1560–1563
75. Nowak MA, May RM (1992) Evolutionary games and spatial chaos. Nature 359(6398):826–829
76. Nowell PC (1976) The clonal evolution of tumor cell populations. Science 194(4260):23–28
77. Nunner H, van de Rijt A, Buskens V (2022) Prioritizing high-contact occupations raises effectiveness of vaccination campaigns. Sci Rep 12(1):737
78. Ohtsuki H et al (2006) A simple rule for the evolution of cooperation on graphs and social networks. Nature 441(7092):502–505
79. Ohtsuki H, Nowak MA, Pacheco JM (2007) Breaking the symmetry between interaction and replacement in evolutionary dynamics on graphs. Phys Rev Lett 98(10):108106
80. Ohtsuki H, Pacheco JM, Nowak MA (2007) Evolutionary graph theory: breaking the symmetry between interaction and replacement. J Theor Biol 246(4):681–694
81. Pacheco JM, Traulsen A, Nowak MA (2006) Coevolution of strategy and structure in complex networks with dynamical linking. Phys Rev Lett 97(25):258103
82. Peña J et al (2016) Evolutionary games of multiplayer cooperation on graphs. PLoS Comput Biol 12(8):e1005059
83. Perc M et al (2013) Evolutionary dynamics of group interactions on structured populations: a review. J Royal Soc Interface 10(80):20120997
84. Shai Pilosof et al (2017) The multilayer nature of ecological networks. Nature Ecol Evolut 1(4):0101
85. Piraveenan M et al (2021) Optimal governance and implementation of vaccination programmes to contain the COVID-19 pandemic. Royal Soc Open Sci 8(6):210429
86. Porco Travis C et al (2012) When does overuse of antibiotics become a tragedy of the commons? PLSO ONE 7(12):e46505
87. Richard D (2015) Branching process models of cancer. Springer International Publishing, Newyork, pp 1–63
88. Risa Tori and Jun Tanimoto (2022) A study on prosocial behavior of wearing a mask and self-quarantining to prevent the spread of diseases underpinned by evolutionary game theory. Chaos, Solitons Fract 158:112030
89. Roca CP, Cuesta JA, Sánchez A (2009) Evolutionary game theory: temporal and spatial effects beyond replicator dynamics. Phys Life Rev 6(4):208–249
90. Lynn Sagan (1967) On the origin of mitosing cells. J Theor Biol 14(3):225–274
91. Larry Samuelson (2016) Game theory in economics and beyond. J Econ Perspect 30(4):107–130
92. Santos FC, Pacheco JM (2005) Scale-free networks provide a unifying framework for the emergence of cooperation. Phys Rev Lett 95(9):098104

93. Santos FC, Pacheco JM, Lenaerts T (2006) Evolutionary dynamics of social dilemmas in structured heterogeneous populations. Proce Natl Acad Sci 103(9):3490–3494
94. Santos FC, Rodrigues JF, Pacheco JM (2006) Graph topology plays a determinant role in the evolution of cooperation. Proce Royal Soc B Biol Sci 273(1582):51–55
95. Santos FC, Santos MD, Pacheco Jorge M (2008) Social diversity promotes the emergence of cooperation in public goods games. Nature 454(7201):213–216
96. Santos MD, Dorogovtsev SN, Mendes JFF (2014) Biased imitation in coupled evolutionary games in interdependent networks. Sci Rep 4(1):4436
97. Karl Sigmund (2010) The calculus of selfishness. Princeton University Press
98. Sigmund K, Nowak MA (1999) Evolutionary game theory. Curr Biol 9(14):R503–R505
99. Soares CE, Denise L, Kleber D-C (2018) Protection mutualism: an overview of ant-plant interactions mediated by extrafloral nectaries. Oecol Aust. https://doi.org/10.4257/oeco.2018.2204.05
100. Soltanolkottabi M, Ben-Arieh D, Chih-Hang W (2020) Game theoretic modeling of infectious disease transmission with delayed emergence of symptoms. Games 11(2):20
101. Souza MO, Pacheco JM, Santos FC (2009) Evolution of cooperation under N-person snowdrift games. J Theor Biol 260(4):581–588
102. Stadler B, Dixon AFG (2005) Ecology and evolution of aphid-ant interactions. Ann Rev Ecol Evol Syst 36:345–372
103. Staňková K et al (2019) Optimizing cancer treatment using game theory: a review. JAMA Oncol 5(1):96–103
104. Stein A et al (2023) Stackelberg evolutionary game theory: how to manage evolving systems. Philos Royal Soc B 378(1876):20210495
105. Straffin PD Jr (1980) The prisoner's dilemma. UMAP J 1:101–103
106. György Szabó, Csaba Tőke (1998) Evolutionary prisoner's dilemma game on a square lattice. Phys Rev E 58(1):69
107. Tang C-L et al (2006) Effects of average degree on cooperation in networked evolutionary game. Eur Phys J B-Condensed Matter Complex Syst 53:411–415
108. Taylor PD, Jonker LB (1978) Evolutionary stable strategies and game dynamics. Math Biosci 40(1–2):145–156
109. Tomlinson Ian PM (1997) Game-theory models of interactions between tumour cells. Eur J Cancer 33(9):1495–1500
110. Traulsen A, Levin SA, Saad-Roy CM (2023) Individual costs and societal benefits of interventions during the COVID-19 pandemic. Proce Natl Acad Sci 120(24):e2303546120
111. Tucker AW, Straffin Jr Philip D (1983) The mathematics of Tucker: a sampler. Two-Year College Math J 14(3):228–232
112. Turajlic S et al (2019) Resolving genetic heterogeneity in cancer. Nature Rev Gene 20(7):404–416
113. Vega-Redondo Fernando (2007) Complex social networks. 44. Cambridge University Press
114. Vincent TL (1996) Modeling and managing the evolutionary component of biological systems. Ecol Model 92(2–3):145–153
115. Zhen Wang et al (2015) Evolutionary games on multilayer networks: a colloquium. Eur Phys J B 88:1–15
116. Wang X et al (2020) Vaccination behavior by coupling the epidemic spreading with the human decision under the game theory. Appl Math Comput 380:125232
117. Wang B, Chen X (2012) Wang L (2012) Probabilistic interconnection between interdependent networks promotes cooperation in the public goods game. J Stat Mech Theory Exp 11:P11017
118. Waser Nickolas M, Forrest Jessica RK (2014) "Pollination by animals". In: Encyclopedia of life sciences. John Wiley & Sons, Ltd
119. Dominik Wodarz, Natalia Komarova (2014) Dynamics of cancer: mathematical foundations of oncology. World Scientific
120. Wölfl B et al (2022) The contribution of evolutionary game theory to understanding and treating cancer. Dyn Games Appl 12(2):313–342
121. Xingru Chen and Feng Fu (2019) Imperfect vaccine and hysteresis. Proce Royal Soc B 286(1894):20182406
122. Yang Y et al (2019) Efficient vaccination strategies for epidemic control using network information. Epidemics 27:115–122
123. Yang G et al (2021) Strategically positioning cooperators can facilitate the contagion of cooperation. Sci Rep 11(1):1127
124. Yong JC, Choy BKC (2021) Noncompliance with safety guidelines as a free-riding strategy: an evolutionary game-theoretic approach to cooperation during the COVID-19 pandemic. Front Psychol 12:646892
125. Zhang J et al (2017) Integrating evolutionary dynamics into treatment of metastatic castrate-resistant prostate cancer. Nature Commun 8(1):1816

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Authors and Affiliations

Christo Morison[1] · **Małgorzata Fic**[2,3] · **Thomas Marcou**[4] · **Javad Mohamadichamgavi**[5] · **Javier Redondo Antón**[6] · **Golsa Sayyar**[7] · **Alexander Stein**[8] · **Frank Bastian**[9] · **Hana Krakovská**[10,11] · **Nandakishor Krishnan**[12,13] · **Diogo L. Pires**[14] · **Mohammadreza Satouri**[15] · **Frederik J. Thomsen**[16] · **Kausutua Tjikundi**[6,17] · **Wajid Ali**[18]

✉ Wajid Ali
wajid.ali@liverpool.ac.uk

1 School of Mathematical Sciences, Queen Mary University of London, London, UK

2 Department of Theoretical Biology, Max Planck Institute for Evolutionary Biology, Plön, Germany

3 Center for Computational and Theoretical Biology, University of Würzburg, Würzburg, Germany

4 Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic

5 Institute of Applied Mathematics and Mechanics, University of Warsaw, Warsaw, Poland

6 Department of Computer Science, University of Turin, Turin, Italy

7 Bolyai Institute, University of Szeged, Szeged, Hungary

8 Evolutionary Dynamics Group,Centre for Cancer Evolution, Barts Cancer Institute, Queen Mary University of London, London, UK

9 School of Mathematical Sciences, University College Cork, Cork, Ireland

10 Institute of the Science of Complex Systems, Center for Medical Data Science, Medical University of Vienna, Vienna, Austria

11 Complexity Science Hub Vienna, Vienna, Austria

12 Institute of Evolution, HUN-REN Centre for Ecological Research, Budapest, Hungary

13 Doctoral School of Biology, Institute of Biology, Eötvös Loránd Universit, Budapest, Hungary

14 Department of Mathematics, City, University of London, London, UK

15 Institute for Health Systems Science, Faculty of Technology, Policy and Management, Delft University of Technology, Delft, Netherlands

16 Institute of Applied Mathematics, Delft University of Technology, Delft, Netherlands

17 ISI Foundation, Turin, Italy

18 Department of Mathematical Sciences, University of Liverpool, Liverpool, UK