Understanding Structured Eco-Evolutionary Systems

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Contents

Abstract

Natural systems frequently exhibit structure in various forms, including temporal and spatial aspects like social connections, family ties, age distribution, and geographical arrangements. Incorporating these structural elements into modelling frameworks can provide valuable insights into the behaviour of natural systems. Evolutionary game theory models traditionally involve pairwise interactions between agents, but individuals often interact with numerous others. The quantity and nature of these interactions can differ across time and space. Integrating structure into game theoretical models can significantly alter the dynamics of such systems.

My PhD research incorporates complexities into the classical frameworks to expand and enrich our understanding of eco-evolutionary biological and social dynamics. In Chapter 2, I examine the disease evolution and spread in epidemiology and oncology in complex environments. The chapter reviews the use of evolutionary game theory in healthcare and posits possible knowledge transfer opportunities between the two fields. In Chapter 3, I consider how age structure can proxy for time delays in multiplayer games. The model introduced in the chapter illustrates the influence of time on interactions and provides a tool to analyse these effects. In Chapter 4, I study the impact of social networks on human interactions and the dissemination of trust and beliefs within small populations. Additionally, I analyse the effects of minorities and influential individuals on evolutionary dynamics in those populations. Lastly, in Appendix C, I show how geographical structures, such as varied dispersal paths between species, influence predator-prey dynamics. The conclusions presented in the Appendix point to the value of data-informed modelling and the importance of the effects of anthropomorphic changes on ecological systems.

Be it social, temporal or spatial, structure is ubiquitous in the world around us. In this thesis, I show the importance of structure in eco-evolutionary dynamics across scales of organisation. The models presented in this thesis vary in the level of generality, providing an overview of how structure can be introduced on all the levels of specificity. By introducing complexities into evolutionary game theoretical models, I aim to represent the real world more accurately, bringing the theoretical frameworks closer to the reality they portray.

Kurzfassung

Die Einbeziehung dieser strukturellen Elemente in Modellieransätze kann wertvolle Einblicke in das Verhalten natürlicher Systeme liefern. Evolutionäre spieltheoretische Modelle beinhalten traditionell paarweise Interaktionen zwischen den Akteuren, aber Individuen interagieren oft mit zahlreichen anderen. Umfang und Art dieser Interaktionen können sich zeitlich und räumlich unterscheiden. Die Integration von Struktur in spieltheoretische Modelle kann die Dynamik solcher Systeme erheblich verändern.

Im Rahmen meiner Doktorarbeit habe ich diese Komplexität in den klassischen Ansätzen integriert, um unser Verständnis von öko-evolutionären biologischen und sozialen Dynamiken zu erweitern und zu bereichern. In Kapitel 2 untersuche ich die Entwicklung und Verbreitung von Krankheiten in Epidemiologie und Onkologie in komplexen Umgebungen. Das Kapitel gibt einen Überblick über die Anwendung der evolutionären Spieltheorie im Gesundheitswesen und zeigt Möglichkeiten des Wissenstransfers zwischen den beiden Bereichen auf. In Kapitel 3 betrachte ich, wie die Altersstruktur stellvertretend für Zeitverzögerungen in Multiplayer-Spielen stehen kann. Das in diesem Kapitel vorgestellte Modell veranschaulicht den Einfluss der Zeit auf Interaktionen und bietet ein Instrument zur Analyse dieser Effekte. In Kapitel 4 untersuche ich die Auswirkungen sozialer Netzwerke auf menschliche Interaktionen und die Verbreitung von Vertrauen und Überzeugungen innerhalb kleiner Populationen. Außerdem analysiere ich die Auswirkungen von Minderheiten und einflussreichen Personen auf die evolutionäre Dynamik in diesen Populationen. In Anhang C zeige ich schießlich, wie geografische Strukturen, wie etwa unterschiedliche Ausbreitungswege zwischen den Arten, die Räuber-Beute-Dynamik beeinflussen. Die im Anhang dargestellten Schlussfolgerungen verdeutlichen den Wert datengestützter Modellierung und die Bedeutung der Auswirkungen anthropomorpher Veränderungen auf ökologische Systeme.

Ob sozial, zeitlich oder räumlich, Struktur ist in der Welt um uns herum allgegenwärtig. In dieser Arbeit zeige ich die Bedeutung von Struktur in öko-evolutionären Dynamiken über verschiedene Ebenen der Organisation hinweg. Die in dieser Arbeit vorgestellten Modelle variieren in ihrem Allgemeinheitsgrad und geben einen Überblick darüber, wie Struktur auf allen Ebenen der Spezifität eingeführt werden kann. Durch die Einführung von Komplexität in evolutionäre spieltheoretische Modelle möchte ich die reale Welt genauer darstellen und die theoretischen Modelle näher an die Realität bringen, die sie abbilden.

1

Introduction

From cells to human societies, natural systems are organised in various ways. Be it spatial positioning, social ties or temporal aspects, structures are ubiquitous. Incorporating those structures in the modelling frameworks allows us to capture more accurately the intricacies of the real world. In this thesis, I present various ways structure can be incorporated into evolutionary game theory models and discuss its impact on evolutionary dynamics. The thesis presents models of systems across the scales of organisation and with varying levels of generality. Hence, the versatility of the proposed approaches is highlighted. The following chapters discuss social, spatial, and age structures in detail. The analysis expands evolutionary game theoretical models by adding time delays and network structures.

Evolutionary Game Theory

Evolutionary game theory (EGT) is a powerful mathematical tool that can be used to explore dynamics of biological and social processes. First introduced in 1973 by Maynard Smith, it incorporates the notion of evolution into the economic framework of strategic interactions[1,2]. EGT abandons the concept of rational players deciding on actions. Instead, it treats strategies, or types, as inheritable traits, passed down from generation to generation according to the principles of Darwinian evolution[3]. Changes in the population composition are driven by natural selection and the ”survival of the fittest”[4]. Yet, selected for strategies may seem to contradict that notion, as the cooperative behaviours, where an individual favours the well being of the group over their own, emerge[5].

Evolution of cooperation, defined as incurring a cost to provide others with a benefit, is the central theme of EGT[6]. Nowak present 5 mechanisms for evolution of cooperation: kin selection, direct reciprocity, indirect reciprocity, network reciprocity and group selection[7]. Each of them can be viewed through the lens of an underlying structure: family ties, a network of favours, also including higher-order (indirect) connections, interaction graphs or networks of subpopulations.

Hence, introduction of structure is a natural way of expanding EGT models to correspond closer the complexity of real world.

As in the classical game theory, in the framework of EGT the fitness of an individual depends on their strategy and the strategy of their opponent (or opponents). In the simple case of two-player, two-strategy symmetric games, the game can be characterised by the following matrix:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \tag{1.1}$$

.

In the game two actions are possible: cooperate (C) and defect (D). The strategy of the focal player is represented by the rows (top row - C, bottom - D) and the columns indicate the action of the opponent (left - C, right - D). The game is symmetric, meaning that each of the players is characterised by the same payoff matrix[8].

The relationship between the four entries of the payoff matrix (1.1) can be used to characterized four game types[9]:

1. for $T > R$ and $P > S$ the games is known as the Prisoner's Dilemma (PD). In this game defection is always the best reply, regardless of the opponent's strategy[10–13];

2. for $T > R$ and $S > P$ the game becomes the Snowdrift Game (SG), also knows as the hawk - dove, chicken or anticoordination game. In this class of games the best reply to any strategy is to play the other one: cooperating when faced with a defector and defecting when faced with a cooperator[13,14];

3. for $R > T$ and $P > S$ the game is called the Stag Hunt (SH), also referred to as the trust game or the coordination game. The best reply in this type of games is to chose the same strategy as the opponent, with mutual cooperation being favoured[15];

4. for $R > S > P$ and $R > T > P$ the game, known as the Harmony Game, is not a cooperative dilemma, as cooperation is always the favoured strategy[16].

Two player games are a very convenient modelling device to represent pairwise interactions. However, many real-world relations include more than two individuals at the same time. To model those interactions multiplayer games can be used[17,18]. Each of the 2-player game classes can be translated into their respective N-player games[19]. The multiplayer PD is also knows as the Public

Goods Game (PGG)[20,21] and the N-player SG can be seen as the threshold PGG[22]. Both of those games are further explored in the Chapter 2. Similarly, the multiplayer SH game[23] is introduced and analysed in Chapter 4.

Introduction of structure in EGT models is shown to have a significant effect on the evolutionary dynamics. I particular, in this thesis, I focus on temporal, social and spatial organisation to highlight the importance of structure in the framework.

Time delays

Introduction of temporal characteristics, like time-scales[24] or age structure, into EGT models is a complex endeavour. Being associated with higher complexity of the models, the aspect of time is often omitted for the sake of simplicity and tractability of the model. Yet, time is an important element of any dynamic system[25]. In particular, in the context of EGT time is often introduced in the form of delays.

The effect of delays on game theoretical dynamics vary[26–28]. Introduction of delays can not only change the value of steady states of the systems, effectively modifying parameters of the underlying games, but also lead to a change in stability of existing equilibria or appearance of new ones. In those cases delays induce a change in the type of the game played, rendering conclusions made based on the original game inaccurate. Hence, consideration of temporal aspects of the modelled systems is crucial in its faithful representation in the modelling.

Delays in evolutionary games can be caused by different underlying processes. Alboszta and Miękisz specify two classes of delays: biological and social[29] . In the former, the delay is said to arise due to the time between an interaction between the parents and the consequent addition of a new individual in the population. In the latter class of delayed models the time discrepancy is caused by a delay in information transmission and processing[30]. The effects of strategy-dependent delays on game theoretical dynamics are especially interesting[31,32]. However, due to the complexity of the problem, the analysis proves to be challenging, as shown by Miękisz and Bodnar[33]. In order to overcome that challenge, Mohamadichamgav et al. present a small delay approximation model, which reduces the complexity of the system while providing a good intuition on effects of delays[34]. However, that model is limited by considering only "small" values of delays. To overcome that restriction, in Chapter 3 another approximation model of the biological delays is introduced and analysed.

Games on networks

Many EGT models consider well-mixed populations - that is, populations in which each pair of individuals is as likely to interact[35]. However, the real world is characterised by complex interactions patterns induced by social and spatial connections present[36]. In order to account for those patterns, network structures can be added in EGT models[37]. Commonly used networks include regular graphs like lattices[38] and rings, random networks[39] like scale-free[40] and small-world networks[41] as well as real-world networks[42]. In those models individuals interact only with their neighbours, rather than all other players in the populations[43]. Network structures are also a convenient way of introducing multiplayer games, played with all neighbours at the same time instead of one at a time[44,45]. Different underlying networks have varying effects on emergence and evolution of cooperation, from leading to emergence of chaos[46], inhibiting cooperation levels[47] to favouring it[48].

Certain properties of underlying network topologies are shown to influence the evolution of cooperation[49], including average degree[50] and degree distribution[51]. Well connected nodes of networks, or hubs, can also influence the emergence of cooperative behaviour[52–54], as well as strategic placement of cooperators on the graph[55]. The effects of these network properties are further discussed and analysed in Chapter 4.

Recently, multilayered networks have been used to incorporate additional complexities into modelling frameworks[56–58]. Multilayer networks, also known as networks of networks, consist of multiple layers (networks) connected with multilayer edges. This versatile construct can represent various aspects, including multiple types of individuals and interactions, temporal and spatial structures or communities[59]. In the context of EGT, multilayer networks are shown to impact evolutionary dynamics and promote cooperation significantly[60–69]. Appendix C presents a simple model of predator-prey dynamics, showcasing the impact of multilevel networks on modelling ecological processes.

Structure of the thesis

The main body of this thesis is divided in three chapters, spanning different scales of organization and levels of generality, examining the effects of structure on the evolution of cooperation. The structure of the thesis is presented in Figure 1.1 detailing the diversity of the contents on the two aforementioned axes.

First, in Chapter 2, a review of the importance of EGT, and specifically evolutionary Public Goods Games, in modelling disease evolution and spread is presented. The chapter provides a brief introduction to EGT models and games in spatially structured populations, before focusing on its use in mathematical epidemiology and oncology. The chapter does not present a specific system, but rather showcases the versatility of the framework, providing examples of EGT models in representing both human and cellular (cancer) behaviour. Moreover, the review draws parallels between the two domains, displaying possible areas in which the two could learn from one another.

Secondly, in Chapter 3, an approximation model of time delays in EGT is introduced. The derivation of the mathematical model is presented, as well as analytical and numerical results. The chapter provides a simple and mathematically tractable alternative to complex delayed differential equation models, maintaining qualitatively matching results. Presented results include analysis of the PD, SG and SH. The study showcases the importance of incorporating time aspects into EGT frameworks not only due to the changes in the dynamics of specific games but also notably because of the possibility of transitions between game classes.

Chapter 4 presents the most particular model in this thesis. The chapter presents a study of spread of narratives and their effect on emergence and stability of cooperation in socially structured populations engaging in a multiplayer SH game. The effects of network topology properties and targeted introduction of novel strategies on game dynamics are investigated. Furthermore, the power of minorities to influence populations is examined. Additionally, Appendix B contains the Supplementary Material, presenting more detailed analysis of impact of network size and clustering coefficient as well as game properties on evolutionary dynamics.

Lastly, Appendix C contains preliminary results of a multilevel network model of predator-prey dynamics. The model considers two species of predator-prey dynamics with dispersal, in which a different dispersal network characterizes each species. The conclusions drawn from a three-patch system suggest the importance of species-specific dispersal on the ecological dynamics, leading to significant changes in the system's oscillatory behaviour.

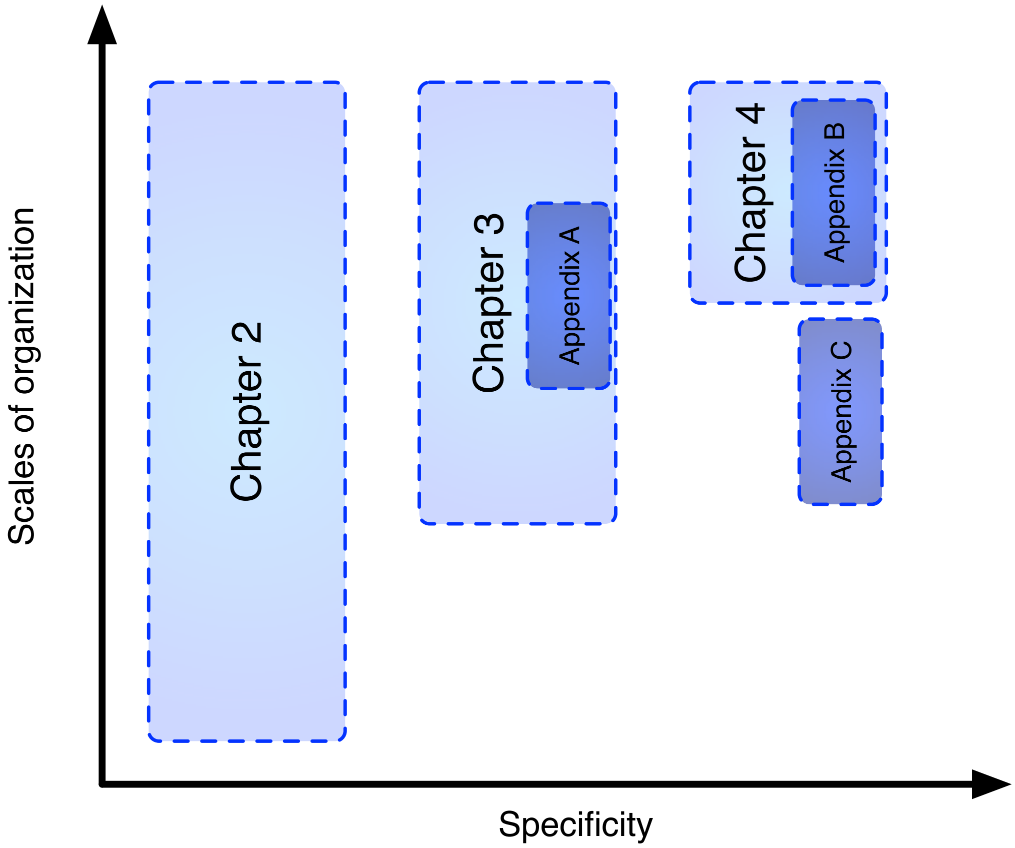

Figure 1.1: The three main chapters of the thesis span different scales of organization and levels of generality. Chapter 2 does not present a specific model but a general review of literature on Public Goods Games in modelling disease spread and evolution. The games considered in the chapter are played by cells of the body, viruses and other pathogens, as well as people in modern societies. Then, Chapter 3 introduces an approximation model of time delays in 2-player, 2-strategy evolutionary games, particularly PD, SG and SH. Following the biological-type delays, the approach can be applied to model reproduction in many systems, from animals to humans. Lastly, in Chapter 4 a model of spread of narratives in structured populations is presented. The chapter focuses on a specific game (multiplayer SH) and an effect of beliefs, a concept unique to humans. The model is further explored in the Appendix B. Additionally, in Appendix C, a predator-prey model in a patchy environment is presented, with species-specific dispersal networks. The analysis is focused on a particular 3-patch example in order to highlight the possible effects of species-specific dispersal on the ecological dynamics.

2

Public Goods Games in Disease Evolution and Spread

The following chapter has been publish as a preprint on *Zenodo* and has been submitted to *Dynamic Games and Applications*.
C. Morison*, **M. Fic***, T. Marcou, J. Mohamadichamgavi, J. Redondo Antón, G. Sayyar, A. Stein, F. Bastian, H. Krakovská, N. Krishnan, D. Pires, M. R. Satouri, F. J. Thomsen, K. Tjikundi, and W. Ali "Public goods games in disease evolution and spread", 2024

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Abstract

Cooperation arises in nature at every scale, from within cells to entire ecosystems. In the framework of evolutionary game theory, public goods games (PGGs) are used to analyse scenarios where individuals can cooperate or defect, and can predict when and how these behaviours emerge. However, too few examples motivate the transferal of knowledge from one application of PGGs to another. Here, we focus on PGGs arising in 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 and compare. 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: evolutionary game theory | public goods game | cancer | epidemics

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. Evolutionary game theory (EGT) inspects interactions within a population, translating the payoffs of game theory into evolutionary fitness[1]. In this framework, players are not overtly rational, and strategies (types) are inherited according to principles of Darwinian evolution rather than rationally chosen. Consequently, natural selection leads to changes in the frequency of strategies depending on their relative fitness[4]. Some of these strategies, at first glance, seem to contradict Darwinian selection: for instance, the emergence of behaviours favouring the group over the individual[5].

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[70]) or reproductive services (e.g., pollination[71] or seed dispersal[72]), often in exchange for resources like food or nutrients[73]. It can also be found at the microscale: for instance, eukaryotes evolved from primitive unicellular organisms (including the predecessors to mitochondria), once capable of independent existence, via a cooperative process called endosymbiosis[74]. 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[7], 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, which they then benefit from, regardless of whether they contributed or not[75]. 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[10,11] and used to study cooperation for decades[12]. 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[76,77], agent-based models[78,79], or stochastic processes[80,81], whereas including social structure involves borrowing tools from network science[82]. 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[83]. On the other hand, cells that evolve to be cancerous are both defecting from the healthy population[84] and cooperating with one another in support of the new entity called the tumour[85], whose cells are sometimes even considered a distinct species[86]. In reviewing these two areas, we will discuss the appearance of PGGs and discuss some ways in which each domain may be able to inform the other.

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[21]. In this game, we consider a group of N players, each endowed with a resource c, which they can invest in a public pool (a strategy called Cooperate) or not (a strategy called Defect). 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 Figure 2.1a). If n_c players cooperate, the payoff of a defector is $P_d = rcn_c/N$, and that of a cooperator is $P_c = P_d - c$, since the cooperators incur the additional cost of investing in the public good[87]. 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). Nevertheless, though there are incentives for players to invest for the benefit of the group, there also exist incentives to free ride off others' contributions[21,88] (see Figure 2.1b). A rise in the frequency of defectors may lead to a phenomenon commonly referred to as the "tragedy of the commons", where selfish behaviour leads to a depletion of the common good[89]. 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[90]). 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 Figure 2.1a), the player cannot always refrain from using the good (for example, because of needing sustain oneself); this creates a tension between balancing current and future consumption.

When $N = 2$, the PGG can be formulated as the PD[12,91]. Similarly to the multiplayer game, cooperation involves costs 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 in Table 2.1.

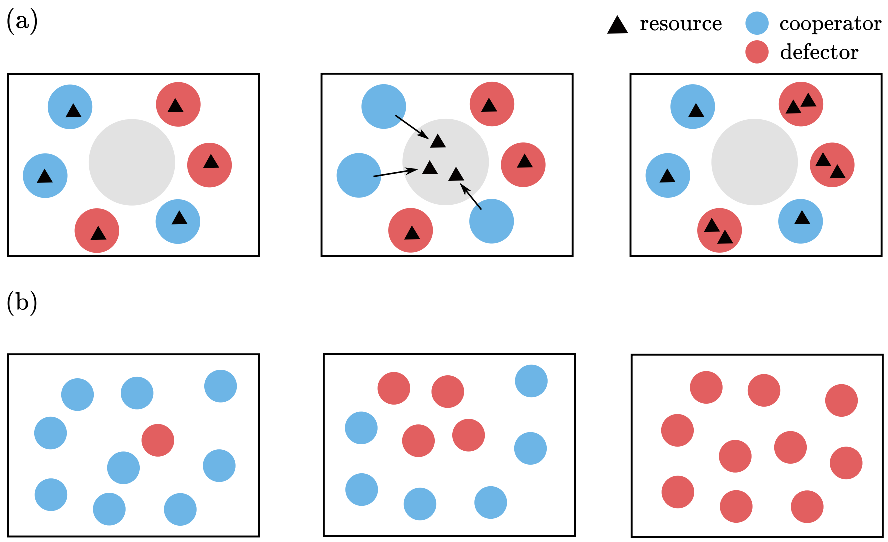

Figure 2.1: **(a)** In public good games, individuals are presented with a choice to either contribute an amount c to a common pot (Cooperate) or not (Defect). All contributions are then multiplied by a factor r (in the example depicted, $r = 2$) and shared equally amongst all players, regardless of 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[7]. (This figure was created with Inkscape 1.1.2, `https://inkscape.org/release/inkscape-1.1/?latest=1`.)

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

Table 2.1: The matrix representing the payoffs received by Player 1 with respect to its strategies and the strategies of Player 2 in the Prisoner's Dilemma.

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[22].

Historically, the emergence of cooperation was examined with well-mixed population models that assume all-to-all interactions[35], with evolutionary dynamics most commonly described by the replicator equation, wherein strategies providing higher payoffs increase in frequency[92] (as in Figure 2.1b). Nevertheless, these models fail to capture the complexity of real-life interactions[36]. Introducing networks into the framework of EGT allows for the inclusion of some of those complexities, like spatial and temporal structure or social relations. Individuals are then represented as nodes and interactions as edges. Players interact locally with their neighbours, either with one at a time, in two-player games, or with all neighbours simultaneously, in N-player games.

Strategies are updated according to a specified rule, which typically involves choosing an individual to replicate and a neighbour to die (or vice versa), with selection acting on one of the two events[93]. Successful strategies then spread, and depending on the update rule, different dynamics can be witnessed: for example, Ohtsuki *et al.* observed that cooperation was favoured when selection acted on the second event, unlike when it acted on the first[94].

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[93]. Successful strategies then spread, and depending on the update rule, different evolutionary outcomes may be achieved: for example, Ohtsuki *et al.* observed that network reciprocity alone allowed cooperation to evolve when selection acted on the second event, unlike when it acted on the first[94].

By studying various network structures, it has been shown that the interaction topology impacts strategy evolution[49]. For example, the spread of cooperation in the PD varies across lattice[38,46], small-world[95], regular[48], and real-world networks[42]. The impact of other topological aspects of networks on cooperation has been studied: some examples include the average degree of the network[50], the degree distribution heterogeneity[96], the presence of hubs on scale-free networks[53], as well as the strategic placement of cooperators[55]. 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[97,98], as well as on regular graphs and heterogeneous scale-free networks[44,99].

Additionally, multilayer networks can represent multiple types of interactions and individuals, add temporal and spatial context or depict communities[58,59]. They are shown to have a significant impact on the evolutionary dynamics and can promote the evolution of cooperation in the PD[60,65], multiplayer PGGs[61] and when several games are present[62,66].

EGT's strength 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[100], or the international refugee crisis, wherein governments must navigate providing for citizens versus people seeking shelter and balancing domestic resources with human rights ideals[101]. In light of these examples, it is evident that defection is not inherently morally wrong or selfish in the context of evolutionary PGGs. Instead, EGT 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.

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[102] and cancer[103,104]. Spurred by the recent COVID-19 pandemic and high incidence rates of cancer worldwide, they have been used even more widely in these areas. Here, we focus on the appearance of PGGs in both contexts by reviewing the literature and suggesting ways the two fields may learn from one another.

Epidemics

Epidemiology is the study of the distribution and determinants of health-related events in populations[105]. 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[106] 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[102]. Since then, 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 2.2. Importantly, social interactions can be incorporated in each case by adding structure to the populations.

Herd immunity is established within a population when a sufficiently large fraction has undergone immunisation, either naturally or via vaccination, ensuring

Public good	Cooperate	Defect
Herd immunity (e.g.[107])	Immunisation	Susceptibility
Pathogen-free environment (e.g.[108])	Following non-pharmaceutical interventions, such as mask mandates or social distancing	Not following non-pharmaceutical interventions
Sensitivity to antibiotics (e.g.[109])	Not overusing antibiotics	Overusing antibiotics

Table 2.2: Examples of public goods found in epidemiological modelling, with corresponding cooperating and defecting strategies.

that the disease cannot persist as an endemic condition[77]. 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[107]. Through this lens, immune individuals are cooperators, and those susceptible are defectors. If enough of the population is immune—that is, if n_c/N is greater than some threshold, typically around 90%, depending on the disease[107]—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 Figure 2.2a), and the vaccination game with herd immunity can be seen as a threshold PGG[110]. The game can be introduced into classical SIR-type models to better understand individual behaviour in the face of voluntary vaccination[83]. These models can be further enriched by introducing an incubation period between infection and symptom onset. Soltanolkottabi *et al.* (2020) show 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[111]. The model also includes a community structure wherein individuals get vaccinated when their (vaccinated) neighbours obtain a higher payoff. Fu *et al.* (2011) relax that assumption, introducing uncertainty into the decision to vaccinate. The model showcases social structure's ability to either promote voluntary vaccinations or facilitate disease spread[112]. Wang *et al.* (2020) further investigate the motivation behind vaccination decisions. Two reasons are considered for getting vaccinated: conforming and increasing one's payoff. A multilayer network approach then decouples the epidemic dynamics from the vaccination behaviour and captures the multi-levelled nature of human interactions[113]. These results display the importance 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[114,115] and quarantining[116]. Here, rather than

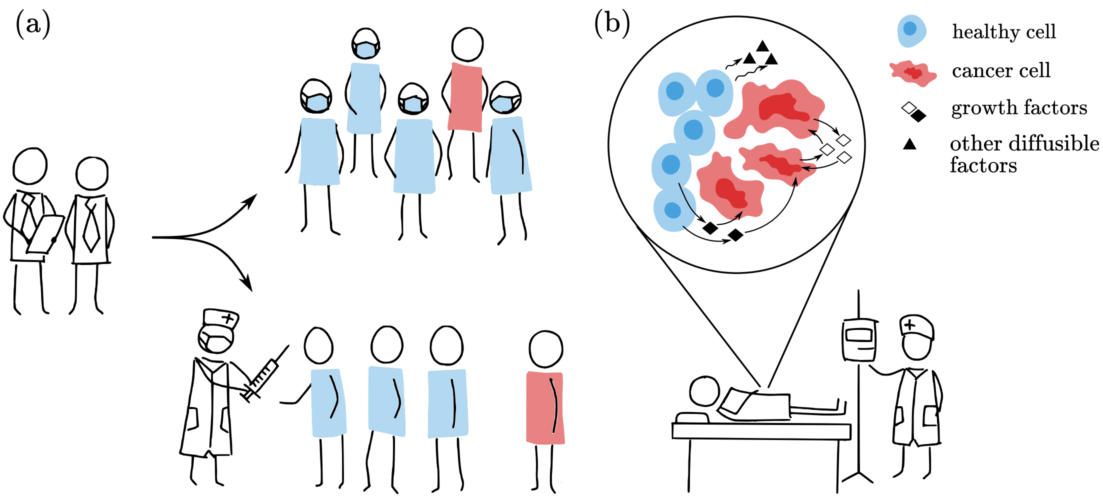

Figure 2.2: **(a)** During an epidemic, policy-makers are faced with implementing intervention policies aiming at disease containment and eradication. These approaches include vaccines as well as non-pharmaceutical interventions such as mask mandates, lockdowns, etc. PGG models can inform policy-makers by providing insights into how both infectious disease and individual behaviours evolve in the population. Here, defecting individuals are shown in red and cooperating individuals in blue. **(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 can 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`.)

herd immunity, the pathogen-free environment can be seen as a public good, which is depleted when individuals do not comply with interventions[108]. For example, Traulsen *et al.* (2023) highlight the importance of individual preference in designing intervention campaigns, including mask mandates, social distancing and vaccinations[117]. Hence, 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[118].

Although the 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[109]. From the point of view of a doctor, it is always better to treat their patient with antibiotics, even when the diagnosis is uncertain. However, drug overuse accelerates the evolution of resistance, leading to the tragedy of the commons[109]. Thus, PGGs can model the use of antibiotics and provide insight into possible strategies to avoid antibiotic overuse and resistance evolution[119].

Cancer

Cancers are evolutionary diseases initiated in a process termed carcinogenesis, in which normal cells transform into malignant tumour cells[120]. EGT models have been used to study interactions occurring during disease progression and treatment at different scales: between cancer cells and cancer cells[121], cancer cells with the tumour microenvironment[122], and cancer cells with the physician[123]. In particular, frequency-dependent modelling in oncology began with tools from optimal control[124] before being formalised as EGT[103,104]. One of its most significant applications has been modelling the emergence of resistance to treatment[85,125]. In particular, PGGs have been used to study the evolution of cooperation in cancer, both from the perspective of cancer cells defecting from the healthy population as well as cooperation amongst the cancer cells themselves[126], as depicted in Table 2.3.

Public good	Cooperate	Defect
Growth factors (e.g.[127])	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.[128])	Producing diffusible factors	Not producing
Adhesion (e.g.[126])	Producing adhesion molecules	Not producing

Table 2.3: Examples of public goods found in cancer modelling, with corresponding cooperating and defecting cell types.

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”[84]. On the other hand, an established tumour can also be modelled as a collection of cooperating subpopulations[129]. Many cancer processes rely on the production of diffusible factors by the cancer cells to promote growth[130] (see Figure 2.2b). 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[131]. For example, Archetti *et al.* (2015) modelled insulin-like growth factor II (IGF-II) as a public good amongst pancreatic cancer cells in mice. This led to coexistence between cooperators (producers of IGF-II) and defectors (non-producers), whose bistability was predicted by PGG dynamics[127].

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[132] can be considered public goods. Axelrod *et al.* (2006) argue 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[130]—involve shareable resources[128]. Threshold PGGs can also model direct contact between cells and their neighbours. Here, the public good (adhesion between cells) is provided so long as a minimum number of cells contribute adhesion molecules[126].

Moreover, Archetti (2021) has proposed leveraging cooperation amongst cancer cells to improve treatment. 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[133]. Hence, PGGs could join other evolutionary concepts in mathematical oncology that have led to novel treatment strategies such as adaptive[134], double-bind[135] and extinction therapies[136].

Discussion

Mathematical models in epidemiology and oncology can inform public health officials and clinicians in their quest to manage and eradicate infectious diseases and cancers. EG The evolution of tumours and the spread of pathogens have been studied with PGGs; however, their uses have been fairly disjoint. Here, we outline some opportunities for future avenues of research.

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[137]; likewise, antibiotic resistance threatens one's ability to eliminate pathogenic bacteria[138]. Just as sensitivity to antibiotics is a public good to a population of (possibly infected) individuals (see Table 2.2), 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. On the other hand, it has been shown that bacteria resistant to antibiotics can help shield their sensitive counterparts, increasing the survival capability of the whole population[139]. With these parallels in mind, recall Archetti's engineered defector cells and their role in collapsing intratumour cooperation[133]. 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 doesn't produce a certain metabolite[140], thus defecting in the PGG though not evolving antibiotic resistance.

Introducing network structure in EGT models allows for more accurate representations of real-world dynamics[37]. For instance, knowledge of the underlying social network during an epidemic can help identify the most influential individuals to vaccinate[141]. However, during dynamical processes—such as the evolution and spread of diseases—these structures are rarely static[142] and often co-evolve with the strategies[143] or even independently[144]. Another class of spatial models considers individuals moving through networks, allowing for the inclusion of complex, ever-changing social interaction patterns[145]. 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 (as reviewed in[85]) and could also benefit from dynamical networks.

Another recent addition to EGT that shows promise to improve treatment modelling are Stackelberg games, which can describe the leader-follower dynamics between a clinician and a tumour. Here, the cancer cells are themselves also playing an evolutionary game, which allows the clinician to apply evolutionarily-informed treatments by anticipating the evolution of the disease[146]. 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. For example, targeting vaccinations can be optimised in pursuit of the public good of herd immunity[147]. 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.

3

Kindergarten Model: Approximating Time Delays in Evolutionary Games

The following chapter is in preparation for submission to *Journal of Theoretical Biology.*

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Abstract

Real-world processes often exhibit temporal separation between actions and reactions - a characteristic frequently ignored in many modelling frameworks. Adding temporal aspects, like time delays, introduces a higher complexity of problems and leads to models that are challenging to analyse and computationally expensive to solve. In this work, we propose an intermediate solution to resolve the issue in the framework of evolutionary game theory. Our compartment-based approximation model includes time delays while remaining relatively simple and straightforward to analyse. We show that the approximation yields qualitatively comparable results with models incorporating explicit delays. Particularly, we focus on the case of delays between parents' interaction and an offspring joining the population, with the magnitude of the delay depending on the parents' strategy. We analyse the stag-hunt game, the snowdrift game and the prisoner's dilemma and show that strategy-dependent delays are detrimental to affected strategies. Additionally, we present how including delays may change the effective games played in the population, subsequently emphasising the importance of considering the studied systems' temporal aspects to model them accurately.

Keywords: evolutionary game theory | time delays

Introduction

Evolutionary game theory provides a robust framework for modelling many biological and social interactions[148]. Traditional models largely exclude time delays, instead assuming that the actions of an individual are instantaneous and their impacts on fitness are immediate. However, real-world processes frequently exhibit temporal separation between actions and their effects across scales of biological organisation. Sporulation, the response to nutrient deprivation observed in bacteria like *Bacillus subtilis*, takes about 8 to 10 hours to be completed after being triggered[149]. A seed bank in weeds leads to the sprouting of plants even years after the seed has been produced[150]. In the animal kingdom, the delays are also abundant. In the case of marine midges *Clunio marinus*, the time between reproduction and emergence is strictly correlated with the lunar cycle and takes from about 15 or 30 days, as compared to their relatively short adult lives of 2 hours[151]. Similarly, pregnancy and nurturing are temporally disconnected actions that culminate in adding a new, mature individual to the population[152]. Social systems, too, display such delays, evident in long-term financial investments or latency in information transmission and processing[153,154]. Thus, incorporating temporal factors could refine evolutionary game theoretical models, capturing realistic dynamics more accurately.

The effects of time delays on replicator dynamics were discussed at length in the literature[26–29,31,33,155–162]. In[155], the authors introduced a social-type model in which individuals at time t imitate a strategy with a higher average payoff at time $t-\tau$ for some time delay τ. They showed that the interior stationary state of the resulting time-delayed differential equation is locally asymptotically stable for small time delays. In contrast, it becomes unstable for big ones, and oscillations appear. In[29], a biological type model was constructed in which individuals are born τ units of time after their parents played. This type of delay leads to a system of equations of strategy's frequency and population size. The authors showed the absence of oscillations — the original stationary point is globally asymptotically stable for any time delay. Recently, models with strategy-dependent time delays were introduced[31,33,158,161,162].

In[33,162], the authors discussed the biological-type model of[155] with strategy-dependent time delays. They reported a novel behaviour, showing that stationary states depend continuously on time delays. Moreover, at specific time delays, an interior stationary state may disappear, or another interior stationary state may appear. The equation for the stationary state of frequencies of strategies was derived and solved numerically in[33] for stag-hunt, snowdrift and prisoner's dilemma games. In[163], a small-time delay approximation was proposed. The authors derived an explicit formula for the stationary state, which approximates well the exact results of[33].

Here, we introduce a model that shares the analytical tractability of[163] without assuming small delays. We extend the approach of Miękisz and Bodnar[33] and derive a system of ordinary differential equations that is easier to analyse through either closed-form solutions of stationary states or existing bifurcation software. In the model, time delays are represented by rates at which an offspring grows and can participate in games. More precisely, in our Kindergarten model, a newly born offspring is located in an inactive compartment. Then, with some strategy-dependent intensity, juveniles become players and move to an active compartment (this is reminiscent of models of delayed protein degradation in gene expression present in[164]). This approach allows us to derive explicit analytical formulas for stationary states of the strategies. Our results quantitatively agree with those in[33]. Notably, our model can be extended to multi-player and multi-strategy games.

In Section 3, we recall the model of Miękisz and Bodnar[33] and present our approach to model time delays. Results are described in Section 3, and Conclusions follow in Section 3.

Materials and Methods

Model with explicit time delays

We begin by reintroducing the delay model constructed by Miękisz and Bodnar[33].

We will consider two-player symmetric games with two strategies: cooperation (C) and defection (D) given by the following payoff matrix:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}, \tag{3.1}$$

where the $i\ j$ entry is the payoff of the first (row) player when it plays the strategy i and the second (column) player plays the strategy j, with $i, j \in \{C, D\}$. We assume that both players are the same, and hence, payoffs of the column player are given by the matrix transposed to (3.1); such games are called symmetric.

Now we follow[33] closely.

Let us assume that during a time interval of length ϵ, only an ϵ-fraction of the population takes part in pairwise competitions, that is, plays games. Let $p_i(t)$ with $i \in \{C, D\}$, be the number of individuals playing at time t the strategy C and D, respectively. Then $p(t) = p_C(t) + p_D(t)$ is the total number of players and $x(t) = \frac{p_C(t)}{p(t)}$ is the fraction of the population playing C.

The expected payoffs of an individual is given by

$$U_C(t) = Rx(t) + S(1 - x(t)), \tag{3.2}$$

and

$$U_D(t) = Tx(t) + P(1 - x(t)), \tag{3.3}$$

for cooperators and defectors, respectively.

Now we consider that individuals are born some time units after their parents played. We assume that time delays depend on strategies and are equal to τ_C and τ_D respectively.

Miękisz and Bodnar[33] proposed that the growth of the population playing a particular strategy is given as

$$p_i(t + \epsilon) = (1 - \epsilon)p_i(t) + \epsilon p_i(t - \tau_i)U_i(t - \tau_i); i = C, D. \tag{3.4}$$

and derive a system of coupled delayed differential equations for the fraction using the first strategy $x(t)$ and the population size $p(t)$,

$$\begin{aligned}\frac{dx(t)}{dt} =& \frac{x(t - \tau_C)p(t - \tau_C)U_C(t - \tau_C)(1 - x(t)))}{p(t)} \\ &- \frac{(1 - x(t - \tau_D))p(t - \tau_D)U_D(t - \tau_D)x(t)}{p(t)},\end{aligned} \tag{3.5}$$

$$\frac{dp(t)}{dt} = -p(t) + (p_C(t - \tau_C)U_C(t - \tau_C)) + p_D(t - \tau_D)U_D(t - \tau_D) \tag{3.6}$$

Then, the authors provided an equation for the stationary state of x and solved it numerically for various games.

Here, we propose another type of model to deal with time delays. We do not have to track the population's size, and we are able to derive analytical formulas for the frequency of strategies in stationary states. This provides more insight into the dynamics of more complex games and can easily be expanded to multi-player, multi-strategy games.

We will compare our results with those presented in[33] to check for the robustness and accuracy of our approximation.

Kindergarten model

Here, we construct a model where time delays are represented by the inverse of rates at which an offspring grows and can participate in games. More precisely, in our Kindergarten model, newly created offspring are located in inactive compartments. Then, with some strategy-dependent rates, they become players and move to the active compartment.

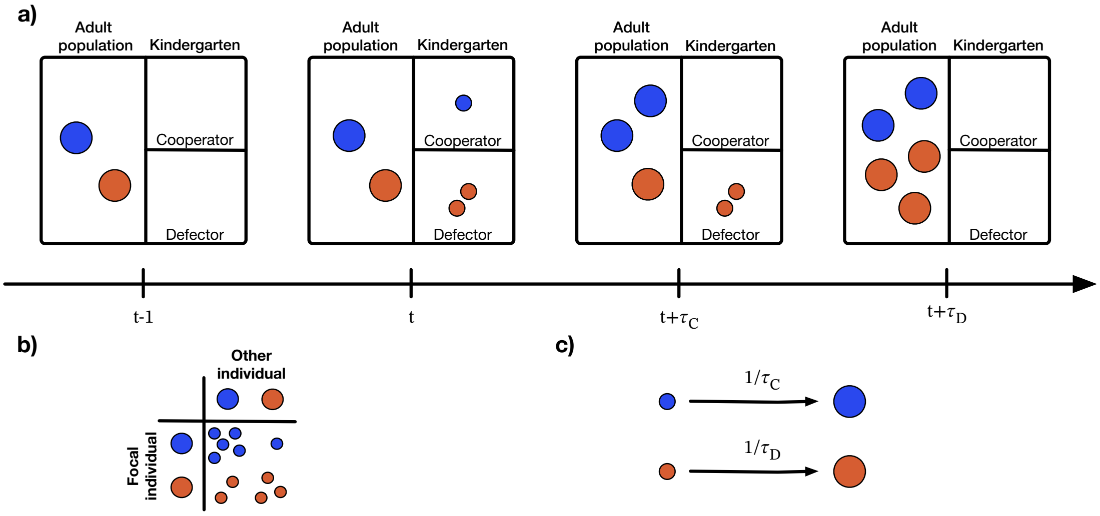

Figure 3.1: **a)** Individuals in the adult population interact with one another and receive payoff (offspring) based on those interactions. Offspring created at time t join the strategy-specific kindergarten. After an offspring matures, it joins the adult population and can reproduce. **b)** The payoff matrix indicates the expected number of offspring created in each interaction. **c)** Maturation rate depends on the parent's strategy and equals $1/\tau_C$ and $1/\tau_D$ for cooperators and defectors, respectively.

Let us denote by k_i kindergartens for offspring which inherited the i-th strategy with $i \in \{C, D\}$. Juveniles leave the kindergarten to join the adult population at a specific strategy-dependent rate.

The size of the kindergarten for the strategy i at time $t+\epsilon$ is given by

$$k_i(t+\epsilon) = \left(1 - \frac{\epsilon}{\tau_i}\right) k_i(t) + \epsilon p_i(t) U_i(t) \tag{3.7}$$

Then for the number of adult individuals playing i at a time $t+\epsilon$ we have,

$$p_i(t+\epsilon) = (1-\epsilon) p_i(t) + \frac{\epsilon}{\tau_i} k_i(t) \tag{3.8}$$

Let $y_i(t) = k_i(t)/p(t)$ for $i \in \{C, D\}$ denote sizes of kindergarten compartments relative to the size of the adult population.

Now, in the standard and straightforward way, one can derive differential equations from the above difference equations and get

$$\begin{aligned}
\frac{dx(t)}{dt} &= \frac{y_C(t)(1-x(t))}{\tau_C} - \frac{y_D(t)x(t)}{\tau_D} \\
\frac{dy_C(t)}{dt} &= y_C\left(\frac{\tau_C - 1}{\tau_C} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D}\right) + x(t)U_C(t) \\
\frac{dy_D(t)}{dt} &= y_D\left(\frac{\tau_D - 1}{\tau_D} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D}\right) + (1-x(t))U_D(t)
\end{aligned} \tag{3.9}$$

Similarly, we can obtain the differential equation for the change in population size, given by:

$$\frac{dp(t)}{dt} = p(t)\left(\frac{y_C(t)}{\tau_C} + \frac{y_D(t)}{\tau_D} - 1\right). \tag{3.10}$$

Hence, the size of the population in a stationary state is given by $p(t) = p(0)e^{(y^*_C/\tau_C + y^*_D/\tau_D - 1)t}$ implying the population grow exponentially if

$$\rho(\tau_C, \tau_D) = \frac{y^*_C(t)}{\tau_C} + \frac{y^*_D(t)}{\tau_D} > 1, \tag{3.11}$$

or goes extinct otherwise. Hence, condition (3.11) has to be met for the population not to go extinct.

We should take care of cases of one delay equal to zero separately.

For $\tau_C = 0$ there is no cooperator kindergarten ($y_C = 0$) and the system (3.9) becomes:

$$\begin{aligned}
\frac{dx(t)}{dt} &= x(t)\left(U_C(t)(1 - x(t)) - \frac{y_D(t)}{\tau_D}\right)\\
\frac{dy_C(t)}{dt} &= 0\\
\frac{dy_D(t)}{dt} &= y_D\left(\frac{\tau_D - 1}{\tau_D} - x(t)U_C(t) - \frac{y_D(t)}{\tau_D}\right) + (1 - x(t))U_D(t)
\end{aligned} \tag{3.12}$$

Analogously, for $\tau_D = 0$ the defector kindergarten compartment is empty ($y_D = 0$) and the system (3.9) becomes:

$$\begin{aligned}
\frac{dx(t)}{dt} &= \frac{y_C(t)}{\tau_C} - x(t)\left((1 - x(t))U_D(t) + \frac{y_C(t)}{\tau_C}\right)\\
\frac{dy_C(t)}{dt} &= y_C\left(\frac{\tau_C - 1}{\tau_C} - (1 - x(t))U_D(t) - \frac{y_C(t)}{\tau_C}\right) + x(t)U_C(t)\\
\frac{dy_D(t)}{dt} &= 0
\end{aligned} \tag{3.13}$$

The system of equations (3.9) has two trivial stationary states, $x = 1, 0$, of full cooperation and full defection, and two possible internal stationary states whose existence depends on the game parameters and delays.

Let us notice that for strategy-independent delays, i.e. $\tau_C = \tau_D$, equations simplify greatly, and the system has only one possible internal stationary state: $x = (P - S)\,/\,(R - T + P - S)$ equal to the one for replicator dynamics without time delays.

In the following, we study Eqs. (3.9) through the lenses of dynamical systems and bifurcation theory. That is, we investigate stationary states of Eqs. (3.9) by setting $f(x, y_C, y_D) = 0$ and perform a linear stability analysis of the stationary states[165]. These might be given in a closed form for special payoff matrices, allowing us to analyse the change in x depending on the delay values and payoff matrix entries. In the case of a general payoff matrix, the stationary states are obtained through numerical continuation done by the Julia package BifurcationKit[166]. In particular, we consider three specific games - the stag hunt, snowdrift and the prisoner's dilemma game and compare them with results presented in[33].

Results

Stag hunt game

In the stag hunt game, two individuals decide between cooperating and hunting a stag together (C) or pursuing a hare independently (D). Hunting a hare does not require help from the other individual and results in a specific payoff b; however, a stag provides a higher payoff value a[15]. The following payoff matrix characterises the stag hunt game:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R = a & S = 0 \\ T = b & P = b \end{pmatrix} \end{array} \tag{3.14}$$

where $a > b > 0$. In the case of no delays, i.e. $\tau_D = \tau_C = 0$, Eq. (3.9) collapses to a well-studied replicator equation with two stable equilibria: $x_0 = 0$ and $x_1 = 1$ and an unstable equilibrium at $x_2 = b/a$.

For the stag hunt game, the system (3.9) becomes:

$$\begin{aligned} \frac{dx(t)}{dt} &= \frac{y_C(t)(1 - x(t))}{\tau_C} - \frac{y_D(t)x(t)}{\tau_D} \\ \frac{dy_C(t)}{dt} &= y_C \left(\frac{\tau_C - 1}{\tau_C} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D} \right) + ax^2(t) \\ \frac{dy_D(t)}{dt} &= y_D \left(\frac{\tau_D - 1}{\tau_D} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D} \right) + b(1 - x(t)) \end{aligned} \tag{3.15}$$

The system (3.15) is characterised by three possible equilibria in the interval $[0, 1]$. The full defection equilibrium $x_0 = 0$ becomes

$$e_0 = \left(0, 0, \frac{1}{2} \left(\tau_D - 1 + \sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1} \right) \right). \tag{3.16}$$

For the condition (3.11) to be met and the population in this equilibrium to grow exponentially, the following needs to be true:

$$\frac{1}{2\tau_D} \left(\tau_D - 1 + \sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1} \right) > 1. \tag{3.17}$$

For that to be true, an additional condition needs to hold: $b \geq 1$.

The full cooperation equilibrium x_1 becomes

$$e_1 = \left(1, \frac{1}{2}\left(+\tau_C - 1 + \sqrt{4a\tau_C + \tau_C^2 - 2\tau_C + 1}\right), 0\right). \tag{3.18}$$

Again, we check the condition (3.11), which in this equilibrium becomes:

$$\frac{1}{2\tau_C}\left(\tau_C - 1 + \sqrt{4a\tau_C + \tau_C^2 - 2\tau_C + 1}\right) > 1. \tag{3.19}$$

For the condition to held, we need an additional constraint: $a \geq 1$.

Lastly, the internal equilibrium x_2 takes the following form:

$$e_2 = \left(x_2^*, -\frac{\tau_C x_2^* y_D^*}{\tau_D(x_2^* - 1)}, y_D^*\right) \tag{3.20}$$

where

$$x_2^* = \frac{\tau_C + (\tau_D - \tau_C)\sqrt{(4b-2)\tau_D + \tau_D^2 + 1}}{2a\tau_D^2} + \frac{2b\tau_C - \tau_C + \tau_D - 1}{2a\tau_D}, \tag{3.21}$$

$$y_D^* = -\frac{(x-1)\tau_D\left(\tau_C - 1 + \sqrt{(4ax-2)\tau_C + \tau_C^2 + 1}\right)}{2\tau_C}. \tag{3.22}$$

For the condition (3.11) to be met in e_2, that is for

$$-\frac{\tau_C x_2^* y_D^*}{\tau_D \tau_C (x_2^* - 1)} + \frac{y_D^*}{\tau_D} > 1 \tag{3.23}$$

to hold true, we need $x_2^* \geq 1/a$.

For the population to grow exponentially in all the equilibria, an additional constraint on the game parameter needs to be introduced: $b > 1$. Moreover, the value of the internal equilibrium x_2^* cannot fall below $1/a$.

Homogeneous equilibria. We conduct stability analysis of e_0 and show that it is always a stable equilibrium. The equilibrium e_1 is stable unless the following condition is met: $\tau_C \geq m$ where $m = \frac{(b-1)b\sqrt{\frac{(a-b)^2(\tau_D(4b+\tau_D-2)+1)}{(b-1)^2b^2}} + a(2b-1)\tau_D + a - b\tau_D - b}{2(b-1)b}$. For a large enough cooperator delay full cooperation loses its stability. Details of the analysis are presented in Appendix A.

Internal equilibrium. If no delays are present, the internal stationary point x_2^* always exists and equals to b/a. The increase of τ_C leads to an increase in the stationary point value. Then, the equilibrium reaches full cooperation ($x_2^* = 1$) and disappears when $\tau_C = m$. An increase in τ_D always leads to a decrease in x_2^*. In the limiting case of $\tau_D \to \infty$ we have $x_2^* \to 1/a$. The latter result coincides with the limit presented in[33]. It also ensures that condition (3.11) is met. When the internal equilibrium e_2 exists, it is always unstable, as shown in Appendix A.

One delay present. We consider the limiting case of each delay to be equal to 0. We solve the systems (3.12) for $\tau_C = 0$ and (3.13) for $\tau_D = 0$ and check the behaviour of e_2 in the corresponding limits. If it exists, the internal equilibrium of the system (3.12) takes the following form:

$$\tilde{e}_2 = (\tilde{x}_2, 0, -a\tau_D(\tilde{x}_2 - 1)\tilde{x}_2) \tag{3.24}$$

where

$$\tilde{x}_2 = \frac{\tau_D - 1 + \sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1}}{2a\tau_D}. \tag{3.25}$$

The solution coincides with the value of e_2 in the limit of $\tau_C \to 0$. Additionally, we can show that: $\lim_{\tau_D \to 0} \tilde{x}_2 = b/a$. Hence, in the limiting case of no delays, we recover the solution of the standard stag-hunt game. Similarly, for $\tau_D = 0$, we solve the system (3.13). The system has only one stationary solution in the game-theoretic relevant interval of $\bar{x} \in (0, 1)$:

$$\bar{e}_2 = (\bar{x}_2, b\tau_C\bar{x}_2, 0) \tag{3.26}$$

where

$$\bar{x}_2 = \frac{b(b\tau_C - \tau_C + 1)}{a}. \tag{3.27}$$

Again, we can show that $\lim_{\tau_D \to 0} x_2^* = \bar{x}_2$ and $\lim_{\tau_C \to 0} \bar{x}_3 = b/a$. So, the internal solution represented by e_2 can be used in the limiting cases of either or both delays approaching 0.

We show that in the classical stag-hunt game, the introduction of delay is insufficient to destabilise complete defection. However, it is possible to destabilise full cooperation. Moreover, we prove that increasing delay of one of the strategies leads to shrinking of the basin of attraction of the equilibrium consisting of individuals following only that strategy.

Example. Below, we present an analysis of the stag hunt game characterized by the payoff matrix used in[33]:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R = 5 & S = 0 \\ T = 3 & P = 3 \end{pmatrix} \end{array} \tag{3.28}$$

In the case of no delay, the game has two stable equilibria corresponding to the two homogeneous states. The unstable equilibrium, dividing the basins of attraction of the two equilibria, is $x^* = 0.6$.

Figure 3.2 explores the change in the stability of the stationary states of the system (3.15) in the parameter space of the delays. In most of the parameter

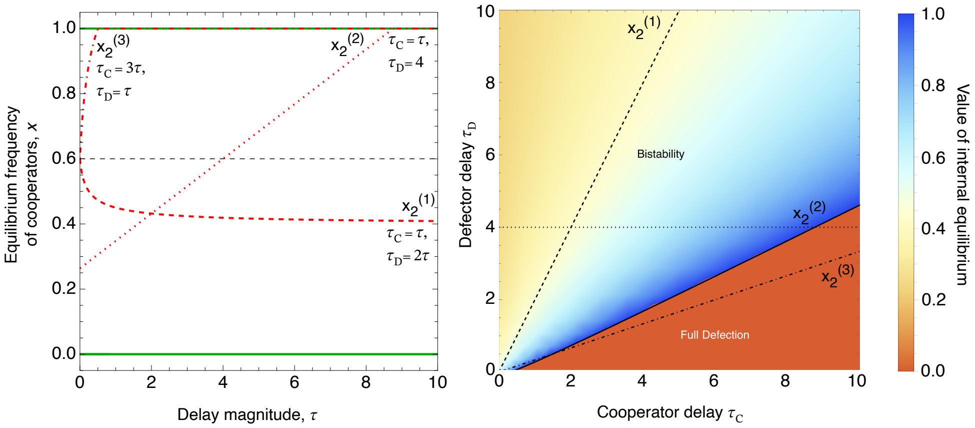

Figure 3.2: Stability of the equilibria of the stag hunt game represented by matrix (3.28). On the left, the stationary state values for the specific values of delays are plotted. The dashed line represents the internal stationary state $x_2^{(1)}$ as a function of τ, when $\tau_C = \tau$, $\tau_D = 2\tau$. An increase in τ leads to a decrease in stationary state value. The dotted line represents internal stationary state $x_2^{(2)}$ as a function of τ, when $\tau_C = \tau$, $\tau_D = 4$. The internal stationary state disappears for big enough τ, and full cooperation loses its stability. The dot-dashed line represents the internal stationary state $x_2^{(3)}$ as a function of τ, when $\tau_D = \tau$, $\tau_C = 3\tau$. An increase in τ leads to an increase in the stationary state value until its disappearance. On the right, the stability of the system in the parameter space τ_C and τ_D is shown. The solid black line indicates the point of bifurcation. In the "Full Defection" region, only e_0 is stable. In the "Bistability" region, both e_0 and e_1 are stable, and their basins of attraction are divided by the unstable internal equilibrium. The colour indicates the value of the internal stationary state. The values considered on the left are represented by dashed ($x_2^{(1)}$), dotted ($x_2^{(2)}$) and dot-dashed ($x_2^{(3)}$) lines, respectively. The effects of only one delay can be observed on the left and bottom edges of the plot.

space, we observe full cooperation and defection bistability. The value of x_2^* decreases with τ_D, reaching the limiting value of 0.2 ($1/a$). With the increase in τ_C, an increase in the value of the x_2^* is observed. As the internal equilibrium value approaches 1, one of the stable equilibria disappears, leaving full defection as the only stable equilibrium. The curve dividing the region of bistability and full defection marks the bifurcation point.

Snowdrift Game

Next, we analyse the snowdrift game, also known as the chicken game or the hawk-dove game. In this game, two players choose between contributing to a common good (C) or not (D). The cost of the good (c) is divided equally between all contributors. If at least one of the individuals contributes, each player, regardless of their strategy, obtains the benefit b[167]. Hence, the game can be represented by the following matrix:

$$\begin{array}{ccc} & C & D \\ C & R = b - c/2 & S = b - c \\ D & T = b & P = 0 \end{array} \tag{3.29}$$

Where $b > c > 0$. The game with no delays has two unstable equilibria $x_0 = 0$, $x_1 = 1$ and one stable internal equilibrium $x_2 = (b - c)/(b - c/2)$.

For the payoffs specified in the matrix (3.29) the system (3.9) becomes:

$$\begin{aligned} \frac{dx(t)}{dt} &= \frac{y_C(t)(1 - x(t))}{\tau_C} - \frac{y_D(t)x(t)}{\tau_D} \\ \frac{dy_C(t)}{dt} &= y_C \left(\frac{\tau_C - 1}{\tau_C} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D} \right) + x(t)(\frac{c}{2}x(t) + b - c) \\ \frac{dy_D(t)}{dt} &= y_D \left(\frac{\tau_D - 1}{\tau_D} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D} \right) + bx(t)(1 - x(t)) \end{aligned} \tag{3.30}$$

The system (3.30) can have four equilibria. The trivial equilibrium x_0 becomes:

$$e_0 = (0, 0, \tau_D - 1)\,, \tag{3.31}$$

if $\tau_D > 1$. Then, the population would grow exponentially if $1/\tau_D < 0$. Additionally, when $\tau_D \leq 1$, $y_D = 0$. As the delay cannot take negative values, we can see that the population always goes extinct in the full defection equilibrium.

The full cooperation equilibrium x_1 becomes:

$$e_1 = \left(1, \frac{1}{2} \left(\tau_C - 1 + \sqrt{\tau_C(4b - 2c + \tau_C - 2) + 1} \right), 0 \right). \tag{3.32}$$

In the full cooperation equilibrium, the condition (3.11) becomes:

$$\frac{1}{2\tau_C} \left(\tau_C - 1 + \sqrt{\tau_C(4b - 2c + \tau_C - 2) + 1} \right) > 1 \tag{3.33}$$

and holds when $(1 < b < 2 \wedge 0 < c \leq 2b - 2) \vee (b \geq 2)$.

Additionally, two internal equilibria may be present:

$$e_2 = \left(x_2^*, \frac{\tau_C x_2^* y_D^{(2)}}{\tau_D - \tau_D x_2^*}, y_D^{(2)} \right) \tag{3.34}$$

$$e_3 = \left(x_3^*, \frac{\tau_C x_3^* y_D^{(1)}}{\tau_D - \tau_D x_3^*}, y_D^{(3)} \right) \tag{3.35}$$

where

$$
\begin{aligned}
x_2^* =& \frac{1}{(c\tau_D - 2b\tau_C)^2} \\
& \Big((\tau_C - \tau_D)\sqrt{o} \\
& + \tau_D \left(4b^2\tau_C - 2b(2c\tau_C + \tau_C - 1) - c(\tau_C + 1)\right) \\
& + \tau_C(2b(\tau_C - 1) + c) + c\tau_D^2(-2b + 2c + 1)\Big), \qquad (3.36) \\
x_3^* =& \frac{1}{(c\tau_D - 2b\tau_C)^2} \\
& \Big((\tau_D - \tau_C)\sqrt{o} \\
& + \tau_D \left(4b^2\tau_C - 2b(2c\tau_C + \tau_C - 1) - c(\tau_C + 1)\right) \\
& + \tau_C(2b(\tau_C - 1) + c) + c\tau_D^2(-2b + 2c + 1)\Big), \qquad (3.37) \\
y_d^{(i)} =& -\frac{1}{2}(x_i^* - 1)\left(\tau_D - 1 + \sqrt{4b\tau_D x + \tau_D^2 - 2\tau_D + 1}\right), \qquad (3.38) \\
o =& 16b^3\tau_C + 4b^2(\tau_C(-4c + \tau_C - 2) - 2c\tau_D + 1) \\
& + 4bc(2c\tau_D + \tau_C(-\tau_D) + \tau_C + \tau_D - 1) + c^2(\tau_D - 1)^2. \qquad (3.39)
\end{aligned}
$$

In the internal equilibira, the condition (3.11) takes the following form:

$$
\frac{x_i^* y_D^{(i)}}{\tau_D - \tau_D x_i^*} + \frac{y_D^{(i)}}{\tau_D} > 1. \qquad (3.40)
$$

The condition is met when one of the following constraints holds true:

$$
\begin{aligned}
& \Bigg(1 < b \leq 2 \land \Bigg((0 < c \leq b - 1) \\
& \lor \left(b - 1 < c < 2b - 2 \land \frac{-2b + 2c + 2}{c} \leq x_i^* < 1\right)\Bigg)\Bigg) \qquad (3.41) \\
& \land \left(b > 2 \land \left((0 < c \leq b - 1) \right.\right. \\
& \left.\left. \lor \left(b - 1 < c < b \land \frac{-2b + 2c + 2}{c} \leq x_i^* < 1\right)\right)\right)
\end{aligned}
$$

Now, we combine conditions (3.33) and (3.41) and obtain the following constrains on the game parameters: $(1 < b \leq 2 \land c < 2b - 2) \lor b > 2$. Additionally, when $b < c + 1$, the following constraint needs to be applied to the internal stationary state values: $\frac{-2b+2c+2}{c} \leq x_i^*$ for $i \in 2, 3$.

Homogeneous equilibria. We perform stability analysis of the trivial equilibria. The analysis of the full cooperation equilibrium e_1 shows that it is stable if $\tau_D > n$ where $n = \frac{4b^2\tau_C - 2bc\tau_C - 4b\tau_C + c\tau_C + c}{4b^2 - 4bc - 4b + c^2 + 2c} + \sqrt{\frac{4bc^2\tau_C - 2c^3\tau_C + c^2\tau_C^2 - 2c^2\tau_C + c^2}{(4b^2 - 4bc - 4b + c^2 + 2c)^2}}$. Hence, full cooperation can be stable if the defector delay is large enough and the cooperator delay is small enough. We show that full defection equilibrium e_0 is stable if the following conditions are met $(0 < c \leq 2 \wedge (2+c)/c < b < c+1 \wedge \tau_D > p) \vee (c > 2 \wedge c < b < c+1 \wedge \tau_D > p)$ where $p = \frac{1}{2}\sqrt{\frac{4b\tau_C - 4c\tau_C + \tau_C^2 - 2\tau_C + 1}{(b-c-1)^2}} + \frac{-\tau_C - 1}{2(b-c-1)}$ and is never stable if $\tau_D < 1$. The specific form of the payoff matrix of the snowdrift game causes the assumption of exponential growth to be violated whenever full defection is a stable equilibrium. Therefore, any parameter combination leading to stability of full defection needs to be noted as leading to the possible extinction of the population. As population extinction is excluded from the model's assumptions, we only analyse the parameter space when it is not possible. Hence, we assume that $b \geq c+1$. The details of the stability analysis are presented in Appendix A.

Internal equilibrium. Next, we analyse the two possible internal equilibria (e_2, e_3) in the interesting interval $(0, 1)$. When the cooperator delay is greater than the defector delay ($\tau_C > \tau_D$), only one internal equilibrium, e_2, exists in the interval $(0, 1)$. In that region of the parameter space, the equilibrium is always stable. With the increase of cooperator delay, the internal equilibrium value x_2^* decreases. In the limit of $\tau_C \to \infty$ x_2^* approaches a limiting value $1/b$. Notably, for all considered game parameters $1/b > (-2b + 2c + 2)/c$, hence the population always grows exponentially in the internal equilibrium. An increase in the defector delay τ_D leads to an increase in the value of x_2^*. In the limit of the delay τ_D approaching τ_C, the stationary state approaches the limiting value, the internal equilibrium of the system with no delays, $(b-c)/(b-c/2)$.

If the defector delay is greater than the cooperator delay ($\tau_D > \tau_C$), both internal equilibria may exist in the interesting interval $(0, 1)$. In particular, the existence of the equilibrium e_3 depends on the parameter values of the game: the equilibrium can exist only if certain conditions are met. Otherwise, only e_2 can exist. The two regions of the b, c parameter space are represented in Figure 3.3.

Both internal equilibria may exist in the parameter region indicated in purple in Fig. 3.3. Particularly, when $0 < \tau_C < q$, where $q = \frac{8b^3 - 4b^2(3c+2) + 4bc(c+2) - c^2}{2\sqrt{2}\sqrt{b(2b^3 - 2b^2(2c+1) + bc(2c+3) - c^2)}} - 2b + c + 1$ the two equilibria coexist, with $x_2^* < x_3^*$, e_2 being stable and e_3 unstable. At the point $o = 0$, the two equilibria collide at a fold bifurcation and disappear. e_3 collides with the full cooperation equilibrium e_1 at $\tau_D = n$ and the two switch stability.

In the gray region in Fig. 3.3 or when $\tau_C \geq q$ only e_2 exists. The value of x_2^* decreases with cooperator delay τ_C and increases with defector delay τ_D, colliding with the full cooperation equilibrium at $\tau_D = n$. In the limit of $\tau_C \to \tau_D$ the fraction of the cooperators approaches $(b-c)/(b-c/2)$. If it exists, the internal equilibrium is always stable.

One delay present. To analyse the system (3.12), we must consider the game parameter values and the two regions in Fig. 3.3. In the grey region only one

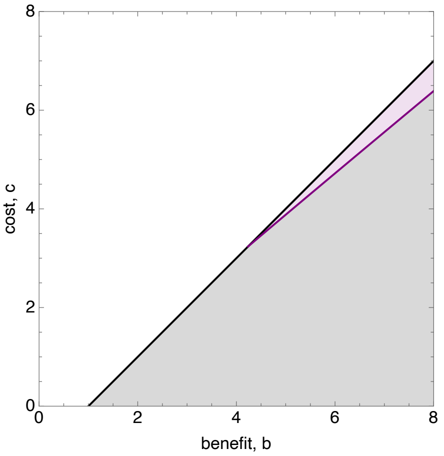

Figure 3.3: The existence of one or two internal in the snowdrift game parameter (b and c) space. In the grey region, only e_2 can exist. In the purple region, both e_2 and e_3 may exist. Outside of the coloured region, the population is at risk of extinction.

internal equilibrium can exist, the fraction of cooperators coinciding with x_2^* in the limit of $\tau_C \to 0$:

$$\begin{aligned}\tilde{x}_2 =& \frac{1}{c^2\tau_D}(b(2-2c\tau_D)+2c^2\tau_D+c\tau_D-c\\ &-\sqrt{b^2(4-8c\tau_D)+4bc(2c\tau_D+\tau_D-1)+c^2(\tau_D-1)^2})\\ =& \lim_{\tau_C\to 0} x_2^*.\end{aligned} \tag{3.42}$$

In the limit of defector delay tending to 0, the internal equilibrium approaches $x_2 = (b-c)/(b-c/2)$.

In the purple region of Fig. 3.3 two internal equilibria can be present, corresponding to e_2 and e_3 such that $\tilde{x}_2$ is given by Eq. (3.42) and $\tilde{x}_3$ by:

$$\begin{aligned}\tilde{x}_3 =& \frac{1}{c^2\tau_D}(b(2-2c\tau_D)+2c^2\tau_D+c\tau_D-c\\ &+\sqrt{b^2(4-8c\tau_D)+4bc(2c\tau_D+\tau_D-1)+c^2(\tau_D-1)^2})\\ =& \lim_{\tau_C\to 0} x_2^*.\end{aligned} \tag{3.43}$$

In the limit of no delays present, only one of the internal equilibria exists in the interval $(0,1)$, in particular $\lim_{\tau_D\to 0}\tilde{x}_2 = (b-c)/(b-c/2)$.

If only cooperators experience delays ($\tau_D = 0$) the system (3.13) has one possible internal equilibrium $\bar{e}_2$. The value of $\bar{x}_2$ is equal to the equilibrium value x_2^* in the limit of no defector delays:

$$\bar{x}_2 = \frac{1}{4b^2\tau_C}(2b\tau_C-2b+c+\sqrt{8b^2\tau_C(2b-2c)+(2b\tau_C-2b+c)^2}) = \lim_{\tau_D\to 0} x_2^*. \tag{3.44}$$

With the cooperator delay approaching 0, the value of the internal equilibrium approaches the no-delay value: $\lim_{\tau_C \to 0} \bar{x}_2 = x_2 = (b-c)/(b-c/2)$.

Examples. We perform numerical analysis on two payoff matrices, each corresponding to one region in Figure 3.3. Matrix (3.45) ($b = 5$ and $c = 2$) corresponds to the grey region and *Example 1* in[33] and the matrix (3.46) ($b = 5$, $c = 3.9$) lies in the purple region.

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R = 4 & S = 3 \\ T = 5 & P = 0 \end{pmatrix} \end{array} \tag{3.45}$$

In the case of no delays, the game characterized by the payoff matrix (3.45) has one stable equilibrium $x = 0.75$ and two unstable equilibria of full cooperation and full defection.

In Figure 3.4, the behaviour of the internal equilibrium is analysed. In the majority of the space, the internal equilibrium exists and is stable. The internal equilibrium disappears above the boundary value of τ_D, and full cooperation becomes stable.

In order to showcase the dynamics in the purple region of Fig. 3.3, we look at another payoff matrix:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R = 3.05 & S = 1.1 \\ T = 5 & P = 0 \end{pmatrix} \end{array} \tag{3.46}$$

In Figure 3.5, the behaviour of the dynamics of the snowdrift game characterized by matrix (3.46) is showcased. For a small interval of values of delays, i.e. $\tau_C < 0.00715429$, we can observe the coexistence of two internal equilibria that collide in a saddle-node bifurcation by increasing the delay magnitude τ_D. In the remainder of the space, the dynamics are similar to the ones observed for matrix (3.45).

Prisoner's dilemma

Lastly, we analyse the prisoner's dilemma. In this game, each player can choose to incur a cost c to provide the opponent with a benefit b (C) or not (D)[168]. Additionally, here, we introduce a base endowment of c so that all of the possible payoffs of the game are non-negative. Hence, the game is represented by the following matrix:

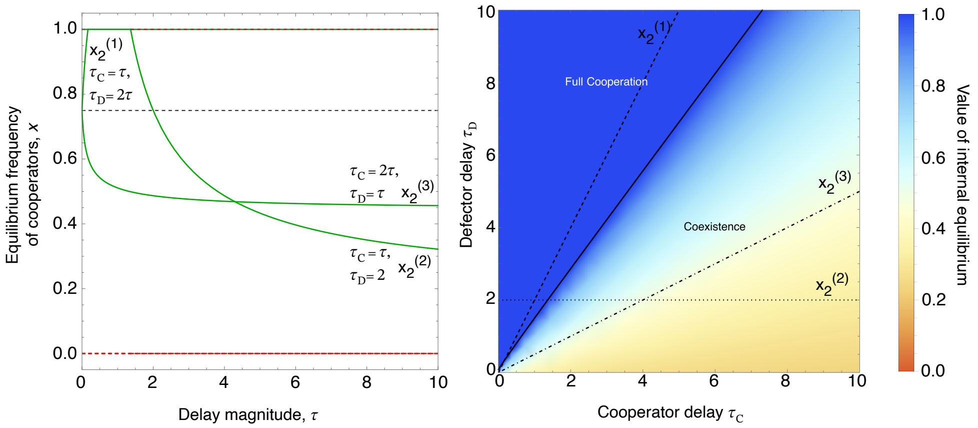

Figure 3.4: Stability of the equilibria of the snowdrift game represented by matrix (3.45). On the left, the stationary state values for specific delays are plotted. The $x_2^{(1)}$ line represents the internal stationary state as a function of τ, when $\tau_C = \tau$, $\tau_D = 2\tau$. An increase in τ leads to an increase in stationary state value. The internal equilibrium ceases to exist for a high enough value of τ, and full cooperation becomes stable. The $x_2^{(2)}$ line represents internal stationary state as a function of τ,when $\tau_C = \tau, \tau_D = 2$. Full cooperation is a stable equilibrium for small values of τ, and no internal equilibrium exists. A stable internal equilibrium appears with the increase in τ, and full cooperation loses stability. The value of the internal stationary state decreases with the increase of τ. The $x_2^{(3)}$ line represents the internal stationary state as a function of τ when $\tau_C = 2\tau$, $\tau_D = \tau$. The internal stationary state's value decreases with an increase in τ. On the right, the stability of the system in the parameter space τ_C and τ_D is shown. The solid black line indicates the point of bifurcation. In the "Full Cooperation" region, only e_1 is stable. In the "Coexistence" region, only e_2 is stable, the fraction of cooperators indicated by the colour. The values considered on the left are represented by dashed ($x_2^{(1)}$), dotted ($x_2^{(2)}$) and dot-dashed ($x_2^{(3)}$) lines, respectively. The effects of only one delay present can be observed on the left and bottom edges of the plot.

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R=b & S=0 \\ T=b+c & P=c \end{pmatrix} \end{array} \tag{3.47}$$

where $b > c > 0$. If no delays are present, the game has one stable equilibrium, full defection ($x_0 = 0$), no internal equilibrium exists, and full cooperation ($x_1 = 1$) is unstable.

For the prisoner's dilemma represented by the payoff matrix (3.47) the system (3.9) becomes:

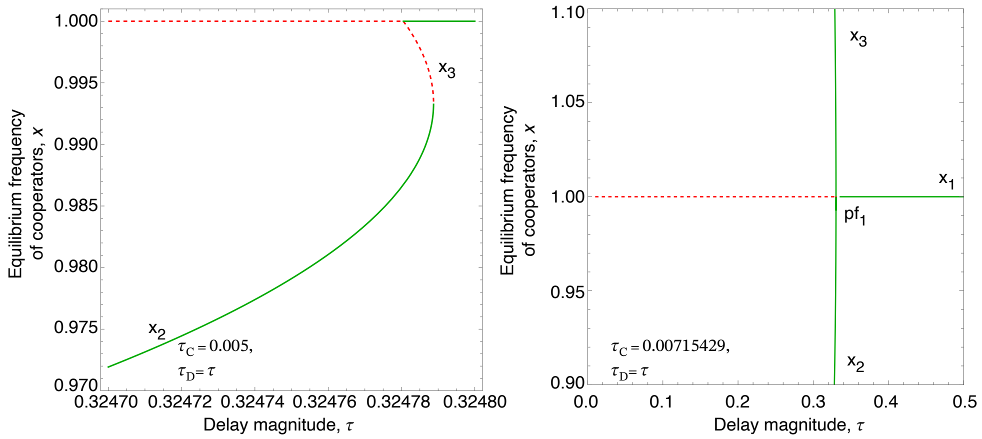

Figure 3.5: The stability and the existence of internal equilibria of the snowdrift game represented by matrix (3.46) depend on the time delays. The left plot represents the internal stationary states' values as a function of τ, when $\tau_C = 0.005$, $\tau_D = \tau$. Two internal equilibria may exist at the same time. The value of x_3^* decreases with τ and x_2^* increases. e_3 is always unstable and appears when full cooperation becomes stable. After the internal equilibria collide, they disappear, and full cooperation is the only stable equilibrium. Full defection is always unstable. As shown on the right plot, the two internal equilibria emerge at $\tau_C = 0.00715429$, and $\tau_D \approx 0.33031257$ as the saddle-node that gives rise to e_2 and e_3 via a pitchfork bifurcation. The details of these mechanisms are further investigated in Appendix A.

$$\begin{aligned}\frac{dx(t)}{dt} =& \frac{y_C(t)(1-x(t))}{\tau_C} - \frac{y_D(t)x(t)}{\tau_D}\\ \frac{dy_C(t)}{dt} =& y_C\left(\frac{\tau_C-1}{\tau_C} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D}\right) + bx^2(t)\\ \frac{dy_D(t)}{dt} =& y_D\left(\frac{\tau_D-1}{\tau_D} - \frac{y_C(t)}{\tau_C} - \frac{y_D(t)}{\tau_D}\right) +\\ & (bx(t)+c)(1-x(t))\end{aligned} \tag{3.48}$$

In the interval $[0, 1]$, three equilibria of the system (3.48) are possible. Full defection (equivalent to x_0) becomes:

$$e_0 = \left(0, 0, \frac{1}{2}\left(\tau_D - 1 + \sqrt{4c\tau_D + \tau_D^2 - 2\tau_D + 1}\right)\right). \tag{3.49}$$

In e_0, the condition (3.11) becomes

$$\frac{1}{2\tau_D}\left(\tau_D - 1 + \sqrt{4c\tau_D + \tau_D^2 - 2\tau_D + 1}\right) > 1. \tag{3.50}$$

For the condition to hold, the following inequality needs to hold: $c \geq 1$

Full cooperation equilibrium (equivalent to x_1) takes the following form:

$$e_1 = \left(1, \frac{1}{2}\left(\tau_C - 1 + \sqrt{4b\tau_C + \tau_C^2 - 2\tau_C + 1}\right), 0\right). \tag{3.51}$$

Then, in e_1 the condition (3.11) becomes

$$\frac{1}{2\tau_C}\left(\tau_C - 1 + \sqrt{4b\tau_C + \tau_C^2 - 2\tau_C + 1}\right) > 1, \tag{3.52}$$

which holds true when $b \geq 1$.

Additionally, an internal equilibrium appears:

$$e_2 = \left(x_2^*, -\frac{\tau_C x_2^* y_D^*}{\tau_D(x_2^* - 1)}, y_D^*\right) \tag{3.53}$$

where

$$\begin{aligned} y_D^* &= -\frac{1}{2}(x_2^* - 1)\left(\tau_D - 1 + \sqrt{\tau_D(4bx_2^* + 4c - 2) + \tau_D^2 + 1}\right) && (3.54) \\ x_2^* &= \frac{1}{2}\left(\frac{-2c\tau_C + \tau_C - \tau_D}{b\tau_C - b\tau_D} + \sqrt{\frac{-4c + \tau_C - \tau_D}{b^2(\tau_C - \tau_D)}}\right). && (3.55) \end{aligned}$$

The population grows exponentially if

$$-\frac{\tau_C x_2^* y_D^*}{\tau_D \tau_C (x_2^* - 1)} + \frac{y_D^*}{\tau_D} > 1. \tag{3.56}$$

The condition is met when $x_2^* > 1/b$.

Hence, for the population to grow in each equilibrium, an additional constraint on the game has to be introduced: $c \geq 1$. In the internal equilibrium, the following needs to hold: $x_2^* > 1/b$.

Homogeneous equilibria. The stability analysis of the full defection equilibrium e_0 shows that it always exists and is always stable. Full cooperation equilibrium e_1 is unstable, unless the following condition is met: $\tau_D > c/(-b + b^2) \wedge \tau_C < r$ where $r = \frac{2(b-1)b\tau_D - c\left(-2b\tau_D + \tau_D + 1 + \sqrt{\tau_D(4b+4c+\tau_D-2)+1}\right)}{2(b+c-1)(b+c)}$. Full cooperation becomes stable for a big enough delay of defectors and a small enough delay of cooperators. Details of the stability analysis are presented in Appendix A.

Internal equilibrium. The system does not have an internal equilibrium if no delays are present. Then, for $\tau_D > c/(-b + b^2)$ and $\tau_C = r$ the internal stationary state appears at $x_2^* = 1$. A further increase in τ_D leads to a decrease in x_2^*. An increase in τ_C always leads to an increase in x_2^* until it disappears again when $\tau_C > r$. Notably, x_2^* attains positive values only if $\tau_D > \tau_C$. In the limit of defector delay approaching infinity, $\tau_D \to \infty$, x_2^* approaches a limiting value $1/b$, ensuring population growth in the internal equilibrium.

One delay present. We analyse the system's behaviour when only one of the delays is present. For $\tau_C = 0$ the system (3.12) has one internal equilibrium in the interval $(0, 1)$, which coincides with the limit of the internal equilibrium x_2^*:

$$\tilde{x}_2 = \frac{1 + \sqrt{\frac{4c}{\tau_D} + 1}}{2b} = \lim_{\tau_C \to 0} x_2^*.$$

In the case of no defector delay ($\tau_D = 0$) the system (3.13) does not have an internal solution in the $(0, 1)$ interval. This result is explained by the fact that the existence of the internal equilibrium of the general prisoner's dilemma depends on the presence of the defector delay. Consequently, we see that in the limit of $\tau_D \to 0$, the internal solution takes a value that is always less than 0: $\lim_{\tau_D \to 0} x_2^* = \frac{-2c+1+b\sqrt{\frac{\tau_C-4c}{b^2\tau_C}}}{2b} < 0$.

We show that in the prisoner's dilemma in the cost-benefit form (transformed for all payoff to be non-negative), complete defection is always stable, regardless of the delays. However, it is possible for full cooperation to become stable and for the unstable internal equilibrium to appear. If both extreme equilibria are stable, an increase in the strategy's delay leads to a decrease in the size of the basin of attraction of the respective equilibrium.

Example. For the numerical analysis, we use the following payoff matrix:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R = 3 & S = 0 \\ T = 5 & P = 2 \end{pmatrix} \end{array} \tag{3.57}$$

Figure 3.6 explores the change in the system stability in the parameter space of delays. In the majority of the parameter space full defection is the only stable equilibrium. As the delay of defectors increases, full cooperation becomes stable, as indicated by the colourful region in the plot, the colours representing the value of the internal equilibrium.

Game transitions.

In our analysis, we show that introducing delays may not only influence the game's properties but also change the type of the game entirely. Introducing strategy-specific delay is detrimental to the strategy affected. Thus, with a high enough cooperator delay, a stag hunt may effectively become a prisoner's dilemma. And vice-versa, a defector delay may transform a prisoner's dilemma into a stag hunt. Similarly, the transition between a snowdrift and harmony (a game where all cooperation is always stable) can be achieved. The possible game changes are represented in Figure 3.7, with open circles representing the original games and the closed ones showing the effective games played in the presence of delays. In order to recover the effective game payoff matrix for specific delay values, we need to obtain the numerical values of $\frac{dx(t)}{dt}$ given in (3.9) depending on $x(t)$, assuming $\frac{dy_i(t)}{dt} = 0$ for $i \in C, D$. Then, the parameters of the effective game are determined by fitting the replicator equation $x(t)(1 - x(t))(U_C(x) - U_D(t))$ to the obtained data, using the least-squares fit.

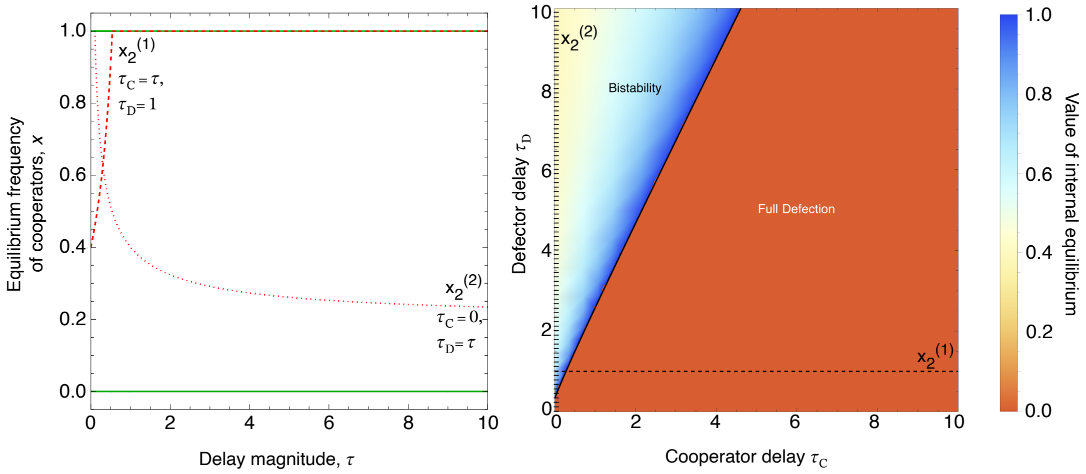

Figure 3.6: Stability of the equilibria of the prisoner's dilemma represented by matrix (3.57). On the left, the stationary state values for specific values of delays are plotted. The dashed line represents the internal stationary state $x_2^{(1)}$ as a function of τ, when $\tau_C = \tau$, $\tau_D = 1$. An increase in τ leads to an increase in stationary state value. The internal equilibrium ceases to exist for a high enough value of τ, and full cooperation is not stable anymore. The dotted line represents internal stationary state $x_2^{(2)}$ as a function of τ, when $\tau_C = 0, \tau_D = \tau$. Full defection is the only stable equilibrium for small values of τ, and no internal equilibrium exists. With the increase in τ, the internal equilibrium appears, and full cooperation becomes stable. The value of the internal stationary state decreases with the increase of τ. On the right, the stability of the system in the parameter space τ_C and τ_D is shown. The solid black line indicates the point of the bifurcation. In the "Full Defection" region, only e_0 is stable. In the "Bistability" region, both e_0 and e_1 are stable, and their basins of attraction are divided by the unstable internal equilibrium. The colour indicates the value of the internal stationary state. The values considered on the left are represented by dashed ($e_2^{(1)}$) and dotted ($e_2^{(1)}$) lines, respectively. The effects of only one delay present can be observed on the left and bottom edges of the plot.

This result emphasizes the importance of delays in the analysis of games and the impact they have on the evolutionary dynamics. Notably, game transitions presented in Figure 3.7 result from cost-benefit forms of the games used in the results section 3. However, other transitions can be observed by considering the general form of the payoff matrix (3.1). In particular, a change between the prisoner's dilemma and the snowdrift occurs, showing the possibility of a vertical shift in the coordinate system. A numerical analysis of a possible transition is presented in Appendix A.

Conclusions

Differential equations with time delays are infinite-dimensional dynamical systems, and therefore, any analytical solutions are difficult to obtain and, therefore,

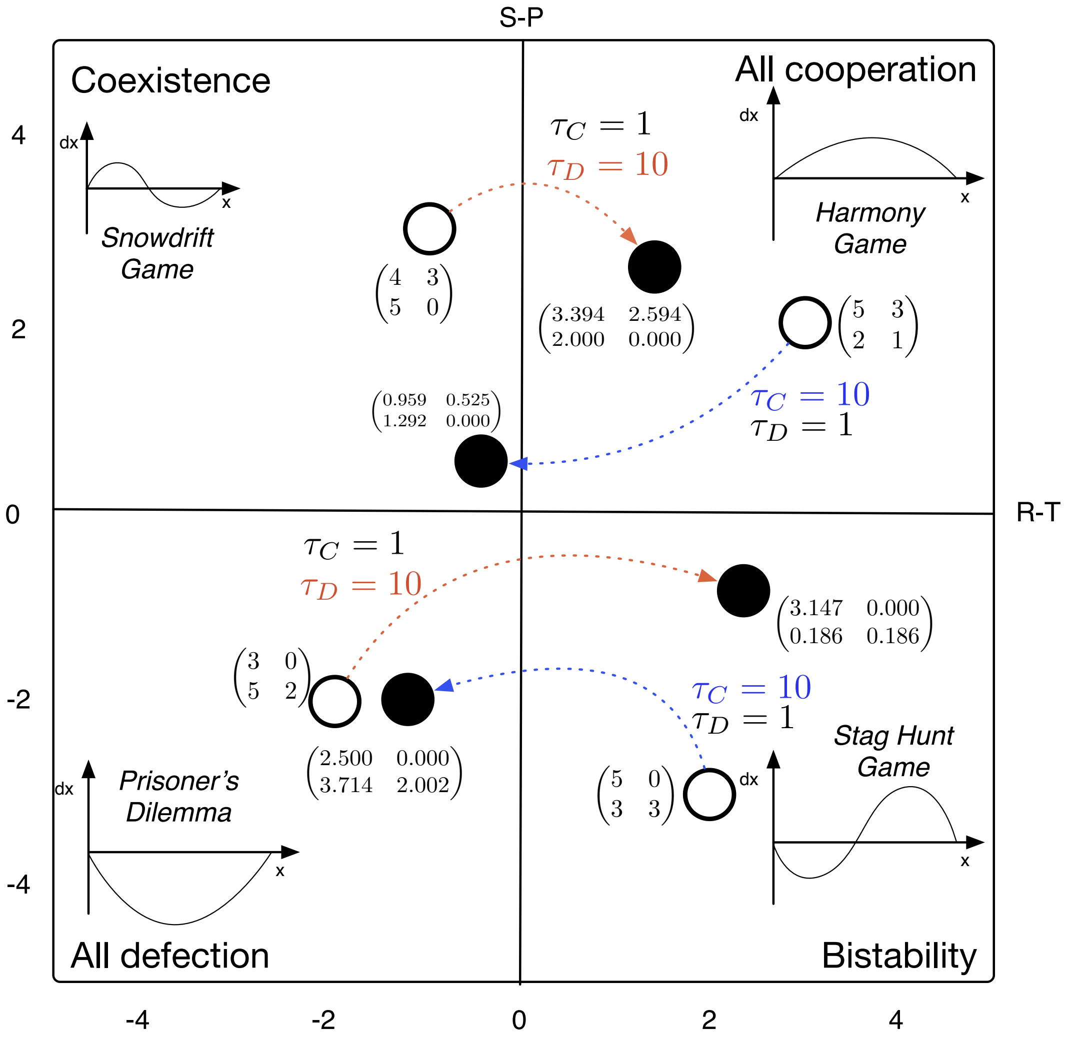

Figure 3.7: The games described by the general Matrix (3.1) can be classified into four classes depending on the sign of the advantage of cooperators playing against cooperators $(R-T)$ and the advantage of defectors against defectors $(S-P)$. The introduction of strategy-dependent delays changes the effective game played in the population. With high enough values of delays present, the stag hunt game becomes a prisoner's dilemma and vice-versa. An analogous transition can be observed between the snowdrift and harmony games. The open circles represent the original games as discussed in Section 3. The filled circles show the effective game obtained by introducing delays, as indicated on the arrows. An increase in cooperator delay leads to a transition from right to left of the coordinate system and an increase in defector delay - from left to right. The possible transitions between the games are limited by the assumptions made on the forms of the games.

are scarce. Here, we presented a different approach to model time delays in evolutionary games, namely in replicator equations. In our Kindergarten model, time delays correspond to rates at which offspring leave kindergarten and are able to play games; kindergartens are strategy-dependent. Our qualitative results coincide with conclusions presented in[33] while providing benefits of lower complexity and easier analysis.

We derive explicit formulas on the change of the fraction of cooperators in population x linked back to the underlying population via the kindergarten compartments y_D and y_C. This allows the direct study of the fraction x, yielding closed-form formulas for internal stationary states for special payoff matrices and the study of a general payoff matrix through continuation.

Namely, we show that in the stag hunt game, a delay of a specific strategy leads to a decrease in the size of the basin of attraction of the corresponding absorbing state. Through high enough cooperator delays, it is possible to destabilise full cooperation. The same cannot be said about full defection, which is stable regardless of delay values. Similar behaviour can be observed in the prisoner's dilemma. With the introduction of time delays, full cooperation can become stable, and the internal unstable equilibrium can be affected like in the stag hunt. Again, it is not possible to destabilise full defection.

In both games, cooperation can be leveraged when we introduce stochasticity in finite populations. According to the "one-third rule" introduced by[6], generalized in[169], a mutant of strategy A can overcome an initial disadvantage and take over a population of strategy B if its frequency is 1/3. Hence, even if the full defection is always stable, decreasing its basin of attraction by introducing delays can give the cooperators the needed advantage to take over the population.

The snowdrift game represents a reverse situation to the stag hunt and prisoner's dilemma - in the benefit-cost version of this game, full defection can never be stable. However, full cooperation can become stable. If the internal equilibrium exists, it is stable, and its value depends on the delays. An increase in the delay of a given strategy decreases its fraction in the coexistence equilibrium. Moreover, an additional, second internal equilibrium may appear.

The effects of delays are not limited to shifting the dynamics within the game class but, additionally, can lead to a change in the nature of the game itself. We show that introducing strategy-specific delays alters the effective games played and, subsequently, leads to a change in optimal strategies. This result underlines the importance of considering the temporal structure of the studied system.

Our approach can be used in games with more than two strategies and multiplayer games.

Competing interests

The author(s) declare no competing interests.

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4

Catalysing Cooperation: The Power of Collective Beliefs in Structured Populations

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Abstract

Collective beliefs can catalyse cooperation in a population of selfish individuals. We study this transformative power of collective beliefs, an effect that intriguingly persists even when beliefs lack moralising components. Besides the process itself, we consider the structure of human populations explicitly. We incorporate the intricate structure of human populations into our model, acknowledging the bias brought by social and cultural identities in interaction networks. Hence, we develop our model by assuming a heterogeneous group size and structured population. We recognise that beliefs, typically complex story systems, might not spontaneously emerge in society, resulting in different spreading rates for actions and beliefs within populations. As the degree of connectedness can vary among individuals perpetuating a belief, we examine the speed of trust build-up in networks with different connection densities. We then scrutinise the timing, speed and dynamics of trust and belief spread across specific network structures, including random Erdös-Rényi networks, scale-free Barabási-Albert networks, and small world Newman-Watts-Strogatz networks. By comparing these characteristics across various network topologies, we disentangle the effects of structure, group size diversity, and evolutionary dynamics on the evolution of trust and belief.

Keywords: evolutionary game theory | stag hunt game | beliefs | networks

Introduction

Working together, or cooperation, is imperative for developing societies[170–172]. Even though cooperative behaviour yields the results desired from the group's point of view, it is costly and risky for the individuals involved. Evolutionary game theory can be used to model and understand these instances[2,12,173]. This work focuses on a specific game, namely the stag hunt game[15,174], and how it can be used to model trust. In the game, also known as the trust dilemma, cooperators can only succeed if they coordinate with other cooperators. Hence, cooperation is a reasonable option only if one trusts that the others will cooperate.

Trust is crucial to social and economic interactions[175]. It is foundational to exchanges and contracts - in an entirely rational population, entering any agreement is reasonable only if all parties believe that others will respect it. Establishing trust would not be difficult in a risk-free, mutually beneficial setting. However, the uncertainty about the actions of others often makes it difficult to achieve and maintain[176]. Hence, the trust problem usually involves some temptation to break it or risk not being reciprocated. We define trust as an individual's conviction that a partner (or partners) will work with them towards a common goal[177].

Not all individuals are as likely to interact with one another. Individuals are likelier to meet their family, neighbours or co-workers than strangers in a different city. To account for that, a network structure can be introduced[51]. The dynamics of evolutionary games played by spatially structured populations differ substantially from their well-mixed counterparts[95,178]. In particular, networks are shown to facilitate cooperation in games like the prisoner's dilemma or the snowdrift game[46,179–183]. However, the stag hunt game, representing a different class of games focused on coordination and trust, has received less attention. Studies of the game dynamics on random networks show that structure can promote cooperation and trust[23,184,185]. In this work, we follow suit, considering the dynamics of the multiplayer stag hunt game in structured populations and examining the effects of particular network parameters in the presence of an additional layer of complexity brought by collective beliefs.

The participating individuals' experiential histories, convictions and commitments shape their social interactions. Individual decisions are not always based solely on facts but are often biased by personal beliefs, preferences and constraints[186]. For example, opinions and decisions about vaccination can be induced not by scientific facts but rather by one's emotions and anecdotal, non-reliable, persuasive storytelling. The beliefs may develop from events irrelevant to the current decision or spillover from past experiences[187,188]. Social norms can, however, stimulate coordination and cooperation in a population[189–191]. The introduction of money, an object with no physical worth but rather a value derived from a collective belief in its worth, allows for successful coordination within economies[192]. Collectively agreed-upon rules spread in the population via narratives and tales, like stories from Agta, a Filipino hunter-gatherer population, and promote moral behaviours[193]. The existence of non-moralising beliefs, or beliefs with no explicit instruction or morals behind them, cannot be explained by their direct effect. However, they may still act as a cooperation catalyst. This effect is significant when beliefs can spread evenly between individuals[191]. However, the effect of non-moralising collective beliefs on the dynamics on a structured population is rarely discussed. Hence, in this work, we study how network properties influence game dynamics in the presence of distinct beliefs.

Results

Takeover

Introducing a structure into a population often facilitates cooperation[194,195]. For multiplayer games, this effect is robust to evolutionary dynamics (birth-death or death-birth, pairwise comparison) or updating strategy (synchronous, asynchronous); hence, we only present results obtained for the birth-death process with synchronous strategy-updating[194]. However, we note that analysis of the interplay of beliefs and evolutionary dynamics could interest future work.

The simulation results presented in this work portray evolutionary dynamics with mutations in small finite populations. Hence, high levels of stochasticity are present, and all simulations result in the stag-hunting equilibrium for all types of networks. Therefore, our focus metric is the takeover time[196,197]. *We define takeover as the first instance when all the individuals in the population are stag hunters.* We measure the time in generations, which could also be easily represented in the number of birth-death events since each generation consists of exactly Z events. After the takeover, some hare hunters may appear due to mutations; however, they cannot take over the population.

The introduction of structure can promote cooperation in the system due to the varying group size and network parameters. Hence, unsurprisingly, all simulations performed on the random graphs led to a faster stag hunter takeover than the well-mixed population. In particular, in the presence of only one belief (achieved by setting $\mu_B = 0.0$), the takeover time in a well-mixed population is on average 7.2 times longer than on the Newman-Watts-Strogatz (NWS) and 3.4 times longer than in the Erdös and Rényi (ER) and Barabási-Albert (BA) networks. For higher values of belief mutation μ_B, the difference between the well-mixed and structured populations reduces but exists. Therefore, in our case, the network structures facilitate the spread of cooperative behaviour and trust.

In all explored regimes, introducing the second belief ($\mu_B \neq 0.0$) leads to faster stag hunter takeover, as shown in Fig. 4.1. Increasing the value of belief mutation rate μ_B from 0.0 to 0.01 decreases the average takeover time on all network types, with a similar reduction of around 65% for ER and BA and around 50% for the NWS. Thus, introducing the second narrative benefits the fast spread of cooperation and trust.

In the BA and ER network populations, the takeover happens slower than in the NWS networks for every considered parameter set. This result suggests that a higher clustering coefficient (0.44 for the NWS) in the network expedites the spread of cooperative behaviour more effectively, as compared to the lower values (0.23 and 0.31 for ER and BA, respectively)[198,199]. The Supplementary Material (Supplementary Figure B.8) presents the effect of clustering on takeover time. Although the low network diameter is also said to promote cooperative behaviour[200], the effect is less pronounced. A relatively low diameter of 3.22 and 3.02 for ER and BA networks does not lead to a more effective cooperation spread than the NWS network, which is characterised by an average diameter of 3.61. In particular, for $\mu_B = 0.0$ (only one belief present), the average takeover time on the ER network is comparable to BA and over 2.1 times longer than on the NWS network.

Hence, we hypothesise that the high clustering coefficient is more effective in promoting cooperation. However, the beneficial effect of beliefs is amplified more effectively by a lower network diameter, as indicated by the higher impact of change in belief mutation on the ER and BA networks compared to the less notable impact for the NWS network.

Hitherto, we assumed that the belief mutation assignment happened at random. Each individual had the same probability of changing their convictions. We acknowledge that, in practice, these assumptions can be violated; hence, this part of our model serves as a null expectation but helps focus on the network properties. The characteristics of network structures can be used to target specific individuals and further accelerate takeover times. In the following section, we analyse how introducing mutations on specific types of nodes of the network influences the dynamics.

Targeting belief spreaders

Not everyone is as likely to be introduced to a novel belief system as others. An individual's characteristics can influence the probability of exposure to different worldviews or the propensity to internalise a new belief. Subsequently, the properties of an individual may also influence the probability of further spread of the novel belief. In particular, in a structured population, the connectivity of a

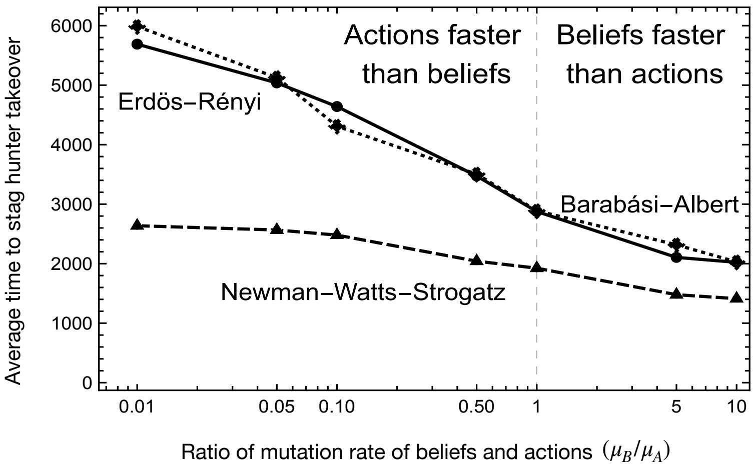

Figure 4.1: Takeover time for stag hunters. The level of action mutation (μ_A) is constant in all simulations. Hence, the mutation rate ratio change is caused by manipulating the belief mutation rate (μ_B). Increased belief mutation frequency leads to a lower takeover time, meaning higher belief diversity promotes a faster spread of cooperators in a population. The takeover is notably faster on the NWS networks, but the effect of belief is more pronounced on the ER and BA networks. The results are averaged over 1000 runs per network type and parameter set.

node can be an essential factor in determining whether a belief mutation occurs and spreads.

Our model assumes that an externality causes the mutation in beliefs and is not easy to induce in principle. The origins of such beliefs and underlying processes are a vast topic in itself and beyond the scope of this study. However, the presence of beliefs promotes a faster spread of cooperative behaviour. Hence, we check whether it is possible to choose specific kinds of individuals to introduce the new beliefs such that the takeover time is reduced.

The concept of changing the properties of a node based on its connectivity is thoroughly explored in epidemiology. A degree of a node, interpreted as multiple social interactions, can be used to identify high-risk individuals[141,201] to target them in vaccination campaigns. The importance of network hubs in epidemiology is apparent[141,201]. The influence of more connected individuals in a network can also be observed in the context of information spreading in social networks[202]. However, the involvement of hubs can also have the opposite impact. They can act as “firewalls" and prevent information from spreading[203]. Hence, it is beneficial to sometimes target the less connected “middle-class" nodes.

We use a degree-based scheme to choose the node for introducing the mutant[54]. The probability of being chosen is given by $p_j = e^{\alpha k_j} / \sum_{i \in N} e^{\alpha k_i}$ with k_i being the degree of a vertex i. Parameter α controls the impact one's connectivity has on its role. In particular, a positive value of α moves the belief mutation to the hubs, $\alpha = 0$ is equivalent to randomly placing the mutant on any node, and $\alpha < 0$ increases the probability of the mutation arising at the periphery.

Similarly to the random mutation allocation, all simulations for targeted mutation placement resulted in a stag hunt takeover. Varying values of α did not affect the overall average fraction of each strategy in the population; hence, we focus on its effect on the takeover times. We compare the takeover times relative to the random belief mutation placement ($\alpha = 0$).

The effect of targeted belief mutation differs notably between different types of networks, as seen in Fig. 4.2. For the BA networks, there is a striking distinction between positive and negative values of α (a difference between targeting the hub or the periphery). For the lowest mutation rate $\mu_B = 10^{-5}$ on the BA network (depicted on the bottom panel of Fig. 4.2), the takeover times for all analysed values of α do not vary significantly and are shorter than the random case. However, as the mutation rate increases, the differences arise, with negative values of α leading to a similar takeover time as $\alpha = 0$ and positive values leading to a slower takeover. Differences between parameter values are more visible as the mutation rate increases. This lack of notable differences between negative values of α and $\alpha = 0$ can be caused by the fact that the periphery in the scale-free network is significantly larger than the hubs. Hence, if the mutation is introduced randomly, it is more likely to occur on a less connected node. This result indicates that targeting less influential (connected) individuals on the scale-free network accelerates takeover.

A similar effect is found on the ER network (the top panel of Fig. 4.2). The takeover times for higher mutation and negative values of α converge to values for random mutation placement and positive values of α lead to a slower takeover. The effect of changing the belief mutation rate value is less notable.

The introduction of targeted mutation has a different effect on the NWS network (middle panel of Fig. 4.2). As the degree distribution of nodes is not as divided as in the case of the scale-free network, different values of α do not affect the takeover times in such a diverse way. Almost all non-zero values of α lead to a lower takeover time for a low belief mutation probability. As the mutation value increases, the relative takeover time grows and oscillates around one.

Thus, the impact of targeted belief mutation depends highly on the network type and node degree distribution. We show that the most influential or connected individuals do not always induce a change in social behaviour in a structured population. However, a committed minority of regular individuals can alter social conventions. We thus delve deeper into how different network structures can impact the power of commoners.

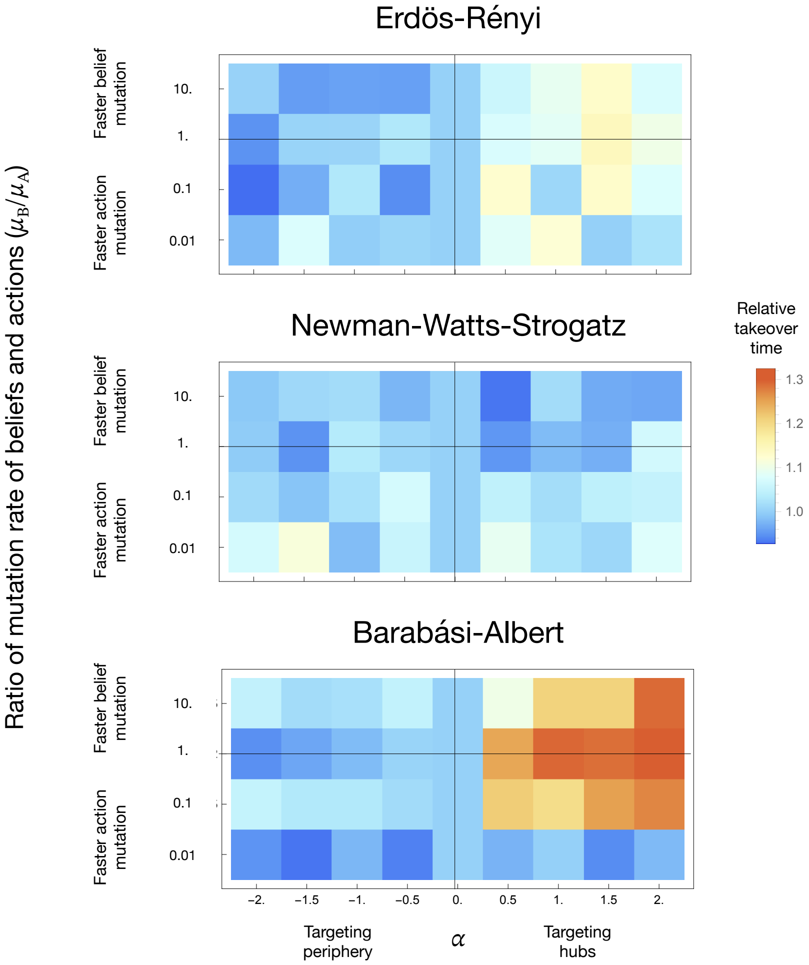

Figure 4.2: Relative time for stag hunters to take over with node targeting. For each value of μ_A/μ_B, the time to takeover is compared to the case of random belief mutation placement ($\alpha = 0$). The impact of varying parameter α is most visible on networks with high node degree heterogeneity (BA and ER) and negligible on the NWS network, characterized by high node degree homogeneity. Positive values of α lead to the targeting of hubs, which increases the takeover time. The time to takeover can be decreased by targeting the periphery ($\alpha < 0$). The presented results are averaged over 1000 runs per network type and parameter set.

Social tipping points

Theoretically, a committed minority can produce a "bandwagon" effect and cause a population-wide social change. The importance of the commitment to the cause, rather than the wealth and power of its supporters, is indicated in critical mass theory[204]. The threshold, which the minority group has to cross to ensure a successful change at the societal level, varies across the literature, ranging from 10% of the population up to 30%-40%[205–208]. Among others, the value of the tipping point may depend on the underlying network structure of the population[209].

We analyse our results to determine an average tipping point value (and standard deviations) for the network types used and three values of $\alpha = \{-2.0, 0.0, 2.0\}$ (Fig. 4.3). We assume a given fraction of stag hunters to be a tipping point if, after surpassing it for the first time, the proportion does not fall below it. In other words, the population did not reach the tipping point ever before and did not fall below it after crossing it.

The belief mutation rate affects the tipping point's average value prominently. Mean and standard deviation increased with increasing mutation rate on all considered network types; see Fig. 4.3. Thus, a competing minority can hinder the spread of a strategy. With a high mutation rate, a second novel strategy can show up in the population before the takeover by the previous invader. The appearance of the new mutant can slow down or even revert the growth of a desired strategy. Thus, the takeover must occur to ensure growth before a new contender can appear. With an increase in the mutation rate, only a larger group can take over the population uninterrupted, leading to a higher value of the tipping point. Hence, we can conclude that in the absence of a competing group, a minority of around $15 - 30\%$ has enough power to alter the social behaviour of the population. High mutation rates result in increased stochasticity and an increase in the standard deviation.

The value of the tipping point varies between the network types, with the value for small mutation and negative α being 19% for NWS and 25% and 28% for ER and BA, respectively. As shown in Fig. 4.1, the NWS network's takeover time is shorter than other network types. Hence, a single mutant appearing on a network can take over faster, reducing the possibility of another invader appearing and hindering the process. In this case, the effect of targeted belief spreading α is not drastic. The differences in values may be due to the stochasticity present in the system, and also, the parameter does not change the portion of new belief followers in the population.

We thus show that the type of underlying network structure can have a crucial impact on the tipping point value. We observe the tipping point value of 19% on networks with a high clustering coefficient. A lower clustering leads to a higher

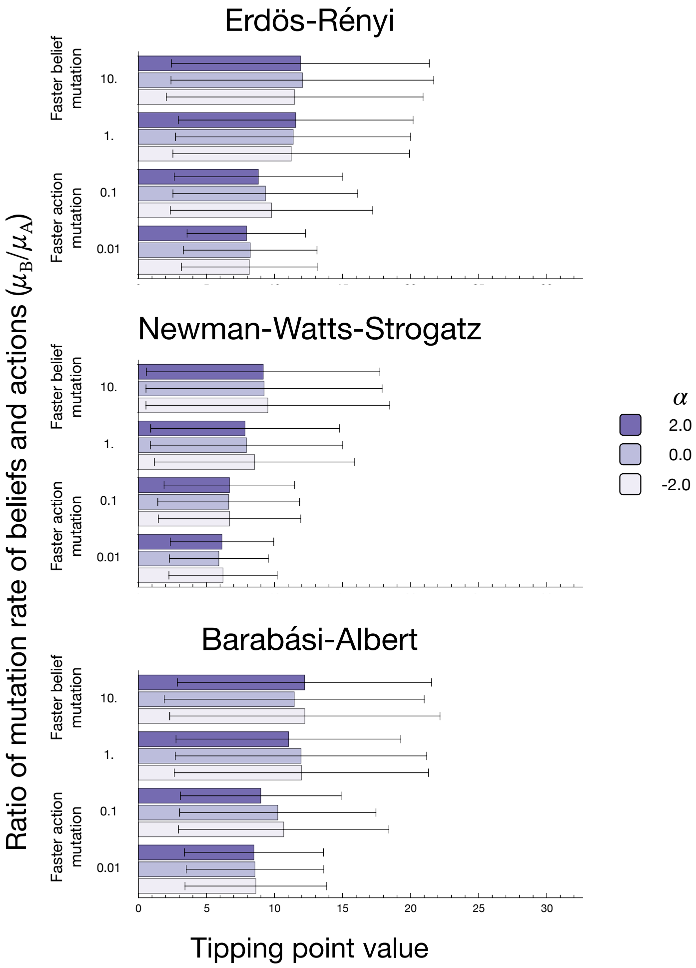

Figure 4.3: Average values and standard deviation of tipping points. The coloured bars represent the average tipping point value and the error bars represent the standard deviation. The tipping point values for the ER and BA networks are similar since both types of networks share similar values of parameters. The NWS network is characterised by a higher clustering coefficient, which leads to lower tipping point values. Increasing the value of the mutation rate introduces more stochasticity in the system and leads to a higher value of the average tipping point and a higher standard deviation value. The parameter α does not visibly affect social tipping points. The results are averaged over 1000 runs per network type and parameter set.

value of the tipping point of around $25\% - 30\%$.

Discussion

Our study illuminates the role of collective beliefs in fostering cooperation and trust among self-interested, rational individuals[191,210,211]. Similar to influential tags or symbolic markers, these beliefs are unbound by specific actions, catalysing a swift spread of cooperative behaviours in structured populations. Our work proposes a framework for future research to explore the dynamic interplay between consensus mechanisms and network structure, including the pivotal role of charismatic leaders[212], conformity dynamics and eventual impacts on actions. Gokhale et al.[191] explored the importance of consensus-forming mechanisms such as frequency-dependent decision-making, majority vote and random narrative choice. While these various processes have the potential to change the outcome of the dynamics in this study, we have focused on the frequency-dependent (“Group Think") mechanism[213].

Structured populations are a hotbed for cooperation[95,194,195]. Networks allow cooperators to flock together and interact with one another, subsequently protecting them from being exploited by the defectors. Many parameters of real-life social networks, like the degree distribution, are said to sustain cooperative behaviour[214,215]. To determine the effects of specific network properties on the evolution of cooperation, we implement three classes of random networks. While random networks such as scale-free networks might not be an appropriate representation of empirically observed ones[216], performing simulations on multiple random networks allows us to focus on general network properties rather than the effects of specific social structures. We show that specific network attributes like a higher clustering coefficient or low diameter are powerful accelerators for spreading cooperation and trust, mainly when high belief diversity exists. Thus, harnessing network structures and understanding their properties is necessary to propel the diffusion of desired behaviours. This concept, already applied successfully in targeted vaccination campaigns[217–219], has profound implications, especially in scale-free networks[220,221]. In this context, the role of well-connected individuals, or “hubs," is crucial[201]. Strategically targeting these hubs can amplify the dissemination of critical information, from marketing messages to disaster response updates[202,222]. However, this double-edged sword can impede the desired spread[203]. Introducing mutations on hubs can trigger cascading effects and propagate defectors[181,223]. Our simulations reveal that belief mutations on the network periphery are more effective in bolstering cooperation than targeting hubs. Remarkably, this phenomenon emerges only in networks with discernible hubs and periphery, suggesting a novel strategy: focusing on less influential individuals can be the key to fostering cooperation.

The impact of network structure on minority power is profound. Lower belief mutation values tip the scales, decreasing the average tipping point. In comparison, higher values may slow the takeover by a desired minority (Figure 4.3). With this understanding of social network structure and individual belief systems, it may be possible to strategise to ignite social change for good. Introducing novel beliefs to less connected individuals proves to be a potent catalyst, expediting cooperation diffusion. This insight explains why the most impactful social change often emerges from grassroots movements[224].

Methods

The problem of trust - the Stag Hunt

To formalise the problem of trust, we use the stag hunt game[15]. In the traditional form of the game, two hunters set out on a hunt to obtain food. Both players can choose to hunt either a stag or a hare. Hunting a stag is difficult and cannot be done alone; however, it yields a higher payoff than a hare. Hence, if both players coordinate on hunting a stag, each obtains a high payoff of P_S. However, if only one of them hunts a stag, they get a payoff of 0, as the hunt is unsuccessful. Conversely, hunting a hare is easy and can be accomplished alone. Thus, the payoff of a hare hunter is always equal to P_H, regardless of their partner's decision. The payoff matrix of the game and the resulting game dynamics are represented in Figure 4.4

This work focuses on an N-player version of the stag hunt, as introduced by[23]. In particular, a hunting party consists of N individuals. Each one has an action of hunting a hare or a stag. Pursuing a hare brings a risk-free payoff of $\Pi_H = P_H$ to each hare hunter, where P_H is the value of a hare. For a stag hunt to succeed, at least M stag hunters need to participate. Thus, if the number of stag hunters is less than M, then the hunt is unsuccessful, and the payoff of a stag hunter is $\Pi_S = 0$; else, a successful hunt yields $\Pi_S = P_S$. The value of the caught quarry thus grows linearly with the number of participants in the hunt. This expansion of the 2-player stag hunt allows us to preserve an essential feature of the 2-player game - successful cooperation always brings a higher payoff than defection. This need not be the case in other versions of the game, which could lead to different interesting dynamics but are not considered in this work.

Similarly to the 2-player version of the game, in a population predominantly hunting hare, choosing a stag is risky - an individual is not guaranteed to assemble a hunting party consisting of enough other stag hunters. Only if a significant enough fraction of players hunt stag is it safe to choose the bigger prey. How does one overcome the initial risk of hunting stag in a fully hare-hunting population to move to the more profitable endeavour of pursuing a stag?

A solution to the above dilemma is posited via the inclusion of collective narratives by Gokhale et al.[191]. The authors assume that each individual believes in narrative one (or two) personally, and the group believes in one of those narratives. The individuals then condition their actions on the narrative chosen by the group. Therefore, each player's strategy consists of three elements -

- action taken by the individual when the group believes in narrative one
- action taken by the individual when the group believes in narrative two and,

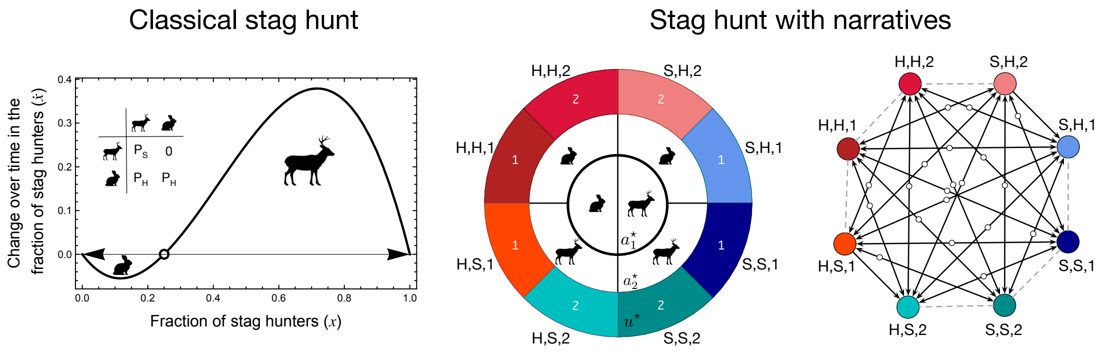

Figure 4.4: Left panel: In the classical two-player stag hunt game, two individuals decide to hunt for a stag or a hare. If both choose to hunt a stag together, they successfully hunt one. Hunting a stag brings a larger payoff than hunting a hare, but hare-hunting does not require any coordination of actions and can be achieved alone. However, the players do not know their partner's action preferences. In an infinite population, change in the fraction of stag hunters ($\dot{x}$) depends on the current value of x. If there are enough stag hunters in a population, hunting a stag is profitable. However, stag hunting is not favoured if the fraction of stag hunters is low $x < x^*$. The value of x at which the direction of the change shifts (the unstable internal equilibrium x^*) is represented with an open dot. How do we convert a population of hare hunters to stag hunters? Introducing collective narratives provides a solution. Central panel: In the stag hunt with narratives, the strategy of each individual consists of three elements. The centremost layer (a_1^*) corresponds to the action taken by an individual when they find themselves in a group believing in narrative 1, the options being stag or hare. The middle layer (a_2^*) shows the two possible actions that can be taken in the group believing in narrative 2. The outermost layer (u^*) depicts an individual's two possible beliefs in narrative 1 or 2. A strategy is then represented as ($a_1^*, a_2^*, u*$). Thus, in all, there can be eight strategies. Right panel: Like the two-strategy outcome (left panel), the right panel shows the result of the eight-strategy case in an infinitely large, well-mixed population. White points represent the unstable equilibria. If two strategies have the same payoff when played against each other, the change in composition may happen by neutral drift - indicated by the grey dashed lines. Here, we see two paths from a hare hunting population ((H,H,1) or (H,H,2)) to stag hunting. If an initial population consists of only (H,H,1) individuals, it may be taken over by (H,S,1) individuals by chance. From there, the dynamics would lead to a takeover of (H,S,2) individuals, and the population would end up drifting neutrally between the stag-hunting strategies without the possibility of reverting to hare hunting. A similar transition may also occur if first (H,H,2) and then (S,H,2) individuals take over the initial population via drift. The plots are generated for $N = 5$, $M = 4$, $P_H = 1$, $P_S = 4$ with $N = 2$, $M = 2$ for the two player case. The central and right panels have been adapted from Gokhale et al.[191].

- narrative the player personally believes in.

For example, a (H,S,1) player would hunt a hare if the hunting party believes in narrative one and a stag if the party believes in narrative two. The individual personally believes narrative one to be true. Thus, eight strategies can be present, as shown in Figure 4.4.

Importantly, we do not make assumptions about the narratives' contents. Beliefs held by individuals neither impact their payoffs nor the actions taken directly. Believing in either of the narratives does not make players prone to choose specific actions, and it does not give them additional payoff for choosing them. Still, introducing collective narratives leads to rich game dynamics, as shown in Figure 4.4.

Different ways of determining the collective narrative can exist, such as groupthink[213], majority vote[225,226], dictatorship, charismatic individuals[212] and so forth. In this model, hunters make decisions based on a frequency-dependent process. The choice of the narrative believed in by the group is random and depends on the composition of the hunting party. The probability of each of the narratives to be chosen is proportional to the fraction of the believers in the given narrative in the group.

Narratives can act as coordination devices, allowing stag hunting to take over the population[191]. Thus, the model explains how moral-free beliefs can influence game dynamics but assumes that the players interact within a well-mixed population.

In a realistic society, social ties, family connections or geographic closeness can cause specific individuals to interact more frequently than by chance. Similarly, organically formed hunting parties can be expected to include a different number of participants rather than be an artificially chosen, constant size. Varying group sizes can significantly impact the game dynamics[19,227]. The analysis of the effect of group size diversity on our game is presented in the Supplementary Material. Hence, the assumption of well-mixed populations cannot always be substantiated.

Structured populations

Random networks represent human societies more accurately than complete ones[228]. We implement three classes of random networks frequently considered in the literature to analyse the impact of particular network properties on evolutionary dynamics.

Erdös and Rényi[229] proposed a random network to model real social networks. The Erdös-Rényi (ER) network is characterised by a high degree of homogeneity. It is formed by generating n_v nodes and n_e random edges connecting them.

Many social networks are said to have "small-world" properties[230–233], meaning that any two individuals in the network can reach one another via a small number of links (steps). Hence, our analysis implements a small-world network generated by the Newman-Watts-Strogatz (NWS) algorithm[234]. In this algorithm, first, a d-dimensional lattice is generated. Then, a new edge is drawn for each vertex with probability p. An NWS network has a high clustering coefficient and a small average path length between any two vertices.

Furthermore, some members of society are typically more connected and, as a result, more influential than others. These individuals are represented by hubs - vertices of the network with a high degree. However, the majority of the population is not as well connected. Such diversity within the individuals is not present in either of the networks mentioned above. Hence, we use a Barabási-Albert network (BA)[40], with a power-law degree distribution. The Barabási-Albert algorithm is based on preferential attachment. A network grows at each time step by adding one node and connecting it to m nodes already present. The probability of a vertex being connected to the new one is proportional to the attachment function $A(k)$, with k being the node's degree. The attachment function $A_{BA}(k) \propto k$.

Differences in degree distribution between the three networks are presented in Figure 4.5.

For the results obtained for networks generated by different algorithms to be comparable, we keep the network size ($Z = 32$) constant. The parameters of the generating algorithms were chosen so that the networks would have a similar number of edges. First, the minimal connectivity of the BA network was selected to be equal to the stag-hunting threshold ($m = M$). By construction, all BA networks with the same minimal connectivity are characterised by the same number of edges, computed as $m(m-1)/2 + (Z-m)m$. Then, this value is used to parametrize the ER network ($n_e = m(m-1)/2 + (Z-m)m$). Due to the random component of the NWS algorithm, it is not possible to set a given number of edges in the network. However, the expected number of edges can be computed as $k(d+p)$ (or $(d-1)(1+p)$ if d is odd). Hence, the probability of adding an edge p and initial lattice dimensionality d were chosen for the expected number of edges to equal the other networks. The parameters of interest of the networks are presented in Table 4.1.

The similarity in the network size and number of edges allows us to focus on the effects of the properties of interest, like the degree distribution, global clustering coefficient and diameter.

Table 4.1: Parameters of networks used in simulations.

	Erdös-Rényi	Newman-Watts-Strogatz	Barabási-Albert
Algorithm	Randomly generated edges	Randomly generated edges	Preferential attachment
Size	32	32	32
Average degree	7.375	7.375	7.375
Average number of edges	118.0	118.0	118.0
Parameters	Number of edges $n_e = 118$	Initial lattice dimension $d = 6$ Probability of adding an edge $p = 0.24$	Minimal connectivity $m = 4$
Average global clustering coefficient	0.23	0.44	0.31
Average diameter	3.22	3.61	3.02

All networks used in the simulations share the same size and a similar average node degree. The effects of different degree distribution and varying values of clustering coefficient and diameter are of interest.

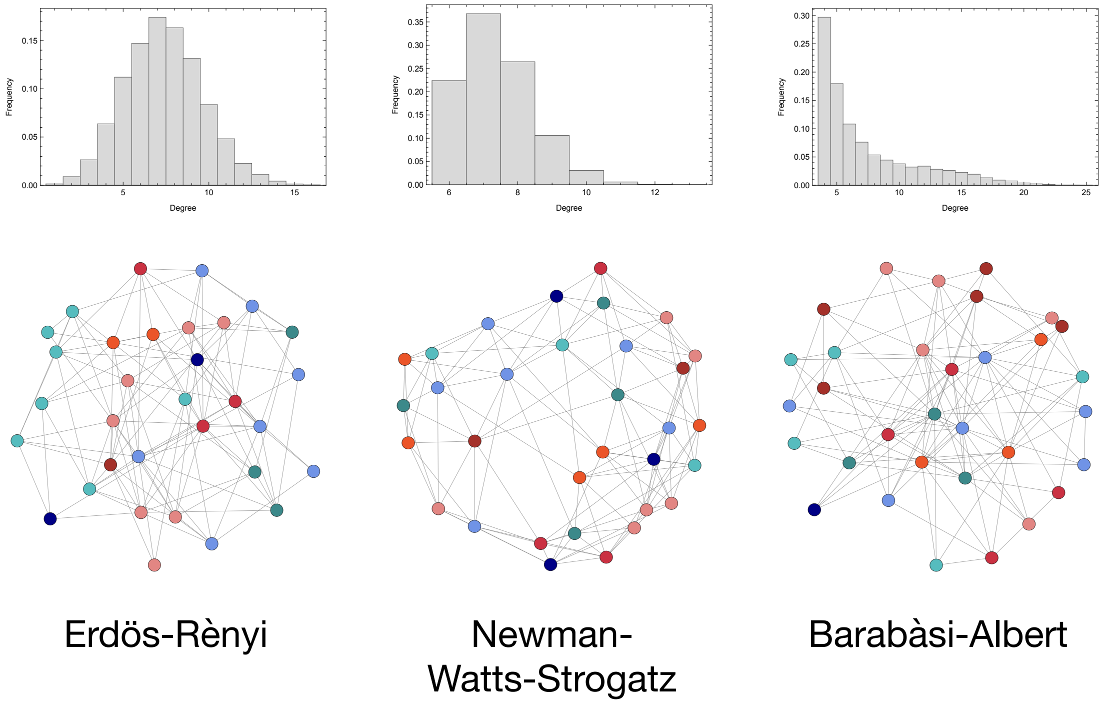

Figure 4.5: Degree distribution and an example of the three types of graphs used in the simulations. In the Erdös Rényi, the edges are generated randomly. The Newman-Watts-Strogatz graph is a small-world network. In the Barabási-Albert network, some vertices (hubs) are characterised by much higher connectivity as compared to the rest (periphery). For all graphs, $Z = 32$. The colors of the vertices represent strategies according to the scheme presented in Figure 4.4. An analysis of varying network sizes from 32 to 252 is provided in the Supplementary Material (Supplementary Figure B.3).

Updating actions and beliefs

A belief frequently involves a complex system of stories, values, orientation, perspective, and more[235]. Due to its complexity, it is unlikely to appear in society spontaneously at the same rate as new behaviours do. Individuals are far less likely to invent a new belief system or culture than explore novel behaviours[236]. Arguments can also be made in the opposite direction, and hence, we assume that actions and beliefs appear at different rates. Namely, we introduce two uncorrelated mutation rates - μ_A and μ_B. The former applying to actions taken by an individual (two first elements of the strategy) and the latter influencing the belief (the third element of the strategy). We assume that change in actions happens during reproduction, capturing the notion of offspring being prone to experiment and try actions different from those displayed by their parents. In this setup, a "mutation of actions" occurs at most once in an individual's lifetime and can be seen as a cumulation of all the changes they have undergone. Simultaneously, we assume that a change in belief is more likely to happen in a later stage of life and is caused by a cultural externality. Hence, the "belief mutation" occurs independently from reproduction. Once appeared, actions and beliefs spread in the population in the same evolutionary process. Hence, we can use the ratio of the two mutation rates to proxy the timescale ratio between the action and belief propagation processes.

Interaction dynamics

Birth-death. Our model uses a birth-death Moran process[6,237]. Every generation consists of Z discrete time steps (Z corresponding to the population size) so that (on average) every individual has an opportunity to reproduce. In each time step, a belief mutation occurs with probability μ_B - a belief (the third element of the strategy) of a randomly chosen individual is set to one of the two existing beliefs, each with equal probability. Subsequently, the fitness of all individuals is determined. In each time step, one player reproduces with probability proportional to its fitness. The offspring is identical to the parent unless a mutation occurs (with probability μ_A). If a mutation occurs, actions (the first two strategy elements) are drawn from four possibilities (H-H, S-H, H-S or S-S). Regardless of the action mutation, the offspring inherits the belief from the parent unchanged. One of the neighbouring individuals (or the parent itself) is randomly chosen to die and be replaced by the offspring. The schematic of the process is presented in 4.6.

Fitness. The fitness of an individual (ψ_i) depends on a payoff received after engaging in one hunting game with all its neighbours (Π_i) and the selection intensity (ω)[6] as $\psi_i = 1 + \omega\Pi_i$, where $\Pi_H = P_H$ and $\Pi_S = P_S$ if the hunt is

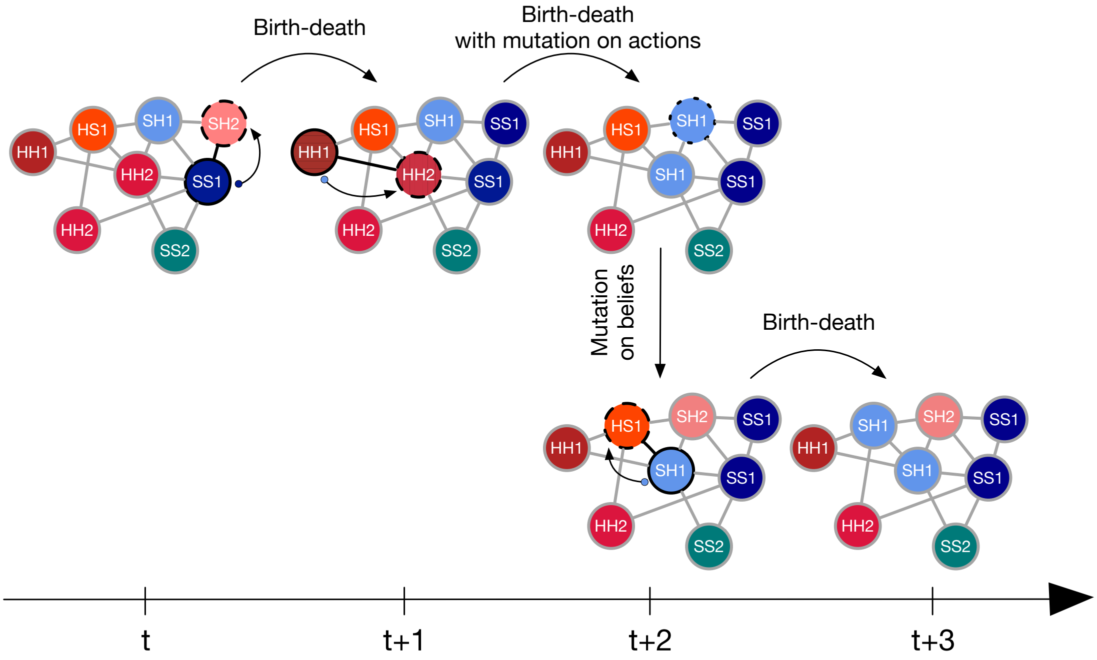

Figure 4.6: Scheme of the dynamics Strategies are updated by the birth-death process. An individual is chosen to reproduce (represented by a solid black outline on the figure) with probability proportional to their fitness. A neighbour of the reproducing individual is chosen randomly to die (indicated by a dashed black outline) and gets replaced by an identical offspring of the reproducing individual (as represented by an arrow and a small dot). In each step of the birth-death process, a mutation of actions might occur with probability μ_A. If a mutation occurs, the newly produced offspring has different actions than the parent but the same belief. A belief mutation can occur in each time step with probability μ_B. The belief of a randomly chosen individual (represented by a dotted black outline) is randomly set to one of the two beliefs present in the population.

successful and $\Pi_S = 0$ otherwise. The selection intensity can be used as a proxy for the importance of the hunt relative to other activities affecting one's fitness. That is, for $\omega = 0$, the game (and therefore one's strategy) does not affect the fitness and increasing ω enhances the game's impact on the fitness[238]. In the main text, we continue with $\omega = 1$ while different values of selection intensity are further explored in the Supplementary Material (Supplementary Figure B.4).

Simulation parameters. The simulation results presented in this work were obtained for populations of size $Z = 32$. For computational ease, we choose a population size that could characterise a local hunter-gatherer residential group[239], but large enough to examine differences in network properties. Results of simulations for varying population sizes are presented in the Supplementary Material (Supplementary Figure B.3).

We start with an egoistic population, everyone following the (H,H,1) strategy. Thus, they always hunt hares, and only belief one is present. Starting with a single belief allows us to analyse the effects of introducing the second belief.

As mentioned above, three types of networks were implemented - Erdös-Rényi with 118 edges, Newman-Watts-Strogatz with initial lattice dimension $d = 6$ and probability of adding an edge $p = 0.24$ and Barabási-Albert with minimal connectivity of a node $m = 4$. The parameters and properties of the generated networks are specified in Table 4.1. Due to the random nature of the ER network, in a small proportion of the cases, individuals had fewer neighbours than necessary for the stag hunt to be successful (the number of neighbours never falling below 1). Despite some hunting parties being too small to support cooperation, the average results for these networks do not differ from the ones with only big enough groups. Further investigation of the issue is presented in the Supplementary Material. Additionally, we compare the results on random graphs with ones obtained in a well-mixed population, where individuals play the stag hunt game with 8 random players. At each time step, any two individuals can be chosen to reproduce and die. Each simulation lasts for a maximum of 5×10^5 generations, where each generation consists of Z time steps. We use $\mu_A = 0.001$, $P_H = 1$, $P_S = 4$, $M = 4$, $\omega = 1$, $Z = 32$. For an exploration of some of these parameters, see the Supplementary Material. Ten networks were generated for each parameter set and network type, and 100 simulations were run on each. The results for each network type are thus averages over 1000 realisations.

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Author contributions

M.F. developed the algorithm and ran the simulations. Both authors conceived the study, developed the model, analysed the results and wrote the manuscript.

Competing interests

The author(s) declare no competing interests.

Data availability

Data used in the analysis is available on Github at `https://github.com/tecoevo/structured_beliefs`.

Code availability

Appropriate computer code describing the model is available on Github at `https://github.com/tecoevo/structured_beliefs`.

5

Discussion

Mathematical modelling of social and biological phenomena is invaluable for understanding the underlying processes[240–242]. Although simplifications are necessary for creating tractable and functional models, introducing more complexities is critical to represent the real world accurately. Faithful modelling of those dynamics ensures drawing accurate conclusions and predictions. To capture complex aspects of natural systems, elements of structure can be introduced[243,244]. In Evolutionary Game Theory (EGT) models, structure can be understood in many ways[245], for example, social[37], spatial[246], and temporal[49]. In this thesis, I have shown how introducing those structures can significantly change model results, proving the importance of complex model extensions.

The three main chapters of this thesis demonstrate an overview of different kinds of models, with varying levels of generalisation present in each as presented in Figure 1.1. I am beginning with Chapter 2, which shows a broad overview of the topic at hand, through Chapter 3, introducing a more specific model, which can still be applied in a variety of systems, and finishing on the most specialised Chapter 4, which focuses on a specific system. Each of those approaches serves a different purpose and is appropriate to use depending on the aim of the study[247]. Literature reviews and synthesis provide the reader with an overview of the field and facilitate the detection of new connections and niches. Although those general approaches highlight fundamental processes and universal trends, they may not be sufficient for explaining particular behaviours seen in specific systems. On the other side of the spectrum, models are created to represent given phenomena, as presented in Chapter 4. Those models sacrifice generality to accurately represent the issue and ensure a thorough analysis of its causes and results. Showcasing a variety of models across the spectrum displays the importance of structure in EGT, not only in specialised models but also in the general framework as a whole.

The evolution of cooperation is a unifying theme in this thesis. Cooperating behaviours can be observed across organisation scales from groups of cells[248] and microbes[249] to human populations[37,96]. Consequently, conclusions from studying particular systems can enlighten research in seemingly unrelated areas. The development of multidisciplinary research leads to discovering non-trivial connections. Researchers use EGT in a plethora of areas, including but not limited to ecology[173], oncology[123], economics[250], and epidemics[251]. The benefits of transferring knowledge and adapting modelling frameworks between those fields are undeniable, yet more challenging to obtain than it may seem. As more and more emphasis is placed on interdisciplinary research, new challenges arise in the community, and more interdisciplinary collaborations are required[252]. Chapter 2 represents an example of an effort to facilitate the recognition of possible collaboration opportunities, drawing connections between two rapidly developing healthcare modelling areas. In particular, the chapter reviews the development of Public Goods Games (PGGs) in epidemiology and oncology, providing an introduction to quantifying cooperation in disease modelling. Considered cases vary from modelling the behaviour of cancer cells to human decision-making in the face of a pandemic, showing the breadth of applicability of the EGT framework across the scales of organisation. Simultaneously, by paralleling the use cases of PGGs in the two fields, the review indicates possibilities of knowledge transfer. This chapter provides a general introduction to EGT models and showcases the adaptability of the framework.

While space and social or family ties are a common addition in EGT models, temporal aspects are largely overlooked. Still, time is an essential element of numerous real-life systems and significantly affects observed processes[25,253,254]. Hence, introducing temporal structures into the modelling frameworks and understanding their impact on evolutionary dynamics is noteworthy. Notably, an effect of time delays caused by consideration of the duration of different processes is of interest, particularly when different types of individuals experience delays differently[31,255]. However, those model extensions act as a two-edged sword, leading to a significant increase in model complexity and reducing the possibility of analysis of the dynamics. In order to combat the challenges posed by the increased complexity, multiple solutions were proposed, including numerical solutions for simple games[33] f or small-delay approximation[34]. In Chapter 3, another approach is proposed, and a compartment approximation model of strategy-specific delays is presented. The model is then shown to approximate the dynamics of the delay system accurately. The presented results indicate that a delay is detrimental to the concerned strategy. Introducing a delay of a strategy leads to a decrease in its frequency in the equilibrium or a reduction in its basin of attraction if it can take over the population. Subsequently, the results show that the delays lead to a discrepancy between the original game and the effective game played, pointing towards possible transitions between Prisoner's Dilemma (PD) and Stag Hunt (SH) and Snowdrift (SG) games, as well as SG and Harmony (all cooperative) game. These results prove the significance of time delays in EGT modelling, as they impact the nature of the game and, hence, the dynamics present.

Although the importance of strategy-specific time delays in game dynamics is evident, the effect on more complex games has yet to be studied extensively[31,162,256]. Due to its relative simplicity, the Kindergarten model, introduced in Chapter 3, can be easily extended to accommodate multiplayer games and games with more than two strategies. The study of delays in those complex games is an interesting future research direction, allowing for drawing more general conclusions about delay effects in games.

Aside from time, space structure has a significant impact on evolutionary dynamics. Hence, elements of network theory have historically been a significant part of the development of EGT models[37,88,257,258]. Starting with regular graphs[38] and moving to random networks, the networked structure is a crucial component influencing evolutionary dynamics in games. Similarly, multilevel and higher order networks are a promising avenue for future studies in the field[62,259]. As recounted in Chapter 2, they provide an excellent toolbox for representing complex, multidimensional or indirect interactions and processes. Appendix C further displays the potential effect of multilevel networks on evolutionary dynamics. In the presented model, a predator-prey interaction is considered, with both species moving across a network of habitat patches. Notably, the dispersal networks are specific to a given species and do not have to coincide. A variety of factors can cause this discrepancy: properties of the considered species, like size or speed, or due to the terrain conditions themselves. The preliminary results presented in the Appendix examine the dynamics on a 3-patch network while the rate of movement of a predator is changed on a single network edge. Still, even in such a small network, the impact of the multilevel network is evident. With only one patch and no movement, osculations in the number of prey a predator is observed. However, after introducing the dispersal network, and depending on the dispersal rates, the dynamics may lead to an extinction of predators on some or all of the patches or stabilisation of the dynamics at positive values for both species. The preliminary results presented in Appendix C indicate a promising direction of studies of structured games and, subsequently, their use in modelling ecological interactions.

Elements of ecological systems are rarely static. As shown in Appendix C, introducing dispersal in the predator-prey model can significantly impact the dynamics. Likewise, other EGT models are impacted by the inclusion of movement. When players can travel between network nodes, the size and composition of groups in the game are no longer constant, leading to more complex dynamics[145,260]. Moreover, with strategic movement, individuals have more agency over their situation. Subsequently, cooperators can co-evolve assortative behaviour to gain the upper hand over defectors and avoid being exploited[261]. Similarly, in social settings, the networks of interactions are not stable. Individuals may sever a link with another player and seek other connections to improve their payoff. A plethora of mechanisms can be introduced to govern the re-linking decisions, including dependence on strategies of co-players[143,262,263], strategy-independence[144,264] or based on secondary player characteristics like attractiveness[265], reputation[266] and satisfaction[267]. Both movement and re-linking allow for the inclusion of additional complexities into the EGT models, representing a type of process that can co-evolve with cooperation in structured populations[142].

As the structure is proven to be a significant element of EGT models, more complex tools are necessary to analyse them[268]. Those developments call for including elements originating from fields like network science, dynamical system theory or complex systems. Random and real-world networks are examples of model extensions which limit the possibility of analytical study of the system and require the use of other solutions[269]. Large, random networks are particularly challenging to analyse due to the stochasticity present. Stochastic simulations are a suitable tool for examining the dynamics on those networks. Using the Monte Carlo method[270], that is, performing multiple stochastic simulations on a range of networks assures that the results obtained do not arise solely due to the properties of a specific graph but rather general attributes of a network class. In Chapter 4, an agent-based model[271] is used – a simulation framework which allows the tracking of change in individuals players strategies over time. Subsequently, the model provides insight into the effects of spatial and social structure on evolutionary dynamics and the impact of individual positioning in that structure on their behavioural dynamics.

Chapter 4 examines the effect of network structure on the evolution of cooperation in the presence of collective beliefs in a multiplayer SH game. Three classes of random networks are considered: Erdös-Rényi[39], Barabási-Albert[40] and Newman-Watts-Strogatz[234], each characterized by different properties. The introduction of structure leads to a significant change in the evolutionary dynamics, accelerating the spread of cooperative behaviours in the population. Moreover, specific properties of underlying social networks, like high clustering coefficient or low diameter, are shown to be accelerators for cooperation spread. Subsequently, the results point to network parameters that could be altered to benefit cooperators. Still, transforming the network structure is a challenging task. Hence, the study proposes a targeted belief mutation scheme as an alternative solution. By basing the probability of introducing a new belief to an individual on their position on the network, it is possible to harness the network properties to favour cooperators. Surprisingly, focusing on the most connected individuals in the population, or hubs, is not the optimal strategy and can even be detrimental to the goal of spreading cooperation. Instead, targeting the periphery of a network makes it possible to support cooperators. Following the theme of the effects of less connected individuals on population dynamics, the study looks at the impact of minorities. Again, different network classes had a distinct effect on the value of the tipping point of the number of cooperators needed for the strategy to take over the population. By considering a range of network types, results presented in Chapter 4 provide an insight into the effects of network properties on game theoretical dynamics in structured populations. Moreover, due to the implementation of the agent-based modelling framework, the study shows the effect of influencing particular network nodes, leading to a better understanding of network positioning on evolutionary dynamics.

Change in beliefs may lead to change in actions. As shown in Chapter 4, sharing a belief system may promote cooperation among individuals. Hence, shifts in beliefs and opinions are a vital process that should be investigated to understand dynamics governing social change[272,273]. With the rise of social media popularity, a large source of data is created, providing researchers with readily available information on opinion and behavioural dynamics in the population with a clear underlying interaction network accessible[274,275]. The data collected in that manner can be used to inform studies on the public's attitude towards controversial topics[276], spread of fake-news[277] or the effects of information bubbles and echo chambers[278,279]. Using real-world data allows for the validation of the theoretical models and informs future modelling attempts.

Evolutionary Game Theory is a powerful tool used across a myriad of disciplines. Consideration of structure is a meaningful development in the field. This thesis introduces structure in terms of time, space, and social connections. Presented models range across scales of organisation and levels of generality, indicating the versatility of the framework and the importance of structure in it. By providing them with additional complexity, the structure allows models to depict the real world more closely, leading to a more accurate analysis of the underlying processes.

A

Appendices: Kindergarten Model: Approximating Time Delays in Evolutionary Games

The following include the Appendices of the manuscript
Kindergarten Model: Approximating Time Delays in Evolutionary Games
M. Fic, F. Bastian, J. Miękisz, C.S. Gokhale

Stability Analysis

Stag hunt

We perform a stability analysis of the stag hunt game's full defection equilibrium e_0. Its eigenvalues are given by:

$$\lambda_{0,1} = -\frac{\sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1}}{\tau_D} \tag{A.1}$$

$$\lambda_{0,2} = -\frac{\tau_D - 1 + \sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1}}{2\tau_D} \tag{A.2}$$

$$\lambda_{0,3} = \frac{\tau_D + 1 - \sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1}}{2\tau_D} - \frac{1}{\tau_C}. \tag{A.3}$$

$$\tag{A.4}$$

This equilibrium is always stable.

In contrast, the full cooperation equilibrium e_1 can change its stability. The eigenvalues of the equilibrium are given by:

$$\lambda_{1,1} = -\frac{\sqrt{(4a-2)\tau_C + \tau_C^2 + 1}}{\tau_C} \tag{A.5}$$

$$\begin{aligned}\lambda_{1,2} =& \frac{1 - \sqrt{4a\tau_C + \tau_C^2 - 2\tau_C + 1}}{2\tau_C} \\ & - \frac{1 + \sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1}}{2\tau_D}\end{aligned} \tag{A.6}$$

$$\begin{aligned}\lambda_{1,3} =& \frac{1 - \sqrt{(4a-2)\tau_C + \tau_C^2 + 1}}{2\tau_C} \\ & - \frac{1 - \sqrt{4b\tau_D + \tau_D^2 - 2\tau_D + 1}}{2\tau_D}\end{aligned} \tag{A.7}$$

.

The change in the stability of the equilibrium happens via transcritical bifurcation when $\lambda_{1,3} = 0$, which takes place when $\tau_C = m$. At this point, we observe the internal equilibrium reaching the full cooperation equilibrium ($e_1 = e_2$) and the stability of the two equilibria exchanges. For $\tau_C \geq m$, the full cooperation equilibrium e_1 is unstable, and e_2 does not exist. When e_2 exists, it is unstable, and the full cooperation equilibrium is stable.

Snowdrift Game

First, we present the stability analysis of the full cooperation equilibrium $e_1$of the snowdrift game. The eigenvalues are given by:

$$\lambda_{1,1} = -\frac{\sqrt{4b\tau_C - 2(c+1)\tau_C + \tau_C^2 + 1}}{\tau_C} \tag{A.8}$$

$$\lambda_{1,2} = \frac{1 - \sqrt{4b\tau_C - 2(c+1)\tau_C + \tau_C^2 + 1}}{2\tau_C} - \frac{1 + \sqrt{(4b-2)\tau_D + \tau_D^2 + 1}}{2\tau_D} \tag{A.9}$$

$$\lambda_{1,3} = \frac{1 - \sqrt{4b\tau_C - 2(c+1)\tau_C + \tau_C^2 + 1}}{2\tau_C} - \frac{1 - \sqrt{(4b-2)\tau_D + \tau_D^2 + 1}}{2\tau_D} \tag{A.10}$$

.

The change in stability of the equilibrium happens via a transcritical bifurcation when $\lambda_{1,3} = 0$. The bifurcation takes place when $\tau_D = n$. At this point, we observe one of the internal equilibria (e_2 or e_3 depending on the parameter values) and the full cooperation equilibrium exchange stability. For $\tau_D > n$, full cooperation is a stable equilibrium.

We perform the stability analysis of the full defection equilibrium e_0. The eigenvalues are given by:

$$\lambda_{0,1} = -\frac{|\tau_D - 1|}{\tau_D} \tag{A.11}$$

$$\lambda_{0,2} = -\frac{1 + \sqrt{\tau_C(4b - 4c - 2) + \tau_C^2 + 1}}{2\tau_C} + \frac{1 - |\tau_D - 1|}{2\tau_D} \tag{A.12}$$

$$\lambda_{0,3} = -\frac{1 - \sqrt{\tau_C(4b - 4c - 2) + \tau_C^2 + 1}}{2\tau_C} + \frac{1 - |\tau_D - 1|}{2\tau_D} \tag{A.13}$$

.

The equilibrium changes its stability via a transcritical bifurcation when $\lambda_{0,3} = 0$, which occurs when $(b < c + 1 \wedge \tau_D = p)$. The full defection equilibrium is stable if $(b < c + 1 \wedge \tau_D > p)$ and unstable otherwise. For the model assumptions not to be violated, we assume that $b < c + 1$ and hence, the full defection equilibrium e_0 is always unstable.

Prisoner's dilemma

We perform the stability analysis of the full defection equilibrium e_0. The eigenvalues of the equilibrium are given by:

$$\lambda_{0,1} = -\frac{\sqrt{(4c-2)\tau_D + \tau_D^2 + 1}}{\tau_D} \tag{A.14}$$

$$\lambda_{0,2} = -\frac{\tau_D - 1 + \sqrt{(4c-2)\tau_D + \tau_D^2 + 1}}{2\tau_D} \tag{A.15}$$

$$\lambda_{0,3} = \frac{1 - \sqrt{4c\tau_D + \tau_D^2 - 2\tau_D + 1}}{2\tau_D} + \frac{\tau_C - 2}{2\tau_C} \tag{A.16}$$

.

The full defection equilibrium is always stable.

Now, we perform the analysis of the full cooperation equilibrium e_1. The eigenvalues are given by:

$$\lambda_{1,1} = -\frac{\sqrt{(4b-2)\tau_C + \tau_C^2 + 1}}{\tau_C} \tag{A.17}$$

$$\begin{aligned}\lambda_{1,2} = &-\frac{1 + \sqrt{\tau_D(4b+4c-2) + \tau_D^2 + 1}}{2\tau_D}\\ &+\frac{1 - \sqrt{(4b-2)\tau_C + \tau_C^2 + 1}}{2\tau_C}\end{aligned} \tag{A.18}$$

$$\begin{aligned}\lambda_{1,3} = &-\frac{1 - \sqrt{\tau_D(4b+4c-2) + \tau_D^2 + 1}}{2\tau_D}\\ &+\frac{1 - \sqrt{(4b-2)\tau_C + \tau_C^2 + 1}}{2\tau_C}\end{aligned} \tag{A.19}$$

.

Full cooperation can change its stability via a transcritical bifurcation when $\lambda_{1,3} = 0$, which takes place when $\{\tau_D > c/(-b+b^2) \wedge \tau_C = r\}$. At the bifurcation point, we have $e_1 = e_2$ and the internal equilibrium exchanges stability with full cooperation equilibrium. For $\tau_D > c/(-b+b^2) \wedge \tau_C < r$ full cooperation is stable. In this parameter region the internal equilibrium e_2 exists in the relevant interval ($x_2^* \in (1,0)$) and is unstable. Outside this parameter space equilibrium e_2 does not exist and full cooperation is unstable.

Transition from a snowdrift to prisoner's dilemma

In Sec. 3, game transitions caused by time delays are discussed. Here, we are interested in exploring a less restricted parameter regime in the form of a general payoff matrix (3.1) and observed game transitions. In particular, we investigate the transition from the snowdrift game into a prisoner's dilemma, meaning from a game (snowdrift) that can exhibit two internal states[33] to the game of full defection, which can, in turn, become a bistability game. This implies we are interested in the case when the inequality $P < S$ (snowdrift) of the general payoff matrix becomes $P > S$ (prisoner's dilemma). We use the payoff matrix (3.46) as a case study, meaning if $P > 1.1$, the snowdrift game has become a prisoner's dilemma.

We start by continuing the branch of mixed equilibria e_2 in Fig. 3.4 outside of the interval $[0, 1]$ i.e. $x_2 > 1$ and observe that at $\tau_C \approx 0.65833239$ a saddle-node bifurcation sn occurs, which gives rise to e_2 as depicted in Fig. 3.4. Throughout the following discussion, we are particularly interested in the location of sn and the associated changes in the effective game with time delays. We explore the P, τ_C parameter plane where sn is depicted by the blue curve in Fig.A.1 a).

At $P \approx 0.91624583$, and $\tau_C \approx 0.761597$ the fold bifurcation sn enters the relevant domain ($0 \leq x \leq 1$) by colliding with the transcritical bifurcation tr_1 forming a codimension 2 supercritical pitchfork bifurcation pf_1; see Fig.A.1 b). Further increasing of P results in the unfolding of the pitchfork bifurcation pf_1 and the formation of two internal equilibria like Fig. 3.5. It appears that such configuration is quite robust in the parameter space as already indicated in Fig. 3.3 and noted by Miękisz and Bodnar[33] in the original DDE model. By further increasing P, we observe a second transcritical bifurcation tr_2 for sufficiently large time delay τ_C as indicated by the corresponding one-dimensional bifurcation diagram for $P = 1.15$ in Fig.A.1 c). Notably, we are already in the prisoner's dilemma parameter domain, but due to the time delay τ_C, we still have two internal equilibria similar to the snowdrift game. As indicated by Fig.A.1 a), this behaviour is robust until the saddle-node leaves the interesting interval $[0, 1]$. If P is further increased, sn leaves the interesting interval $[0, 1]$, similar to the pitchfork pf_1 caused by the collision of sn and tr_1. Indeed, sn collides for $P \approx 1.19206938$ and $\tau_C \approx 0.589708546$ with the previously observed tr_2 at a subcritical pitchfork bifurcation at $\tau_D \approx 0.589708546$ (see A.1 d)).

Extinction in a snowdrift game due to time delay

In A, we investigated the transition from snowdrift game to prisoner's dilemma and the change in the associated bifurcation structure, which depended on the location of the saddle-node bifurcations sn. Here, we consider a similar scenario of investigating the dynamics of changing P in the following general payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R = 2.0 & S = 0.5 \\ T = 2.95 & P = 0.01 \end{pmatrix} \end{array}. \tag{A.20}$$

In the following analysis, we always vary τ_C and keep $\tau_D = 5.0$ fixed. The corresponding bifurcation diagram, in Fig. A.2 b), depicts the x-component of

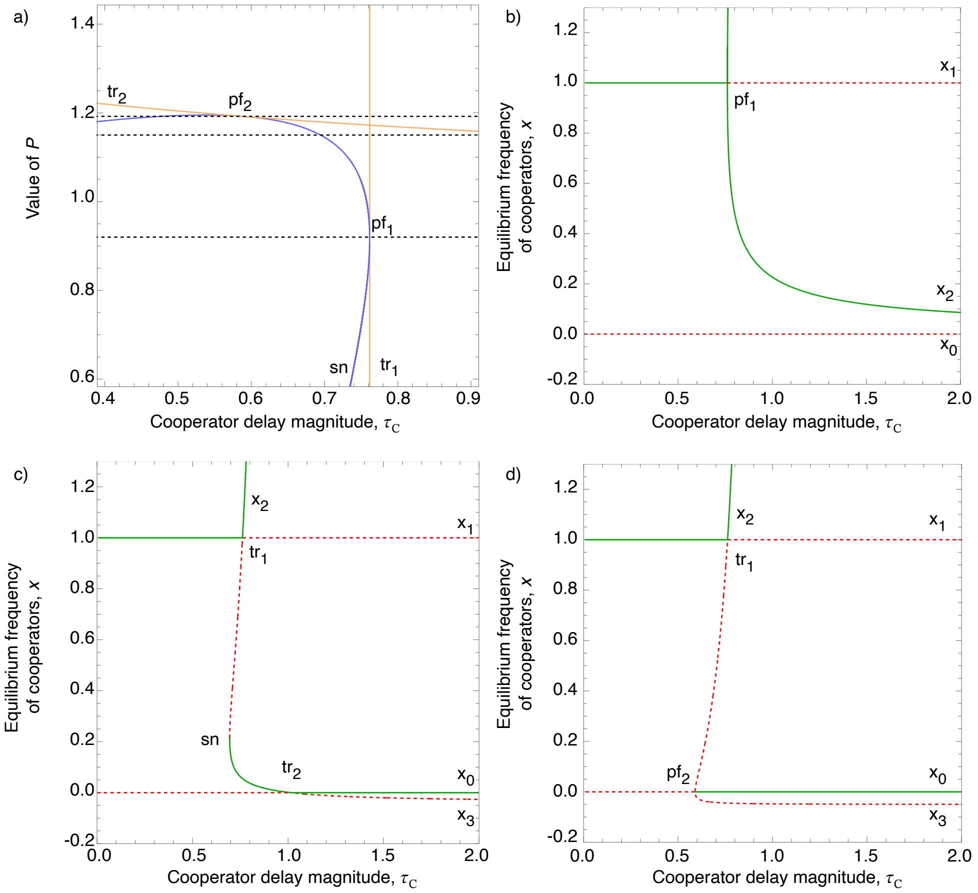


Figure A.1: a) The saddle-node bifurcation sn collides with the transcritical bifurcation tr_1 in a codimension two pitchfork bifurcation pf_1 and with the transcritical tr_2 in a supercritical pitchfork pf_2. **b)** At $P \approx 0.91624583$, $\tau_C \approx 0.761597$, the saddle-node bifurcation sn enters the biologically relevant interval $[0, 1]$ via a supercritical bifurcation pitchfork pf_1 giving rise to two internal mixed equilibria see **c)** and leaves the interval of interest via a supercritical pitchfork bifurcation at $P \approx 1.19206938$ and $\tau_C = 0.589708546$ (see **d)**). The remaining parameter are $R = 3.05$, $S = 1.1$, $T = 5$, $P = 0$, and $\tau_D = 2.0$.

the respective branch of equilibria. First, we note that both trivial equilibria e_0 and e_1 exchange stability at transcritical bifurcation tr_1 and tr_2 respectively. In particular, the scenario at tr_1 is similar to Fig. 3.5, as the associated branch e_2 will collide at the saddle-node sn_1 with e_3 giving rise to two internal equilibria. The extinction condition Eq. (3.11) $\rho_{2,3}(\tau_C, \tau_D = 5.0)$ (see the corresponding black dashed line) of both internal branches e_2, e_3 is larger than 1, implying the growth of underlying population.

However, we also observe an additional branch e_5 associated with tr_2. This branch bifurcates with e_4 at a second saddle-node sn_2. As indicated by $\rho_{4,5}(\tau_C, \tau_D = 5.0)$, the population of both branches goes extinct since $\rho_{4,5} < 1$. Therefore, by increasing the time delay τ_C, we note the effective game for Matrix (A.20) transition from bistability (separated by the repelling branch x_4)

to a prisoner's dilemma to coexistence.

Similar to A, we increase P of the payoff matrix (A.20), which results in the collision of sn_1 and sn_2 at a cusp bifurcation $\tau_C \approx 2.07708$, $P = 0.025$ as depicted in the two-dimensional bifurcation diagram in Fig. A.2 a). At the cusp bifurcation for $P = 0.025$ (see Fig. A.2 c), sn_1 and sn_2 are connected via a transcritical bifurcation for varying τ_C. For this degenerated case, the population of the connecting branch x_3 remains constant since $\rho_3 = 1$. Additionally, the population of x_2 decreases if $\tau_C < 2.07708$ since $\rho_2 < 1$ and increases for $2.07708 < \tau_C < 2.17929239$ until x_2 leaves the relevant interval at tr_1 with $\tau_C \approx 2.17929239$.

Further increase of P results in a detaching of x_2 and x_3. The $P = 0.03$ case is depicted in Fig. A.2 d). The branch x_2 is repelling separating cooperating and defection for $\tau_C < 1.97722372$, denoting tr_2 and x_3 entering the $[0, 1]$ interval. However, $\rho_3(\tau_C) < 1$ and the equilibrium e_3 is attractive, meaning the associated population goes extinct. In other words, in this scenario, an increase in the time delay causes the population to go extinct.

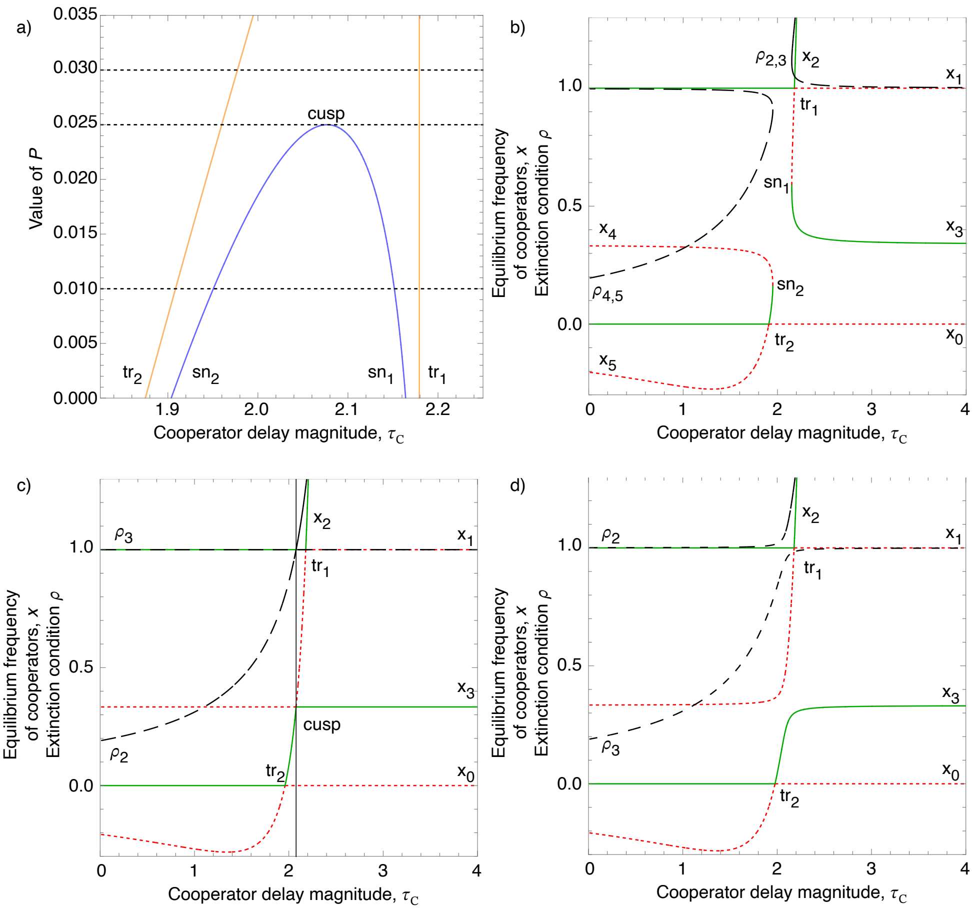


Figure A.2: **a)** The saddle-node bifurcations sn_1 and sn_2 colide at a cusp bifurcation. **b)** The branches e_4 and e_5 are associated with an decreasing population since $\rho_{4,5}(\tau_C) < 1$ (black dashed line) while the branches e_2 and e_3 are associated with an increasing population since $\rho_{2,3}(\tau_C) > 1$ (black dashed line). **c)** At the cusp bifurcation, the population of e_3 remains constant since $\rho_3(\tau_C) = 1$, and the growth of population of e_2 depends on the time delay τ_C, i.e. for $\tau_C < 2.07708$ the population goes extinct and grows otherwise. **d)** The detaching of e_2 and e_3 leads to an extinct population or sufficiently large enough time delay, since for $\tau_C > 2.17929238$ only e_3 remains as a single attractor in the interval $[0, 1]$ and is associated with a decreasing population. The remaining parameter are $R = 2.0$, $S = 0.5$, $T = 2.95$, and $\tau_D = 5.0$.

B

Supplementary Material: Catalysing Cooperation: The Power of Collective Beliefs in Structured Populations

The following Appendix contains Supplementary Material of the manuscript publish as **M. Fic**, C.S. Gokhale ”Catalysing Cooperation: The Power of Collective Beliefs in Structured Populations”, *npj Complexity*, vol. 1, no. 1, p. 6, 2024.

Varying hunting party size

The model presented by Gokhale et al.[191] assumes that individuals form groups of a constant size. However, social systems often exhibit group-size heterogeneity[231,280]. Group size diversity can impact the qualitative outcomes of the evolutionary games[19,227]. Therefore, we assess how varying the hunting party size affects cooperation in our model.

A mutant strategy can arise in a population consisting of otherwise homogeneous individuals. In the context of human social behaviour, the deviation from the status quo can be caused by a human's natural inclination to explore available options[281]. Suppose the change happens at a low enough rate. In that case, the novel behaviour can either take over the population or go extinct before a new type appears. Hence, it is sufficient to analyse the impact of group-size diversity on dynamics between pairs of strategies. In particular, we are interested in how the fraction of hare hunters ((S,H,2), (H,S,1), (H,H,1) or (H,H,2)) changes when confronted with stag hunters ((S,H,1), (H,S,2), (S,S,1) or (S,S,2)) in the presence of beliefs.

Considering a pair of strategies, (H,H,1) and (S,H,1) is equivalent to a basic N-player stag hunt game with no beliefs involved. We denote the fraction of stag hunters, (S,H,1), as x and the group size as n. Thus, the difference between the average payoff of a stag hunter and a hare hunter, $f(x,n)$, is given as,

$$\begin{aligned} f(x,n) &= \sum_{j=0}^{n-1} \binom{n-1}{j} x^j (1-x)^{n-1-j} [\Pi_S - \Pi_H] \\ &= \sum_{j=0}^{n-1} \binom{n-1}{j} x^j (1-x)^{n-1-j} [P_S \theta(j+1-M) - P_H] \qquad \text{(B.1)} \end{aligned}$$

where $\theta(x) = 1$ for $x \geq 0$ and 0 if $x < 0$, Π_H is a payoff of a hare hunter, Π_S is a payoff of a stag hunter, P_H is a value of hare and P_S is a value of a stag.

As per Jensen's inequality,[227] show that group size does not affect the game if $h(x,n) \equiv nf(x,n)$ is a linear function in n. Since $\frac{\partial^2 h}{\partial n^2} \neq 0$ for $n \geq M$, the stag hunt game will be affected by varying the size of the hunting party. The effect of changing n is unclear as $h(x,n)$ is neither convex nor concave concerning n.

Similarly, analysis can be performed for any pair of strategies ((a_1, a_2, u) and (a_1^*, a_2^*, u^*)). We denote an action chosen by an individual playing the first strategy in a group choosing their preferred narrative as a_u and in a group choosing a narrative preferred by the other strategy as a_{u^*}. The same principle is also used to denote the action taken by individuals playing the second strategy. The payoff of an individual depends on their action, which is indicated by an appropriate subscript. The difference between the average payoffs can be calculated as

$$\begin{aligned} f(x,n) = &\sum_{j=0}^{n-1} \binom{n-1}{j} x^j (1-x)^{n-1-j} \\ &\left[\frac{j+1}{n} \Pi_{a_u} + \frac{n-j-1}{n} \Pi_{a_{u^*}} - \frac{j}{n} \Pi_{a^*_u} - \frac{n-j}{n} \Pi_{a^*_{u^*}} \right], \end{aligned} \tag{B.2}$$

with x denoting the fraction of players choosing the first strategy.

In particular, for a pair of strategies (S,H,1)and (S,H,2), $f(x,n)$ takes a form of:

$$f(x,n) = \frac{P_S - P_H}{n}. \tag{B.3}$$

Hence, it is straightforward to show that the function $h(x,n) \equiv n f(x,n)$ is linear with respect to n. Analogous analysis can be performed for strategies (H,S,2) and (H,S,1). In those cases, the stag hunting strategy dominates the hare hunting, and the group size does not influence the dynamics (provided that $n \geq M$).

Except for these two strategy pairs, ((S,H,2), (S,H,1) and (H,S,1), (H,S,2)), $h(x,n)$ is not linear in n. Hence, it is reasonable to assume that group size diversity will impact a population's cooperation (stag hunting) level.

Based on animal group-size distributions, we perform a numerical analysis for three group-size distributions - truncated Poisson, geometric, and Waring[282,283]. In particular, the Waring distribution exhibits power-law degree distribution, a characteristic often obtained by preferential attachment[40]. We assume the average group size to be constant across the cases. For $E[N] \approx 8$, $M = 4$, $P_S = 4$, $P_H = 1$ the analysis shows, in Figure B.1, that varying group size strengthens cooperation, regardless of underlying group size distribution.

Impact of small groups

The ER network is generated randomly. Hence, some individuals may end up with fewer neighbours than the minimal size of the successful stag hunt (M). In simulations presented in this work, such small groups constituted 1.03% of all hunting parties. To check whether the presence of these groups influenced the results, we compared the average takeover time on the networks containing the small groups with the one on the remaining graphs. A two-sample t-test has been used. The results of all the tests are presented in Supplementary Figure B.2 The comparison was done within each of the 37 parameter sets considered.

No networks with small groups were present in one of the parameter sets. In three parameter sets, the simulations performed on the networks with small

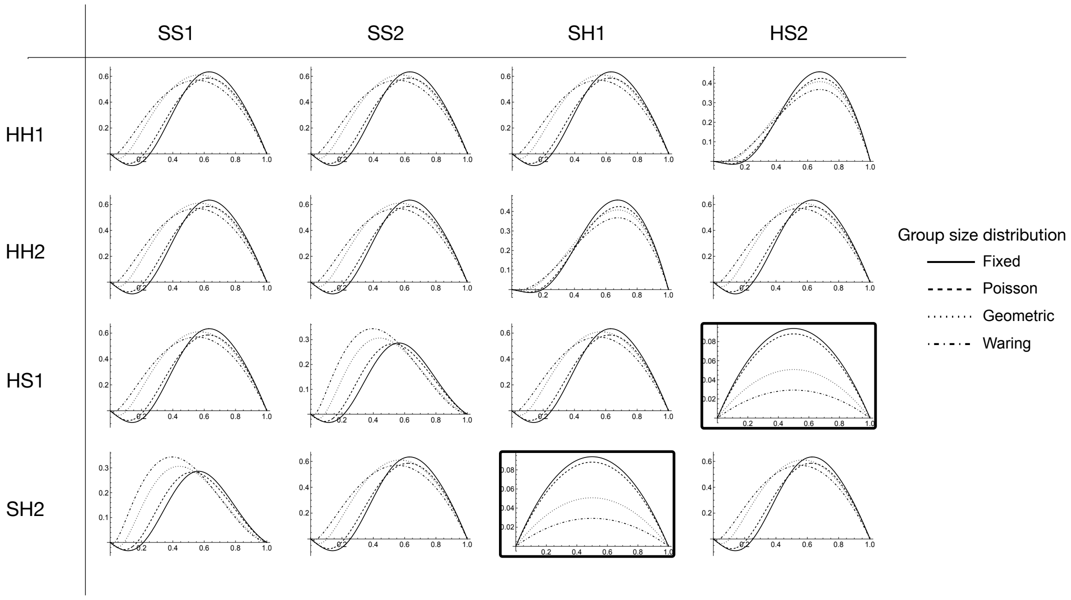


Figure B.1: Change in dynamics between two strategies depending on the group size distribution. Stag hunting strategies (columns) were compared with hare hunting strategies (rows). Each panel of the plot represents a dynamics between the two strategies, with x representing the fraction of stag hunters. Varying the group size moves the internal fixed point of the dynamics to the left, enlarging the basin of attraction of the all stag hunt equilibrium. Bold frame panels: For pairs (H,S,2), (H,S,1) and (S,H,1), (S,H,2) the dynamics lead to all stag hunt equilibrium regardless of the group size distribution. The parameters for each of the considered distributions are $E[N] \approx 8$, $M = 4$, $P_S = 4$, $P_H = 1$. Four distributions were considered: fixed group size 8, Poisson distribution with mean $\mu = 8$, geometric distribution with probability parameter $p = 0.111$ and Waring distribution with $\alpha = 2.25, \beta = 0.5, n = 20$.

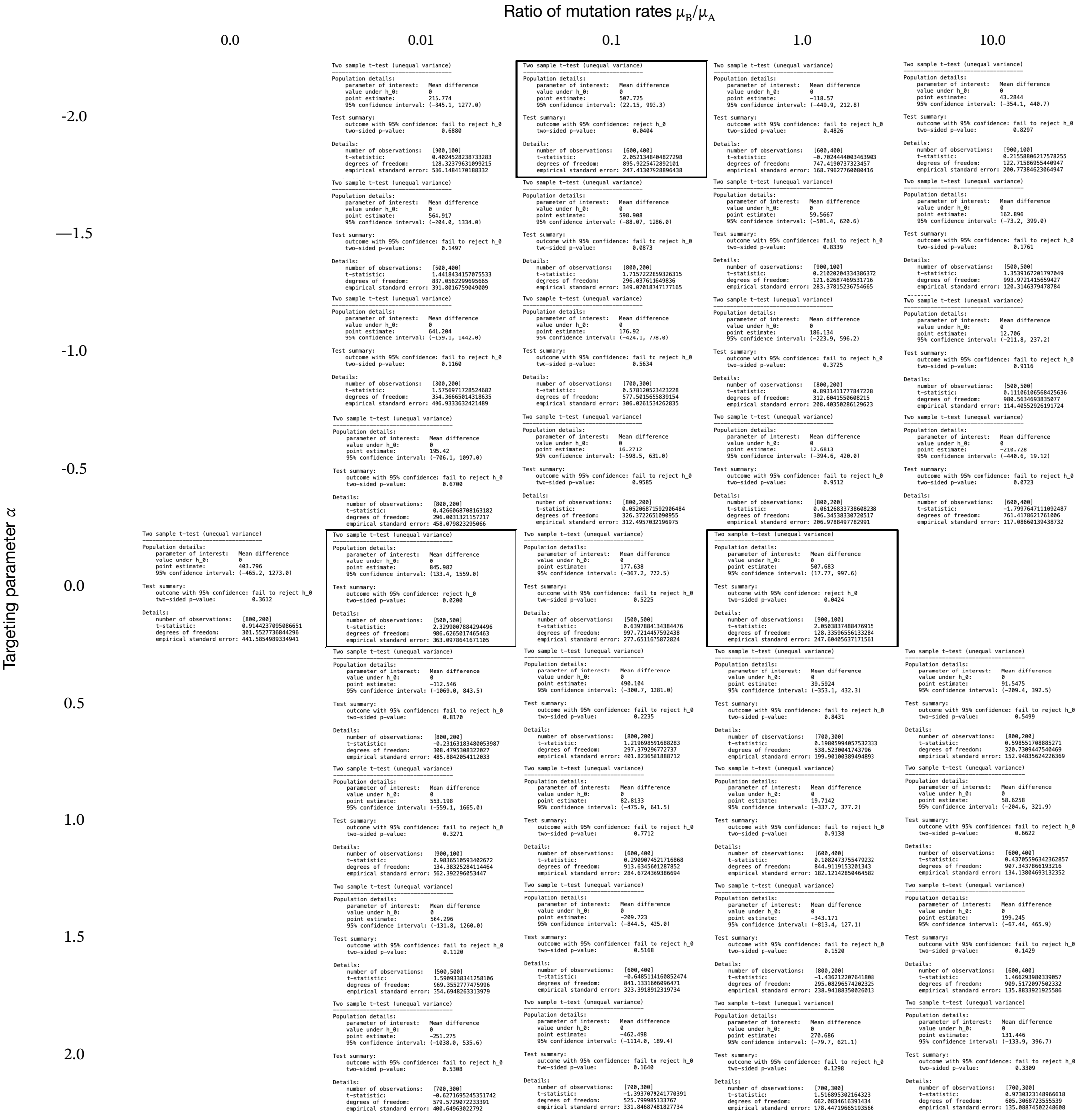
groups were characterized by a faster takeover. In thirty-three parameter sets, we observed no difference between the two types of networks. Hence, we conclude that any differences between the networks with and without small groups are not significant and result from the parameters of the individual networks and stochasticity rather than the attribute of interest.

Different network generating algorithms

The main study generated the small world networks using the Newman-Watts-Strogatz algorithm[234]. Similar network properties can also be obtained by using the Watts-Strogatz algorithm[41], where a network is created by deleting a fraction P of links in a d dimensional regular lattice.

The Watts-Strogatz (WS) networks are used as an example of small-world networks in the following sections.

An Erdös-Rényi random network can be generated either by specifying a number of edges[229] or a probability of each edge being generated[39]. Both of



```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          215.774
    95% confidence interval: (-845.1, 1277.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.6880

Details:
    number of observations:   [900,100]
    t-statistic:              0.4024528238733283
    degrees of freedom:       128.32379631099215
    empirical standard error: 536.1484170188332
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          507.725
    95% confidence interval: (22.15, 993.3)

Test summary:
    outcome with 95% confidence: reject h_0
    two-sided p-value:           0.0404

Details:
    number of observations:   [600,400]
    t-statistic:              2.0521348404827298
    degrees of freedom:       895.9225472892101
    empirical standard error: 247.41307928896438
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          -118.57
    95% confidence interval: (-449.9, 212.8)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.4826

Details:
    number of observations:   [600,400]
    t-statistic:              -0.7024444003463903
    degrees of freedom:       747.4190737323457
    empirical standard error: 168.79627760080416
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          43.2844
    95% confidence interval: (-354.1, 440.7)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.8297

Details:
    number of observations:   [900,100]
    t-statistic:              0.21558806217578255
    degrees of freedom:       122.71586955440947
    empirical standard error: 200.77384623064947
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          564.917
    95% confidence interval: (-204.0, 1334.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1497

Details:
    number of observations:   [600,400]
    t-statistic:              1.4418434157075533
    degrees of freedom:       887.0562299695665
    empirical standard error: 391.8016759049009
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          598.908
    95% confidence interval: (-88.07, 1286.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.0873

Details:
    number of observations:   [800,200]
    t-statistic:              1.7157222859326315
    degrees of freedom:       296.037611649836
    empirical standard error: 349.07018747177165
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          59.5667
    95% confidence interval: (-501.4, 620.6)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.8339

Details:
    number of observations:   [900,100]
    t-statistic:              0.21020204334386372
    degrees of freedom:       121.62687469531716
    empirical standard error: 283.37815236754665
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          162.896
    95% confidence interval: (-73.2, 399.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1761

Details:
    number of observations:   [500,500]
    t-statistic:              1.3539167201797049
    degrees of freedom:       993.9721415659427
    empirical standard error: 120.3146379478784
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          641.204
    95% confidence interval: (-159.1, 1442.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1160

Details:
    number of observations:   [800,200]
    t-statistic:              1.5756971728524682
    degrees of freedom:       354.36665014318635
    empirical standard error: 406.9333632421489
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          176.92
    95% confidence interval: (-424.1, 778.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.5634

Details:
    number of observations:   [700,300]
    t-statistic:              0.578120523423228
    degrees of freedom:       577.5015655839154
    empirical standard error: 306.0261534262835
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          186.134
    95% confidence interval: (-223.9, 596.2)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.3725

Details:
    number of observations:   [800,200]
    t-statistic:              0.8931411777847228
    degrees of freedom:       312.6041550608215
    empirical standard error: 208.40350286129623
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          12.706
    95% confidence interval: (-211.8, 237.2)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.9116

Details:
    number of observations:   [500,500]
    t-statistic:              0.11106106568425636
    degrees of freedom:       980.5634693835077
    empirical standard error: 114.40552926191724
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          195.42
    95% confidence interval: (-706.1, 1097.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.6700

Details:
    number of observations:   [800,200]
    t-statistic:              0.4266068708163182
    degrees of freedom:       296.0031321157217
    empirical standard error: 458.079823295066
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          16.2712
    95% confidence interval: (-598.5, 631.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.9585

Details:
    number of observations:   [800,200]
    t-statistic:              0.05206871592906484
    degrees of freedom:       326.3722651090955
    empirical standard error: 312.4957032196975
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          12.6813
    95% confidence interval: (-394.6, 420.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.9512

Details:
    number of observations:   [800,200]
    t-statistic:              0.06126833738608238
    degrees of freedom:       306.34538330720517
    empirical standard error: 206.9788497782991
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          -210.728
    95% confidence interval: (-440.6, 19.12)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.0723

Details:
    number of observations:   [600,400]
    t-statistic:              -1.7997647111092487
    degrees of freedom:       761.4178621761006
    empirical standard error: 117.08660139438732
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          403.796
    95% confidence interval: (-465.2, 1273.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.3612

Details:
    number of observations:   [800,200]
    t-statistic:              0.9144237095086651
    degrees of freedom:       301.5527736844296
    empirical standard error: 441.5854989334941
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          845.982
    95% confidence interval: (133.4, 1559.0)

Test summary:
    outcome with 95% confidence: reject h_0
    two-sided p-value:           0.0200

Details:
    number of observations:   [500,500]
    t-statistic:              2.3299007884294496
    degrees of freedom:       986.6265017465463
    empirical standard error: 363.0978641671105
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          177.638
    95% confidence interval: (-367.2, 722.5)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.5225

Details:
    number of observations:   [500,500]
    t-statistic:              0.6397884134384476
    degrees of freedom:       997.7214457592438
    empirical standard error: 277.6511675872824
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          507.683
    95% confidence interval: (17.77, 997.6)

Test summary:
    outcome with 95% confidence: reject h_0
    two-sided p-value:           0.0424

Details:
    number of observations:   [900,100]
    t-statistic:              2.0503837488476915
    degrees of freedom:       128.33596556133284
    empirical standard error: 247.60405637171561
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          -112.546
    95% confidence interval: (-1069.0, 843.5)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.8170

Details:
    number of observations:   [800,200]
    t-statistic:              -0.23163183480053987
    degrees of freedom:       308.4795308322027
    empirical standard error: 485.8842054112033
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          490.104
    95% confidence interval: (-300.7, 1281.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.2235

Details:
    number of observations:   [800,200]
    t-statistic:              1.219698591688283
    degrees of freedom:       297.379296772737
    empirical standard error: 401.8236581888712
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          39.5924
    95% confidence interval: (-353.1, 432.3)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.8431

Details:
    number of observations:   [700,300]
    t-statistic:              0.19805994057532333
    degrees of freedom:       538.5230041743796
    empirical standard error: 199.90100389494893
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          91.5475
    95% confidence interval: (-209.4, 392.5)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.5499

Details:
    number of observations:   [800,200]
    t-statistic:              0.598551708885271
    degrees of freedom:       320.7309447540469
    empirical standard error: 152.94835624226369
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          553.198
    95% confidence interval: (-559.1, 1665.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.3271

Details:
    number of observations:   [900,100]
    t-statistic:              0.9836510593402672
    degrees of freedom:       134.38325284114464
    empirical standard error: 562.392296053447
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          82.8133
    95% confidence interval: (-475.9, 641.5)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.7712

Details:
    number of observations:   [600,400]
    t-statistic:              0.2909074521716868
    degrees of freedom:       913.6345601287852
    empirical standard error: 284.6724369386694
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          19.7142
    95% confidence interval: (-337.7, 377.2)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.9138

Details:
    number of observations:   [600,400]
    t-statistic:              0.1082473755479232
    degrees of freedom:       844.9119153201343
    empirical standard error: 182.12142850464582
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          58.6258
    95% confidence interval: (-204.6, 321.9)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.6622

Details:
    number of observations:   [600,400]
    t-statistic:              0.43705596342362857
    degrees of freedom:       907.3437866193216
    empirical standard error: 134.13804693132352
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          564.296
    95% confidence interval: (-131.8, 1260.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1120

Details:
    number of observations:   [500,500]
    t-statistic:              1.5909338341258106
    degrees of freedom:       969.3552777475996
    empirical standard error: 354.6948263313979
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          -209.723
    95% confidence interval: (-844.5, 425.0)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.5168

Details:
    number of observations:   [600,400]
    t-statistic:              -0.6485114160852474
    degrees of freedom:       841.1331606096471
    empirical standard error: 323.3918912319734
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          -343.171
    95% confidence interval: (-813.4, 127.1)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1520

Details:
    number of observations:   [800,200]
    t-statistic:              -1.436212207641808
    degrees of freedom:       295.08296574202325
    empirical standard error: 238.94188350026013
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          199.245
    95% confidence interval: (-67.44, 465.9)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1429

Details:
    number of observations:   [600,400]
    t-statistic:              1.466293980339057
    degrees of freedom:       909.5172097502332
    empirical standard error: 135.8833921925586
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          -251.275
    95% confidence interval: (-1038.0, 535.6)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.5308

Details:
    number of observations:   [700,300]
    t-statistic:              -0.6271695245351742
    degrees of freedom:       579.5729072233391
    empirical standard error: 400.64963022792
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          -462.498
    95% confidence interval: (-1114.0, 189.4)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1640

Details:
    number of observations:   [700,300]
    t-statistic:              -1.3937079241770391
    degrees of freedom:       525.799985133767
    empirical standard error: 331.84687481827734
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          270.686
    95% confidence interval: (-79.7, 621.1)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.1298

Details:
    number of observations:   [700,300]
    t-statistic:              1.516895302164323
    degrees of freedom:       662.0834616391434
    empirical standard error: 178.44719665193566
```

```
Two sample t-test (unequal variance)
------------------------------------
Population details:
    parameter of interest:   Mean difference
    value under h_0:         0
    point estimate:          131.446
    95% confidence interval: (-133.9, 396.7)

Test summary:
    outcome with 95% confidence: fail to reject h_0
    two-sided p-value:           0.3309

Details:
    number of observations:   [700,300]
    t-statistic:              0.9730323148966618
    degrees of freedom:       605.3068723555539
    empirical standard error: 135.08874502248608
```

Figure B.2: Summaries of two sample t-tests between simulations run on networks with and without hunting parties of size at most 3. For the parameter set ($\alpha = 0.0$, $\mu_B = 0.01$) no networks with small groups were present. For three parameter sets (indicated with a frame) the simulations run on networks with small hunting parties were characterized with a significantly shorter takeover time. However, the difference is only siginifcant with the confidence level 0.05 and not 0.01.

the algorithms result in a random network with similar properties.

The ER algorithm's latter formulation (depending on specifying the probability of edge generation) is used in the following sections.

Moving away from small networks

Our main text results focus on a small population of size $Z = 32$. However, we presume that our conclusions from the analysis hold for other small population sizes. To check that we run an additional set of simulations with the following parameters: $Z \in \{52, 73, 92, 112, 132, 152, 172, 192, 212, 232, 252\}$, $\mu_A = 10^{-3}$, $\mu_B \in \{10^{-5}, 10^{-4}, 10^{-3}, 10^{-2}\}$, $P_H = 1$, $P_S = 4$, $M = 4$, $\omega = 1.0$, $\alpha = 0.0$. For each parameter set, ten graphs were generated, and simulations were run ten times on each graph. The results are then averaged over those 100 simulation runs.

In the smallest considered network $Z = 32$, we observe a decrease in takeover time with an increase in belief mutation rate μ_B. The same trend can be observed in the bigger network. However, for a big enough network size, the trend is reversed at $\mu_B = \mu_A = 10^{-3}$, and increasing belief mutation leads to an increase in takeover time. For each network type, the size threshold at which the shift in the direction of the effect of belief mutation varies. For the WS networks, the downward trend can be observed until $Z = 132$. For BA and ER, the size at which high mutation still leads to a decrease in takeover time equals $Z = 92$ and $Z = 152$, respectively. The change in the trend is depicted in Figure B.3 .

These results suggest that our conclusions are applicable to small networks, where the exact definition of a small network depends on the network type. The effects of introducing collective beliefs on larger networks remain an interesting future direction of study.

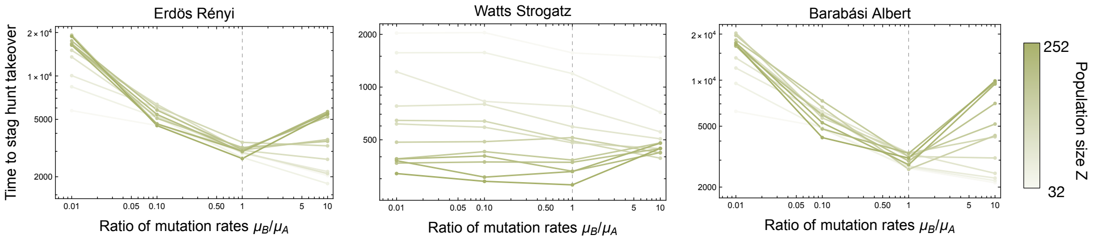


Figure B.3: Time to stag takeover depending on the population size Z and the ratio of mutation rates μ_B/μ_A. For small enough network sizes increase in the mutation rate leads to a decrease in takeover time. However, with an increase in network size, too high mutation rates may cause an increase in takeover time. The population size at which the change of direction occurs depends on the network type. The presented results are averaged over 100 runs per network type and parameter set.

Impact of selection intensity

The importance of the game (interaction) on the overall dynamics can be modelled by varying the value of the ω parameter[238]. For $\omega = 0$ all strategies are equivalent, as the hunt does not influence the fitness.

An additional set of simulations was conducted to determine the importance of ω on the dynamics. We use $Z = 32$, $\mu_A = 10^{-3}$, $\mu_B \in \{0.0, 10^{-5}, 10^{-4}, 10^{-3}, 10^{-2}\}$, $P_H = 1$, $P_S = 4$, $M = 4$, $\omega \in \{0.0, 0.25, 0.5, 0.75\}$, $\alpha = 0.0$. Each simulation is run for 10^5 generations. Presented results are averaged over 10 graphs per network type (ER, WS, BA) and 100 runs per graph.

As expected, for $\omega = 0.0$ (first row in Figure B.4), the proportion of stag hunters in the population, in the long run, is equal to approximately 50% for all values of belief mutation, as there is no advantage to any of the strategies. As the parameter's value increases slightly (subsequent rows in Figure B.4), the proportion of stag hunters grows to 98%. The effect of belief mutation can also be observed, as the percentage of stag hunters decreases with the mutation rate due to increased stochasticity.

The same effect is not so visible for an abundance of different belief followers, represented as grey bars in Figure B.4, as the belief itself does not impact one's fitness. Additionally, the belief abundance depends highly on the mutation rate at which the second belief is introduced. The proportion of belief followers increases significantly with the increase of μ_B. A slight increment can also be observed with the growing value of ω, suggesting that the second belief is essential for the game dynamic and acts as a coordination device.

Varying value of Stag

The takeover of the stag hunters may be caused, or at least aided, by a relatively high value of the stag compared to the hare. To determine whether the high payoff of stag hunters is required for their prevalence, we conduct simulations considering a smaller value of stag. In particular, we use the following parameters: $Z = 32$, $\mu_A = 10^{-3}$, $\mu_B \in \{10^{-5}, 10^{-4}, 10^{-3}, 10^{-2}\}$, $P_H = 1$, $P_S =\in \{1, 2, 3\}$, $M = 4$, $\omega = 1.0$, $\alpha = 0.0$. Each simulation is run for a maximum of 10^5 generations. The results are averaged over 10 graphs per network type and 10 simulation runs on each graph.

Surprisingly, almost all simulations still led to stag hunt takeover, even for $P_S = 1$. Only for the lowest value of belief mutation, $\mu_B = 10^{-5}$ and lowest value of stag $P_S = 1$ stag hunters were not able to take over the population in 23% and 17% of cases on the BA and ER networks respectively. On the WS network, all simulations led to a stag hunter takeover. This result clearly shows the power of

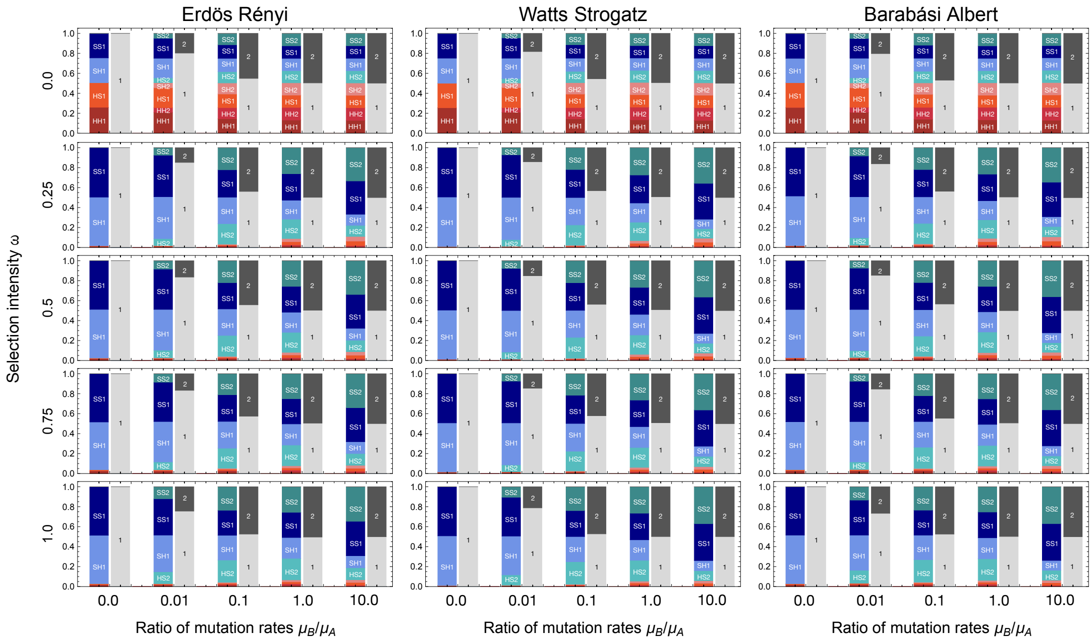


Figure B.4: Equilibrium frequency of each strategy and belief in the population depending on the selection intensity ω and the ratio of mutation rates μ_B/μ_A. While selection intensity ω equals 0, all strategies are equally likely to appear in the population. An increase in the parameter leads to a swift rise in the fraction of stag hunters. The frequency of each of the two narrative believers depends mainly on the value of the mutation rate, showing that the beliefs do not impact the payoff directly. The presented results are averaged over 100 runs per network type and parameter set.

collective narratives to entail coordination.

Let us analyse how stag hunters can take over a population with their payoff being at most equal to the one of hare hunters. Without the collective beliefs in place, it would be almost impossible for stag hunters to arise in the population - any single stag hunter that would appear due to mutations would have minimal chances of surviving. However, in the presence of beliefs, an individual can be a hare hunter in one narrative and a stag hunter in another, and that way, exist and reproduce while hunting a hare until they are surrounded by like-minded individuals, at which point a change in belief may cause them to hunt stags. In particular, we can imagine a group of (H,S,1) individuals who are hare hunters with the possibility to hunt stags. By introducing a belief mutation to one of them, we can create a (H,S,2)individual. If the hunter with the new belief can convince their hunting party of their belief (which can always happen by chance), stag hunting may emerge. While the takeover of stag hunters in that scenario would be rapid if they had a payoff advantage, it is still possible to observe the same effect by drift. Having the same payoff as hare hunters gives the singular stag hunters the same chance to reproduce as their less cooperative neighbours. Hence, it is still possible for stag hunters to take over the population. However, it is not guaranteed for them to remain in power, as the drift may cause a shift in the opposite direction. Additionally, the takeover is much slower since the change is driven by drift rather than selection (Supplementary Figure B.5).

Even so, assuming a here and a stag to be worth the same is unrealistic and negates the game's purpose. Hence, we focus on analysing the results for slightly higher values of a stag. Even for $P_S = 2$, all simulations lead to a stag takeover. Increasing the value of a stag leads to a faster takeover. Moreover, as shown in Figure B.5, we can see that the difference between low and high stag values is diminished with increased belief mutations, showing that introducing collective beliefs leads to a faster and more effective spread of cooperative behaviours.

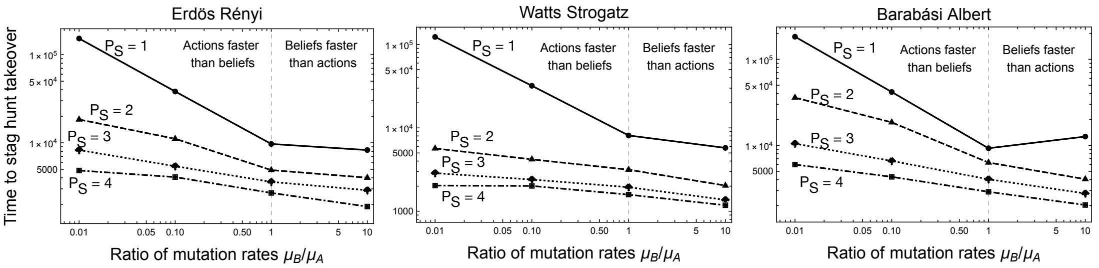


Figure B.5: Time to stag hunter takeover depending on the value of Stag P_S and the ratio of mutation rates μ_B/μ_A. For $P_S = P_H = 1$, not all simulations resulted in stag takeover. However, when stag hunters had an advantage over hare hunters, they could always take over the population. An increase in the value of stag led to a decrease in takeover time. The presented results are averaged over 100 runs per network type and parameter set.

Varying value of M

Hunting a stag is a group effort. In our model, we assume that at least M hunters need to partake in the effort for the hunt to be successful. The value of that hunting threshold may affect the game dynamics, especially in structured populations. As the necessary number of hunters grows, it is more probable that the group size is smaller than the threshold. To investigate the effect of the threshold, we run additional simulations while varying the parameter M. We use $Z = 32$, $\mu_A = 10^{-3}$, $\mu_B \in \{10^{-5}, 10^{-4}, 10^{-3}, 10^{-2}\}$, $P_H = 1$, $P_S = 4$, $M = \in \{2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15\}$, $\omega = 1.0$, $\alpha = 0.0$. For each parameter set, 10 graphs were generated, and 10 runs were conducted on each graph. The presented results are averaged over 100 runs.

The networks used in the simulations were generated for $M = 4$, with minimal connectivity of the BA network set to that value. Hence, as the threshold value increased, the probability of the group being too small to succeed in the stag hunt increased. Subsequently, the probability of a stag takeover decreased with the increase of M, as exhibited on Figure B.6. This effect was particularly apparent for $\mu_B = 10^{-5}$, as the takeover was generally the slowest for low belief mutation rate. For the highest value of the threshold considered, $M = 15$, the simulations ended with the stag takeover in 50% on BA networks, 35% on WS and 34% on ER. The relatively better performance of the BA networks may be regarded as the effect of the degree distribution of the networks. The long tail of the degree distribution of the BA networks ensures that at least some stag hunters can appear in the population and meet the threshold value, leading to a higher probability of stag takeover. For higher belief mutation rates, stag hunters are more likely to take over. For $\mu_B = 10^{-2}$, even for $M = 15$, all simulations on all network types ended in stag hunt takeover.

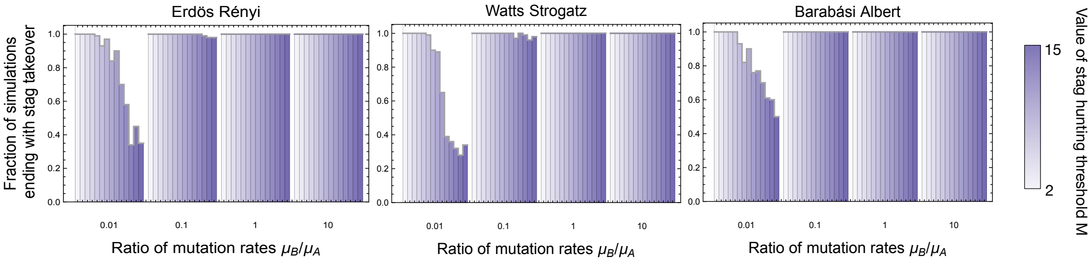


Figure B.6: Fraction of simulations ending in stag takeover depending on the vale of M and the ratio of mutation rates μ_B/μ_A. For low mutation values and high threshold value M only part of simulations led to stag takeover. However, with a lower threshold or higher belief mutation, all simulation runs ended with a stag takeover. The presented results are averaged over 100 runs per network type and parameter set.

We measure conditional time to stag takeover, i.e. the time to takeover for each threshold value, given that the takeover takes place. The effects of a high hunting threshold are the most apparent for low belief mutation rates. Still, the conditional time to takeover increases with the threshold increase for all belief mutation values, as shown in Figure B.7.

The effect of the belief mutation rate on takeover time for each value of M varies. There is no trend for low threshold values ($M \in \{2, 3\}$, represented by the lightest colours in Supplementary Figure B.7), and differences between takeover times for different mutation rates are minimal. Hence, if hunting a stag is relatively easy, collective narratives do not have a meaningful effect, as the population would become stag hunters regardless. For intermediate values of M, we observe a decrease in takeover time with the increase in mutation rate, as discussed in the main manuscript. As the value of M increases, we observe a change in the trend and an increase in the takeover time between $\mu_B = 10^{-3}$ and 10^{-2}. This suggests that as stag hunting is more challenging to sustain, too high belief mutation rate may jeopardise the stag takeover. For these parameter values, strategies must spread among more individuals for the population to switch to a stag hunt. If the belief mutation rate is too high, the change in belief happens before enough potential stag hunters are present and the hunt is unsuccessful. However, this effect dissipates if M is increased even more. For a high enough threshold value, we again observe the monotonous decrease in takeover time with increased mutation rates. For high enough values of the hunting threshold, stag hunters are too disadvantaged and struggle to take over the population. The takeover is then facilitated by a rapid mutation of beliefs, which may randomly cause the takeover. However, since the switch is caused by the random factor rather than the genuine advantage of stag hunters, the stag hunt equilibrium is not guaranteed to be retained. The limiting values of M vary between the network types considered.

The hunting threshold M proves to be an essential parameter of the model. Setting it too low makes stag hunt easy to obtain and renders collective beliefs unimportant. However, higher values of the parameter allow for collective beliefs to showcase their power - first as a coordination device between players and later, when stag hunt is almost impossible to achieve, by introducing an additional level of stochasticity and facilitating the switch. Notably, if the stag hunters are not guaranteed to succeed in their hunt even in a population of all stag hunters, that is if the threshold is larger than the group size, their takeover is a random process and the population can revert to hare hunting.

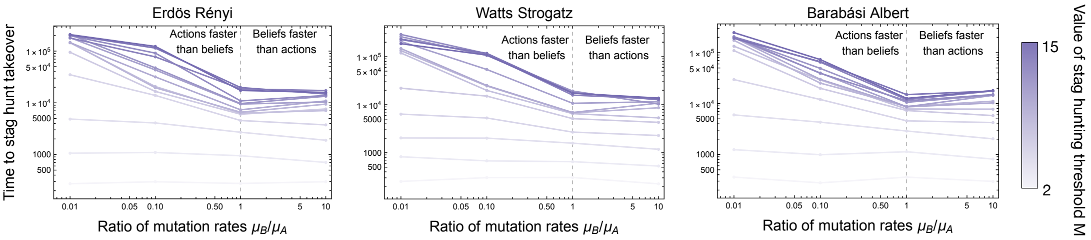


Figure B.7: Conditional time to stag takeover depending on the vale of M and the ratio of mutation rates μ_B/μ_A. If hunting a stag is easy (low values of M) narratives are not very important and the time to takeover does not depend on the belief mutation rate. However, as hunting requires more and more participants, beliefs become more important and we observe a decrease in takeover time with an increase in mutation rate. For very high values of M, a slight increase in takeover time can be observed if the mutation is too high - showing that too rapid mutation turnover may hinder cooperation. The presented results are averaged over 100 runs per network type and parameter set.

The effect of clustering

We hypothesise that high clustering promotes the spread of cooperative behaviour[198,199]. We use the Watts-Strogatz network to check if that is the case. By varying the rewiring parameter while generating the network, we can produce a set of graphs varying from regular to random. Subsequently, we vary the clustering coefficients of the graphs from the highest in the regular graph to the lowest in the random network. We use $Z = 32$, $\mu_A = 10^{-3}$, $\mu_B \in \{10^{-5}, 10^{-4}, 10^{-3}, 10^{-2}\}$, $P_H = 1$, $P_S = 4$, $M = 4$, $\omega = 1.0$, $\alpha = 0.0$, $p \in \{0.0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0\}$, where p is the rewiring probability in the WS network generating algorithm. For each set of parameters, 10 graphs were generated, and 10 runs of the simulation were run on each of the graphs.

An increase in p leads to decreased clustering in the network[41]. The results of the simulations show that an increase in p leads to an increase in takeover time, as shown in Figure B.8. In other words, lowering the clustering coefficients leads to a slower cooperator takeover. These results confirm our claim about the beneficial impact of clustering on levels of cooperation.

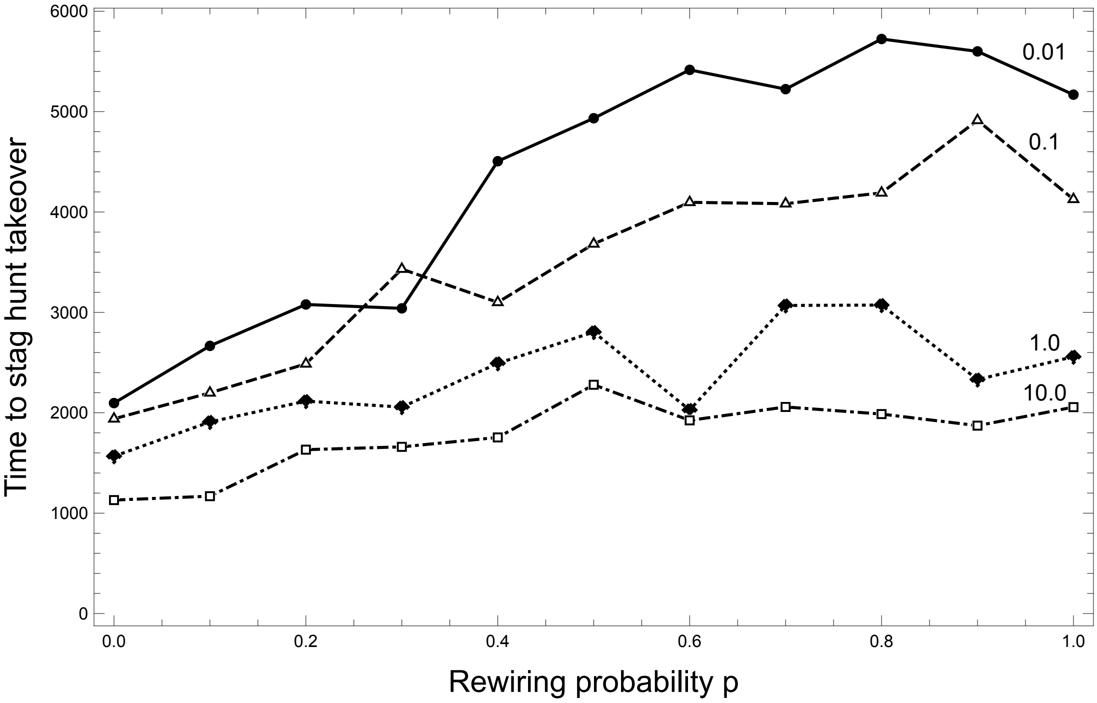


Figure B.8: Time to stag takeover depending on the vale of rewiring probability p and the ratio of mutation rates μ_B/μ_A. High rewiring probability leads to low global coefficients in the network. Simulations run on networks characterized by lower clustering result in higher takeover time across all mutation rates. The presented results are averaged over 100 runs per network type and parameter set.

C

Predator-prey dynamics with species-specific dispersal in structured populations

The work presented in the following Appendix has been initiated during a secondment at City University, under the supervision of Prof. Mark Broom

Introduction

In the complex world surrounding us, no species exists in isolation. Hence, to model the ecological dynamics of a given species, its direct interactions with others must be considered. The Lotka-Voltera model can be used to represent simple predator-prey dynamics[284,285]. The model allows for describing intra- and interspecific interactions in a population of multiple species.

The immense complexity of the real world is not limited to species richness or complex interactions between them. The space in which the species interact proves to be as important. The animals are not static in one place but dynamically dispersed around multiple habitat patches. The movement can be caused by environmental factors like weather and access to food and water. Behaviour of other species, including excessive hunting or a limited amount of prey, can also have a significant impact. Hence, dispersal patterns and habitat heterogeneity are crucial in modelling predator-prey dynamics[286,287].

Despite population structure being extensively discussed in the literature, the understanding of the species-specific spatial dispersal seems to be restricted to specific spatial structures and dispersal rules[288,289]. Multiple reasons (like different animal size, average speed, landscape perception or the nature of the landscape[290,291]) can lead to dispersal path heterogeneity, which can in turn lead to significant changes in the ecological dynamic in the system. Understanding of these effects can be beneficial for accurate modelling of predator-prey systems.

A spatial distribution and dispersal can be introduced via the metapopulation dynamics[292] and the multiplex network framework[59]. A multiplex network consists of multiple layers, each layer sharing the same set of nodes. In the context of modelling species interactions, nodes represent habitat patches and

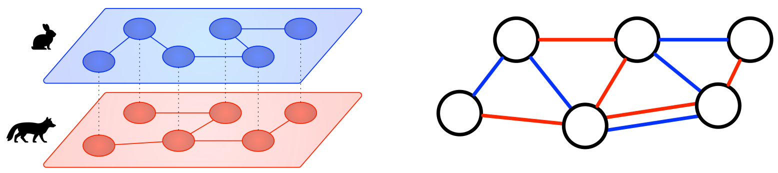


Figure C.1: The two species – predator (red) and prey (blue)– share the habitat patches, however each species is characterized by a different dispersal network between specific patches. The differences between the dispersal networks can be represented by a multilayer network, where each species moves on its own layer (left). Both layers share the same set of nodes (habitat patches) but have different sets of links (dispersal paths). Alternatively, the distinct links can be represented by multicoloured edges on the same graph (right).

links between them represent paths along which migration can take place. Each of the network layers can be characterized by a distinct set of edges, representing a species-specific dispersal path - each layer corresponding to one species. A given species can migrate between patches if they are connected on its respective layer, as shown on Figure C.1.

Lotka Volterra predator prey models in patchy environment have been extensively discussed in literature. However, proposed models introduce notable limitation with the assumptions made. Namba[293] presents a N-patch model which includes diffusion on random graphs. Importantly, diffusion networks of predator and prey species do not have to coincide. On each path between two patches movement of a given species takes place with the same rate and depends on the density on the patch of origin. The model is described by a system of $2N$ differential equations.

$$\frac{du_i}{dt} = (a - Ku_i - bv_i)u_i - \sum_{j=1}^{N} D_{ij}^u (u_i - u_j),$$

$$\frac{dv_i}{dt} = (-c - Lv_i + dv_i)v_i - \sum_{j=1}^{N} D_{ij}^v (v_i - v_j)$$

where u_i and v_i are densities of prey and predators on the i-th patch respectively. All parameters are non-negative constants. The model incorporates crowding effects with parameters K and L. The movement of species p from patch i to j is governed by coefficients D_{ij}^p, taking positive values only if given species can move on between the patches. Importantly, it is assumed, that movement from i to j can happen with the same rate as form j to i. Nature of the landscape can lead to violation of this assumption, for example if dispersal takes place via streams with strong current or on steep terrain. Additionally, the model assumes that there are no isolated compartments, or groups of compartments.

It is shown that in a spatially homogenous environment, dispersal cannot stabilize the oscillations in the system. Moreover the system is shown to be asymptotically spatially homogenous. Hence the effect of diffusion is not substantial.

Gao and Liu[294] generalize the N-patch dispersal model, by introducing boundary conditions between patches. Additionally, in the model each patch has a distinct set of parameters. Hence, the system is represented by a set of equations:

$$\frac{du_i}{dt} = (r_i - b_i u_i - e_i v_i)u_i + \sum_{j=1}^{N} d_{ij}^u (u_j - \alpha_{ij}^u u_i),$$

$$\frac{du_i}{dt} = (-\gamma_i - \delta_i v_i + \epsilon_i u_i)v_i + \sum_{j=1}^{N} d_{ij}^v (v_j - \alpha_{ij}^v v_i),$$

with α_{ij} representing the boundary condition between patch i and j. There is no explicit assumptions on the relationship between diffusion rates from i to j and from j to i. However, the model assumes dispersal matrices to be irreducible and the existence of at least one patch k such that $b_k > 0$ or $\delta_k > 0$. Moreover, it is assumed that there exists $\lambda \geq 0$ such that $\lambda d_{ij}^x \epsilon_i x_j^* = d_{ij}^y e_i y_j^*$ for $1 \leq i, j \leq n$, or $d_{ij}^x \epsilon_i x_j^* = \lambda d_{ij}^y e_i y_j^*$. This assumption poses strong limitations on the network structure and it is unclear, whether the results would hold if the assumption was relaxed.

If the positive equilibrium of that system exists, it is proven to be globally asymptotically stable. This result shows that introduction of dispersal can stabilize the oscillating behaviour usually encountered in Lotka Volterra models.

The assumptions made on the structure of the dispersal networks and their coupling do not allow for analysis of effects of arbitrary, random dispersal networks.

Materials and Methods

Effect of dispersal in three patch system

Different effects of heterogeneous dispersal in predator prey model can be observed in a three patch system. Movement between the patches can lead either to stabilization of the dynamics in a positive equilibrium, oscillations, extinction of one or more subpopulations or unbounded growth of some subpopulations.

The following system of differential equations is considered:

for $i \in 1, 2, 3$

$$\frac{du_i}{dt} = (r - \sum_{j=1}^{3} d_{ij}^u - bu_i - ev_i)u_i + \sum_{j=1}^{3} d_{ji}^u u_j$$

$$\frac{dv_i}{dt} = (-\gamma - \sum_{j=1}^{3} d_{ij}^v - \delta v_i + \epsilon u_i)v_i + \sum_{j=1}^{3} d_{ji}^v v_j$$

Here $u = (u_1, u_2, u_3)$ and $v = (v_1, v_2, v_3)$ represent the population densities of prey and predators, respectively, on three habitat patches. The prey population has a constant birth rate r and a death rate e caused by the predators. Additionally, there is an intra-specific competition rate b. The growth of the predator population depends on the rate ϵ and the amount of prey present on the patch, some natural death rate γ and intra-specific competition represented by δ. Patches are homogeneous with respect to the model parameters. Migration rate of species a from patch i to patch j is represented by $d_{i,j}^a$. The parameter $d_{i,j}^a$ takes positive values only if movement of a given species is possible on a given path, and is equal to 0 otherwise.

In the considered example, following values of the parameters were adopted: $b = 0, e = 0.02, r = 0.1, \delta = 0, \epsilon = 0.02, \gamma = 0.4$. In the absence of movement, the subpopulation of each patch oscillates around the positive equilibrium ($u_i = 20, v_i = 5$) (provided that each non of the species is extinct in time 0 and the subpopulation does not begin in the equilibrium).

Introduction of movement can significantly change the dynamics in the system. Some general effects of movement can be observed. In the absence of predator movement and influx of prey to the patch, the subpopulation of the patch i goes extinct if $\sum_{j=1}^{N} d_{ij}^u > r$. If the outflux of prey is faster than the natural birth rate, the species will go extinct on the patch, leading to the subsequent extinction of the predator on that patch. The effect can be offset by introducing an influx of prey from another patch. Moreover, if $\sum_{j=1}^{N} d_{ij}^u = r$ (and no other movement to or from the patch) it is possible for the prey subpopulation to stabilize on some positive level and the predators to go extinct. In that case, the constant influx of prey to other patches leads to the decrease in oscillations and stabilization of the subpopulations on those patches on the positive equilibrium.

Similarly, introduction of predator movement can cause the stabilization of the dynamics. The influx of predators from another patch (given that the population on the source patch does not go extinct) causes the osculations to decrease and the system to eventually stabilize, regardless of the outflux of predator (for no prey movement present).

Results

Changing the capacity of one path can have a crucial effect on the dynamics, moving the system form convergence to stable equilibrium to divergence, leading to predator extinction and undisturbed pray growth.

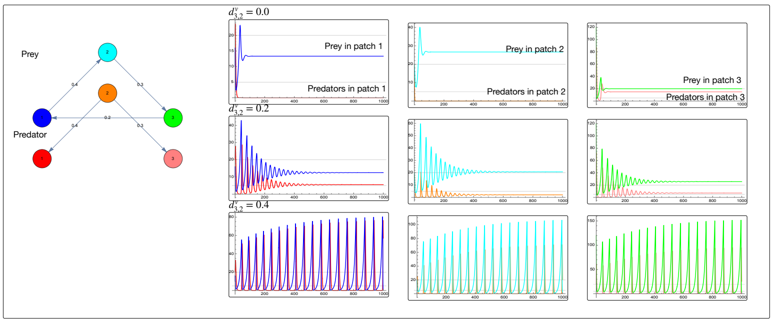


Figure C.2: The network considered in the example (left). The prey (upper layer) can move in a clockwise circle between all three patches. Predators (lower layer) can only move out of patch two. Varying the value of $d^v_{3,2}$ can change the dynamics from extinction of predators in two of the patches (upper row), a stable positive equilibrium (middle row) and divergence from the equilibrium, resulting in extinction of predators in the long run (lower row).

Consider a three patch system introduced above, with the initial conditions $u = (20, 20, 20)$, $v = (20, 20, 20)$. We begin the analysis with a prey moving in a clock-wise circle and predators only leaving patch 2. We consider following parameters: $du_{1,2} = 0.4, d^u_{2,3} = 0.3, d^u_{3,1} = 0.2, d^v_{2,1} = 0.4, d^v_{2,3} = 0.3$ and all other dispersal rates equal to 0, as presented on Figure C.2. We analyse the effect of introducing predator movement from patch 3 to 2.

Before introduction of predator movement from 3 to 2, the system goes to a stable equilibrium $u = (13.333, 26.667, 20), v = (0, 0, 15)$. The extinction of predators on patches 1 and 2 can be prevented by introduction of movement from patch 3 to 2. For small positive values of $d^v_{3,2}$ the subpopulations of predators are rescued and stabilize on low but positive values of equilibrium. The equilibrium is an attractor for $0 < d^v_{3,2} < 0.3034$ and becomes a repeller for higher values. If movement from patch 3 to 2 happens with a high rate, all the predator subpopulations go extinct, which leads to rapid and uninterrupted growth of prey subpopulations (since there is no intra-specific competition in this example).

This example shows how introduction of movement and change in one dispersal rate can drastically change the dynamics in the three patch system and lead to either stabilization or destabilization of the equilibrium.

Discussion

Nothing in nature is static. Neither in time, nor in space[295]. It is then natural to assume that animals disperse among multiple habitat patches, rather than stay in one place. Although different species of animals may share this tendency to migrate between habitat patches, they do not necessarily need to share the speed and paths on which the movement is performed. With different size, speed or movement abilities, dispersal networks may vary among the species. In this work it has been shown, using a simple, 3-patch example, how consideration of species-specific dispersal patterns can influence the ecological dynamics. The considerable effect of altering the movement pattern of just one species between two habitat patches exemplifies the importance of dispersal patterns in modelling attempts and subsequently drawn conclusions on animal behaviour. These results also emphasise the importance of dispersal data, which has historically been shown to be lacking[296].

Modelling of intraspecific interactions is an essential element of conservation initiatives[297]. Faithful modelling allows for accurate predictions of effects anthropogenic interventions may have on ecological systems[298]. With that notion in mind, the conclusions presented in this work suggest that species specific dispersal patterns could be a viable addition to the pre-existing models, enriching the dynamics and providing a more accurate conclusions.

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Publications list

M. Fic and C. S. Gokhale, ”Catalysing cooperation: The power of collective beliefs in structured populations”, *npj Complexity* 2024*

C. Morison, **M. Fic**, T. Marcou, J. Mohamadichamgavi, J. Redondo Antón, G. Sayyar, A. Stein, F. Bastian, H. Krakovská, N. Krishnan, D. Pires, M. R. Satouri, F. J. Thomsen, K. Tjikundi, and W. Ali ”Public goods games in disease evolution and spread”, *Zenodo* 2024*

M. Fic, F. Bastian, J. Miękisz and C.S. Gokhale, ”Kindergarten Model: Approximating Time Delays in Evolutionary Games”, *in preparation**

*These manuscripts are part of this dissertation

Statement of individual author contributions

Description of the specific contributions of the PhD-candidate to a publication with several co-authors and confirmation by the co-authors

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Publication details	Description of the own contribution
Writing of the article Which parts of the article have been written to which extent by the candidate?	The primary draft of the manuscript has been written by C.M and **M.F.**. The review of the manuscript has been done by all coauthors. The final draft has been rewritten and edited by C.M and **M.F.**.
Performed research Which experimental procedures have been conducted by the candidate?	The literature review has been performed by all co-authors.
Conceptual design of the research To which extent did the candidate contribute to the conceptional design of the research project?	The initial design of the study has been conceptualized by all coauthors.
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Publication details	**Description of the own contribution**
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Performed research Which experimental procedures have been conducted by the candidate?	**M.F.** developed the algorithm and ran the simulations.
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