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ENGINEERING AND THE ENVIRONMENT
Aeronautics, Astronautics and Computational Engineering Unit

Challenges and applications of computational models in theoretical anthropology

by

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ABSTRACT

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CHALLENGES AND APPLICATIONS OF COMPUTATIONAL MODELS IN THEORETICAL ANTHROPOLOGY

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Theoretical anthropology tries to develop models of human biology and culture. In this thesis, we investigate how different computational models from theoretical biology can be applied to evolutionary anthropology. We study two different types of models, applying them to two different sub-fields of evolutionary anthropology, and highlighting alternative choices in their construction.

On the one hand, we observe that the evolutionary simulations are composed of three main components: an updating rule, a game and a population structure. We find that the updating rule can alter the qualitative and quantitative evolutionary outcome of a model. A dominant language is more resilient to learning errors and more frequent when selection primarily weeds out maladapted individuals, instead of promoting well-adapted ones.

We study the evolution of cooperation and institutional punishment. Group selection can support cooperation, even when implemented through the selection of individual agents migrating between communities at different rates. Institutional punishment on the other hand is highly complex and cannot arise from simpler strategies in either well-mixed or community-structured populations.

On the other hand, Bayesian inference models used for linguistic phylogenies can incorporate highly correlated typological information, without a priori knowledge about the underlying linguistic universals.

While close in subject, models in theoretical biology and profound anthropological expertise express all but disjoint theories in terms of scope and complexity. This thesis acknowledges this challenge and contributes to bridging the gap.

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Declaration of Authorship

I, Gereon A. Kaiping, declare that the thesis entitled *Challenges and applications of computational models in theoretical anthropology* and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
- where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help;
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
- parts of this work have been published as:

  [1] G. A. Kaiping, G. S. Jacobs, S. J. Cox, and T. J. Sluckin. "Nonequivalence of updating rules in evolutionary games under high mutation rates". In: *Physical Review E* 90.4 (Oct. 2014), p. 042726. DOI: `10.1103/PhysRevE.90.042726`.

  [2] Gereon A. Kaiping. *Fitness-based Migration in policed Public Goods Games.* eng. Conference Talk. Paris, June 2015.

  [3] Gereon A. Kaiping. *Structured populations facilitate cooperation in policed Public Goods Games.* Leicester, May 2015.

- parts of this work have been submitted as:

  [4] Gereon A. Kaiping. *Correlated evolution of typological features in Bayesian phylogeny inference.* en. http://lorentzcenter.nl/lc/web/2015/767/info.php3?wsid=767&venue=Oort. Leiden, Oct. 2015.

  [5] G. A. Kaiping, S. J. Cox, and T. J. Sluckin. “Cooperation and Punishment in Community-Structured Populations”. In: *Journal of Theoretical Biology* (2015). Under review.

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Signed:..

Date:..

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Nomenclature

Parameter	Symbol	Default value
Contribution to the public good	c	0.8
Local selection strength	w_1	0.1
Across-community selection strength	w_2	1
Linear scaling of public good	r	3
Community size	N	20
Community count	M	20
Fine	β	20
Punishment cost	γ	10
Mutation probability	μ	0.0025
Migration probability	m	0.05
Taxpayer's tax	t	0.025
Pool punisher's tax/punishment cost	t'	0.18

Table 1: Symbols used throughout the thesis.

Chapter 1

Introduction

Anthropology, from Greek *ἄνθρωπος* (*ánthrōpos*), "man", and *-logy*, denoting a field of study, denotes the science of humanity. A core interest of anthropology is the empirical study of culture, society and humanity. Anthropology raises deep philosophical questions about the human condition. By contrast with traditional philosophical investigations, it derives its answers from empirically studying human lives under different conditions. Anthropology thus provides two types of insights: the science studies the actual cultural variation in the world, and offers theoretical perspectives and tools "to explore, compare and understand these varied expressions of the human condition"[6]. A core method of anthropology is thus field work, collecting first-hand data from members of different cultures acting as informants. Other data is provided eg. from archaeological evidence, media (such as art or literature) or human biology.

One particular anthropological field of study goes back to Wilson [7]. Socioecology[1], and evolutionary anthropology in general, tries to understand human culture and society using the framework of natural evolution.

Over generations, both life forms and human culture change. The evolution of life happens over very long time frames, while cultural trends can emerge and vanish again over a fraction of a single human lifetime. Therefore the fact that aspects of cultures, in particular languages, are related by descent from a common "ancestor" was actually postulated first. The idea gained momentum and was formalised from the mid 18th century onwards. Linguists such as Sir William Jones (1746–1794), Friedrich von Schlegel (1772–1829) and Franz Bopp (1791–1867) discovered striking similarities between the Indian Sanskrit language on the one hand and classical Latin and Greek on the other. The first to discover systematic rules, according to which language change occurs, were Rasmus Christian Rask (1787–1832) and Jacob Grimm (1785–1863) in the middle of the 19th

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[1] While Wilson originally used the term "sociobiology", the term *socioecology* is now used more widely, because it does not imply that adaption is driven by genetics [8].

century. By describing a consistent set of regular sound changes, they were able to explain the descent of words in the Germanic languages from a postulated proto-Germanic ancestral language.

The idea that life forms, such as plants or animals, do change in a regular way, adapting to their environment, also arose in the early 19th century. Jean-Baptiste Lamarck was the first to propose such laws from 1800 onward. Some decades after the Grimm brothers had identified natural laws of sound change in languages, Charles Darwin postulated one coherent natural mechanism to explain the evolution of life. This mechanism explained the established hierarchical taxonomy of species, as founded on the works of Carl Linnaeus (1707–1778), as a genealogical or phylogenetic tree.

Darwin suggested that offspring are not copies of their parents in a deterministic way, but that they will be subject to random variation. Some of this variation is beneficial to the descendant in their current environment, increasing the probability that they survive and pass the variation on to their offspring. Other variation will increase their probability of dying, thus increasing the chance that it is not passed to the next generation. This very simple mechanism uses only heredity and variation to explain all life as descendants of a single common ancestor.

Replication with variation is not restricted to biological systems, but also applies to human culture. The framework and any generic conclusions of evolutionary theory therefore apply to biological evolution as well as cultural evolution [9]. In this framework, it is thus not only possible to study and explain the actual biological or cultural variation we can observe. Instead, we can also shed light on what evolutionary pathways are theoretically possible or impossible under given external conditions.

Using methods developed since, the fundamental mechanism of evolution driven by variation and inheritance is well-attested. The circumstances that lead to a variation being beneficial or detrimental for its bearer are however much more difficult to grasp. Particularly our own evolutionary history provides puzzling data for this aspect of the theory [10–12]. Two specific properties set humanity apart from other species. Firstly, humans cooperate on a very large scale with each other, even where the degree of kinship is immeasurably wide, showing a very detailed division of labour in the process. Secondly, language provides humans with a symbolic system that can express signals of arbitrary complexity. Through cumulatively building on previous generations' work, language therefore enables this high level of specialisation and human culture in general to persist and grow. The two questions may be related: language facilitates coordination and thus cooperation [13], and on the other hand, social policing may be a significant factor in stabilising complexity and diversity [14].

Both of these aspects of anthropological evolution have been studied using computational and other mathematical models in the past. The study of the evolution of cooperation has come to focus on certain types of models, neglecting other options that may *a priori* be considered equally realistic for the purpose. The computational study of linguistic data on the other hand heavily uses methods derived for the inference from biological data, and it is not always clear what implications this has on the results obtained, and what alternatives might be considered instead. This thesis contributes to both these points by studying the structure of both types of stochastic models in theoretical anthropology. We identify default assumptions in this structure, and discern alternatives and the impact of those choices on the results of evolutionary models.

1.1 The Puzzle of Cooperation

The puzzle of the evolution of cooperation has given rise to the mathematical field of evolutionary game theory [15]. Game theory in general uses mathematical models to understand interactions between separate individuals. Interactions are characterised in terms of decisions for the individuals and numerical values (“payoffs”) characterising the benefit or detriment of possible outcomes of the interaction.

Already the very simple, symmetric case, in which only two individuals each simultaneously choose between two options A and B, gives rise to a broad theory. If the choices (A, A) and (B, B) are not equal, we can (up to renaming the choices) assume that the payoff for (A, A) is $P = 0$ and for (B, B) is $R = 1$ and characterise all such games by the remaining two payoffs T for (A, B) and S for (B, A). Such a game is often described by a payoff matrix, such as

$$\begin{array}{c|cc} & A & B \\ \hline A & P=0 & T \\ B & S & R=1 \end{array} \tag{1.1}$$

Each cell of the matrix gives the payoff for the “row” player (the player who decides which row they obtain the payoff from) dependent on the choice of the “column” player. Note that in a symmetric game the payoff which row receives for playing B when column chooses A is the same as the payoff which column receives for playing B when row chooses A, but the payoffs T for (A, B) and S for (B, A) need not be the same.

Characterising the games in this way shows that there are 12 fundamentally different game structures, as illustrated in Fig. 1.1. The best known of these games is the Prisoner’s Dilemma. The best-known presentation of the game is due to Poundstone [17], and goes as follows.

> Two members of a criminal gang are arrested and imprisoned. Each prisoner is in solitary confinement with no means of speaking to or exchanging messages with the other. The prosecutors do not have enough evidence to

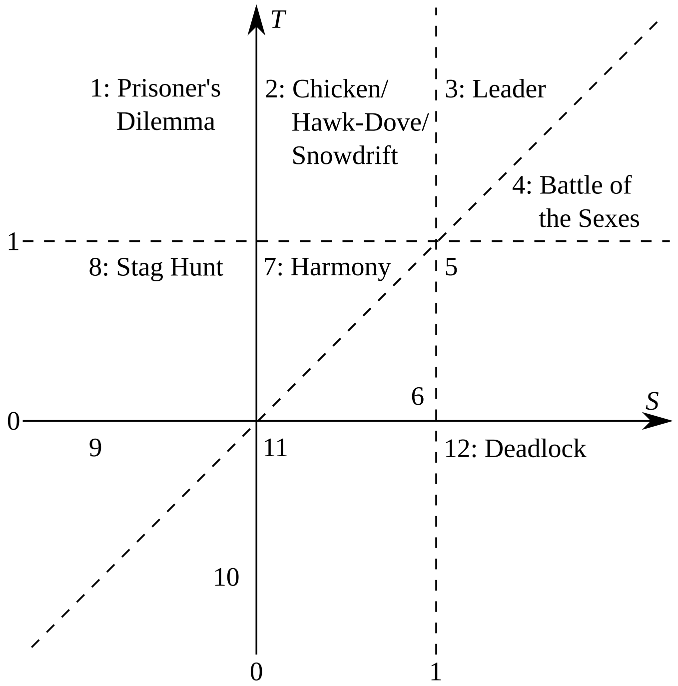

Figure 1.1: The twelve fundamentally different symmetric 2 × 2 games, characterised by the two parameters T and S for $P = 0$, $R = 1$. The most interesting ones of these have been named 1: Prisoner's Dilemma; 2: Hawk-Dove; 3: Leader; 4: Battle of the Sexes; 7: Harmony; 8: Stag Hunt; 12: Deadlock. [16]

> convict the pair on the principal charge. They hope to get both sentenced to a year in prison on a lesser charge. Simultaneously, the prosecutors offer each prisoner a bargain. Each prisoner is given the opportunity either to: betray the other by testifying that the other committed the crime, or to cooperate with the other by remaining silent. Here is the offer:
>
> 1. If A and B each betray the other, each of them serves 2 years in prison
> 2. If A betrays B but B remains silent, A will be set free and B will serve 3 years in prison (and vice versa)
> 3. If A and B both remain silent, both of them will only serve 1 year in prison (on the lesser charge)

The two choices are usually referred to as *Cooperate* with the other player or *Defect* to the police. With this convention, the payoff matrix for the PD in this case can be written as

$$\begin{array}{c|cc} & \text{Defect} & \text{Cooperate} \\ \hline \text{Defect} & -2 & 0 \\ \text{Cooperate} & -3 & -1 \end{array} \tag{1.2}$$

In general, any game with $S < P < R < T$ and $S + T < 2R$ is referred to as an instance of the Prisoner's Dilemma. The particular interest of the PD for the evolution of cooperation and punishment comes from this general payoff structure. If one player chooses to cooperate, the other player will be better off defecting, because $T > R$. Similarly, the other player will be better off defecting when one player chooses to defect, as $P > S$.

No player can therefore improve their own position by unilaterally moving away from (D, D). Strategy combinations with this property are known in Game theory as *Nash equilibria* [15].

On the other hand, each player would be better off if both were to cooperate, because the payoff for (C, C) is $R > P$. Experiments with human experimental subjects show [18, 19] that humans widely decide to cooperate even though defection would be in their immediate material self-interest. Indeed, humans prevalently choose C even when they have never met their co-player, are not apparently related to them and unlikely to ever interact with them again. The puzzle of how such a strong tendency for cooperation between unrelated individuals can develop in the context of Darwinian evolution has led to the construction of many evolutionary models trying to replicate such behaviour.

The concept of the Nash equilibrium requires minimal assumptions on the rationality of agents. The core assumption of evolutionary game theory, by contrast, is that individual agents are not rational. Instead, the space of strategies is analysed in terms of Darwinian evolution. The model is constructed such that strategies generating a higher payoff produce more offspring. Thus, a model in evolutionary game theory consists of multiple components. The core interaction to be studied by the model is given in terms of a game, which defines the payoffs for combinations of strategies actualised by the players. Formally [15], a game is specified by a set of players P, a pure-strategy set S_n for each player $n \in P$, and a payoff function $\pi : \prod_n S_n \mapsto \mathbb{R}^P$.

For much of this thesis, the example model will be a cooperative dilemma similar to the Prisoner's Dilemma. The game is known as the Public Goods Game (PGG) and is defined for any number of players. For the 2-player case, the PGG gives rise to a Prisoner's Dilemma. The formal definition of the PGG will be given in Chapter 3. In addition to the game, however, a game-theoretical model needs to specify at least two things.

Firstly, the evolving population of game players needs to be specified. In the simplest case, the population is well-mixed. In a well-mixed population, all interactions between players are equivalent. Well-mixed populations are easier to study analytically, because their symmetry permits many mathematical simplifications, and analytical methods have been derived for similar systems from statistical physics. Alternatively, the population can have an arbitrarily rich structure [20]. Population structure is often given in terms of a constant graph [21], in which the nodes correspond to players and the edges to interactions between players. Typical choices for such a graph are regular lattices [22–

27] or graphs with properties inspired by real-world interaction networks, such as scale-free social networks [28]. In addition, researchers have studied more complex population structures. Examples include multiplex networks, composed of stacks of static networks, where agents can follow different strategies on different layers of the network, but with their fecundity depending on the payoff from all layers [29], or time-dependent graphs, for instance geometric networks of agents moving about in 2-dimensional space [30].

In this thesis we will however concentrate on populations with a minimal structure, consisting of a finite number of well-mixed subpopulations, where individuals can interact across subpopulations, as well, but only in a weak manner. Similar population structures have been considered in evolutionary modelling for a long time, starting with Wright's considerations of migration [31]. We will refer to this metapopulation structure as *community-structured population*, identical or similar population structures are also known eg. as patch-structured populations or finite island dispersal models [32].

Individuals in the population are assigned a genotype, which informs what strategy the player is following. In the simplest case, genotypes correspond 1-to-1 with discrete pure strategies, but this is not necessarily the case. In models studying the mapping from genotype to phenotype in particular this mapping does not depend purely on the genotype, but in many models the space of genotypes directly corresponds to a set of pure or mixed strategies of the game to be played.

Lastly, a model needs to specify how the population develops in time, in order to incorporate evolutionary effects. A very simple approach assumes that the population is of constant size, and develops over discrete time steps corresponding to separate generations. The composition of the population at time step $t+1$ consists of offspring of the population at time t, where each individual at $t+1$ is a copy (up to mutation) of an individual at t, drawn from the whole population with replacement. The probability to draw an individual from the parent generation is given by its fitness, which is derived from the game payoff. This model is known as the Wright-Fisher model. It can be extended to a model with overlapping generations, if in every time step not the whole population, but only one individual is replaced. In this case, there are two choices each time step: It has to be specified which individual procreates, but also, which one dies. If death is random, while birth is proportional to fitness, this type of updating is known as the Moran process. This process can be generalised to other ways of choosing who copies whom. We will refer to this general family of updating rules as *generalised Moran process*, and discuss it in more detail in Chapter 2.

As populations grow, the stochastic element inherent in the generalised Moran process becomes less relevant. The time evolution of the system can then be approximated using partial differential equations. For large populations, the probability distribution over the state space can be approximated through a continuous probability density obtained by way of a Fokker-Planck differential equation [33]. As population size grows so large

```
Input: A population $P$ at time $t$
Output: The population $P$ at time $t+1$
foreach $n \in P$ do
    calculate payoff $\pi_n$ calculate fitness $f_n$ ;
end
randomly select $j \in P$ with probability $p(j = n) \propto f_n$ ;
randomly select $k \in P$ (uniformly $p(k = n) \propto 1$) ;
/* $j$ procreates and $k$ dies */
replace $k$ with a copy of $j$ ;
```

Algorithm 1: A Moran process model

that stochastic effects become negligible, the behaviour becomes deterministic and can be described by an ordinary differential equation corresponding to the drift term of the Fokker-Planck equation [34]. This latter approach also shows the strength and direction towards a mutation-selection equilibrium, and is therefore useful when illustrating the dynamic behaviour of a model.

For large time scales, in which new mutants regularly arise and invade a population depending on a continuous trait, the evolutionary dynamics can even give rise to differential equations usually known from an ecological context, such as the Lotka-Volterra equations of predator and prey [35].

Generalised Moran processes are often used to model selection in evolutionary simulations. The updating rule in classical Moran processes is a birth-death process, i. e. selection according to fitness of an individual to give birth, followed by the death of a random individual. The time evolution of a generalised Moran model is therefore given by Algorithm 1. For well-mixed populations with only two strategies this updating rule is known to be equivalent to selecting unfit individuals for death and then selecting randomly for procreation (biased death-birth process). It is however known that this equivalence does not hold when considering structured populations. Here we study whether changing the updating rule can also have an effect in well-mixed populations in the presence of more than two strategies and high mutation rates. We find, using 2 models from different areas of evolutionary simulation, that the choice of updating rule can change model results. We show e. g. that going from the birth-death process to the death-birth process can change a public goods game with punishment from containing mostly defectors to having a majority of cooperative strategies. From the examples given we derive guidelines indicating when the choice of the updating rule can be expected to have an impact on the results of the model.

Given a generalised Moran model, different methods of analysis give insight into different time scales of the evolution of the model. In many cases, the focus of interest is on the long-term behaviour and stability of the model. As a Markov process, the stochastic model has a steady state distribution. Even if the equilibrium distribution cannot be obtained directly, some of its properties can often be approximated through various means.

If mutation rates are low [36] and the model has a finite number of strategies, it is often assumed [37, 38] that the model will be in a fixed state with only one strategy most of the time. The proportion of time the system spends in each fixated state can then be expressed as the stable state distribution of a far simpler Markov chain, where the states are the fixed states of the underlying model. The probability of a transition from fixed state A to fixed state B is then the fixation probability ρ_{AB}, *i. e.* the probability that a single mutant of type B will fixate in a population that consist of only individuals of type A otherwise.

Evolutionary models are used to explore a diverse range of research topics, from cancer cell spread [39] and particle systems [40] to the evolution of language traits [41] and cooperation [42]. As such, results from these models greatly inform our characterisation of many systems, with implications for how we view the world and our own social behaviour. Predictions and policies are based on findings from evolutionary game theory [43–45]. Conclusions about factors governing language evolution would for example be relevant in governmental decision-making on language affairs, such as the support of minority languages. General results from models in evolutionary anthropology might also be used by corporations deciding on how best to implement changes in policy or corporate culture. We therefore expect that as anthropological evidence becomes incorporated into computational models, their results and conclusions will be applied on a wider basis than their underlying assumptions directly warrant, in order to inform policy-making. Given this, an awareness of how implicit assumptions in evolutionary models can impact their outcomes is vital. We will thus identify default assumptions, and discern alternatives and the impact of those choices on the results of evolutionary models. If results are highly dependent on implicit choices, the generality of derived results is cast into doubt.

1.2 The Evolution of Language

The reality of cooperation and social structures in the evolutionary history of humanity is difficult to reconstruct. As the last surviving species of the genus Homo, we lack close relatives in the evolutionary tree to compare our behaviour with, and behavioural data over evolutionary timescales is hard to come by.

Linguistic data, on the other hand, is ubiquitous around us[2], and both its use patterns and internal structure can give insight into the human condition, both in large and small contexts. Cultural contact can leave traces in the form of language change. This can range from a single word being borrowed into a new language (like the word “tattoo”

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[2] Look! There is some more linguistic data down here!

in the English language, borrowed from Polynesian languages [46]), to a language shift, where a substrate language of lower prestige is replaced by a dominant other language, and the substrate leaves at only minor traces in the superstrate [47].

In addition, language is a fundamental property of the human brain. Considering the complexity of human languages, Chomsky [48, p. 27] deduced that the abstract generative class to which they belong is so large that without serious restrictions on possible structures, it would be impossible to learn a language from the data a language learner has access to. Furthermore, humans find ways to express themselves using linguistic structures, even in contexts where no language is easily available, as can be seen eg. in the spontaneous emergence of Nicaraguan Sign Language in the 1970s [49]. Both of these observations show that the structure of human language is fundamentally connected with the structure of the human brain, and how it perceives and structures data. An even stronger connection between language and the mind is postulated by the *linguistic relativity hypothesis* (popularly known as the Sapir-Whorf hypothesis, after Sapir [50] and Whorf [51]). It states that “Languages, especially members of quite different language families, differ in important ways from one another.”[52] and “The structure and lexicon of one’s language influences how one perceives and conceptualises the world, and they do so in a systematic way.”[52]

We can therefore expect that understanding the constraints and properties of human language would give us indirect insight into the human condition. Most insight into the puzzle of cooperation is derived through models from evolutionary game theory, studying the effect of different components for the evolutionary outcomes. Where direct evidence is lacking, the merit of such hypotheses must be deduced indirectly. Similar methods can be used to gain insight into logical constraints of cultural evolution. We will consider an example of a game theoretical model of language evolution in Section 2.2.2.

But where theoretical anthropology looks towards real-world culture, other types of models are available, as well. We have access to a large trove of coexisting cultures, and in some regions of the world ample imprint of societies gone by. This data can be used to investigate hypotheses of evolutionary history. Evolutionary phylogenies have been constructed for items of human culture, such as the evolution of board games [53] or folk tales [54]. Such evolutionary histories will have implications on the fundamentals of the structure of language evolution as a property induced by the brain.

Chapter 7 will be dedicated to a case study of reconstructing the evolutionary history of languages, using a Bayesian model. The Bayesian approach allows us to construct possible phylogenies from data, and value them not just by theoretical and logical plausibility, but by quantifying how consistent they are with the given data.

1.3 Outline

In this thesis, we want to investigate how different computational models from theoretical biology can be applied to evolutionary anthropology. Through the application and analysis of models well-established in the biological literature, we aim to get twofold insight for theoretical anthropology. Firstly, we will focus on the challenges arising from the particularity of this interdisciplinary approach, and investigate the methodology of theoretical biology from an anthropological perspective. Secondly, we will attempt to meet those challenges, and derive new results aiding in our understanding of the puzzle of cooperation and the evolution of languages.

We will therefore seek to answer the following questions.

- What structures of theoretical models can be applied to evolutionary anthropology?
- When constructing a specific computational model to gain insight into anthropological questions, what makes one model "better" than another one?
- What is necessary to make interdisciplinary research using mathematical modelling in socioecology and evolutionary anthropology fruitful?

In order to do this, this thesis will attempt to meet the following objectives.

- Construct a computational model of cooperation and punishment in competing communities.
- Investigate the choices made in the assembly of this model, and highlight alternatives and their shortcomings.
- Study the influence of these alternatives on other models in theoretical anthropology
- Construct a computational model of the evolution of languages, extending the range of data that can be used in such a model.

The structure of this thesis is as follows. Having identified the three components of simulation models of evolution above, we will proceed to discern and analyse choices for these components in the following chapters. In Chapter 2, we will introduce three Darwinian updating rules for generalised Moran processes. We will apply them to an abstract model of grammar evolution in Section 2.2.2.

We will proceed by investigating the public goods game and its evolutionary dynamics in Chapter 3. After that, we consider the effects of a particular choice of population structure, the third component of such a model, in Chapter 4, where we study metapopulations consisting of weakly linked well-mixed communities, contributing to our understanding of group selection. Having exemplified and discussed the structure of this type of model by example, we proceed to examine punishment in this framework. Chapter 5 will recall variants of the public goods game that have in the past been used to study punishment in that framework, before scrutinising a particular extension deemed to represent the emergence of institutional punishment in Section 5.1. In Chapter 6, we combine the results from the previous two chapters and study how our model of institutional punishment behaves under group selection.

We then change focus to the matter of evolutionary linguistics in Chapter 7, where a different type of model permits the computational reconstruction of evolutionary history from data, incorporating usage of typological data into existing models derived from bio-informatics. In Chapter 8, we complete the thesis by giving a general discussion and conclusions of the matters considered in this thesis.

Chapter 2

The Choice of Updating Rule

[1] Evolutionary models are used to explore a diverse range of research topics, from cancer cell spread [39] and particle systems [40] to the evolution of language traits [41] and cooperation [42]. In this thesis, we will use stochastic evolutionary modelling to study some aspects of the evolution of punishment, with a strong view towards implications on good and bad strategies of policing.

As such, results from these models greatly inform our characterisation of many systems, with implications for how we view the world and our own social behaviour. Predictions and policies are based on findings from evolutionary game theory. For example, Verspagen [45] argues generally how quantitative evolutionary models can be used for policy analysis, van den Bergh [43] and Frank and Sarkar [44] give specific examples of how game theory can help in decision-making for environmental cases. Given such direct applications of model results to real-world policies, an awareness of how implicit assumptions in evolutionary models can impact their outcomes is vital – particularly where policy-makers do not have deep understanding of the underlying assumptions of a model and its limitations in the real world.

In addition to a game and a population structure, any model in evolutionary game theory must incorporate an *updating rule*. This describes the development of the population in time, and therefore needs to capture the core evolutionary properties of the system to be explored. In this chapter, we consider how different updating rule formulations can lead to varied model results, while appearing to capture similar evolutionary properties. Our focus is on a subtlety of the implementation of selection – whether abstract "fitness advantage" is rewarded by increased survival or increased reproduction.

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[1] This chapter is a slight modification of an article published as (Kaiping *et al.* [1]). GAK, SJC and GSJ defined the problem. GAK carried out the calculations and simulations. GAK, GSJ and TJS wrote up the results.

For stochastic models with overlapping generations, there is a small number of updating rules regularly employed in models with fixed population size. We focus on three of these (birth process, death process and link dynamics) as described below, and will comment on their limit cases of strong and weak selection. We postpone their formal definition and detailed description to Section 2.1.

Other updating rules have also been used to model evolutionary processes, but much more rarely. The three updating rules compared in this chapter are based on replication (or imitation) of one individual in each time step. It is known that other families of updating rules, such as myopic best response [55, 56], can lead to entirely different evolutionary dynamics [57, 58]. While they have merit in particular in conjunction with the consideration of other anthropological items of interest, such as the theory of mind [59], we will not consider these updating rules here, instead focusing on purely Darwinian evolution.

Moran [60] introduced a class of evolutionary models which employ an updating rule known as the *birth-death process* (BP) [61] or (biased) invasion process [62]. In these models, the fitness of an individual gives the probability that this individual produces offspring in a given time step. This type of model is intermediate between the discrete-time Wright-Fisher model [31], in which one time step corresponds to one generation of the finite population, and continuous-time approaches using differential equations and infinite populations, with their respective families of updating rules. The Moran process permits the study of overlapping generations in a finite population of fixed size, using a discrete-time Markov chain. The transition probabilities associated with the birth-death process have comparatively easy algebraic expressions (see e. g. [41]), and are therefore often used where algebraic expressions of derived properties like fixation probabilities are relevant. The BP updating rule appears far more frequently in evolutionary models literature than the following two.

The *death-birth process* (DP) [61] was introduced by Williams and Bjerknes [63] and Bramson and Griffeath [64, 65] to study tumor growth and has been independently studied in the context of particle systems under the name “voter model” [39, 40, 66, 67]. We note that although this updating rule is called a “model” in the context of particle systems, we will reserve the term “model” in this chapter for a combination of updating rule, population structure and underlying game. By contrast with BP, in which fitness is proportional to the stochastic birth rate of an individual, in the death-birth process fitness rather governs an individual’s chance of survival.

The *link dynamics* updating rule (LD) [68] arose from the study of structured populations and focuses on pairwise interactions. In most cases, a population structure is given in terms of a (static) graph [69], in which nodes correspond to individuals in the population. A link between two nodes then indicates that in the updating step of the model, one of these nodes can replace the other one. The effect of different population structures on the evolutionary process has been studied for several years now [20, 70–73]. This chapter on the other hand considers only unstructured, well-mixed populations. A variant of LD was introduced by Szabó and Tőke [74] and has been studied under the names “pairwise comparison evolutionary process” [75] and “Fermi process” [36] for the Prisoner’s Dilemma on lattices.

Of particular interest in evolutionary models is the process of fixation of a single mutant in a population of residents. Relevant quantities obtained from a given model are the fixation probability, *i. e.* the probability that a single mutant allele overtakes a homogeneous population of a different allele, and consequent fixation times.

In many evolutionary models, it is a reasonable assumption that at any given point in time, only two different alleles are present in the population. Given a sufficiently small mutation rate μ, the probability that a mutant enters a population already possessing more than one type of allele in it may be regarded as negligible [76, 77]. Thus the population will always only contain residents and possibly at most one type of mutant.

If the population structure is homogeneous, populations where this assumption is true show equal fixation probabilities for all three of the evolutionary processes introduced above, as has been shown by Antal, Redner, and Sood [78]. On generic graphs on the other hand this equivalence between BP, DP and LD is lost [78]. This result entailed investigations into how different updating rules lead to different evolutionary dynamics on various graph structures [79, 80]. While it is known that going from low to high mutation rates in itself can change the evolutionary dynamics of a system [81], the interaction between high mutation rate and varying updating rules has been studied less. A notable result is given by Allen *et al.* [82], who show that the BP updating rule and a similar, non-equivalent updating rule have significantly different evolutionary dynamics under high mutation rates on homogeneous graphs.

In this chapter we investigate the differences between the different updating rules mentioned above when dismissing the two-allele assumption. The error induced by that assumption has been previously studied by Wu *et al.* [36]. Their study employs the Fermi process as updating rule on a well-mixed model of population size N. Of particular interest is their result for coexistence games, in which the best reply to every strategy is a different strategy. They find that the two allele approximation is only reliable if the mutation rate μ behaves as $O(N^{-\frac{1}{2}}\exp(-N))$ (where N is the population size). This is a very restrictive requirement, which is unlikely to hold in practice even for small populations. The expected time between mutations needs to be significantly longer than the age of the universe in order for mutation to be a negligible factor.

For example, using Eqs. (2.27) and (2.30) below, we see that the expected consensus and fixation times of the anticoordination game with payoff matrix $\begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$, between 100 players, is about 1.3×10^{30} time steps, or about 1.8×10^{13} times the age of the universe at a generation time as low as 10 minutes, for any of the three updating rules. In this chapter we therefore drop the assumption that mutation rates are so low that the fixation time is negligible with respect to the time between mutations. Depending on the circumstances, the implications of this relaxation may differ. For some cases, it will be necessary to explicitly study high mutation rates in a model. Alternatively the effects of high mutation can be studied by allowing more than two strategies to be present at one time step in a given system.

The organisation of this chapter is as follows. In Section 2.1, we will recall some general observations from evolutionary game theory, before describing the update rules, birth-death process (BP), death-birth process (DP) and link dynamics (LD) in more detail, giving example calculations from basic evolutionary game theory for each.

We will then present 2 models that show differences in behaviour for the three updating rules in Section 2.2. Model 1 (Section 2.2.2) is a model from evolutionary linguistics, which we use to examine the effect of different updating rules in the context of high mutation rates. We will show that for high mutation values, changing the updating rule not only affects the quantitative values of the equilibria of a model, but also the topology of the equilibrium space.

For another model, we look at cases where more than two strategies are present in the system. Model 2 (Section 2.2.3) is a simple model from abstract game theory. We show explicitly that the equilibria of the model are identical for the three updating rules. Interestingly, however, the choice of updating rule does impact both the quantitative geometry of the equilibria and their basins of attraction.

Finally, in Section 2.3, we conclude with a general discussion of the properties of the updating rules studied. We suggest heuristic criteria as to when changing the updating rule significantly alters the results of the model and in what contexts to employ which updating rule.

2.1 Updating rules

Updating rules such as BP, DP or LD define a discrete Markov process. The states correspond to all possible configurations of the underlying graph. In the commonly treated case of well-mixed populations, for example, every state is completely described by giving the number of individuals having a particular allele. The transition probabilities between states are derived from the fitness values of the alleles, according to the updating rule. The rules considered here are defined such that the population size will be constant.

In order to provide context for our more general study, we first recall well-known results for Markov processes in well-mixed two-allele populations. In what follows we employ the notation and conventions of Antal and Scheuring [83].

Consider a well-mixed population of players, each following one of two different strategies A and B. The state of a population of size N is defined by a single integer $0 \leq n \leq N$, giving the number of individuals in the population following strategy A. Suppose also that at each time step each individual in the population plays a random other individual in a symmetric game. Let the payoff for the row player be given by the payoff matrix

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array} \tag{2.1}$$

for $a, b, c, d > 0$.

The fitness of an individual playing strategy A or B respectively is defined to be its expected payoff, that is

$$f_A(n) = \frac{a(n-1) + b(N-n)}{N-1} \tag{2.2}$$

$$f_B(n) = \frac{cn + d(N-n-1)}{N-1} \tag{2.3}$$

The transition probabilities

$$\lambda_n = P(n \to n+1) = P(\text{One of type } A \text{ procreates}) \cdot P(\text{One of type } B \text{ dies}) \tag{2.4}$$

$$\mu_n = P(n \to n-1) = P(\text{One of type } B \text{ procreates}) \cdot P(\text{One of type } A \text{ dies}) \tag{2.5}$$

are derived from $f_A(n)$ and $f_B(n)$. Each of the three updating rules defines how to obtain λ_n and μ_n from $f_A(n)$ and $f_B(n)$. We discuss this in more detail below. Calculations for Moran's birth process (BP) are given by Eqs. (2.31) and (2.32). The BP updating rule is one of many consistent routes from $f_A(n), f_B(n)$ to λ_n, μ_n. However, whatever route is chosen, an invariant property of (λ_n, μ_n) is that

$$\frac{f_B(n)}{f_A(n)} = \frac{\mu_n}{\lambda_n} = \frac{P(n \to n-1)}{P(n \to n+1)} \tag{2.6}$$

$$= \frac{P(\text{One of type } B \text{ procreates})}{P(\text{One of type } B \text{ dies})} \left(\frac{P(\text{One of type } A \text{ procreates})}{P(\text{One of type } A \text{ dies})} \right)^{-1} \tag{2.7}$$

Thus μ/λ is the quotient of the stochastic growth rates of the A and B populations, justifying the use of the term *fitness* in this context, even when the updating rule is not BP.

For any updating rule, the matrix of all transition probabilities in the Markov process, $P(i \to j)$ for $0 \leq i, j \leq N$, are then given by

$$P(i \to j) = \begin{cases} \lambda_i & \text{for } j = i + 1 \\ \mu_i & \text{for } j = i - 1 \\ 1 - \lambda_i - \mu_i & \text{for } j = i \\ 0 & \text{otherwise} \end{cases} \tag{2.8}$$

For ease of notation, this equation uses $\lambda_N = 0$ and $\mu_0 = 0$.

For any two-allele Markov model with one individual dying and one individual being born every step, we can calculate the probability ϵ_n^+ that the Markov chain starting from state n will hit state N before ever having hit state 0. These probabilities are then given by the system of equations

$$\epsilon_0^+ = 0 \tag{2.9}$$

$$\epsilon_N^+ = 1 \tag{2.10}$$

$$\epsilon_n^+ = \mu_n \epsilon_{n-1}^+ + (1 - \mu_n - \lambda_n)\epsilon_n^+ + \lambda_n \epsilon_{n+1}^+ \tag{2.11}$$

or, equivalently,

$$\epsilon_{n+1}^+ = \left(1 + \frac{\mu_n}{\lambda_n}\right) \epsilon_n^+ - \frac{\mu_n}{\lambda_n} \epsilon_{n-1}^+ \tag{2.12}$$

For convenience of notation, we define

$$q_n = \prod_{j=1}^{n} \frac{\mu_j}{\lambda_j} \qquad q_0 = 1 \qquad s_{n,m} = \sum_{k=n}^{m} q_k \tag{2.13}$$

We remark that q_n and $s_{n,m}$ are polynomials in the variables $\{x_n = \frac{\mu_n}{\lambda_n} \mid n = 1 \ldots N\}$, with no unpaired μ or λ appearing in the coefficients. Using this notation, we have

$$\epsilon_n^+ = s_{0,n-1} \epsilon_1^+ \tag{2.14}$$

(For $n = 1$, we have $s_{0,n-1} = s_{0,0} = \sum_{k=0}^{0} q_k = q_0 = 1$, and assuming we have shown Eq. (2.14) for $n \leq m$, then for $n = m + 1$ we get

$$\epsilon^+_{m+1} = \left(1 + \frac{\mu_m}{\lambda_m}\right) \epsilon^+_m - \frac{\mu_m}{\lambda_m} \epsilon^+_{m-1} \tag{2.15}$$

$$= [\left(1 + \frac{\mu_m}{\lambda_m}\right) s_{0,m-1} - \frac{\mu_m}{\lambda_m} s_{0,m-2}]\epsilon^+_1 \tag{2.16}$$

$$= [s_{0,m-1} + \frac{\mu_m}{\lambda_m} q_{m-1} + \frac{\mu_m}{\lambda_m} s_{0,m-2} - \frac{\mu_m}{\lambda_m} s_{0,m-2}]\epsilon^+_1 \tag{2.17}$$

$$= [s_{0,m}]\epsilon^+_1 \tag{2.18}$$

Therefore Eq. (2.14) follows by induction.)

We recall that state 0 corresponds to a state in which all individuals have allele B. The other absorbing state of each individual playing A is denoted by N. The *fixation probability*, ρ_{AB}, of a single mutant of strategy A in a population of $N - 1$ individuals following strategy B can then easily be calculated from Eq. (2.14) for $n = N$, giving $1 = \epsilon^+_N = s_{0,N-1}\epsilon^+_1$ and therefore

$$\rho_{AB} = \epsilon^+_1 = \frac{1}{s_{0,N-1}} \tag{2.19}$$

As given in Eq. (2.6), we have $\frac{\mu_n}{\lambda_n} = \frac{f_B(n)}{f_A(n)}$, and therefore for the simple game given in Eq. (2.1)

$$\rho_{AB} = \frac{1}{\sum_{k=0}^{N-1} \prod_{l=1}^{k} \frac{f_B(l)}{f_A(l)}} \tag{2.20}$$

$$= \frac{1}{\sum_{k=0}^{N-1} \prod_{l=1}^{k} \frac{cl+d(N-l-1)}{a(l-1)+b(N-l)}} \tag{2.21}$$

For the neutral case $a = b = c = d$ this gives us a fixation probability

$$\rho_{AB} = \frac{1}{\sum_{k=0}^{N-1} \prod_{l=1}^{k} \frac{l+N-l-1}{l-1+N-l}} = \frac{1}{\sum_{k=0}^{N-1} 1} = \frac{1}{N} \tag{2.22}$$

For the case of a mutant with a constant fitness advantage $a = b = r > 1 = c = d$ we obtain the well-known result [60] that the fixation probability is given by

$$\rho_{AB} = \frac{1}{\sum_{k=0}^{N-1} r^{-k}} = \frac{1 - r^{-1}}{1 - r^{-N}} \tag{2.23}$$

The expected time until fixation of i mutants, given that the mutants will fixate, is the *mean conditional exit time* t^+_i, and we are particularly interested in the expected time until fixation of a single mutant t_1^+. Antal and Scheuring [83] give an elementary derivation of this quantity, based on the following ansatz.

Let $P_i^+(t)$ be the probability be the probability of fixating in state N in time step t when the system at time 0 is in state i, with the obvious values $P_i^+(0) = \delta_{i,N}$ and $P_0^+(t) = 0$ for all t and i. Given that the system will fixate at some point, these probabilities will obviously sum up to $\epsilon_i^+ = \sum_{t=0}^{\infty} P_i^+(t)$. As a conditional expectation value, we have

$$t_i^+ = \frac{1}{\epsilon_i^+} E[t \sim P_i^+(t)] = \frac{\sum_{t=0}^{\infty} t P_i^+(t)}{\sum_{t=0}^{\infty} P_i^+(t)} \tag{2.24}$$

Now the $P_i^+(t)$ fulfill a recurrence relation similar similar to Eq. (2.11) above. Multiplying with t and adding it up, this yields

$$\sum_{t=0}^{\infty} t \cdot \left[P_i^+(t)\right] = \sum_{t=0}^{\infty} t \cdot \left[\mu_i P_{i-1}^+(t-1) + (1 - \mu_i - \lambda_i) P_i^+(t-1) + \lambda_i P_{i+1}^+(t-1)\right] \tag{2.25}$$

Using the recurrence relation from Eq. (2.11) above, this simplifies to

$$-\epsilon_i^+ = \mu_i(\epsilon_{i-1}^+ t_{i-1}^+) - (\mu_i + \lambda_i)(\epsilon_i^+ t_i^+) + \lambda_i(\epsilon_{i+1}^+ t_{i+1}^+) \tag{2.26}$$

Due to the alternating summands, this can be rewritten as a recursive equation $\sigma_{i-1}^+ = \frac{\lambda_i^+}{\mu_i^+}\sigma_i^+ - \frac{\epsilon_i^+}{\mu^+}$ for $\sigma_i^+ = \epsilon_i^+ t_i^+ - \epsilon_{i+1}^+ t_{i+1}^+$. After plugging in $t_N^+ = 0$ and simplifying, this recursion formula yields

$$t_{\text{fix}} = t_1^+ = \sum_{n=1}^{N-1} \frac{s_{0,n-1} s_{n,N-1}}{\lambda_n q_n s_{0,N-1}} \tag{2.27}$$

Using the same arguments, we can calculate the expected conditional exit time for extinction instead of fixation. Antal and Scheuring [83] show that the extinction and fixation times are the same for a single B mutant in an otherwise A population as for a single A mutant in an otherwise B population, so we have

$$t_{\text{ext}} = t_1^- = t_{N-1}^+ = (1 - \epsilon_{N-1}^+) \sum_{n=1}^{N-1} q_n \sum_{k=n}^{N-1} \frac{\epsilon_k^+}{\lambda_k q_k} \tag{2.28}$$

In the models we explore below, there are three or more possible strategies. A quantity of relevance in the three-allele problem is the expected time t_{cons} until a two-allele system fixates in either of the two absorbing states. If the mutation rate μ is of the order of magnitude of ${t_{\text{cons}}}^{-1}$ or higher, the probability of a mutation occurring in a non-fixated system can no longer be considered negligible. The *consensus* or *unconditional mean*

```
Input: A population $P$ at time $t$
Output: The population $P$ at time $t+1$
foreach $n \in P$ do
    calculate fitness $f_n$ ;
end
randomly select $j \in P$ with probability $p(j = n) \propto f_n$ ;
randomly select $k \in P$ (uniformly $p(k = n) \propto 1$) ;
replace $k$ with a copy of $j$ ;
```

Algorithm 2: Birth Process

exit time t_{cons} is defined [84] as the expected time until the system reaches either of the absorbing states when starting at $n = 1$. It can be derived analogously, and is

$$t_{\text{cons}} = \epsilon_1^+ t_1^+ + (1 - \epsilon_1^+) t_1^- \tag{2.29}$$

$$= \sum_{n=1}^{N-1} \frac{s_{n,N-1}}{\lambda_n q_n s_{0,N-1}} \tag{2.30}$$

By definition, $\frac{\mu_j}{\lambda_j}$ has the same value for all three updating rules. From Eqs. (2.13) and (2.19) it follows that in the general case the fixation *probabilities* ρ_{AB} will be independent of the specific updating rule chosen. By contrast, the additional λ_n terms in Eqs. (2.27) and (2.30) can mean significant deviations between the expected unconditional mean fixation *times* when comparing the three updating rules.

In what follows we discuss some specific details of the BP, DP and LD processes.

2.1.1 Birth Process

The Moran process, introduced by P. A. P. Moran in 1958 [60], is frequently used as an updating rule in evolutionary simulations. It is also known as the birth process (BP) or biased birth-death process. In every time step, one random individual is replaced by a copy of an individual randomly chosen with probability proportional to its fitness. An individual can be replaced by a copy of itself. The general algorithm can be described in pseudocode as given by Algorithm 2.[2]

---

[2] In cases where multiple individuals execute the same strategy and thus obtain the same fitness, they can be aggregated into groups and fitness values can be calculated for each group. When only two pure strategies are followed, only two fitness calculation steps are necessary.

The transition probabilities in the two-allele case are therefore given by

$$P(n \to n-1) = \mu_n = \frac{(N-n)f_B(n)}{nf_A(n) + (N-n)f_B(n)} \frac{n}{N} \tag{2.31}$$

$$P(n \to n+1) = \lambda_n = \frac{nf_A(n)}{nf_A(n) + (N-n)f_B(n)} \frac{N-n}{N} \tag{2.32}$$

$$P(n \to n) = 1 - \mu_n - \lambda_n \tag{2.33}$$

$$P(n \to j) = 0 \text{ otherwise} \tag{2.34}$$

By way of example, we can calculate the expected times until fixation for the Prisoners' Dilemma with payoff matrix

$$Q = \begin{pmatrix} 1 & 5 \\ 0.1 & 3 \end{pmatrix} \tag{2.35}$$

for a population size of 100. From eq. Eq. (2.27) we obtain that the conditional fixation time is $t_{\text{fix}} \approx 1264.5$ for both a single cooperator among defectors and a single defector among cooperators. Following Eq. (2.30), the average time until the system is in any fixated state again after starting from a single defector is introduced into a population of cooperators is approximately 569.6 updating steps, while for a single cooperator among a population of defectors is close to the life expectancy of that cooperator, because the probability of him reproducing is near 0. Therefore in this case we have $t_{\text{cons}} \approx 105.3$.

2.1.2 Death Process

In the ecological and evolutionary literature, fitness usually corresponds to the mean number of adult offspring per generation. High fitness can thus imply a high fecundity, as seen in the Birth Process. Alternatively, high fitness can be expressed as high probability of survival. This is modelled by the Death Process (DP) updating rule. Just as in BP, in every time step an individual chosen randomly according so some distribution is replaced by a copy of a random individual. However, in DP, the fecundities or birth probabilities of all individuals are assumed to be equal, while the death probabilities are taken to be proportional to the reciprocal of the fitness.

```
Input: A population $P$ at time $t$
Output: The population $P$ at time $t+1$
foreach $n \in P$ do
    calculate fitness $f_n$ ;
end
randomly select $j \in P$ with probability $p(j = n) \propto \frac{1}{f_n}$ ;
randomly select $k \in P$ (uniformly $p(k = n) \propto 1$) ;
replace $j$ with a copy of $k$ ;
```

Algorithm 3: Death Process

The transition probabilities for this updating rule are thus given by

$$\begin{aligned} P(n \to n-1) = \mu_n &= \frac{N-n}{N} \frac{n/f_A(n)}{n/f_A(n) + (N-n)/f_B(n)} \\ &= \frac{N-n}{N} \frac{n f_B(n)}{n f_B(n) + (N-n) f_A(n)} \end{aligned} \tag{2.36}$$

$$P(n \to n+1) = \lambda_n = \frac{n}{N} \frac{(N-n) f_A(n)}{n f_B(n) + (N-n) f_A(n)} \tag{2.37}$$

$$P(n \to n) = 1 - \mu_n - \lambda_n \tag{2.38}$$

$$P(n \to j) = 0 \text{ otherwise} \tag{2.39}$$

Note that $\frac{\mu_n}{\lambda_n} = \frac{f_B(n)}{f_A(n)}$, just as for the birth-death process, and therefore the fixation *probability* for the Death Process is indeed the same as for the Birth Process [78].

This is not however true for the fixation *times* in the Prisoners' Dilemma example with payoff matrix Q as in eq. Eq. (2.35). Here, we have a slightly lower conditional fixation time of $t_{\text{fix}} \approx 1191.0$ for both cases. The expected time until the system is in any fixated state, after starting from a single defector, is slightly longer than in the BP, with a value of 575.3 time steps. Although a single cooperator in a population of defectors has a relatively large probability of reproduction compared to the BP, at $\frac{1}{100}$, the likelihood of dying is very high. As a result, the expected time to elimination is $t_{cons} = 11.4$, significantly less than in the BP case.

2.1.3 Link Dynamics

The third frequently applied updating rule that we study, link dynamics (LD), proceeds as follows. At every time step a random link of the graph describing the population structure is chosen. Two individuals are adjacent to the edge. One of these is chosen randomly as donor k with probability proportional to its fitness. The other individual j is then replaced by a copy of k.

In many cases of numerical simulation, the link dynamics updating rule has a significant computational benefit over BP and DP. The LD rule requires the calculation of the fitness

```
Input: A population $P$ at time $t$
Output: The population $P$ at time $t+1$
randomly select $(x, y) \in P^2$;
calculate $f_x$ and $f_y$;
with probability $\frac{f_x}{f_x+f_y}$ do
    $k := x$, $j := y$;
otherwise
    $k := y$, $j := x$;
endwith
replace $j$ with a copy of $k$;
```

Algorithm 4: Link Dynamics

values for only *two* individuals in every time step. BP and DP, by contrast, necessarily rely on knowing the fitness values of *every* individual in the population.

For the well-mixed case, the population structure contains an edge from every individual to every individual, including itself. The population structure is thus given by a fully-connected graph with self-loops. This is consistent with the assumption made in the previous two subsections for BP and DP, namely that in the same time step an individual can both procreate and die, thereby replacing itself. A pseudocode description is given in Algorithm 4.

The probability that a self-loop is randomly selected as focal link is $\frac{N}{\frac{N(N-1)}{2}+N} = \frac{2}{N+1}$. In the absence of mutation, this implies that nothing happens for such a time step. A model with self-loops corresponds to a model without self-loops in which there is a probability of $\frac{2}{N+1}$ for every time step that nothing happens in that step. Fixation probabilities (as well as other probabilities that are independent of specific times) will remain the same, and expected times, such as t_{fix} or t_{cons} transform between one approach and to the other through a linear re-scaling by a factor $\frac{N-1}{N+1}$. Results given for one approach are therefore easily translated to the alternative.

A related well-known updating rule for well-mixed populations is the Fermi process [84]. In the same way as in the LD updating rule, a random link in the population is chosen. However in case of the Fermi process, both individuals are equally likely to be chosen as donor k. In contrast with LD, where j is always replaced by a copy of k, for the Fermi process this replacement happens only with a probability of $\frac{1}{1+\exp(w[\pi_j - \pi_k])}$.

This probability distribution is known as the Fermi distribution and is eponymous for the updating rule. Here $w > 0$ is a constant describing the strength of selection. In the context of the Fermi distribution, it can be interpreted as an inverse temperature. Lower w corresponds to higher randomness of the system, and thus weaker selection.

The quantities π_x are payoff functions [36]. In contrast to the fitness functions f_x employed in the other updating rules considered here, these payoff functions may take negative values. We also note that, while for BP, DP and LD every time step corresponds to precisely one individual procreating and one individual dying, in the Fermi process there is a probability of $1 - \frac{1}{1+\exp(w[\pi_j - \pi_k])}$ in every time step that no individual procreates and none dies.

We shall in fact show that the Fermi Process is a variant of LD. Let us consider the Link Dynamics updating rule with a fitness function $f_x = \exp(w\pi_x)$. The transition probabilities are then given by

$$
\begin{aligned}
P(n \to n-1) &= \mu_n = 2\frac{n}{N}\frac{N-n}{N}\frac{f_B(n)}{f_A(n)+f_B(n)} && (2.40)\\
P(n \to n+1) &= \lambda_n = 2\frac{N-n}{N}\frac{n}{N}\frac{f_A(n)}{f_A(n)+f_B(n)} && (2.41)\\
P(n \to n) &= 1 - \mu_n - \lambda_n && (2.42)\\
P(n \to j) &= 0 \text{ otherwise} && (2.43)
\end{aligned}
$$

For the Fermi process, we have

$$
\begin{aligned}
P^F(n \to n-1) &= \mu_n^F = \frac{n}{N}\frac{N-n}{N}\frac{f_B(n)}{f_A(n)+f_B(n)}\\
&= \frac{1}{2}\mu_n && (2.44)\\
P^F(n \to n+1) &= \lambda_n^F = \frac{N-n}{N}\frac{n}{N}\frac{f_A(n)}{f_A(n)+f_B(n)}\\
&= \frac{1}{2}\lambda_n && (2.45)\\
P^F(n \to n) &= 1 - \mu_n^F - \lambda_n^F\\
&= \frac{1}{2}(1 - \mu_n - \lambda_n) + \frac{1}{2} && (2.46)\\
P^F(n \to j) &= 0 \text{ otherwise} && (2.47)
\end{aligned}
$$

Comparing Eqs. (2.40) to (2.42) with Eqs. (2.44) to (2.46) respectively indicates a probability of $\frac{1}{2}$ in each time step that the Fermi process behaves like link dynamics, and a probability of $\frac{1}{2}$ that it remains in the same state as before. As a result, one can translate times and expected times obtained through LD to the Fermi process by re-scaling, stochastically or exactly respectively, by a factor of 2.

From the terms for μ_n and λ_n in Eqs. (2.40) and (2.41) we see that, as for BP and DP, we have $\frac{\mu_n}{\lambda_n} = \frac{f_B(n)}{f_A(n)}$. Hence the fixation probabilities for LD and Fermi process are the same as for those two updating rules.

When comparing the transition probabilities for the three updating rules, recalling Eqs. (2.31), (2.36) and (2.40), we see that

$$\mu_n^{\mathrm{BP}} = \frac{n}{N}\frac{(N-n)f_B(n)}{nf_A(n)+(N-n)f_B(n)} \tag{2.48}$$

$$\mu_n^{\mathrm{DP}} = \frac{N-n}{N}\frac{nf_B(n)}{nf_B(n)+(N-n)f_A(n)} \tag{2.49}$$

$$\mu_n^{\mathrm{LD}} = 2\frac{n}{N}\frac{N-n}{N}\frac{f_B(n)}{f_A(n)+f_B(n)} \tag{2.50}$$

$$= \frac{2}{\frac{1}{\mu_n^{\mathrm{BP}}}+\frac{1}{\mu_n^{\mathrm{DP}}}} \tag{2.51}$$

Thus μ_n^{LD} is the harmonic mean of the analogous quantities μ_n^{BP} and μ_n^{DP}. The transition probability λ_n^{LD} is likewise the harmonic mean of the corresponding quantities for BP and DP. The LD updating rule is therefore expected to lead to behaviour that is intermediate between these two rules.

By way of example we see that for the fixation times in the Prisoners' Dilemma with payoff matrix Q from Eq. (2.35), we get precisely the arithmetic mean of the corresponding values from the birth-death process and death-birth process. We obtain $t_{\text{fix}} \approx 1227.7$ for both a single cooperator among defectors and a single defector among cooperators. The expected time until the system is in any fixated state, after starting from a single defector, is 572.5 time steps, and for starting from a single cooperator in a population of defectors we have $t_{\text{cons}} \approx 58.4$.

Due to the exponential function deriving fitness from payoff, and the additional parameter w, a direct comparison between the Fermi process and the BP, DP and LD updating rule is outside the scope of this chapter. For a detailed analysis of the fixation times for the Fermi process for $w \ll 1$ we refer to Altrock and Traulsen [84]. In this reference the authors also give a comparison between the birth-death process generalised to contain a selection strength parameter and the Fermi process for low selection strength.

It is the equality of the fixation probabilities of BP, DP and LD which motivates Antal, Redner, and Sood [78] to refer to these three updating rules as "equivalent" for homogeneous graphs. We remark that this is a very strong term for this specific property. We have indeed seen that for the simple cases of well-mixed mutation-free 2-strategy games considered in this section the long term behaviour of the model, as expressed by the fixation probability, does not change under different updating rules. The vast difference in the consensus times, however, serves as a first indication that applying different updating rules may influence model results. In the next section we will show that different updating rules can indeed lead to different long-term behaviour of otherwise equal evolutionary models.

2.2 Example models

We will now present three examples of systems in which a change to the updating rule also significantly changes its dynamics. Just as for the results given in the previous section, all three examples feature well-mixed populations of discrete strategies. For each of the three examples, we will first describe the model in general, before giving the results for each of BP, DP and LD and comparing the results. However in contrast with the previous section, the examples studied here will not assume that the mutation rate is small enough to be negligible for the dynamics of a non-fixated system. Furthermore fitness functions will not be restricted to the expected payoff from two-player games, but can be arbitrary non-zero functions.

2.2.1 Methodology

Mean field theories are mathematically simplified methods for analysing stochastic well-mixed systems. Using this approach, the Markov chains of an evolutionary model with large population can be approximated by systems of ordinary differential equations. We will use both the mean field approximation as well as stochastic methods to examine the example models below.

On one hand, the large population approximation of the mean field theory has the effect of smoothing the stochastic effects in a system, which are of particular interest when studying frequent mutation. On the other hand, the mean field theory is often more computationally efficient than the individual- or population-based stochastic simulations or the calculation of a Markov chain stationary distribution.

Furthermore, the system of ordinary differential equations allows us to study the equilibria of the mean field theory of an evolutionary system. Equilibria are characterised by the fact that the derivatives of the unknown functions are zero for those states. Depending on their stability, these equilibria can be repellers, saddle points or attractors. If a state is an attractor, a small disturbance will lead to the system returning to that same state. Attractors of the system are therefore evolutionarily stable states. Saddles and repellers lie on the boundaries between the basins of attraction of different evolutionarily stable states. Thus, mean field theory is useful for cataloguing all evolutionarily stable states, together with their basins of attraction.

To obtain the system of analytical ordinary differential equations corresponding to each updating rule, we generalise the method described by Traulsen et al. [34] to the higher-dimensional case. Let $P^\tau(\xi) = P^\tau(\xi_1, \xi_2, \ldots, \xi_n)$ be the probability that a process with n alleles is in state ξ at time τ. Let $F^i(\xi)$ be the fecundity, i. e. the probability that an individual of type i is born when the system is in state ξ, and $M^i(\xi)$ the mortality rate of type i, again taken as probability. Define e_i to be the ith unit vector $(0, \dots, 0, 1, 0, \dots, 0)$. Then the stochastic process is given by the master equation

$$\begin{aligned} P^{\tau+1}(\xi) - P^{\tau}(\xi) = \sum_{j=1}^{n} \sum_{i=1; i\neq j}^{n} & [P^{\tau}(\xi - e_i + e_j) F^i(\xi - e_i + e_j) M^j(\xi - e_i + e_j) \\ & - P^{\tau}(\xi) F^i(\xi) M^j(\xi)] \end{aligned} \tag{2.52}$$

Let $N = \sum_{i=1}^{n} \xi_i$ be the population size. Introducing $x = \xi/N$, $t = \tau/N$ and $\rho(x,t) = NP^{Nt}(Nx)$, we can express the left and right hand side of the previous equation using a multivariate Taylor expansion as follows.

$$P^{\tau+1}(\xi) - P^{\tau}(\xi) = \frac{1}{N}\left[\rho(x, t + \frac{1}{N}) - \rho(x,t)\right] = \frac{1}{N^2}\frac{\partial}{\partial t}\rho(x,t) + o(\frac{1}{N^3}) \tag{2.53}$$

$$\sum_{j=1}^{n} \sum_{i=1; i\neq j}^{n} [P^{\tau}(\xi - e_i + e_j) F^i(\xi - e_i + e_j) M^j(\xi - e_i + e_j) - P^{\tau}(\xi) F^i(\xi) M^j(\xi)] \tag{2.54}$$

$$= \frac{1}{N} \sum_{j=1}^{n} \sum_{i=1; i\neq j}^{n} [\rho(x + \frac{e_j - e_i}{N}, t) F^i(x + \frac{e_j - e_i}{N}) M^j(x + \frac{e_j - e_i}{N}) - \rho(x,t) F^i(x) M^j(x)] \tag{2.55}$$

$$= \frac{1}{N^2} \sum_{j=1}^{n} \sum_{i=1; i\neq j}^{n} \langle e_j - e_i, \nabla[\rho(x,t) F^i(x) M^j(x)] \rangle + o(\frac{1}{N^3}) \tag{2.56}$$

$$= \frac{1}{N^2} \sum_{j=1}^{n} \sum_{i=1}^{n} \frac{\partial}{\partial x_j}[\rho(x,t) F^i(x) M^j(x)] - \frac{\partial}{\partial x_i}[\rho(x,t) F^i(x) M^j(x)] + o(\frac{1}{N^3}) \tag{2.57}$$

$$= \frac{1}{N^2} \sum_{j=1}^{n} \frac{\partial}{\partial x_j}[\rho(x,t) \left(\sum_{i=1}^{n} F^i(x)\right) M^j(x)] - \frac{\partial}{\partial x_j}[\rho(x,t) F^j(x) \left(\sum_{i=1}^{n} M^i(x)\right)] + o(\frac{1}{N^3}) \tag{2.58}$$

$$= -\frac{1}{N^2} \sum_{j=1}^{n} \frac{\partial}{\partial x_j}[(F^j(x) - M^j(x))\rho(x,t)] + o(\frac{1}{N^3}) \tag{2.59}$$

because the F^i and M^j are probabilities for the evolution of the system starting in state x, and all possible birth and death events are encoded in $\{1, \dots, n\}$, so $\sum_{i=1}^{n} F^i(x) = \sum_{j=1}^{n} M^j(x) = 1$.

For $N \to \infty$ the higher-order remainder term $o(\frac{1}{N^3}) \to 0$, so the diffusion term in the corresponding multivariate Fokker-Planck equation vanishes for growing N. Therefore the resulting first-order approximation

$$\frac{\partial}{\partial t}\rho(x,t) = -\sum_{j=1}^{n} \frac{\partial}{\partial x_j}[(F^j(x) - M^j(x))\rho(x,t)] \tag{2.60}$$

gives rise to a system of ordinary differential equations for x given by

$$\dot{x} = F(x) - M(x) \tag{2.61}$$

This means that in the infinite population limit, the rate of change $\dot{x}_i$ of the relative frequency of allele i is given by the difference between its probabilistic fecundity $F^i(x)$ and its probabilistic mortality $M^i(x)$. Model equilibria therefore correspond to states in which $M(x) = F(x)$.

Now let the $F^i(x)$ and $M^i(x)$ be derived from fitness values $f^i(x)$ such that $F^i(x)/M^i(x) = \phi(x)f^i(x)$ for a scalar $\phi(x)$, as is the case for the updating rules without mutation considered here. For a model equilibrium we then need $F(x) = M(x)$, so $F^i/M^i = 1 = \phi f^i$ for all i – that is, in systems without mutation equilibria are given by the condition that the fitnesses of all strategies present be equal. In the presence of mutation it might by analogy be reasonable to assume that a change of updating rule might do no more than perturb the precise value of an equilibrium, while leaving the topology of the equilibrium structure intact. This is however not the case, as the first example (Section 2.2.2) will show.

By contrast, for stochastic systems with finite populations the notion of equilibrium is less clear. For such systems as considered here, the underlying population will have a finite set of alleles, so the state space of the underlying Markov chain is *finite*, as well. If the mutation probability of the model is greater than zero, every state of the underlying Markov chain can be reached from every other state, even though the probability may be very low due to requiring multiple mutations on the way. Such a Markov chain with the property that every state can be reached from every other state in the long run is known as an *irreducible* Markov chain. Lastly, the Markov chain has states in which it remains with probability $0 < P(i \rightarrow i) < 1$, so the number of time steps until it returns to a state cannot be a fixed number. This makes the chain *aperiodic*. Such an aperiodic irreducible finite-state Markov chain has a unique *stationary probability distribution* π, also known as its steady state. This fact is a well-known result from the theory of discrete-time Markov chains, and can be found eg. in [85, Corr. 2.4]

This distribution is a real-valued function over the state space, with local maxima, minima and saddle points. These special points, however, do not correspond to equilibria of the mean field theory. The basins of attraction are derived from the ordinary differential equations in the absence of noise, such as given in Eq. (2.61), which – as argued above – derive from the infinitesimal time-step limit of the Markov chain. Accordingly, basins of attraction indicate properties of the short-term behaviour of the system. The stationary distribution on the other hand is by definition concerned with only the long-term limit. Therefore, the notion of a basin of attraction does not transfer to steady state analysis of the Markov chain.

2.2.2 Model 1: Evolutionary linguistics

In our first example, we examine a model from evolutionary linguistics. The model was constructed by Komarova, Niyogi, and Nowak [41] to study the circumstances under which a single dominant language can evolve, given the fact that language learning is error-prone. Komarova, Niyogi, and Nowak only employ the birth process, but the model is easily modified to use DP or LD instead.

We will use this model to show that the different updating rules can lead to different topologies of the phase spaces of some models with high mutation rates.

Consider a finite population of agents. Each agent speaks exactly one of n different languages. We follow [41] in defining the fitness f_i of an individual speaking language i as

$$f_i = f_0 + \frac{1}{2}\sum_{j=1}^{n}(a_{ij} + a_{ji})x_j \tag{2.62}$$

Here $f_0 > 0$ is the background fitness which does not depend on the agent's language, x_j is the proportion of the population speaking language j, and for the comprehension matrix $A = a_{ij}$ we choose the fully symmetric mutual comprehension matrix, i. e.

$$a_{ii} = 1 \qquad\qquad a_{ij} = a \quad (i \neq j) \tag{2.63}$$

with a constant parameter $0 \leq a \leq 1$. The term $\sum_{j=1}^{n} a_{ij}x_j$ represents an expression for the mean proportion of sentences uttered by random other individuals in the population the actor speaking language i can understand.

We note that a fitness function of this shape is frequently applied in the literature. There is however no explicit reason to assume that the fecundity of an individual should be a linear polynomial in the proportion of other individuals an individual can understand in their population. We will come back to this aspect of updating rules in the context of discussing the general structure of evolutionary models in Section 8.1.2.

In every time step, one individual is replaced by another individual according to the updating rule chosen. Mutation is uniform with probability $\mu > 0$, such that the offspring has a probability of $q_{ii} = q = 1 - \mu$ of speaking the same language as their parent, and a probability of $q_{ij} = \frac{\mu}{n-1}$ for each of the other languages.

Birth Process BP is the original updating rule used in [41]. In BP, the probability of an individual of type j dying is $M^j(x) = x_j$. The birth probability, including mutation, is $F^j(x) = \phi^{-1}\sum_i f_i x_i q_{ij}$, where $\phi = \sum_{m=1}^{n} f_m x_m$. Thus the BP with mutation corresponds to the replicator-mutator differential equation [86] used by Komarova et al.

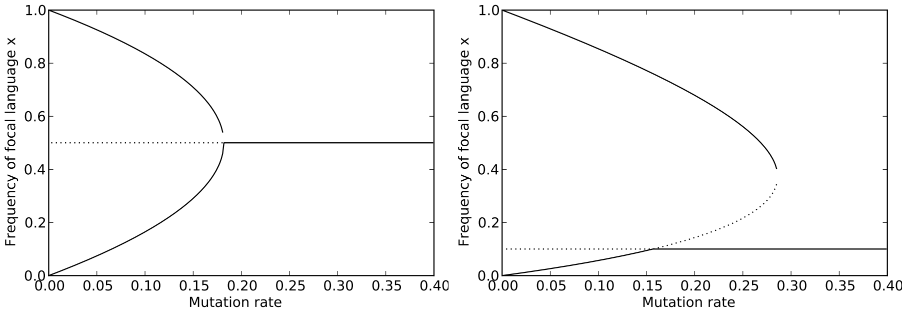


Figure 2.1: Equilibria of model 1 with BP as updating rule for varying μ and $a = 0.2, f_0 = 0.1$. The points on the solid line are stable equilibria for those parameter values, the points on the dotted line are unstable equilibria. (a) for $n = 2$, (b) for $n = 10$

[41]

$$\dot{x_j} = \sum_i f_i x_i q_{ij} - \phi x_j \tag{2.64}$$

under a dynamic re-scaling of time which does not change the equilibria of the model, i. e. the points where $\dot{x_j} = 0$.

Komarova, Niyogi, and Nowak [41] have derived the following results for the equilibria of the model. The equilibrium condition corresponds to a system of degree 3 polynomial equations in the x_j. For all values of the model parameters a, μ, n, f_0, there is an equilibrium in which every language has the same frequency $x_j = \frac{1}{n}$. If all but one language have the same frequency $\frac{1-X}{n-1}$ and the remaining language has frequency X, the system reduces to a single polynomial equation of degree 3, which has one, two or three solutions depending on the sign of a discriminant D. Stable asymmetric equilibria with one dominant language exist if and only if the discriminant

$$D = D^{\mathrm{BP}} = 4[-1 - a(n-2) - f_0(n-1)](1-q)(n-1)(1-a) + (1-a)^2[1 + (n-2)q]^2 \tag{2.65}$$

is positive. For $D > 0$ then also an asymmetric third type of equilibrium exists such that one language i has frequency $x_i = x_{eq}(a, \mu, n, f_0) < \frac{1}{2}$ and all other languages have identical frequency $\frac{1-x_i}{n-1}$. If $x_i < \frac{1}{n}$, this asymmetric equilibrium is stable and the symmetric equilibrium is unstable. Otherwise, the symmetric equilibrium is an attractor and the asymmetric equilibrium is a repeller. The equilibrium structures in this model, as a function of the mutation rate μ, are shown in Fig. 2.1.

We will now generalise the model in order to derive its behaviour under the DP and LD updating rules.

Death Process For the DP, we have $F^j(x) = \sum_i x_i q_{ij}$ and $M^j(x) = \psi^{-1}\frac{1}{f_j}x_j$. Here $\psi = \sum_{m=1}^{n} \frac{x_m}{f_m}$ is again a normalising factor. Thus the system of analytical ordinary differential equations corresponding to Eq. (2.64) is given by

$$\dot{x_j} = \sum_i x_i q_{ij} - \psi^{-1}\frac{1}{f_j}x_j \tag{2.66}$$

We apply the ansatz from [41] to this modified model. An equilibrium is given by $\dot{x_j} = 0$. Using Eqs. (2.62), (2.63) and (2.66), this becomes

$$\frac{1}{(1-a)x_j + a + f_0}x_j = \sum_{m=1}^{n} \frac{x_m}{(1-a)x_m + a + f_0} \sum_i x_i q_{ij} \tag{2.67}$$

Without loss of generality, let $x_1 = X$ and $x_i = \frac{1-X}{n-1}$ for $i \neq 1$. Then

$$\frac{1}{(1-a)X + a + f_0}X = \sum_{m=2}^{n} \frac{1-X}{(n-1)(a+f_0) + (1-X)(1-a)} (\sum_{i=2}^{n} \frac{1-X}{n-1}\frac{1-q}{n-1} + Xq) \tag{2.68}$$

which has the solutions $X = \frac{1}{n}$ and

$$X = \frac{\pm\sqrt{D^{\mathrm{DP}}} + (1-a)(nq-1)}{2(1-a)(nq-1)} \tag{2.69}$$

$$D^{\mathrm{DP}} = -(a-1)(nq-1)(3anq + 4f_0nq - 4an - 4aq - 4f_0n - 4f_0q + nq + 5a + 4f_0 - 1) \tag{2.70}$$

We have thus obtained a similar condition as in the BP case, stating that asymmetric equilibria with one focal language of frequency X and all other languages having frequency $\frac{1-X}{n-1}$ exist if and only if the discriminant

$$D^{\mathrm{DP}} = D^{\mathrm{BP}} + 4(q-1)^2(n-1)(1-a)[(a+f_0)n + (1-a)] \qquad > 0 \tag{2.71}$$

Link Dynamics In the case of the LD update rule, the limit of the stochastic process for increasing population size is given by the ordinary differential equation

$$\dot{x_j} = \sum_i \left(\sum_k \frac{f_i}{f_i + f_k} x_k \right) x_i q_{ij} - \left(\sum_k \frac{f_k}{f_j + f_k} x_k \right) x_j \tag{2.72}$$

because $M^j(x) = \left(\sum_k \frac{f_k}{f_j+f_k}x_k\right)x_j$ and $F^j(x) = \sum_i \left(\sum_k \frac{f_i}{f_i+f_k}x_k\right)x_i q_{ij}$ for LD.

Using the same argumentation as before, it follows from this differential equation that the equilibria are given by

$$0 = \sum_k \left(\sum_i \frac{f_i}{f_i + f_k} x_i q_{i1} \right) x_k - \left(\sum_k \frac{f_k}{f_1 + f_k} X \right) x_k \tag{2.73}$$

Using Eqs. (2.62), (2.63) and (2.72), this is a cubic equation in X,

$$0 = \frac{1-q}{2} \left(X^2 - \frac{(1-X)^2}{n-1} \right) \tag{2.74}$$

$$+ X(1-X) \left(q[(1-a)X + a + f_0] + \frac{2-n-q}{n-1} [(1-a)\frac{1-X}{n-1} + a + f_0] \right) \tag{2.75}$$

with solutions $X = \frac{1}{n}$, and

$$X = \frac{(1-a)(n-1)q \pm \sqrt{D^{\mathrm{LD}}}}{(1-a)(nq+n-2)} \tag{2.76}$$

$$D^{\mathrm{LD}} = D^{\mathrm{BP}} + (q-1)^2(n-1)(1-a)[2(a+f_0)n + 3(1-a)] \tag{2.77}$$

if $D^{\mathrm{LD}} > 0$.

Comparison Comparing D^{DP} (Eq. (2.71)) with D^{BP} (Eq. (2.65)), we see that due to the positive difference

$$D^{\mathrm{DP}} - D^{\mathrm{BP}} = 4(q-1)^2(n-1)(1-a)((a+f_0)n + (1-a)) > 0 \tag{2.78}$$

the asymmetric equilibria exist for a broader range of parameters in the case of DP than in the case of the BP. For those parameter values where $D^{\mathrm{DP}} > 0$ and $D^{\mathrm{BP}} < 0$, such as $a = 0.2, f_0 = 0.1, n = 2, q = 0.2$ (*cf.* Fig. 2.2), both values of the equilibrium Eq. (2.69) are real, so they describe stable equilibria of the model in addition to the unstable equilibrium at $x = \frac{1}{n}$. The corresponding values for the BP will not exist, because the square root of the negative discriminant D^{BP} is not a real number, and only $x = \frac{1}{n}$ will be an equilibrium. Consequently the death process permits a stable asymmetric equilibrium with a dominant language for parameter values that only support a symmetric equilibrium in case of BP.

We see that the discriminant D^{LD} (Eq. (2.77)) still has an additional positive addend as compared to the birth-death process discriminant D^{BP}. On the other hand we have for all reasonable parameter values ($q < 0, n > 1, a < 1, f_0 > 0$), according to Eqs. (2.71) and (2.77),

$$D^{\mathrm{LD}} < D^{\mathrm{LD}} + (q-1)^2(n-1)(1-a)\left(2(a+f_0)n + (1-a)\right) = D^{\mathrm{DP}} \tag{2.79}$$

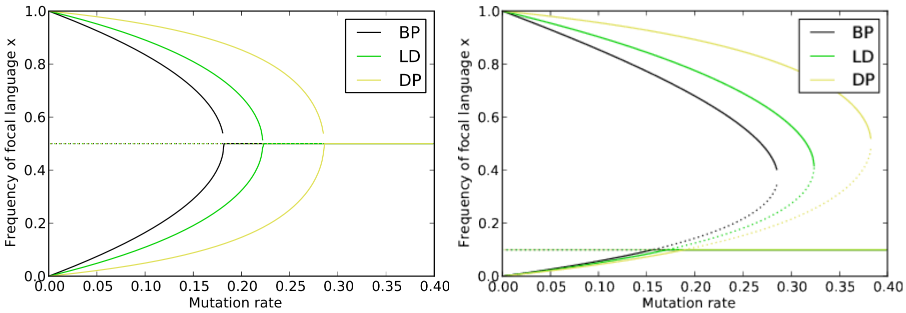


Figure 2.2: Equilibria of model 1 for varying μ for $a = 0.2, f_0 = 0.1$. The points on the solid line are stable equilibria for those parameter values, the points on the dotted line are unstable equilibria. (a) for $n = 2$, (b) for $n = 10$

Thus, just as derived in Eq. (2.51) for the case of two strategies in the absence of mutation, we see that the link dynamics process is a an intermediate updating rule between DP and BP.

In the case of $n = 2$ and $\mu > 0$, $D^{\mathrm{DP}} > D^{\mathrm{LD}} > D^{\mathrm{BP}}$ still holds. Thus for a range of parameters, the equilibrium structure under DP differs from the equilibrium structure under BP even for a model with only two languages.

Interpretation We conclude that, as shown in Fig. 2.2, for low mutation rates $\mu = (1-q)$ the behaviour of the model under all three updating rules is similar. All updating rules lead to stable asymmetric equilibria at similar values. For larger mutation rates, the quantitative difference between the equilibria under different updating rules increases.

When the mutation rate μ grows beyond a critical threshold, the behaviour of the model changes *qualitatively* when changing the updating rule. This first critical threshold is the value of μ such that the BP discriminant $D^{\mathrm{BP}} = 0$, that is

$$\mu = 1 - q_1 = 1 - \frac{4 + 2\sqrt{W}(n-1)^{3/2} - 2f_0(n-1)^2 - 3n - a(2n^2 - 7n + 6)}{(1-a)(n-2)^2} \tag{2.80}$$

where $W_1 = (1 + f_0)[1 + a(n-2) + f_0(n-1)]$. [41]

The behaviour changes again at a second threshold q_2 which is the root of D^{LD} in $[0, 1]$,

$$q_2 = \frac{1 + \sqrt{W_2}(n-1)^{3/2} + 2an - 3a + 2f_0 n - 2f_0}{an^2 - an - a + 2f_0 n^2 - 2f_0 n + n^2 - n + 1} \tag{2.81}$$

$$W_2 = (a + 2f_0 + 1)(2an - 3a + 2f_0 n - 2f_0 + 1) \tag{2.82}$$

For $1 - q_1 < \mu < 1 - q_2$, the BP discriminant is negative, but both LD and DP have a positive discriminant. The end points of this interval are the values of μ where the discriminants $D^{\mathrm{BP}} = 0$ respectively $D^{\mathrm{LD}} = 0$. Accordingly, both LD and DP permit the existence of asymmetric equilibria in this parameter region, while the BP shows only the stable symmetric equilibrium.

A further qualitative change occurs as D^{LD} drops below zero as μ grows larger than $1 - q_2$. From there on, while $\mu < \frac{(1-a)(n-1)}{3an-4a+4f_0n-4f_0+n}$, both BP and LD do not permit the existence of asymmetric equilibria, but the DP still sustains a stable asymmetric equilibrium, in which the dominant language has a frequency of substantially more than half the population.

Only for $\mu > \frac{(1-a)(n-1)}{3an-4a+4f_0n-4f_0+n}$ (*i. e.* for $0 > D^{\mathrm{DP}} > D^{\mathrm{LD}} > D^{\mathrm{BP}}$), do all three models show the same behaviour again, with only a stable symmetric equilibrium present.

These results show that when selection acts by weeding out maladapted individuals, instead of promoting well-adapted ones, a dominant language is more resilient to learning errors, and also more frequent.

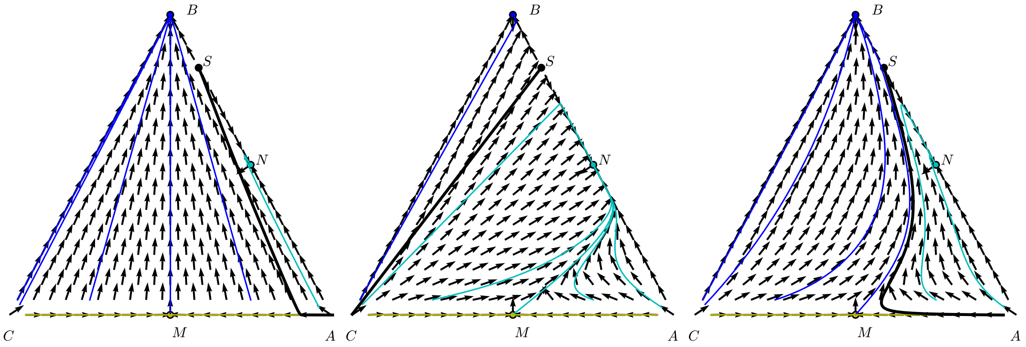
More generally, the conclusion from these calculations is that changing the updating rule does not merely perturb the equilibria, but that it can also give rise to different equilibrium structures. Thus we have illustrated that for high mutation rates the number and structure of evolutionary stable states in a model can depend on the choice of updating rule.

2.2.3 Model 2: Abstract evolutionary game theory

For sufficiently low mutation rates, we have seen that the equilibria of the previous example change only very slightly under different updating rules. The locations and types (attractor, repeller or saddle) of the equilibria in the absence of mutation are dependent only on the fitness functions of the alleles. It might therefore be a reasonable hypothesis that knowledge of the locations of saddle points, stable and unstable equilibria in the fitness landscape is sufficient to fix the topology of the basins of attraction in this landscape. This is however not the case.

We now introduce a different model from the field of abstract evolutionary game theory. We will use it to illustrate that the topology of the basins of attraction of the stable equilibria can change when choosing a different updating rule.

Consider a well-mixed population of size n. Each individual in the population has one of the alleles A, B or C. The fitness of an individual of type A, B and C respectively



(a) Birth Process (b) Death Process (c) Link Dynamics

Figure 2.3: Areas of convergence for BP, DP and LD in Model 2 in barycentric coordinates. The thick black line denotes the boundary between the basins of attraction. Other Lines indicate trajectories through the population state space ending in the mixed A and C equilibrium M, (yellow, bottom line of the triangle), the pure B equilibrium (blue, all trajectories left of the boundary line) and the mixed A and B equlibrium N (cyan, all trajectories right of the boundary line) equilibria.

are frequency-dependent and given by

$$f_A = \exp(3 - 3n_A + \frac{9n_B}{2}) \tag{2.83}$$

$$f_B = \exp(7 + 66n_B - 81n_An_B - 64n_B^2) \tag{2.84}$$

$$f_C = \exp(3n_A - \frac{9n_B}{2}) \tag{2.85}$$

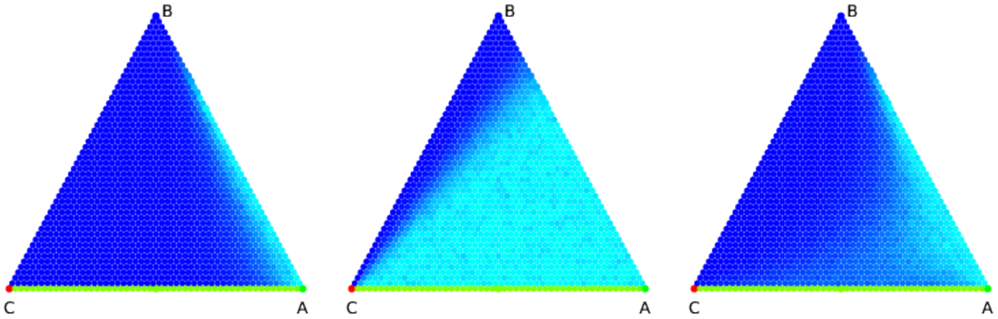
where $0 \leq n_A, n_B \leq 1$ are the relative frequencies of allele A and B respectively.

This example was constructed to show the following behaviour. There is an unstable attractor M between A and C, and an attractor N between A and B. Near M, strategy B has very high fitness, while over much of the state space, C has very low fitness. The coefficients are chosen arbitrarily to achieve this using polynomials of low degree.

We can study the system in the limit for $n \to \infty$, as described in Section 2.2.1. We thereby obtain ordinary differential equations for the behaviour of the system. Numerically solving these ODEs yields the basins of attraction shown in Fig. 2.3.

Running numerical simulations for this model with $n = 50$, starting 500 runs at every location of the simplex and averaging their states when fixated, we obtain the results shown in Fig. 2.4.

Comparison The attractors (M, N and B, coloured circles) and repellers (S, black circle) remain the same under different updating rules. However, while mutation and random drift do not feature in the low mutation limit, the updating rule still has a significant influence on the basins of attraction in the model.



(a) Birth Process (b) Death Process (c) Link Dynamics

Figure 2.4: Numerical simulation results of model 2 in barycentric coordinates. In each sub-float, the colours indicate how many runs starting in that location fixate in what state. In all three cases, the only runs fixating in C (red, bottom left) are those already starting in a fixated C state. All mixtures of of A and C (bottom line) fixate in A (green, bottom right). The rest of the state space is split between states that nearly exclusively fixate in pure B (blue) and states that fixate in either A or B (cyan), with darker colours indicating a higher probability of fixating in B.

For BP, the majority of states lie in the basin of attraction of the pure B equilibrium (blue). This includes the neighbourhood of point M (yellow), which is a mixed equilibrium between A and C (which is stable in the absence of B, but globally unstable). This is apparent both in the numerical and large-population versions of the model. In contrast, given a DP updating rule, the majority of states, including the area around M, lie in the basin of attraction of the stable mixed equilibrium between A and B (cyan). We also see that for LD, the area near M lies in the basin of attraction of B, but close to the boundary between the basins of attraction.

Therefore, we expect that small mutations away from the mixed stable A and C state will lead to fixation in B for the birth process, and to the stable equilibrium between A and B for DP. In the case of LD, the long-term behaviour of the system depends significantly on the stochastic motion of the system. These behaviours are indeed seen in the results of the numerical simulations, Fig. 2.4.

Heuristically, we see that in the BP, trajectories point towards strong attractors, which is most obvious in this example when considering the pure B equilibrium. The DP on the other hand is dominated by the repellers, which can be seen from the fact that all trajectories point away from the unstable pure C equilibrium. Even close to the strong attractor B, the leftmost trajectory follows a nearly straight line away from C. The LD updating rule shows both, with the precise behaviour locally depending on the strength of attraction or repulsion. With only two strategies in a system, the geometry is one-dimensional, and therefore there is no difference between a focus on attractors or repellers, so this effect can only be seen for three or more strategies.

In order to obtain geometrically different basins of attraction such as those described in this example, the system has to contain at least two attractors. Close to an unstable equilibrium between these two attractors, the fitnesses of the alleles must be of different orders of magnitude. In the geometric interpretation, there is a large angle between vectors describing the trajectory away from a strong repeller and that toward a strong attractor. In the example given above, the relevant stable unmixed equilibrium is S with $n_A = \frac{3}{17}$, $n_B = \frac{14}{17}$, $n_C = 0$. Away from this in the direction of C, f_A decreases, but f_B increases significantly, while f_C is very low. Thus the boundary of the basin of attraction has a different orientation close to that point and can differ significantly when followed further. Because by construction f_B is large and f_C is marginal over much of the interior of the state space, the boundary between the two basins of attraction starts in different corners of the state space in this example.

2.3 Discussion

In this chapter, we have studied the impact of the choice of updating rule, that part of a model which describes the manner in which a population changes over time, on the results of well-mixed evolutionary models. Our work complements known results for structured populations, which are able to more closely represent many real-world systems. It has previously been established in the literature that in populations with non-homogeneous graph structures, where nodes have different numbers of links leading to them, changing the updating rule can change the dynamics of an evolutionary model. [78, 79].

Regular graph structures, in particular square or cubic lattices ("spatial games", [22, 24–26, 87, 88]) or "well-mixed" populations (e. g. Komarova et al. in [41]) have been widely used for models in evolutionary game theory. Both lattices and well-mixed populations are homogeneous graphs. Social networks, however, cannot be represented by regular graphs. Rather, they have a degree distribution with a heavy tail, where many nodes have low degrees, but very few nodes have a very high degree each. In the field of evolutionary game theory inhomogeneous graphs have been successfully used to study the evolution of cooperation [42, 68, 89–92], but the impact of changing the updating rule on these results is not fully clear.

Here we have turned our attention back to the most fundamental case of well-mixed populations. We have explored three example models in which the choice of updating rule has a severe impact on the system's behaviour, even in the absence of a structured population. They highlight three additional constraints on results suggesting updating rule equivalence. We have found that for high mutation rates, different updating rules can lead to the presence of non-trivially different equilibria in the system. Even in the absence of mutation, we find that when a system has multiple stable equilibria, their basins of attraction can be topologically different under different updating rules. Differing behaviour can be seen in the mean field approximation as well as in the stochastic simulations. We have further shown that the choice of updating rule can significantly influence relative frequencies of the strategies in the long run if more than two strategies interact non-trivially.

We are therefore led to conclude that the equivalence of updating rules should not be assumed in general. Any generalisation away from investigating fixation probabilities of two-strategy games on homogeneous graphs with low mutation may lead to model results that depend on the updating rule. The shape of the basins of attraction is however strongly dependent on the precise game and its interaction coefficients, and the danger of different behaviour is bigger for strong selection, such as caused by the exponential function in Eq. (2.85).

The properties of evolutionary models with different updating rules outlined in this chapter have a concrete impact on modelling real-world evolutionary processes. It falls to researchers to choose the updating rule based on qualities of the system to be explored. For example, one interpretation sees the three rules as representing different population dynamics. If we consider the death of a random individual, uniformly chosen, to be a normalisation term to keep the population size constant, it is obvious that the dynamics obtained from a Birth Process model approximate a growing population. By the same argument, the Death Process updating rule on the other hand can be considered a renormalised approximation to a shrinking population, and may be significantly better suited for systems where detrimental mutations go extinct quickly. The link dynamics updating rule on the other hand generally behaves like a mean between Birth and Death process, and appears particular suited for models where direct competition between individuals plays a significant role for the dynamics of the system.

It is well-known that selection in growing and shrinking populations are connected to different selection mechanisms [93, 94]. When modelling concrete evolutionary processes, it is therefore important to choose the updating rule based on the population dynamics and selection mechanisms of the reference system.

The study of updating rules in the context of evolutionary game theory is thus important in order to build more realistic models of the systems studied. Far more is known about selection on birth both in models and in reality. Birth Processes are more widespread in modelling, and birth and progeny are easier to study than natural deaths. This applies even more so to cultural variants, some of which leave hardly any traces of their previous existence. Furthermore, in the ecological context of life-history theory it is clear that relative birth rate and survival probability may be determined by different factors, and models accurately representing this phenomenon may be preferred. Incorporating selection terms on birth and death may lead to co-existence of organisms selected for birth and those selected for survival [95, 96]. Understanding the evolutionary dynamics of such systems requires a profound understanding of the impact of selection on birth vs. selection on death.

In this chapter, we have only studied well-mixed populations. However, because it is known that population structure by itself can heavily modify model behaviour, and because many real-world systems show significantly non-trivial population structures, future work needs to study the dynamics of structured populations with different updating rules.

In conclusion, this chapter has highlighted the dangers of blindly following traditional algorithms when designing evolutionary models. Any model should be constructed so as to best represent the system it explores. In cases where a statement on the updating rule is not implied by a problem it is important to confirm that the updating rule does not have a meaningful impact on the model, while recalling that results for the stochastic and deterministic cases can differ. We refer back to Chapter 2, in which we noted that not only our understanding of the world, but also policies affecting our interactions with it, are sometimes informed by evolutionary models. It would be unfortunate to find ourselves misled by unexpected quirks of model behaviour.

Having considered the intricacies of one of the three fundamental components necessary in models of evolutionary game theory, we now turn to the central component of the models of policed cooperation to be studied in this thesis, and formally introduce the Public Goods Game with peer punishment.

Chapter 3

The Public Goods Game with Punishment

The *Public Goods Game* is a well-understood game-theoretical model, which is frequently used to study the social dilemma known as the *Tragedy of the Commons* [97]. Consider a public resource that needs maintenance, but can be used for a large benefit, such as an irrigation system. Given that maintaining the resource comes at personal effort, but the benefits of it are shared between all consumers of the resource, every individual consumer is tempted to shirk from their share of maintaining the resource, and to free-ride on the benefits produced by other agents contributing.

The basic *Linear Public Goods Game* (LPGG), which we summarise in this section, formalises this interaction. It is a symmetric game, involving N players. The fundamental definition and notation of the Public Goods Game chosen in this thesis follows the implementation given by Traulsen *et al.* [81] and proceeds as follows.

All of the N agents playing the LPGG choose simultaneously to either contribute a fixed cost c, which they invest into sustaining a public resource, or to abstain from investing. Contributing players are called *cooperators* (C), abstaining players are referred to as *defectors* (D). The investments into the public venture are then scaled up by a linear factor $1 < r < N$ and split between all players, no matter whether they contributed or not.

This game is often extended by a *peer punisher* (P) strategy. The concept was introduced to the experimental economics literature in 1986 by Toshio Yamagishi [98], and became very popular in the field after experiments by Ernst Fehr and Simon Gächter [99, 100]. The experiments showed that humans tend to punish defectors even if the punishment is designed to be not in the immediate material self-interest of the experimental subjects. Players following strategy P do not only provide for the public good, but additionally punish defectors. After the first stage payoff has been declared as described above, each punisher pays a punishment cost $\frac{\gamma}{N}$ per defector, in order to inflict a fine $\frac{\beta}{N}$ each on every defector. An overview of the parameters used in this chapter is given in Table 1.

The payoff structure of the resulting *public goods game with peer punishment* (PGG/P) with n_s players following strategy s respectively is therefore given by

$$\pi_{\mathrm{D}} = \Pi - \beta \frac{n_{\mathrm{P}}}{N} \tag{3.1}$$

$$\pi_{\mathrm{C}} = \Pi - c \tag{3.2}$$

$$\pi_{\mathrm{P}} = \Pi - c - \gamma \frac{n_{\mathrm{D}}}{N} \tag{3.3}$$

where

$$\Pi = rc\frac{n_{\mathrm{C}} + n_{\mathrm{P}}}{N} \tag{3.4}$$

is the individual's share in the public good, and $c, \beta, \gamma > 0$ and $1 < r$.

In case $r > N$ we have $\Pi - c > 0$ even for a single cooperator surrounded by defectors. This effect makes cooperation have a net benefit for the cooperating individual. The parameters are therefore often restricted to $0 < r < N$ in models and experiments using the public goods game [24, 26, 101, 102]. Because this net benefit in payoffs does not translate to a gross benefit in fitness relative to defectors, we will not need to restrict r to be less than N in our models.

For $N = 2$, and without punishment, the public goods game becomes a Prisoner's Dilemma, with payoff matrix

$$\begin{array}{c|cc} & \mathrm{D} & \mathrm{C} \\ \hline \mathrm{D} & P = 0 & T = \frac{r}{2}c \\ \mathrm{C} & S = \frac{r-2}{2}c & R = (r-1)c \end{array} \tag{3.5}$$

for the row player. In general, the payoffs are structured such that in a well-mixed population in the absence of punishers (and even in the presence of punishers, as long as $\frac{n_{\mathrm{P}}}{N} < \frac{c}{\beta}$), defectors dominate cooperators. When all three strategies are present, cooperators dominate punishers.

Throughout most of this thesis we will consider the Public Goods Game with Peer Punishment or some variant of it, to exemplify the implications of default assumptions in evolutionary modelling and to study policing. The precise connections between punishers and benefits, population structure, and division of labour are still not well-understood.

While most models assume costly "Peer punishment" to enforce cooperation in a system, results from the anthropology and economics literature [103–105] cast doubt on the general validity of this assumption.

Guala [103], for example, argues that public goods experiments with punishment show a strong social preference for cooperation in the lab, but that cooperation in the real world is not usually sustained by costly punishment. Both Guala and Ostrom, Walker, and Gardner [105] argue that cheap punishment actions (criticism, ridicule, punishment by a strong coalition) are far more important for cooperation in real life than risky, violent action, which is more likely to lead to group fission. While we will focus on the traditional setup of the PGG/P with $\gamma \gg 0$ here, we will nonetheless consider the case of small punishment costs γ where appropriate.

As a baseline to compare with, we will now consider the evolutionary dynamics of the PGG/P in a well-mixed population, employing all three updating rules introduced in Chapter 2. We will then review some extensions to the PGG/P in Chapter 5, before concentrating on one particular challenge in Section 5.1: Starting from the observed preference for police, *i. e.* a division of labour between a purely supportive majority and a dedicated minority of enforcers, we study whether a simple mechanism can explain the emergence of institutional punishment from peer punishers.

3.1 Evolutionary Dynamics of the PGG/P

In Chapter 2, we saw that the impact of the choice of updating rule can be quite large even for stochastic simulations. In this section, we consider the evolutionary dynamics of the PGG/P under these three updating rules, in order to confirm which of them is appropriate for further investigations.

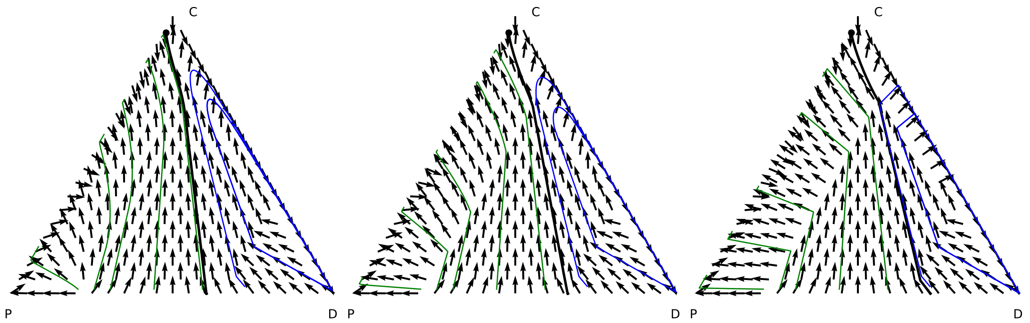
Payoffs from the public goods game can be negative. It is therefore not immediately obvious what the fitness in the evolutionary dynamics should be. One obvious consideration is to cut off fitnesses less than $\epsilon > 0$. Otherwise, the fitness is taken to be proportional to the payoff. The fitnesses for the four strategies are then given by

$$f_{\mathrm{D}} = \max(\epsilon, rc\frac{n_C + n_P}{N} - \beta\frac{n_P}{N}) \tag{3.6}$$

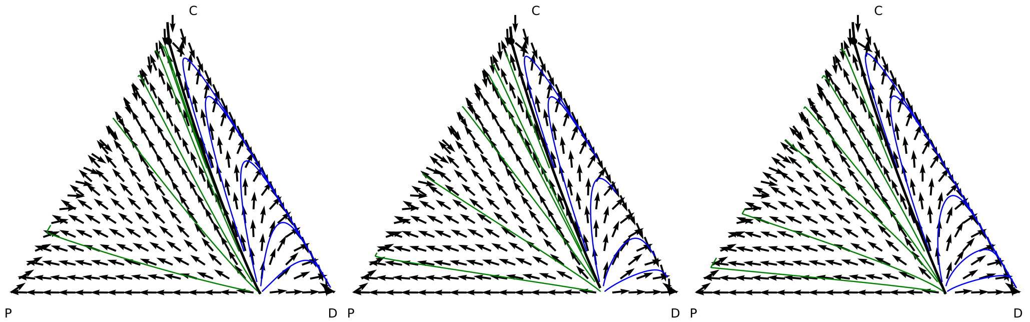
$$f_{\mathrm{C}} = \max(\epsilon, rc\frac{n_C + n_P}{N} - c) \tag{3.7}$$

$$f_{\mathrm{P}} = \max(\epsilon, rc\frac{n_C + n_P}{N} - c - \gamma\frac{n_D}{N}) \tag{3.8}$$

This definition would however imply that for much of the state space, D and P are neutral. Furthermore, for high enough fines β, much of the area around pure defection would be neutral. This can be seen in Figs. 3.1a to 3.1c. In the bottom-right corner (near



(a) Linear fitness, Birth Process (b) Linear fitness, Link Dynamics (c) Linear fitness, Death Process



(d) Exponential fitness, Birth Process (e) Exponential fitness, Link Dynamics (f) Exponential fitness, Death Process

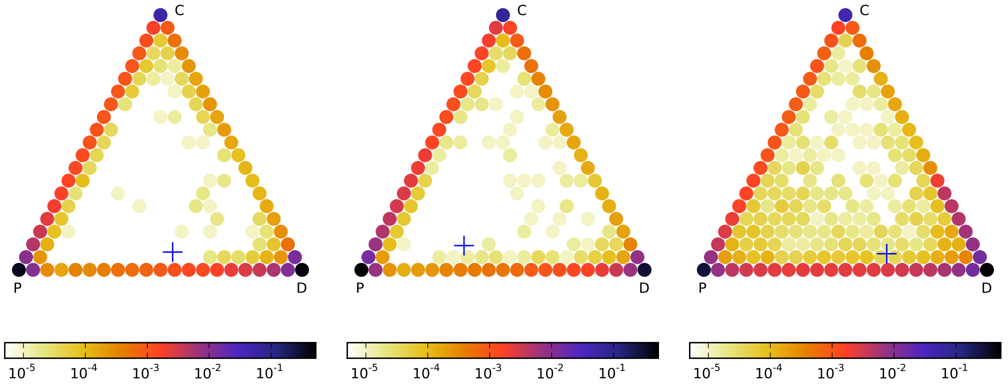
Figure 3.1: Areas of convergence for BP, DP and LD in the evolutionary Public Goods Game in barycentric coordinates, for parameters given in Table 1. Top line: With linear fitness, cut off at $\epsilon = 10^{-6}$; Bottom: With exponential fitness. The thick black line denotes the boundary between the basins of attraction. Other lines indicate trajectories through the population state space ending near the pure D equilibrium (blue, all trajectories right of the boundary line) and on the neutral line between C and P (green, all trajectories left of the boundary line). Note that for linear fitness, the blue trajetories approach a limit cycle.

the pure D state) of each of these figures, the vector field, which indicates the mean effect of selection and mutation, points towards the middle of the triangle. All three strategies earn negative payoff, so their fitness will be ϵ. In this case, mutation drives the system in the direction of an equal distribution of D, C and P each. Due to this cutoff effect, the linear models contain a limit cycle instead of an attractor point near pure defection.

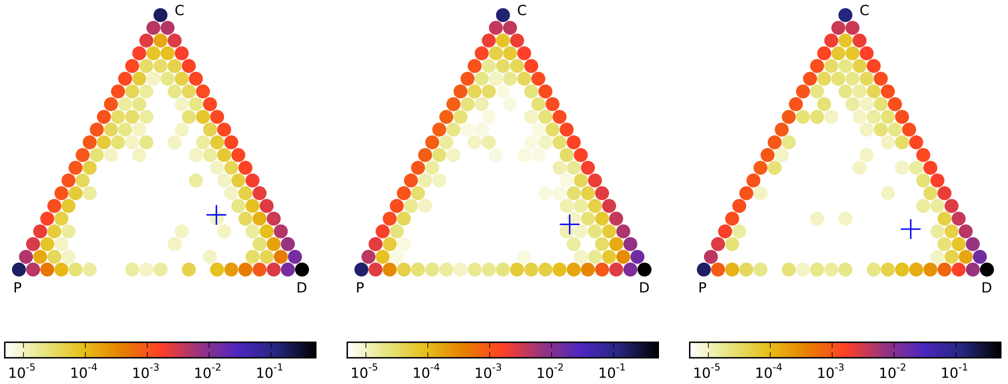
We therefore follow the choice frequently made in the literature [26, 28, 38, 89, 106–108] and define the fitness to be an exponential function of the payoff,

$$f_s = \exp(w\pi_s) \tag{3.9}$$

and, by contrast with the results of Section 2.2.3, the vector fields for reasonable parameter values, as shown in Figs. 3.1d to 3.1f, do not show large differences between the three different updating rules.



(a) Linear fitness, Birth Process (b) Linear fitness, Link Dynamics (c) Linear fitness, Death Process



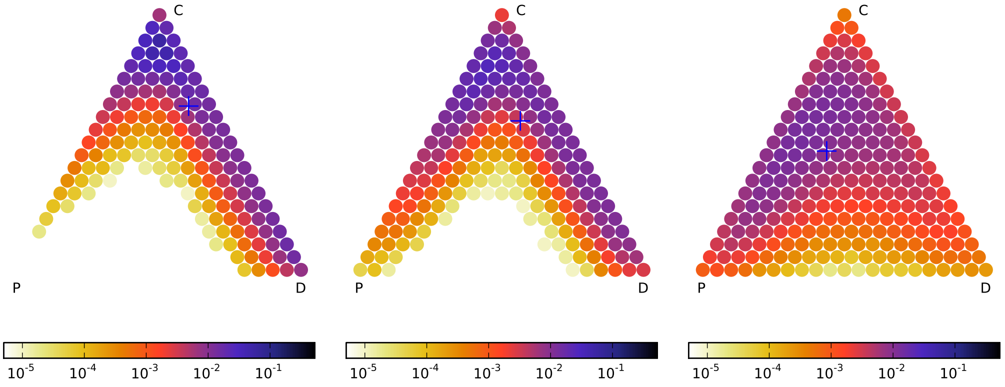
(d) Exponential fitness, Birth Process (e) Exponential fitness, Link Dynamics (f) Exponential fitness, Death Process

Figure 3.2: Stationary distribution of the Markov chain induced by the public goods game with punishment, for different ways of calculating fitness, and different updating rules. Darker colour indicates a higher probability of the corresponding state in the stationary distribution. The mean of each distribution is marked with a blue +. For parameters given in Table 1. Top line: With linear fitness, cut off at 0; Bottom: With exponential fitness.

In this case, the state where all individuals follow the D strategy (up to mutation) is an attractor. In the absence of Defectors, Cooperators and Punishers are indistinguishable. Every state not in the basin of attraction of the pure D state will converge towards a mixed C and P state. The fitness functions close to the unstable equilibrium on the D-P line are $f_{\mathrm{C}} \gg 0$, $f_{\mathrm{D}} = \epsilon$ and $f_{\mathrm{P}} = \epsilon$. By the arguments given in Section 2.3 it is therefore not surprising that the geometry of the basin of attraction changes only slightly when changing the updating rule.

Changing the update rule used for the public goods game will therefore have an influence on the long term behaviour of the system only when stochasticity plays a significant role. We will now investigate the effect of different updating rules on the stationary distribution of the Markov chain.

Figure 3.2 shows the stationary distribution of the Markov chain induced by the public



(a) $w = 0.1$, $\mu = 0.18$ (b) $w = 1$, $\mu = 0.18$ (c) $w = 100$, $\mu = 0.18$

Figure 3.3: Stationary distribution of the LD-induced Markov chain induced by the public goods game with punishment, for different selection strengths w and $\mu \gg 0$. Darker colour indicates a higher probability of the corresponding state in the stationary distribution. The means are marked with a $+$. For parameters given in Table 1.

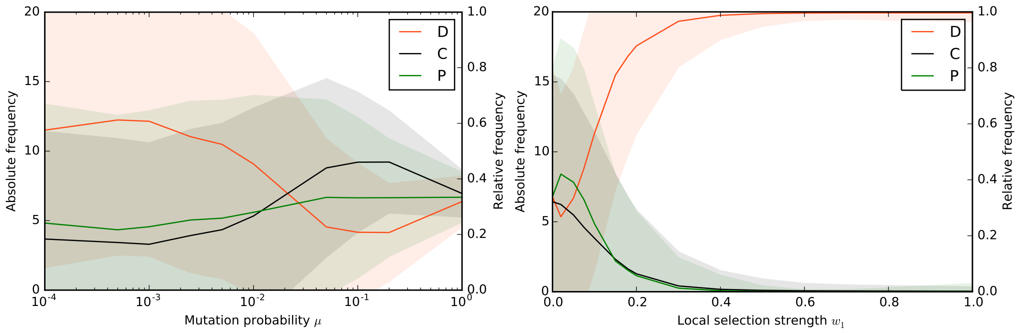
goods game with punishment and different updating rules. The values have been numerically obtained through power iteration of the transition probability matrix P. Darker colour indicates a higher probability of the corresponding state in the stationary distribution. In the case of linear fitness, the stationary distribution obtained from LD shows a slightly higher probability of presence for states in the interior of the state space than the birth process case. Under DP, this probability rises even more, again supporting the hypothesis that LD generally behaves as a mixture of BP and DP.

In the following, we will employ the link dynamics updating rule, but vary other parameters of the model.

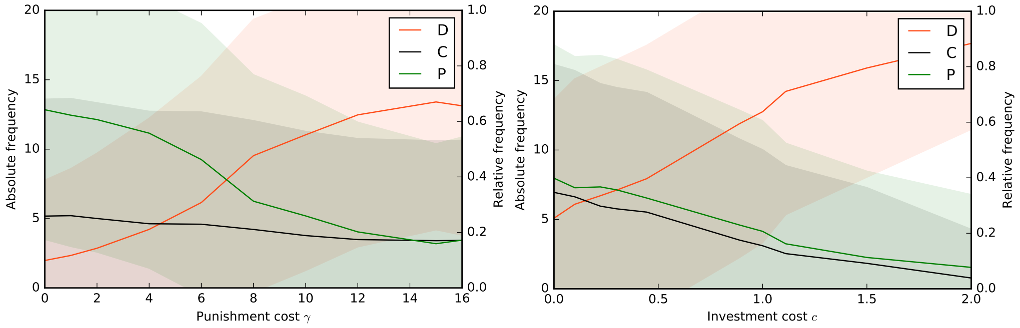
Traulsen *et al.* [81] have studied the evolutionary dynamics for the PGG/P for infinite populations under strong (*i. e.* $w \to \infty$) link dynamics selection for high mutation rates. They have found that mutation counteracts the forces of neutral drift or selection towards the edges of the simplex. In the expectation, all strategies are therefore always present for large μ. Defectors are therefore always punished, and cannot invade the population, while punishers bear the punishment cost at all times. Cooperators are thus able to outperform both other strategies. Without punishers, defection would continue to be dominant even for very high mutation probabilities.

We find that this behaviour in general still holds for finite populations (Fig. 3.3c). If selection is weak, the disadvantage of Punishers when compared to Cooperators is however lessened, so that not only the variance, but also the mean frequencies of the different strategies change.

Considering the dependency of the long-term behaviour of the system on other other parameters, we find the following results. The evolutionary dynamics under the Fermi process, *i. e.* for link dynamics with exponential fitness, do not depend on the scaling r



(a) Varying mutation rate μ (b) Varying selection strength w



(c) Varying punishment cost γ (d) Varying contribution c

Figure 3.4: Frequencies of strategies in the equilibrium state of the PGG/P in a well-mixed population, under variation of different parameters. All other parameter are as given in Table 1. Solid lines show the mean of the frequency in the long-time limit, the shaded area denotes the $\pm 1\sigma$ band around it.

of the investments to benefits from the public good. Dependency on other parameters is however strong. Mutation begins to strongly affect the system around N^{-2}, as Fig. 3.4a shows. For lower mutation rates, defectors consistently outperform cooperators and punishers, but as μ increases, punishers and particularly cooperators become more frequent than defectors, but as mutation rates go to 1, the relative frequencies of cooperators, punishers and defectors approach ca.[1] $\frac{1}{3}$ each.

A different way to increase cooperation through added randomness is by way of weak selection strength w, as can be seen in Fig. 3.4b. By contrast with frequent mutation, weak selection does benefit punishers more than cooperators. In addition, strong selection ($w \gg 0$) reduces cooperation levels to be negligible even for small mutation rates, whereas cooperative strategies persist at low frequencies for low mutation probability, but weak selection.

For punishment cost $\gamma = 0$, P and C are neutral strategies even in the presence of defectors. But since a population of pure cooperators can be far more easily invaded by defectors than a population of pure punishers, punishers are more than twice as frequent as cooperators in the mean of the equilibrium distribution for $\gamma = 0$. As the punishment

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[1] The proportions are not precisely 1/3 each, because mutation in our model is restricted to produce an offspring different from the parent. A type of parent producing *more* offspring will therefore be *less* frequent in the mean for $\mu = 1$.

cost γ increases from 0, the frequency of punishers steadily decreases, even below the frequency of cooperators. The frequency of cooperators goes down, as well, but not as steeply. The influence of the fine β is similar, but far slower. While defectors can be suppressed by high fines, this only happens when $\beta \gg Nc$.

The contribution c could be absorbed into the selection strength w under adjustment of the punishment parameters γ and β. It is therefore expected behaviour that for high c defectors dominate the population, but their number decreases as $c \to 0$. For very low values of c, we therefore see that, just as for weak selection, randomness allows cooperation to prevail by a small margin.

Chapter 4

Metapopulations

[1] We have now looked at two of the main components of evolutionary models targeted at solving the puzzle of cooperation. We have seen that three different updating rules in the generalised Moran process can lead to differing results even for well-mixed populations, and we have reviewed the evolutionary dynamics of the well-known public goods game in well-mixed populations, focussing on frequent mutation. Mutation is however not the only source of randomness which might support cooperation and punishment.

It is well-known [20, 89, 90, 109] that the structure of an evolving population has great influence on the evolutionary dynamics of a model. Cooperation, where other individuals gain a benefit at a cost to a cooperator, is known to be able to evolve if the structure of the population ensures that those benefits are mostly received by other cooperators, rather than being distributed uniformly. Hamilton's rule [110] gives a quantitative criterion for the increase of a cooperative allele in a system based on relatedness.

This effect is not restricted to populations on lattices or arbitrary graphs, but also apparent in island- or community-structured populations [106]. Similar population structures have been considered in evolutionary modeling for a long time, starting with Wright's considerations of migration [31]. These models have become known under a variety of names, such as deme-structured populations [111], patch-structured populations [32], finite island dispersal models [32], or viscous populations [112].

In this chapter, we study effects of group selection on the evolutionary dynamics of the linear PGG/P. We construct a meta-population that consists of separate communities. Group competition may play an important role in the evolution of cooperation. Even more, Gavrilets [113] has argued that competition between groups is more likely to be a driver for the evolution of collaborative ability, which is then beneficial also in overcoming

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[1] This chapter is a slight modification of an article submitted to Journal of Theoretical Biology, with authors G. A. Kaiping, S. J. Cox and T. J. Sluckin. SJC, TJS and GAK defined the problem. GAK carried out the calculations and simulations. GAK and TJS wrote up the results.

other exterior challenges. Agents play the public goods game and produce offspring in their local community according to a Moran-like process with a Fermi updating rule [1, 36, 84], but have a small chance of producing offspring in a different community. The chances of successfully producing offspring into a different community will depend on the specific model of interaction. We investigate how these different interactions between communities affect the long-term behaviour of the system.

We compare the effects of three different types of interactions between different communities. Our models draw on previous contributions concerning multi-level selection by Boyd *et al.* [114] and Wang *et al.* [106], and transfer their models into a common framework where they can be compared. As baseline, we present a model of migration at constant rates. It has however long been suggested that competition between groups can increase the cooperativeness of a system. We will therefore model direct conflict between groups leading to group extinction, using an approach based on [114]. Finding that we can reproduce previous results that direct competition between groups can sustain cooperation, we then aim to weaken the assumption of multi-level selection that entire communities need to go extinct and reproduce together. We therefore consider a model of individual migration where fitter individuals have a higher chance of migrating. This fitness-based migration model is a special case of [106], without a second-level public goods game.

Migration according to symmetric, constant migration rates polarises the system between punishing regimes and defecting regimes through greater mixing. Direct competition between groups and fitness-based migration, on the other hand, can sustain cooperation in new regions of the parameter space. Fitness-based migration does so only in a smaller parameter region, and favours cooperators over punishers.

The structure of this chapter is as follows. First, in Section 4.1 we describe the general structure of the model that we study in subsequent sections. Then, in Section 4.2, we investigate the case where migration between any two communities occurs with a single constant rate, as a baseline model of meta-population interactions. We consider a case where entire communities interact and can go extinct, being replaced by others, in a model of multi-level selection in Section 4.3. In Section 4.4, we then study the case where fitness gained inside a community governs the process of producing offspring somewhere else, before we compare our different models in Section 4.5. Finally, in Section 4.6, we discuss our three models and present some general conclusions.

4.1 Model Structure

The general structure of the models studied in this chapter is as follows. Consider a population consisting of M disjoint, well-mixed subpopulations (“communities”) of equal

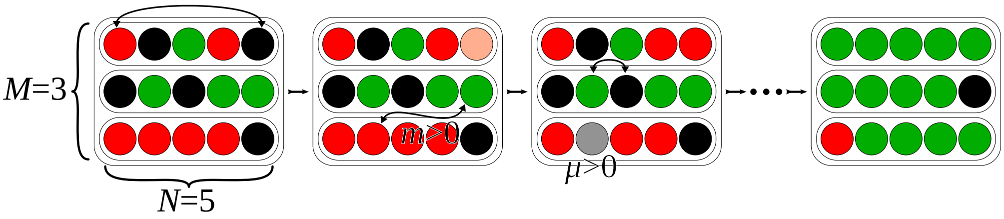


Figure 4.1: A community-structured meta-population, with within- and across-community updating and mutation.

size N. The model evolves in discrete time with overlapping generations. In each time step, either with probability m a cross-community migration step (or a community conflict step) between two focal communities, or with probability $1-m$ a within-community updating step in a single focal community occurs. The cross-community steps will be described in the sections below.

The within-community updating steps implement a Moran-like process with a Fermi process updating rule, following the arguments given in Section 3.1. Each of these local updating steps proceeds as follows. Individuals in the focal community take part in a PGG/P with all other individuals from their community. Two individuals (i, j) are then chosen from the community at random. Their fitness values are calculated from the Public Goods Game payoffs using an exponential function,

$$f_i = \exp(w_1 \pi_i) \tag{4.1}$$

One of the two individuals is then chosen with probability $p(j \to i)$ proportional to this fitness value.

$$p(j \to i) = \frac{f_i}{f_i + f_j} = \frac{1}{1 + \exp(w_1[\pi_j - \pi_i])} \tag{4.2}$$

With probability $p(j \to i)$, j is replaced by an offspring of i. With probability $p(i \to j) = 1 - p(j \to i)$ the opposite happens and j is replaced by an offspring of i. (We note that this is different from the definition of the Fermi process updating rule given in [1, 36], where instead with probability $1 - p(j \to i)$ nothing happens. The resulting re-scaling of time by a factor of 2 is irrelevant for the long-term analysis in this chapter.) With a mutation probability μ, the offspring follows a random pure strategy different from the parent, otherwise it follows the same pure strategy as the parent.

The whole model gives rise to a discrete-time finite-state aperiodic irreducible Markov chain $Y^{(t)}$, which is composed of M equivalent component sub-chains, $Y^{(t)} = (Y_1^{(t)}, \ldots, Y_M^{(t)})$.

Each sub-chain has a state space $\{1, \dots, n\}$. In each time step, each of these chains develops either according to a transition matrix $A = (a_{ij})_{1 \le i,j \le n}$ describing the local interactions, or a random other sub-chain is picked, which will be in state $s \in \{1, \dots, n\}$, and the focal chain is updated according to a different transition matrix $X^{(s)} = (x^{(s)}_{ij})_{1 \le i,j \le n}$.

Whether an individual sub-chain is chosen to be updated or not is independent of the state of the chain. For low m, the states of the sub-chains can be considered independent, because interactions are rare. The time development of the vector of probabilities of presence $y^{(t)}_k = (y^{(t)}_{k,l})_{1 \le l \le n}$ of a single sub-chain $Y^{(t)}_k$ is then given by

$$y^{(t+1)}_{k,i} = \sum_{j=1}^{n} \left[(1-m)(a_{ij}) + m \sum_{s=1}^{n} x^{(s)}_{ij} \frac{\sum_{l \neq k} y^{(t)}_{l,s}}{M-1} \right] y^{(t)}_{k,j} \tag{4.3}$$

or, more compactly,

$$y^{(t+1)}_k = [(1-m)A + mX \cdot \bar{y}^{(t)}_k] y^{(t)}_k \tag{4.4}$$

where $\bar{y}_k$ is the average state vector of the $M-1$ other sub-chains, and the dot product is to be understood as reducing the rank-3 tensor $X = (X^{(s)}) = (x^{(s)}_{ij})_{1 \le i,j,s \le n}$ over the index s.

In the limit of low m, we can assume that $\bar{y}^{(t)}_k = \bar{y}$ is the stable state distribution of a sub-chain. Because the system is symmetric under exchanging sub-chains, this equilibrium distribution $\bar{y}$ has to fulfill

$$\bar{y} = [(1-m)A + mX \cdot \bar{y}]\bar{y} \tag{4.5}$$

From this, it is obvious that in this case of small m, the equilibrium distribution will be independent of M, as long as $M > 1$. While it is not obvious how to find such a $\bar{y}$, we expect that this system of equations is simple and symmetric enough to be accessible to numerical solution even for reasonably large N, but for the results given in this chapter, we have employed Monte Carlo sampling of the Markov chains to obtain approximate equilibrium distributions.

4.2 Migration

In the context of migration, a community-structured meta-population is often described as a network of islands, between which migration occurs at a constant rate [31].

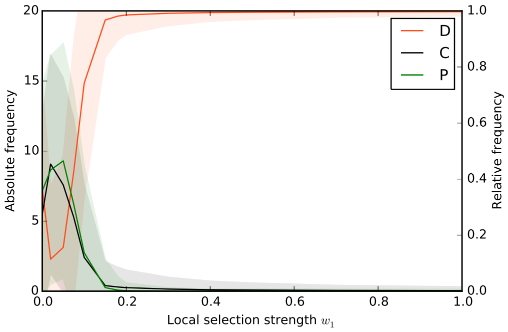
Borrowing from Hauert and Imhof [115], we model migration as follows. When a migration step randomly occurs, two random individuals from the whole population are selected. One of them produces an offspring of its own type with probability $1-\mu$, and a random other type of offspring with probability μ. The offspring then migrates to the community of the other individual and replaces it.

This model of migration corresponds to the special case of the multilevel public goods game model studied by Wang *et al.* [106] in which the second-level public goods game is deactivated ($k_1 = 0$ and $\beta_2 = \gamma_2 = 0$ in their notation) and selection strength across communities is $w_2 = 0$. Wang *et al.* find that for low mutation and migration, defection is more abundant than cooperation unless $w_1 \ll w_2$, and that with a second-level public goods game and large populations, pure punishment is more frequent than pure defection in the stable state distribution of the Markov chain.

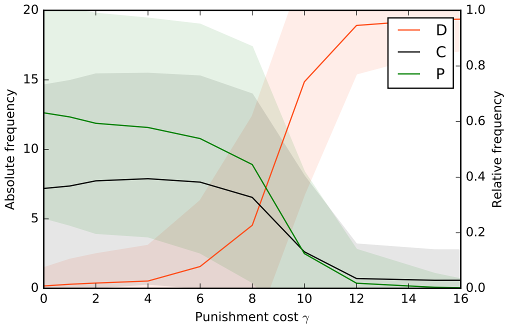
In our model of constant migration, we have $w_2 = \gamma_2 = \beta_2 = 0$, a simpler case not studied in [106]. If their results were to hold for this case, we should expect defection to be the most frequent strategy in every case. For ease of comparison, we will generally assume equivalent values to [106], as given in Table 1.

It is not obvious that the approximations of low migration and mutation rates should hold. One of these interactions, between C and P, is neutral. None of the pairwise interactions is equivalent to an anti-coordination game, i. e. an interaction in which the best response to a strategy is the other strategy. Using the results by Wu *et al.* [36] as a guideline, we therefore need to require that the migration rates be $m \ll N^{-2}$. If want to consider "low" mutation rates, we then have to assume that the population is homogeneous when a mutation step occurs. When $m \ll N^{-2}$ we can assume that each subpopulation is homogeneous when a migration step occurs. We can then assume that migration is a neutral updating step (because there is no selection pressure affecting the direction of migration), operating on homogeneous subpopulations instead of on individuals. For that assumption to hold, we have to require $\mu \ll mM^{-2}$ by analogy. For a meta-population size $N = M = 20$, individuals with a generation time of an hour should under this assumption mutate less than once per year, and even less than this when considering larger populations.

Given what we know about the mutation rates in the real world, this is not a reasonable assumption. We will therefore concentrate on the case where m and μ are large, and generally assume $m = 0.05$ and $\mu = 0.0025$. For $N = M = 20$, this means $m = N^{-1}$ and $\mu = (NM)^{-1}$. The conditions $m \ll N^{-2}$ and $\mu \ll mM^{-2}$ are thus not fulfilled. Just as for the basic PGG in a well-mixed population, and for the same parameter ranges, we do indeed find that the frequency of defectors can be lower than both the frequency of cooperators or punishers. Examples of this behaviour can be found for low values of the punishment cost γ (*cf.* Fig. 4.2b), or for small values of $w_1 > w_2 = 0$ (*cf.* Fig. 4.2a).



(a) Varying local selection strength w_1



(b) Varying punishment cost γ

Figure 4.2: Mean and standard deviations of the frequencies of strategies in the equilibrium state of the PGG/P in a meta-population with constant migration, under variation of different parameters. All other parameters are as given in Table 1.

In general, phases strongly dominated by a strategy for the basic PGG/P on a well-mixed population remain dominated by the same strategy for the migration model. In some cases where no strategy vanishes, migration can decrease the abundance of defectors to be lower than the abundance of contributors, for example for middle values of γ as seen in Fig. 4.2b. The transitions between different such phases are however steeper in the model with migration than in the case of $m = 0$. The following heuristic argument gives some insight as to why this might be the case.

Consider a Markov chain X with states $s_1, \ldots, s_n$, and stable state $x = (x_1, \ldots, x_n)$. An independent product $X \times X$ will then develop the corresponding stable state distribution $x^2 = (x_{11} \ldots x_{1n} \ldots x_{nn})$, where $x_{ij} = x_i x_j$. Now assume instead that the two copies of X can influence each other. In our case, this would be the transition from a collection of well-mixed, separate communities to a meta-population of interacting communities with $m > 0$.

We will now argue that such an interaction will lead to frequent states becoming more frequent and rare states becoming rarer, using some heuristic simplifications. Assume that a mixed state (s_i, s_j) will have a much higher probability of developing towards (s_i, s_i) or (s_j, s_j) in the mid-term, and that it converges to each of these with probability proportional to x_i and x_j respectively. (This only holds in a very rough approximation for the evolutionary dynamics studied here.)

If we assume this happens fast enough that the probabilities x_{ij} for $i \neq j$ in the stable state distribution are negligibly small, the two separate Markov chains might be in different states (s_i, s_j), which without interaction happens during a proportion of $x_i x_j$ of the time, but an interaction will lead to (s_i, s_i) with a probability of $\frac{x_i}{x_i+x_j}$. Each of the two $i \neq j$ pairs therefore contributes $\frac{x_i}{x_i+x_j}$ to x_{ii}, so

$$\begin{aligned} x_{ii} &= x_i^2 + \sum_{j\neq i} 2x_i x_j \frac{x_i}{x_i + x_j} && (4.6)\\ &= x_i^2 (1 - 2\frac{x_i}{x_i + x_i} + 2\frac{x_i}{x_i + x_i} + 2\sum_{j\neq i} \frac{x_j}{x_i + x_j}) && (4.7)\\ &= x_i (2x_i \sum_j \frac{x_j}{x_i + x_j}) && (4.8) \end{aligned}$$

So we have $x_{ii} \geq x_i$ if and only if $2x_i \sum_j \frac{x_j}{x_i+x_j} \geq 1$.

For $x_i = x$, $x_j = \frac{1-x}{n-1}$ otherwise, this simplifies to $(x-1)[(n-2)x+1](nx-1) \leq 0$, which for $n \geq 2$ holds if and only if $\frac{1}{n} \geq x \geq 1$. This is an indication that when x_i is large (bigger than $1/n$), then $x_{ii} > x_i$ will be even larger, and if x_i is small then x_{ii} is even smaller. For metastable states in the equilibrium distribution, mixing therefore increases the probability of presence of frequent states and reduces the probability of infrequent states.

The pure strategy states of the evolutionary PGG/P are such metastable states, because they can only be left when mutation occurs. It is therefore not surprising that rare strategies become rarer and frequent strategies become more frequent when migration is added to a meta-population structure. By this process then phase transitions between cooperative and defective regions in the parameter space become steeper. We have thus seen that migration polarises the evolutionary PGG/P between cooperative and defective regimes, and can only help cooperation dominate in a region of the parameter space where considerable amounts of cooperative strategies are present already for the base game.

In the next section, we consider a second-level selection model, in which communities are in direct competition. A question of particular interest is now whether, in contrast to the case of fixed migration, group competition can allow cooperation to arise in regions of the parameter space where it is scarce in the basic model.

4.3 Group Competition

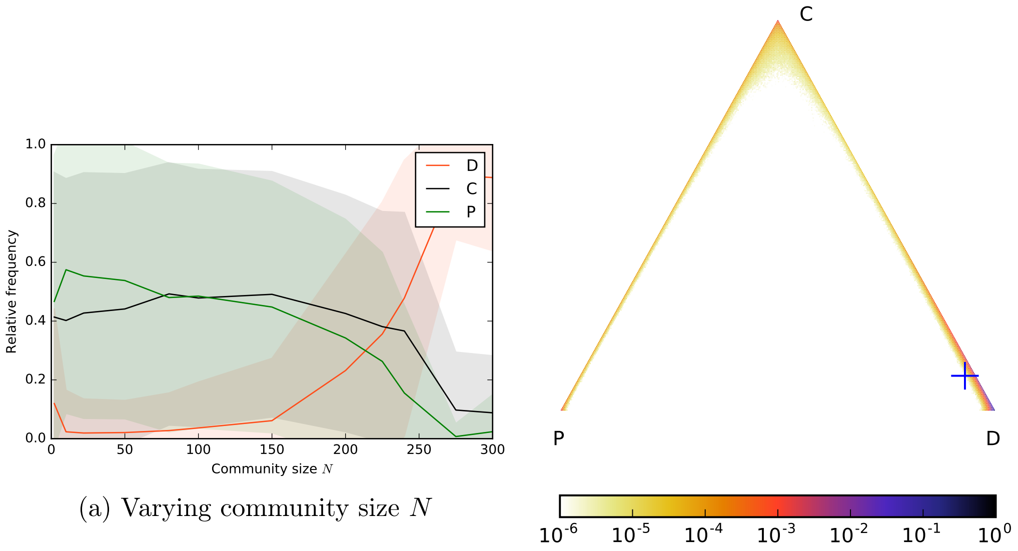
Interactions between communities need not be restricted to individuals migrating. Soltis, Boyd, and Richerson [116] argue that selection between cultural groups can be a viable mechanism to drive human evolution. They investigate real-world anthropological data and find that the effective extinction (where surviving members are quickly assimilated into other communities) of cultural groups, through between-community warfare, may be frequent enough to have an impact on the long-term evolution of cooperation. In this section, we thus study a model of group competition. Second-level selection is implemented through explicit conflict between separate communities, leading to extinction and replacement of one community by another one.

The model presented in this section is closely informed by the one constructed by Boyd *et al.* [114], but we deviate in places to make it compatible with the model framework of this thesis. Boyd *et al.* study a model of inter-group conflict [117]. The model involves a meta-population of fixed-size communities playing an evolutionary Public Goods Game with peer punishment. In addition, randomly paired communities (I, J) are in conflict at a low rate, and community J is replaced by a copy of community I with probability $(1+d_J-d_I)/2$, with d_Q the relative frequency of defectors in group Q. Punishment and its costs are thus not considered in the group conflict step. In addition to groups replacing other groups, however, their model includes imitation steps according to a link-dynamics updating rule with the same positive selection strength as within-group updating. In this work we want to compare this structure of mixing between groups, which we will discuss in more detail in Section 4.4, and direct group competition as described above.

Boyd *et al.* [114] find that this model of group selection can generally sustain cooperation up to a critical population size, for a wide range of parameters. In a variant of the model without punishment, this critical population size is much lower. Therefore, while punishment does not directly contribute to the success of a community in inter-group conflict, it nonetheless benefits cooperation.

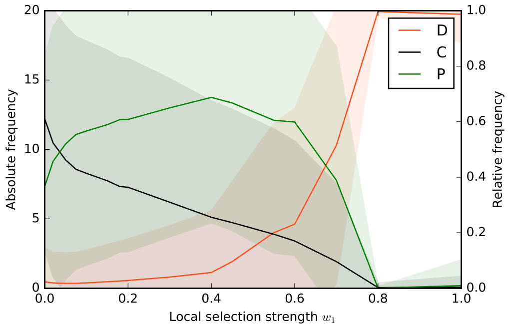
Their model includes both direct group competition and imitation steps across communities with positive selection strength. The latter could be considered an implementation of group competition through selection on individuals, which we will focus on in the next section. In order to investigate those effects separately, our model will not contain both types of cross-community updating steps; in this section, we study a model with within-community updating and whole communities replacing other whole communities only.

In addition, we modify the following properties from [114] to fit our model framework. Their model assumes that punishers and cooperators have a small probability e of defecting instead of cooperating in the first stage of the public goods game. We will not



(a) Varying community size N

(b) Frequency, and mean value (+), of the states according to the simulations for $N = 300$



(c) Varying local selection strength w_1

Figure 4.3: Mean frequencies and standard deviations of strategies in the equilibrium state of the PGG/P for group selection, under variation of the local selection strength w_1. All other parameter as given in Table 1.

follow this assumption, and instead continue to assume that players realise pure strategies. Furthermore we will continue to use exponential fitness in a Fermi updating rule, while Boyd *et al.* [114] use pure link dynamics without an exponential term. We will use exponential fitness also in the group conflict step, such that the results can be compared with fitness-based migration in the next chapter. This means that, as opposed to the referenced model, punishment is actually short-term detrimental in the group conflict step.

In this section, we thus consider a community-structured population as described in Section 4.1. In addition to the local Fermi updating, we consider group conflict steps. Group conflict is also executed through a Fermi updating step. In such a step, two random communities I and J are selected. The average payoffs $\bar{\pi}_I$ and $\bar{\pi}_J$ of individuals in each community are calculated, and the whole community I is replaced by a copy of

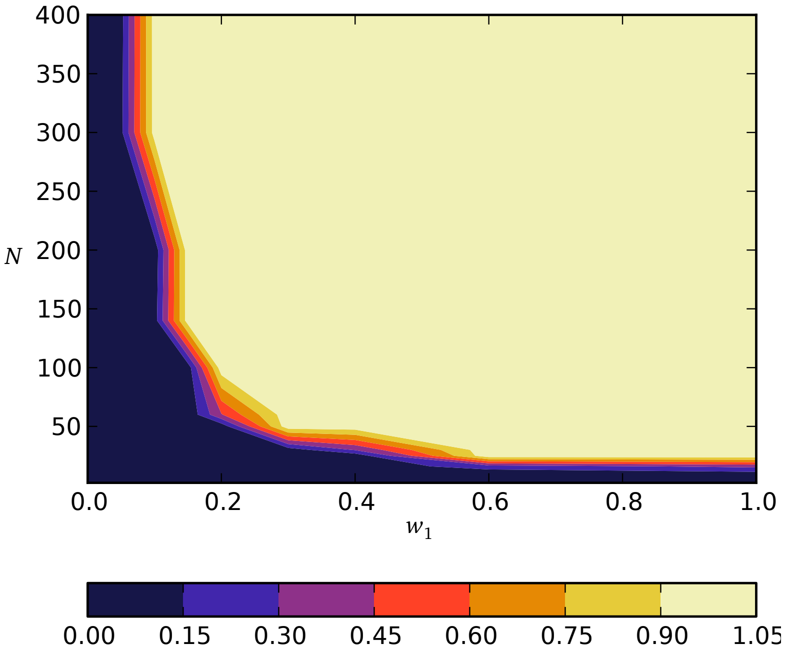


Figure 4.4: Heat map of the mean frequency of defectors in the equilibrium state of the PGG/P for group selection, under variation of w_1 and N. All other parameter are as given in Table 1. For high w_1, cooperation only works in small groups, but for weak local selection, group competition can suppress defection even for very large groups.

of the whole community J with probability

$$p = \frac{1}{1 + \exp(w_2[\bar{\pi}_I - \bar{\pi}_J])} \tag{4.9}$$

or J by a copy of I with probability $(1-p)$. We see that Eq. (4.9) differs from our previous formula for the link dynamics updating step, Eq. (4.2), only in using a different selection strength (w_2 instead of w_1) and using the mean payoff of a community $\bar{\pi}_I$ instead of the payoff of an individual π_i. In order to obtain the same average number of offspring across communities for each local updating step as for the individual migration models studied here, we will assume a probability of such a group conflict step of $m' = \frac{mN}{m(N-1)+1}$.

As Fig. 4.4 shows, having either small groups or weak local selection is sufficient for group conflict to sustain cooperation over a wider range of parameters than the PGG/P in a well-mixed population. In fact, while a well-mixed population on average contains more defectors than punishers or cooperators for the parameter values given in Table 1, group selection leads to a population that is nearly evenly split between cooperators and punishers, with only a marginal number of defectors (*cf.* Fig. 4.3c for $w_1 = 0.1$ or equivalently Fig. 4.3a for $N = 20$).

If selection within communities is weak, roughly for $w_1 < 0.5$ (*cf.* Fig. 4.3c), group competition does in fact lead to cooperation in many reasonable areas of the parameter space. As opposed to the findings of Boyd *et al.* this also holds for quite large community sizes N, as can be seen in Fig. 4.3a. Only for very large community sizes does defection reappear.

The simulations which Fig. 4.3a is based on have been run for 2 500 000 000 time steps (to account for the larger population size, as opposed to the minimum of $25\,000\,000 \gg \frac{N^2}{m\mu}$ time steps used otherwise). For large N, this not bigger than $\frac{N^2}{m\mu}$, so we can not rely on convergence, but given that the simulation is started in pure defection and both the mean results of the simulations for various N and the observed frequencies over the simulation run (*cf.* Fig. 4.3b for $N = 300$) appear very continuous, this will be sufficient for the conclusion that group competition is beneficial for cooperation for at least medium to large N.

For stronger local selection $w_1 \gg 0$, we do however recover the fact that for community sizes above a relatively small critical value $N > N^*$, group selection cannot sustain cooperation. The value of N^* depends on w_1, as can be seen in Fig. 4.4.

In the next section, we will focus on a different, individual-based mechanism also seen in [114], and study how it relates to the stability of cooperation.

4.4 Fitness-Based Migration

While Soltis, Boyd, and Richerson [116] argue that cultural group extinction occurs often enough among human populations to at least mediate the evolution of cooperation, subsequent computational analysis by Boyd *et al.* [114] also contains a secondary mechanism implementing competition between groups. In addition to whole groups replacing each other, individuals can produce offspring into another group. As opposed to the basic migration model described in Section 4.2, this occurs with a rate proportional to fitness, just like within-group reproduction.

The specific model studied in this section is of a meta-population consisting of M well-mixed subpopulations, as generally described in Section 4.1 and used in the previous sections. There are M communities of N individuals each, yielding a total population of MN individuals. The individuals in each community participate in a Public Goods Game with punishment. In addition to local Fermi updating steps occurring with probability $1 - m$, we consider here Fermi updating steps between any two random individuals from the total population with probability m.

In such a cross-community Fermi updating step, one of the individuals is replaced by an offspring of a different individual. In a process analogous to the local Fermi updating steps, two random individuals (i, j) from the *total* population are selected. Then j is replaced by a – possibly mutant – offspring of i with probability

$$p(j \to i) = \frac{f_i}{f_i + f_j} = \frac{1}{1 + \exp(w_2[\pi_j - \pi_i])} \tag{4.10}$$

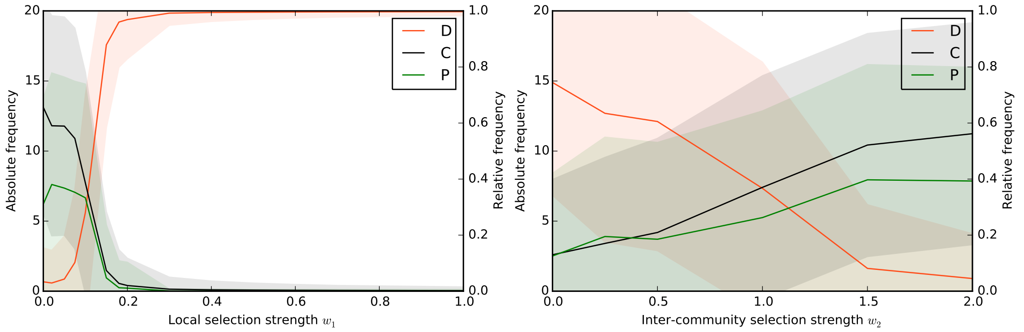
We note that these updating steps differ from the local updating steps according to Eq. (4.2) only in scope – taking individuals from the whole population and not from a single community – and selection strength – w_2 may be different from the parameter w_1 in Eq. (4.2). Individual fitness is therefore pertinent in the migration step, so we describe this mechanism as *fitness-based migration* (FBM). The parameter describes a very similar across-group selection strength to the one that appears in Eq. (4.9). We do not consider a model with both group selection and fitness-based migration, so we will proceed using the same symbol w_2 for the two related quantities.

This mechanism implements a limit case of the general description of a multilevel public goods game given in Wang *et al.* [106]. The second-level public goods game added in [106] is not played, which corresponds to the case of some of their positive parameters being set to zero instead, like in Section 4.2. But whereas in Section 4.2 we have considering the same model under the additional constraint $w_2 = 0$, here we have $w_2 > 0$.

Wang *et al.* argue that for $\mu M \ll m \ll 1/N$, cooperators will be abundant if and only if $w_1 \ll w_2$. This argument is independent of the second-level PGG and therefore also holds in the model studied in this section.

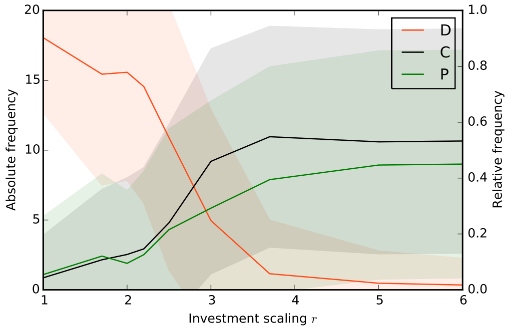
As in previous sections, we will now look at higher migration rates, and study the robustness of cooperation under changes in parameters. Results for different local selections strengths w_1 are shown in Fig. 4.5a. We do see that for low w_1, the most abundant strategy is C, just as for rare migration and mutation. Similarly, for large w_2, cooperators and punishers share the meta-population between them. But for middle values of w_2, the behaviour differs from the limit case of small m and μ. For $0 \leq w_2 < w_2^* \approx 1$, defectors take over the system. This is different from the results shown by Wang *et al.* [106, Fig. 4a], where this phase transition occurs for $w_2^* \approx 4$, and for $w_2 \ll 1$, in a second transition, punishers become abundant and both defectors and cooperators are rare.

Other parameters do not affect the limit behaviour studied in [106], but are relevant in the context of group competition, For instance, Fig. 4.5c shows how strategy frequencies vary depending on the linear scaling parameter r. In well-mixed populations and under constant migration, strategy frequencies were independent of r. We recall that according to Eq. (4.1) fitness is given by an exponential function of payoffs. As Eq. (4.2) shows, this implies that only differences between payoff magnitudes matter. Because all three strategies gain their equal share of the public good Π (Eq. (3.1)), which is the same for all members of the same community, the magnitude of the scaling factor r matters only when fitnesses are compared across communities. This is the case for FBM, but not for



(a) Varying w_1.

(b) Varying w_2.



(c) Varying the investment scaling coefficient r.

Figure 4.5: Mean frequencies and standard deviations of strategies in the equilibrium state of the PGG/P for fitness-based migration. All other parameter as given in Table 1

constant migration. This is an indication that FBM goes beyond being the "migration-like process that causes behaviors to diffuse from one group to another"[114], as which it was originally intended by Boyd *et al.* [114]. We will therefore now compare the three models presented here in more detail.

4.5 Comparison

In the previous sections, we have presented three different models of interactions between different communities in a patch-structured population. We have studied their effect on the evolutionary dynamics of the Public Goods Game with peer punishment, and found various effects.

We have seen that migration according to constant migration rates does not have a strong effect on the long-term evolutionary dynamics of such a meta-population. Both group conflict and to a lower extent fitness-based migration can suppress defection in parameter regions where defectors would strongly dominate for well-mixed populations. For fixed migration, this is no longer the case.

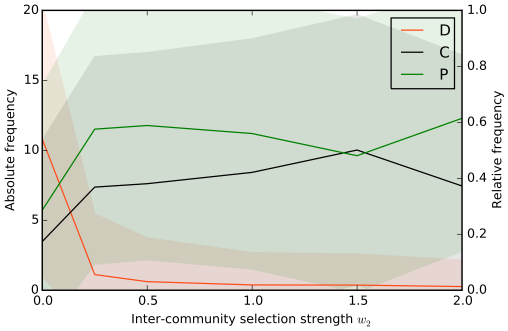


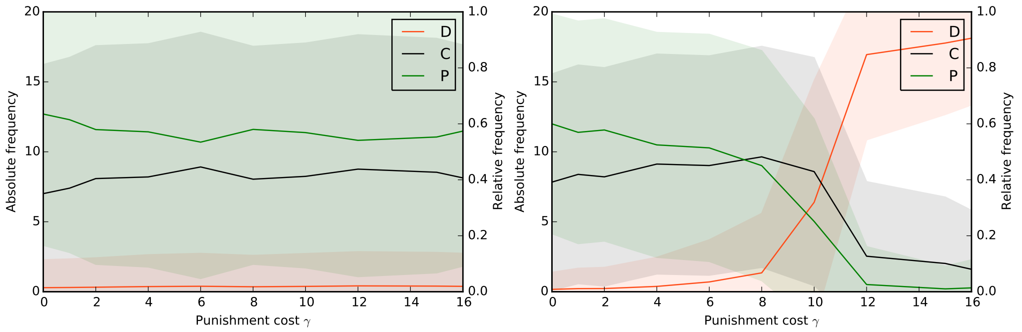
Figure 4.6: Mean frequencies and standard deviations of strategies in the equilibrium state of the PGG/P varying selection strength w_2, in a model of direct conflict between groups. All other parameter as given in Table 1

In a model of direct group conflict, entire subpopulations die out and are replaced by copies of other communities. Here we have seen that for weak local selection and strong second-level selection in the group competition stage, cooperation is generally a dominant strategy. For stronger local selection $w_1 \gg 0$, we were able to confirm the result found by Boyd *et al.* [114] that direct group conflict can sustain cooperation only for small group sizes N, using a slightly different model.

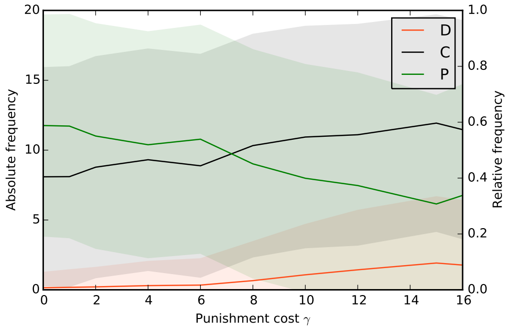
Lastly, we studied a model of fitness-dependent migration, in which the migration probability is proportional to the fitness of an agent. This model allows cooperation to prevail in a wider range of parameters than well-mixed populations or a model of constant migration. For our default values, including $w_1 = 0.1$ and $w_2 = 1$, this effect is however not very strong.

We have shown that strong selection between communities suppresses defection in the case of FBM. This is also true for group competition. The threshold of selection strength, above which group selection maintains cooperation, is however lower; compare Figs. 4.5b and 4.6.

For higher selection strengths, such as $w_2 = 2$, fitness-based migration suppresses defection over a wide range of parameters. An example is shown in Fig. 4.7c. This behaviour for strong selection is similar to the group selection case. We do however find that in the presence of fitness-based migration, cooperation is relatively more abundant than punishment in most cases. For example for varying punishment costs γ, the frequency of both punishers and cooperators are roughly constant under group selection. A model with fitness-based migration on the other hand contains more cooperators than the group selection model for low values of γ. Their number further increases with γ, such that for our chosen default punishment cost, $\gamma = 10$, cooperators have become more frequent than punishers. High selection strength w_2 then continues to maintain cooperation for much higher punishment costs than weak selection (*cf.* Fig. 4.7c), even as the frequency of punishers continues to decrease.



(a) With group competition (b) With fitness-based migration

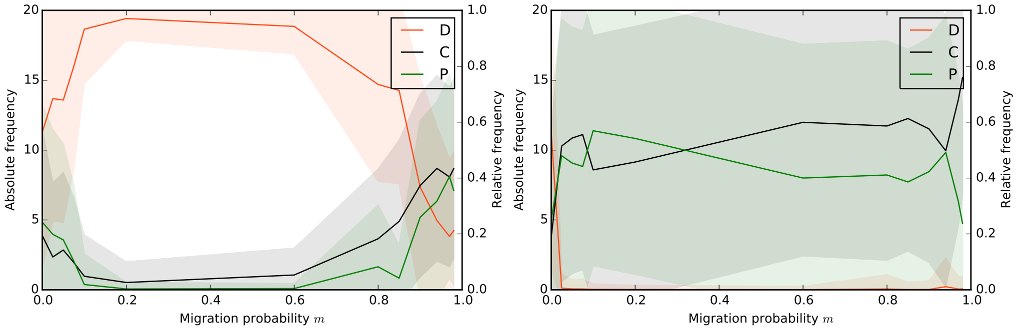


(c) With fitness-based migration, with $w_2 = 2$

Figure 4.7: Comparison of the mean frequencies of strategies in the equilibrium state of the PGG/P for varying punishment cost γ, in models with group competition and fitness-based migration with different selection strengths. All other parameter as given in Table 1

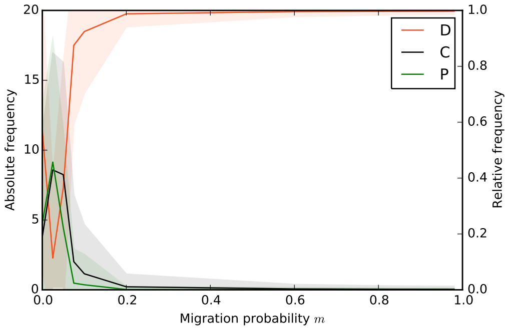
We note that for high migration rates, fitness-based migration behaves differently from both group selection and constant migration. As shown in Fig. 4.8, for high migration rates defection is weak in both the constant migration and the group selection model. This is because migration steps (in the migration model) or group conflict steps (in the group selection model) take place so often that defectors have almost no opportunity to invade through local updating steps. When subject to fitness-based migration, however, defection rates are persistently high. In this case, the model approximates a large well-mixed population of size MN in behaviour, in which the PGG is played in small, rapidly changing groups.

The stable state distributions of well-mixed populations and all three models for the parameter values given in Table 1 are shown in Fig. 4.9. As is expected, the pure states have the highest probabilities, followed by those states where two different strategies are present. In the well-mixed case and for group selection, most states with three strategies have negligible probability of presence in the equilibrium distribution. This holds particularly for those states near the unstable equilibrium between punishers and defectors.



(a) With constant migration

(b) With group competition

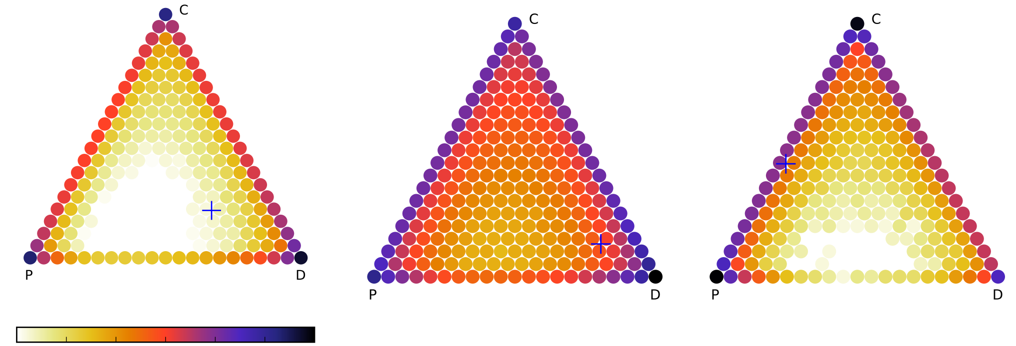


(c) With fitness-based migration

Figure 4.8: Comparison of the mean frequencies of strategies in the equilibrium state of the PGG/P for varying migration probability m in the three different models presented in this article. All other parameter as given in Table 1

For strong selection (Fig. 4.9e), the fitness-based migration population contains on average only very few defectors. This is also true for group selection, shown in Fig. 4.9c. But in the group selection case, this corresponds to low probabilities of the mixed states with many defectors. The pure defection state retains a high probability of presence. In a model using FBM with strong selection on the other hand, mixed states are generally non-negligible. Pure defection however is less likely to be the actual state in the equilibrium distribution than many mixed states containing cooperators and a single other strategy. Fitness-based migration is thus not only capable of increasing the frequency of cooperation overall, but can be seen to decrease the length of time a system spends in pure defection.

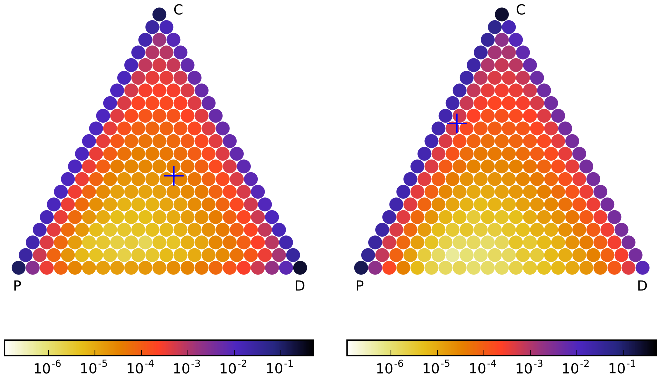
A similar mixing effect explains why punishment is less frequent for fitness-based migration than for group selection: because mixed states are far more frequent for FBM, the likelihood for all three strategies to be present is increased. For example, while the mean frequency of cooperators is similar between Fig. 4.9c and Fig. 4.9d, the latter has more probability mass in the mixed state, making up for a loss of probability in the pure cooperation state. In such cases, cooperators dominate punishers for positive punishment cost $\gamma > 0$, thus leading to an increase in cooperators.



(a) In a well-mixed population

(b) With constant migration

(c) With group competition



(d) With fitness-based migration

(e) With fitness-based migration, with $w_2 = 2$

Figure 4.9: Long-time averages of the evolutionary dynamics shown as a heat map in barycentric coordinates. Each dot corresponds to a possible state of the system, with pure defectors (bottom right), pure cooperators (top) and pure punishers (bottom left) in the corners. Darker dots correspond to a higher probability of presence. Note that the gradient of brightness is logarithmic. The mean of each distribution are marked with a +. Stochastic simulations were run for at least $320\,000\,000 \gg \frac{N^2}{\mu m} = 3\,200\,000$ time steps, to ensure convergence. The parameters used in these simulations are as given in Table 1.

4.6 Discussion and Conclusions

In this chapter, we have considered three different models of interactions in an island- or community-structured meta-population, and illuminated how they influence the long-term behaviour of the Public Goods Game with peer punishment. We have considered explicit conflict between separate groups, and compared it to a model of individual migration proportional to fitness, which shows some capability of approximating group competition, in particular for strong cross-group selection. We have seen that for group competition, as well as for fitness-based migration, defection would take over each community according to local dynamics. But due to direct or indirect competition between groups, highly defective groups are at a disadvantage, and globally cooperation and punishment can prevail.

The fact that global and local trends can differ is not surprising. It is a well known paradox in statistics that a trend that occurs in different groups of data can be reversed when the groups are combined. This effect is known as *Simpson's Paradox* [118, 119]. The terminology was introduced to the literature on the evolution of cooperation by Sober and Wilson [12]. The argument is as follows. Given a set of subpopulations, defection is a dominant strategy in each of them. The relative frequency of defectors, averaged over all subpopulations, will therefore be high. If, on the other hand, subpopulations with high amounts of cooperation have a higher population capacity and contain more individuals [12, 32, 120, 121], the relative frequency of cooperators in the whole meta-population will be large nonetheless.

Fitness-based migration tries to capture some aspects of this behaviour, while keeping the parameter space small and population sizes constant. But in the model presented in Section 4.4, the rise in cooperation does not stem from different subpopulation sizes, as is the case in previous models, but from the fact that copying steps between these subpopulations are biased. As such, the model presented here has two methodological advantages compared with models with variable subpopulation size.

Firstly, the constant subpopulation size reduces the parameter space of the model. If the population capacity of a subpopulation depends on the amount of public good that subpopulation produces, this dependency must be described by additional parameters of the model. If an effect found before for variable population sizes (*cf. eg.* [32]) can already be shown using the simpler model presented here, it is clear that such an effect is more universal than if it can only be shown for certain choices of that dependency.

It should be noted that such an argument would not hold if equally-sized populations were a special case showing the desired effect particularly strongly. There is no indication of such a particularity of the behaviour in our model – and if there was, it would still be worthwile to separately consider the factors of variable population size (influencing for example the speed of local evolution and fixation) and the weight a population has in the migration step (which influences the mixing between subpopulations).

Secondly, the state space of a model with constant population size is comparatively small. For a subpopulation size of $N = 20$ and three different strategies, the Markov transition matrix is a sparse matrix between $(N+1)(N+2)/2 = 231$ different states (up to symmetry), and can be easily calculated and manipulated by computational tools. In the model presented here, the interactions between all subpopulations are symmetric. This suggests that it might be possible to obtain the stable state distribution of the full Markov chain as a solution to an equation of the form $y^k = y^i y^j T_{ij}^k$, as suggested in Eq. (4.5).

The key conclusions of this study are however that we were able to show that direct conflict between groups and second-level selection are not necessary to implement group selection. We were able to decouple two components used by a pioneering modeling study by Boyd *et al.* [114] and show that fitness-based migration, an element introduced by them merely to incorporate an element of diffusion between groups, is by itself capable of serving as a proxy for group selection and thus to support the evolution of cooperation.

In addition to its capability as a proxy for group selection, migration according to fitness increases the probability of mixed states in the public goods game. Punishers therefore move from an abstract strategy that safeguards a population from future invasions by defectors towards playing an active role in suppressing constant defection. Fitness-based migration may therefore be a useful addition to the toolbox with the twofold use of increasing variability while also implementing group selection.

We have now analysed two of the main components of evolutionary models, by focussing on the updating rule and the population structure. Now we will concentrate on the third component, and consider extensions to the public goods game. We start by recalling extensions suggested in the literature, with a focus on the context of punishment.

Chapter 5

Extensions to the PGG/P

The reliance on high randomness, by way of high mutation rates, to explain the prevalence of stable cooperation and punishment, is conceptionally unsatisfying. This holds in particular for biological systems, where random exploration appears to be rare. Yet cooperation has arisen in many unrelated phyla. But also for human social groups, where experiments have shown that levels of strategy exploration can be high [122, 123], persistent exploration rates of 20% to attain stable cooperation with some punishment seem excessive.

One ansatz to solve this issue is the consideration of population structures that benefit cooperation. For social insects, relatedness between workers, which engage in punishment, seems to be a major factor stabilising cooperation and punishment [124–126]. But also for human populations, the social structure seems to be configured to facilitate cooperation. Santos, Santos, and Pacheco [127] showed that scale-free networks, where the degree distribution of nodes in the network follows a power-law, similar to how human social networks are structured, promote the emergence of cooperation. A review of how network structures affect evolutionary dynamics can be found in [20]. We will revisit community-structured populations in Chapter 6.

On the other hand, many researchers extend the space of strategies, to include further options that appear missing in the model. In this chapter we will discuss some such extensions. We will introduce and discuss the evolutionary effects of loners (Section 5.0.1, generalisations of the peer punisher strategy to include rewards or punish other groups than defectors (Section 5.0.2), opportunistic strategies in the context of models with incomplete information (Section 5.0.3), and pool punishers (Section 5.0.4). We then explore the implications of a punishment strategy that will interpolate between the peer and pool punisher strategies, in Section 5.1.

5.0.1 Loners

Many workers in population dynamics literature add *Loners* (L) as additional strategy. This strategy was introduced by Hauert *et al.* [102]. Players who follow this strategy gain a small frequency-independent payoff

$$\pi_{\mathrm{L}} = \sigma < r - 1 \tag{5.1}$$

The rationale for the introduction of L is that participation in potentially cooperative endeavours is in most cases voluntary, rather than a compulsory and possibly exploitative interaction. Choice to not participate should thus facilitate cooperation among those choosing to participate.

It is indeed the case that the presence of loners can give rise to cooperation under a variety of models [102, 121]. Because cooperators fare better than loners, loners dominate in a population rich in defectors and defectors exploit cooperators, the loners, while only an intermediate state of the system, are required for the evolution of cooperation. However, even with the addition of punishment [128], the resulting dynamics show cycles or bi-stability [101]. Nonetheless, L strategies are a frequent ingredient of evolutionary models with public goods games, including many of the articles mentioned in the following.

5.0.2 Extending Reward and Punishment

Costly punishment models the more aggressive punishment possibilities on a wide scale from negative gossip about an individual via fines and ostracism to corporal punishment and execution [104]. In the real world, such punishment is not unlikely to lead to retaliation (in fact, one of the justifications for high punishment costs is to model this risk) [103]. Specific retaliation against punishers can hinder the evolution of cooperation [129], but in more general terms, the observation of retaliation points to a deeper neglect in Public Goods Game models in which only cooperators can punish only defectors.

Consequently, as initiated by Rand and Nowak [130], research has included anti-social punishment, punishment against all cooperators, and in some cases against Loners. While the option to punish any or all of defectors, cooperators and loners hinders the evolution of cooperation [130], fully separating loners from the rest of the public goods game does allow cooperation to evolve [131]. The evolution of cooperation in this context is however still founded on the cyclic dominance of cooperators over loners, loners over defectors and defectors over cooperators and requires the presence of loners to evolve.

5.0.3 Mixed Strategies

Recently, models of punishment in the public goods game, and games with similar structure, such as the gift-giving game, have begun to focus on probabilistic effects. This is particularly relevant in the context of opportunistic strategies. Opportunists, such as the O strategy of [28] or the opportunistic defectors and cooperators introduced in [108], mimic one of two strategies, depending on which one has the higher expected payoff.

In the previous models, randomness is most relevant in the strategy imitation step, so much that Szabó and Fáth [89] identify the reciprocal of the selection strength, $\frac{1}{w}$, as a measure of noise in the system. In particle systems with terms similar to exponential fitness, the corresponding term represents the temperature (and therefore inherent entropy) of the system [22]. Recall also the strong effect of mutation rates on the evolutionary dynamics of evolutionary games [81].

For opportunistic and other mixed strategies, randomness in game step becomes a driving force of different evolutionary dynamics. Interestingly, many models concerning pure strategies [81, 84, 132, 133] and even the articles focusing on strategies involving randomness cited above [28, 108] base their analysis on average payoffs.

In the model of third-party punishment presented by Roos *et al.* [28], opportunists are aware of the general proportion of peer punishers in their neighbourhood, but they cannot predict with whom they will be paired in the punishment step. This uncertainty makes the willingness to punish a strong signal that can lead opportunists to cooperate.

The randomised punishing strategies introduced by Chen, Szolnoki, and Perc [88] are in competition because randomness in the strategy-updating step leads to irregular boundaries between compact domains of different strategies. Individually, those strategies punishing with lower punishment probability are weaker against persistent clashes with defectors and die out, while they have synergy effects in compact groups.

5.0.4 Pool Punishers

Anthropologists and economists [103–105, 134] have argued that the majority of punishment observed in the real world consists of less risky punishment. A frequent implementation of such punishment in experimental and theoretical economics is called pool punishment. Pool punishment is usually understood as follows. Agents have the option to be pool punishers. Pool punishers pay a constant tax t before allocating resources to the public good. If the tax paid is above some threshold, all defectors are punished by a constant amount. Economic experiments have shown that humans prefer institutional punishment to peer punishment when given the choice [103, 135, 136].

The threshold can be less than t, in which case a single pool punisher is sufficient to punish a whole population of defectors at low cost. This reveals a striking feature of the pool punishment strategy. Pool punishers are the only social strategy that can under many reasonable parameter values successfully invade and take over a population of defectors. In turn, pool punishers bear the cost of the institution no matter whether defectors are present or not, and are thus always dominated by cooperators. This Rock-Paper-Scissors–like cycle is in contrast with the evolutionary neutrality of cooperators and punishers in the basic PGG/P.

Many studies have focused on the evolutionary dynamics of the public goods game with pool punishment, in particular in competition with peer punishment [25, 26, 108, 137–139]. They show that, due to the fact that cooperators out-compete pool punishers when only these two strategies are present, institutional punishment is unstable unless supported by second-level punishment, *i. e.* a fitness penalty for cooperators that do not punish. Recent results by Schoenmakers *et al.* [108] show that this instability can be partially mitigated through an opportunistic strategy that cooperates if and only if a punishment institution is set up. If the composition of the groups playing the public goods game is highly random and varies between game steps, opportunists fare relatively badly when they defect when grouped with other opportunists, but cooperate with pool punishers. This leads to the emergence of a stable equilibrium between pool punishers and opportunists, which cannot be easily invaded by other strategies. In this model, pool punishment is therefore highly stable, without having to rely on loners or second-level punishers to emerge.

Models and experiments of pool punishment do pre-suppose the existence of pool punishment institutions. The payments by the punishers to the punishing institution are taken out of the system, and the institution, which avoids evolutionary pressures, bears the risk of high versus low numbers of punishers externally to the system. The transition from peer to pool punishment is not well-studied in evolutionary modelling. In the following section, we consider a model in which the individual punishers supported by the tax t are actively competing with the remainder of the population.

5.1 Evolving pool punishment

In this section, we study whether something similar to pool punishment could evolve in the model from a pair of strategies that generalise from previous definitions of cooperators and peer punishers in a limit. We will compare this model with pool punishers, and study how it fares in competition with that strategy. We will therefore now introduce the model containing both *pool punishers* (I, for their institutions) and a strategy we will dub *tax payers* (T) strategy. Pool punishers behave according to the rules given in [25]: They pay a constant cost t' which may be different from the contribution made by taxpayers.

If any pool punishers paid their cost in this matter, all defectors are punished by a constant amount. We note that for pool punishers, the punishment happens without the necessity for individuals to actually execute it. Without adding new sources of payoff, and keeping the administration of punishment within the model, any approximation of pool punishment must involve modifications to both cooperators and punishers. In addition to providing investment c for the public good, agents following the T strategy will therefore pay a fixed tax t. If any peer punishers are present, the sum of all tax is split among all peer punishers. The payoffs of the strategy is thus as follows.

$$\pi_{\mathrm{D}} = \Pi - \beta \frac{n_{\mathrm{P}} + Z(n_{\mathrm{I}})}{N} \tag{5.2}$$

$$\pi_{\mathrm{C}} = \Pi - c \tag{5.3}$$

$$\pi_{\mathrm{T}} = \Pi - c - t \tag{5.4}$$

$$\pi_{\mathrm{P}} = \Pi - c - \gamma \frac{n_{\mathrm{D}}}{N} + t \frac{n_{\mathrm{T}}}{N} \tag{5.5}$$

$$\pi_{\mathrm{I}} = \Pi - c - t' \tag{5.6}$$

$$\tag{5.7}$$

where

$$\Pi = rc \frac{n_{\mathrm{C}} + n_{\mathrm{P}}}{N} \tag{5.8}$$

is the individual's share in the public good, and Z is a step function such that $Z(0) = 0$ and $Z(X) = 1$ for all $X > 0$. For $t = 0$, this game recovers the usual public goods game with punishment. But when $t > 0$, it is obvious that punishers will trivially dominate taxpayers in the absence of defectors.

Let us first consider the evolutionary dynamics of this model for low mutation rates. In general, the fixation probability of a single A mutant in an otherwise homogeneous population of B is given by [106]

$$\rho_{BA} = \frac{1}{1 + \sum_{j=1}^{N-1} \exp[w \sum_{i=1}^{j} \pi_B(n_A = i, n_B = N - i) - \pi_A(n_A = i, n_B = N - i)]} \tag{5.9}$$

For a constant payoff advantage or disadvantage $a(B, A)$, such as $a(\mathrm{C}, \mathrm{T}) = \pi_{\mathrm{C}} - \pi_{\mathrm{T}} = t$, this simplifies to

$$\rho_{BA} = \frac{\exp[wa(B, A)] - 1}{\exp[wNa(B, A)] - 1} \tag{5.10}$$

and $\rho_{BA} = 1/N$ for a neutral mutant, *i. e.* $a(B, A) = 0$. This is equivalent to the fixation probability for a constant advantage in the symmetric 2-player case as seen earlier in Eq. (2.23).

If mutation is negligibly rare, we can make the usual ansatz and consider the system of fixed states only, where the transition probabilities are given by the fixation probabilities of single mutants ρ_{BA}. If we consider the game with D, C and I only, each strategy has a constant frequency-independent advantage or disadvantage compared to each other strategy, so we can write down the transition matrix M of the reduced Markov chain as

$$M = \begin{pmatrix} 1 - \rho_{\mathrm{DC}} - \rho_{\mathrm{DI}} & \rho_{\mathrm{DC}} & \rho_{\mathrm{DI}} \\ \rho_{\mathrm{CD}} & 1 - \rho_{\mathrm{CD}} - \rho_{\mathrm{CI}} & \rho_{\mathrm{CI}} \\ \rho_{\mathrm{ID}} & \rho_{\mathrm{IC}} & 1 - \rho_{\mathrm{ID}} - \rho_{\mathrm{IC}} \end{pmatrix} \tag{5.11}$$

$$= \begin{pmatrix} 1 - \rho_{\mathrm{DC}} - \rho_{\mathrm{DI}} & \frac{\exp(-wc)-1}{\exp(-wmc)-1} & \frac{\exp(-w(c+t'-\beta/N))-1}{\exp(-wm(c+t'-\beta/N))-1} \\ \frac{\exp(wc)-1}{\exp(wmc)-1} & 1 - \rho_{\mathrm{CD}} - \rho_{\mathrm{CI}} & \frac{\exp(-wt')-1}{\exp(-wmt')-1} \\ \frac{\exp(w(c+t'-\beta/N))-1}{\exp(wm(c+t'-\beta/N))-1} & \frac{\exp(wt')-1}{\exp(wmt')-1} & 1 - \rho_{\mathrm{ID}} - \rho_{\mathrm{IC}} \end{pmatrix} \tag{5.12}$$

The stationary distribution is then given by the (left) eigenvector $\pi M = 1 \cdot \pi$ of M, with $0 \leq \pi_i \leq 1$ and $\sum_i \pi_i = 1$. For 3×3 matrix we can explicitly construct such an eigenvector. The eigenspace is generated by

$$((\rho_{\mathrm{CD}}\rho_{\mathrm{ID}} + \rho_{\mathrm{CI}}\rho_{\mathrm{ID}} + \rho_{\mathrm{CD}}\rho_{\mathrm{IC}}), (\rho_{\mathrm{DC}}\rho_{\mathrm{ID}} + \rho_{\mathrm{DC}}\rho_{\mathrm{IC}} + \rho_{\mathrm{DI}}\rho_{\mathrm{IC}}), (\rho_{\mathrm{DI}}\rho_{\mathrm{CD}} + \rho_{\mathrm{DC}}\rho_{\mathrm{CI}} + \rho_{\mathrm{DI}}\rho_{\mathrm{CI}})) \tag{5.13}$$

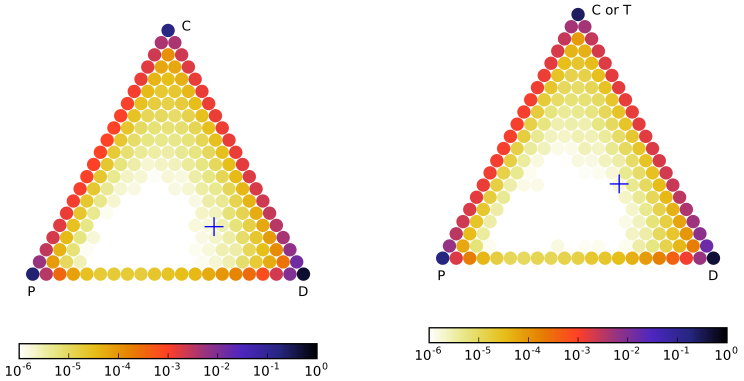
so there is an explicit closed-form formula for the stationary distribution, depending on the parameter values.

For the parameter values given in Table 1, this gives a distribution in the stable state of the Markov chain of about $(0.485, 0.206, 0.309)$.

When considering the model with strategies $\mathrm{D}, \mathrm{C}, \mathrm{T}$ and P, it is not possible to give a simplified expression for the fixation probability, because the payoff differences of P and D, as well as P and T, are not constant. Furthermore, the stable state will be an eigenvector of the 4×4 matrix

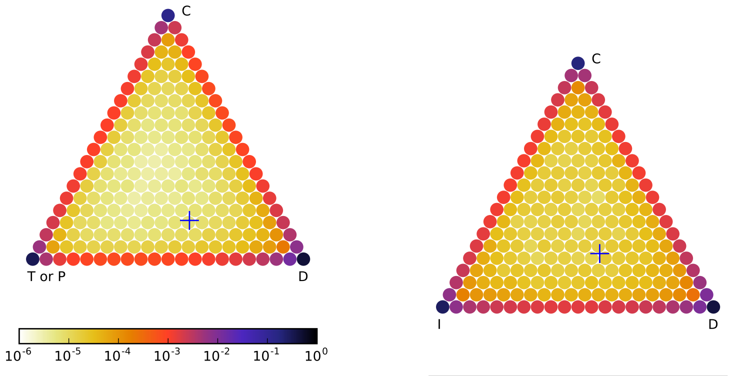
$$\begin{pmatrix} 1 - \dots & \rho_{\mathrm{DC}} & \rho_{\mathrm{DT}} & \rho_{\mathrm{DP}} \\ \rho_{\mathrm{CD}} & 1 - \dots & \rho_{\mathrm{CT}} & \rho_{\mathrm{CP}} \\ \rho_{\mathrm{TD}} & \rho_{\mathrm{TC}} & 1 - \dots & \rho_{\mathrm{TP}} \\ \rho_{\mathrm{PD}} & \rho_{\mathrm{PC}} & \rho_{\mathrm{TP}} & 1 - \dots \end{pmatrix} \tag{5.14}$$

All of $\rho_{\mathrm{TD}}, \rho_{\mathrm{TC}}, \rho_{\mathrm{TP}}, \rho_{\mathrm{DT}}, \rho_{\mathrm{CT}}$ and ρ_{TP}, and therefore also all entries on the diagonal, depend on t. The resulting expression for the frequency of defectors in terms of the parameters, including t, can in theory be given, but deriving valid approximations in order to simplify this unwieldy formula is outside the scope of this work.



(a) The basic PGG/P without pool punishers or tax-payers.

(b) With peer punishers and tax payers. The barycentric coordinates of the states are given by n_D, n_C+n_T and n_P.



(c) With peer punishers and tax payers. The barycentric coordinates of the states are given by n_D, n_C and n_T+n_P.

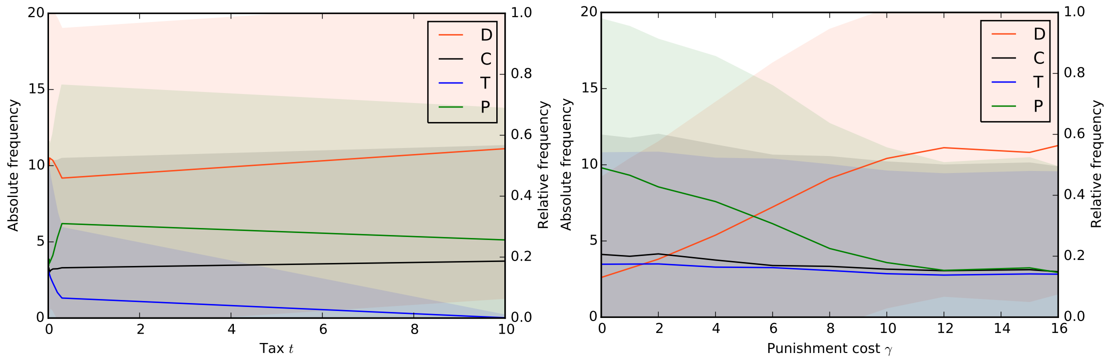
(d) With pool punishers

Figure 5.1: Stationary distribution of the Markov chain induced by the public goods game with punishment, for different strategy sets. Darker colour indicates a higher probability of the corresponding state in the stationary distribution. The means are marked with a +. For parameters given in Table 1.

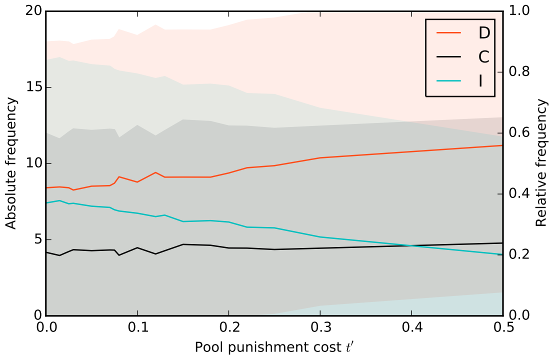
Instead, we consider numerical simulations, which we will do without the then unnecessary restriction of low mutation rates. We use Monte Carlo simulations to calculate the distribution of the Markov chain for 20 000 000 time steps, focusing on the parameter space around the values given in Table 1. We first compare the results for the D, C, I game with the limit result given above. For $\mu = 0.0025 = \frac{1}{N-2}$, the mean of the numerical simulations, $(0.499, 0.200, 0.301)$, is very close to the theoretical limit case.

In both the D, C, I and the D, C, T, P game, and in contrast with the less cooperative basic PGG/P, defectors constitute just below half the population.

The behaviour of the T/P model depends on both tax t and punishment cost γ, as Fig. 5.2 shows. For comparison with pool punishers, we have chosen t' to be 0.18, such that the frequency of defectors in the T/P model matches the frequency of defectors in the I model. We can thus compare the equilibrium distributions in more detail. We



(a) tax t (b) punishment cost γ



(c) pool punishment cost t'

Figure 5.2: Average frequencies of strategies in the fixed-cost punishment models for varying costs and taxes

see that in the pool punishment model mixed states are even more frequent than in the taxpayer model (Fig. 5.1d). The mixed states between institutional punishers and defectors in particular are far more frequent than the corresponding states between peer punishers and defectors.

Fixing these values of the costs t', γ and t, we can compare the pure I strategy with the hypothetical cooperative of peer punishers and tax payers by having them directly compete with each other. In stochastic simulations with all five strategies, we observe that peer punishers often outperform pool punishers slightly. In contrast with results for the competition of institutional and peer punishers in the spatial public goods game [26], we find no strong phase transitions in the explored parameter space. On the contrary, we consistently find that tax-receiving peer punishers have a small advantage over institutional punishers, which in turn perform better than pure cooperators, followed by taxpayers.

We observe different behaviour only for high mutation rates (see Fig. 5.3), where the order of strategies is inverted. For higher selection strength γ, we observe a stronger distinction between the strategies, where peer punishers gain in frequency at the cost of cooperators and taxpayers.

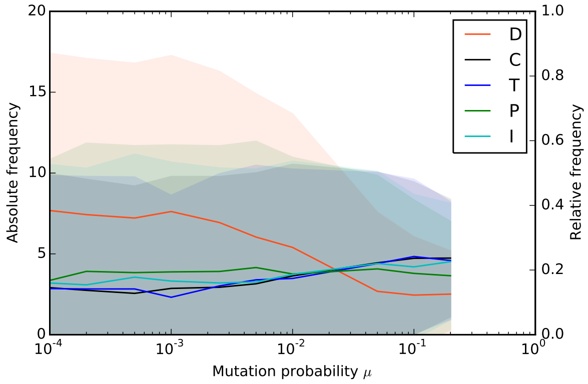


Figure 5.3: Average frequencies of strategies when T, P and I compete, for different mutation rates

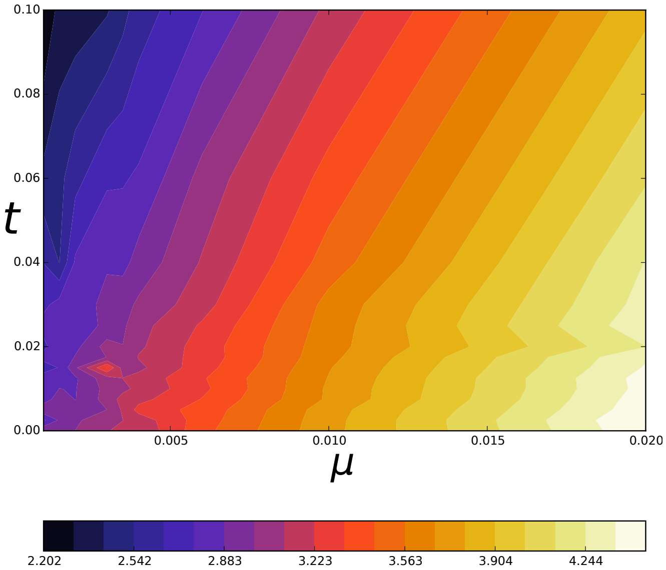


Figure 5.4: Heat map of the frequency of taxpayers in a slice of the parameter space. For any mutation rate μ, n_{T} decreases as t increases.

While both institutional and peer punishers decrease the frequency of defection, mixed states containing both many punishers and many cooperators or taxpayers are still rare. There is however no stable state between punishers and taxpayers, either. In fact, while mixed states containing any other two strategies are present in the stable state distribution with probability 2–4% each, only the states containing both punishers and defectors (0.98%) are more rare in the equilibrium than states with both T and P at 1.8%. This proportion goes up as μ increases, but even for $\mu \gg 0$, the intended synergy between taxpayers and punishers does not come about, and other strategy combinations keep being more frequent than having both T and P players in the population at the same time. Consequently, the frequency of taxpayers dependent on the level of taxes is monotonically decreasing over the whole range of mutation rates, as Fig. 5.4 shows.

Even if taxpayers are strongly selected against due to high taxes $t \gg 0$, a single taxpayer can still significantly compensate punishers, thus forcing defectors out of the system.

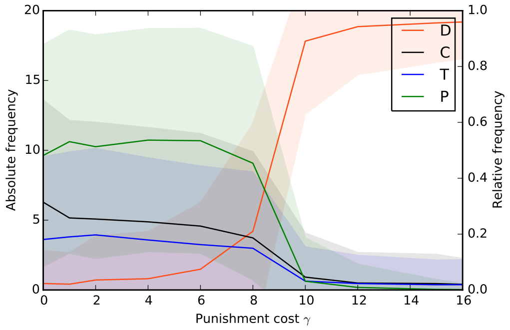
When mutation rates are large, this can suppress defection to some extent, but this is much more an artefact of the model structure than of the system we try to model. We expect more natural outcomes in models incorporating some level of locality, so we will now extend the analysis to the metapopulation structures considered in Chapter 4.

Chapter 6

Taxpayers in community-structured populations

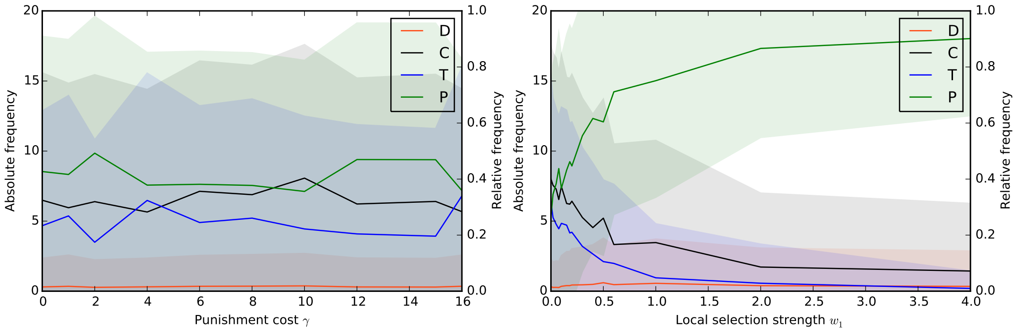
We have seen in the previous section that taxpayers can increase cooperation, but that any increase in tax harms the taxpayers. In Chapter 4, we have seen that a similar monotonicity property for the frequency of cooperators depending on the cooperation cost c is reversed under group selection. We shall therefore now investigate the behaviour of the taxpayer/punisher combination in community-structured populations.

Similarly to the approach in Chapter 4, we will first, as a baseline, consider a model of migration between separate communities. Under migration, the evolutionary outcome is similar to the model without taxpayers. The proportion of the population occupied by cooperators for the basic game is now split between cooperators and taxpayers in



(a) Varying punishment cost γ

Figure 6.1: Frequencies of strategies in the equilibrium state of the PGG/P with taxpayers, in a community-structured population with migration, under variation of different parameters. All other parameter are as given in Table 1. Solid lines show the mean of the frequency in the long-time limit, the shaded area denotes the $\pm 1\sigma$ band around it.



(a) Varying punishment cost γ (b) Varying local selection strength w_1

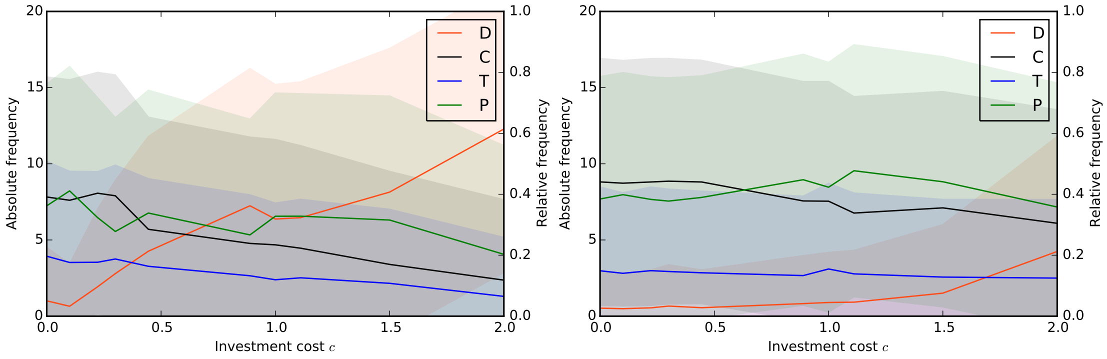
Figure 6.2: Frequencies of strategies in the equilibrium state of the PGG/P with taxpayers, in a community-structured population with migration, under variation of different parameters. All other parameter are as given in Table 1. Solid lines show the mean of the frequency in the long-time limit, the shaded area denotes the $\pm 1\sigma$ band around it.

varying proportions. In regions of high randomness, the average frequency of taxpayers generated by the stochastic simulations is sometimes marginally above the frequency of cooperators. Overall, however, cooperators are generally between one and 3 times as frequent as taxpayers, with little effect on other strategies. For varying punishment cost γ, however, the presence of taxpayers keeps punishment stable for slightly higher γ, thus making the phase transition steeper than in the basic PGG/P (Fig. 6.1a; *cf.* Fig. 4.2b).

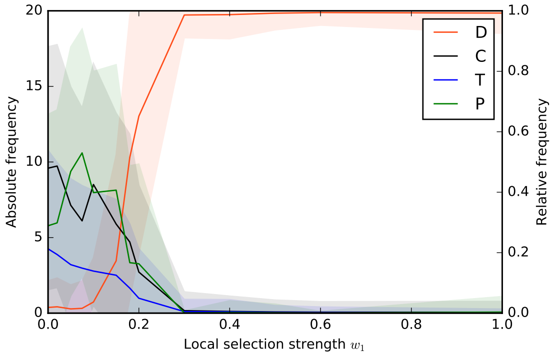
6.1 Group selection

Considering the model with second-level selection, where entire communities can go extinct and reproduce together according to a Fermi process based on the average payoff (*cf.* Eq. (4.9)), we find the following. Just as for the basic model, defection is suppressed for a large region of the parameter space. But when including taxpayers, the new strategy does not only take over part of the basic cooperators, as was the case for the migration model above. Instead, taxpayers compete with both cooperators and punishers, reducing punishers to below half the population where they were constituting the absolute majority before. An example of this is shown in Fig. 6.2a, where the average frequency of the four strategies is plotted against the punishment cost γ.

An even stronger change can be seen in Fig. 6.2b, in comparison with Fig. 4.3c. For increasing local selection strength w_1, we observed that group selection stabilises cooperation up to a critical value $w_1^* < w_2$, above which defection takes over. In contrast with this, the presence of taxpayers allows punishers to suppress defectors for much higher selection strengths. Even more, for strong local selection and group selection, the population consists nearly exclusively of punishers, suppressing not only the first-, but also the second-level free riders. This is the case even though taxpayers are only a marginal



(a) Varying the investment cost c (b) Varying the investment cost c, for $w_2 = 1$.



(c) Varying the local selection strength w_1

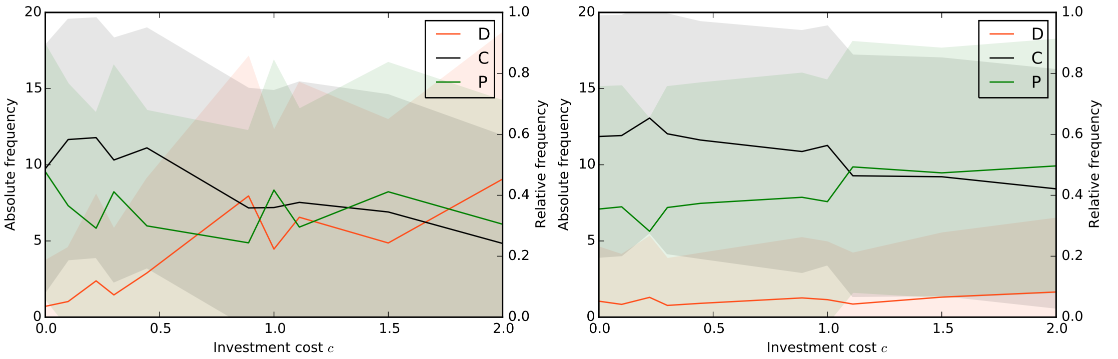
Figure 6.3: Varying parameters for the taxpayer model, under fitness-based migration

minority for strong local selection, and in contrast with the basic PGG, where defectors prevail for high local selection strength.

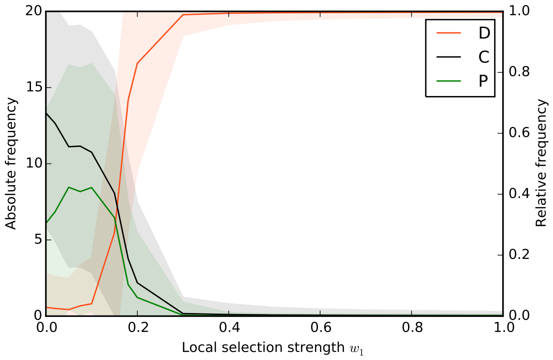
6.2 Fitness-Based Migration

Under fitness-based migration, the public goods game with taxpayers behaves very similar to the basic PGG/P. By contrast with the basic game, however, higher competition between the three cooperative strategies leads to a break-down in cooperation for lower investment costs than in the basic model (compare Fig. 6.3a and Fig. 6.3b with Fig. 6.4a and Fig. 6.4b).

While explicit group conflict sustains cooperation for far higher local selection strengths when tax payers are present, individual-based FBM maintains a similar threshold from which on defection dominates the system both with and without tax-payers (compare Fig. 6.3c and Fig. 6.4c).

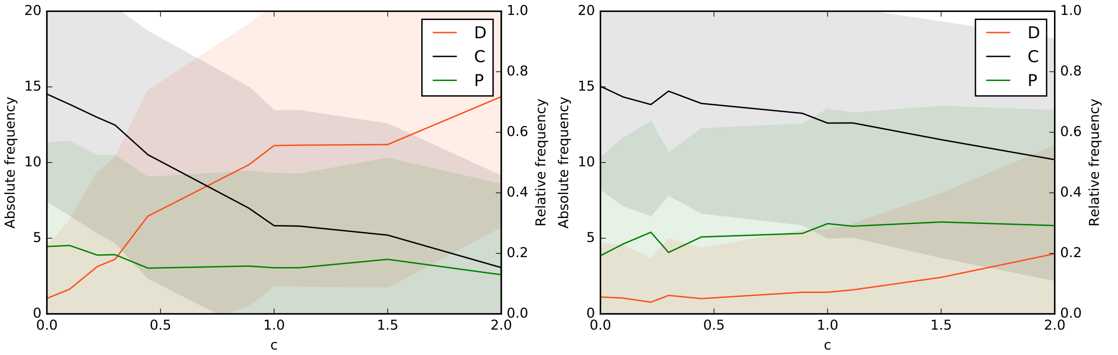


(a) Varying the investment cost c (b) Varying the investment cost c, for $w_2 = 1$.



(c) Varying the local selection strength w_1

Figure 6.4: Varying parameters for the basic PGG/P model, under fitness-based migration



(a) Varying the investment cost c (b) Varying the investment cost c, for $w_2 = 1$.

Figure 6.5: Varying parameters for the basic PGG/P model with asymmetric mutation matrix

6.3 Discussion

We found that in regions where defection is suppressed, introducing taxpayers can actually decrease the frequency of punishers. Instead, we could compare the DCTP model, in which mutation is uniform among all alternatives, to a model with strategies DCP, in which mutating towards C is twice as probable as to D or P.

For this model of non-symmetric mutation, we see similar behaviour in the parameter dependency as in the model with taxpayers, compare Fig. 6.5 with the corresponding figures in Fig. 6.4 and Fig. 6.3. This observation is a special case of the known but little-considered fact that the structure of mutations can have a strong influence on the evolutionary dynamics of a model [38].

More generally, we have tried to see pool punishers emerge in a simple model. Over all, tax payers by themselves are not sufficient to generate a model that captures key properties of pool punishment. The frequency of tax payers is always monotonically decreasing with the level of taxes. In many cases, the presence of taxpayers is even detrimental to cooperation in the system. Even though it appears *a priori* that the opportunity to pay taxes to keep punishers effective should increase cooperation, the availability of the taxpayer strategy changes the structure of mutations, and increases the competition between the cooperative strategies, thus harming cooperation in regions of the parameter space.

We therefore conclude that pool punishment can only evolve in models of higher complexity. But in such systems, it is important to also justify the in- and exclusion of other conceivable strategies of similar complexity, as has been done for peer punishment (*cf.* Section 5.0.2).

Chapter 7

Reconstructing evolutionary histories

In the previous chapters, the focus lay on showing the feasibility of certain evolutionary patterns, given prior assumptions. Another core subject of evolutionary modelling, however, is the reconstruction of evolutionary pathways from real-world data. This chapter will focus on such an application.

The fact that both life on the one hand, and languages on the other, possess genealogical trees, going back to ancient common ancestors, has been established since the early 19th century. Because characteristics change only slowly over time, closely related taxa share many properties. Initially, the structure of the biological tree of life was thus derived from easily accessible physiological features of the species. This is however a problematic approach, because species from different branches in the tree may develop analogous structures (homoplasy) due to convergent evolution under similar environmental pressures. Both analytical methods of biochemistry and computational methods have advanced to overcome the misleading effects of convergent evolution. The discovery of DNA as the carrier of genetic information (Avery-MacLeod-McCarty) gave the field of evolutionary biology a physical focus of study. The recent development of feasible nucleic acid sequencing methods allows evolutionary biologists to obtain the genetic code of entities of interest.

On the other hand, the rise of scientific computing permits to trivially store and manipulate hundreds of such sequences with thousands of bases each. Of particular interest in the context of reconstructing cultural evolution is the development of dedicated models and algorithms to analyse data such as this.

Methods to build phylogenetic trees initially made use of deterministic methods to build trees according to certain optimisation criteria, such as minimising a deterministic measure of evolutionary distance (eg. the number of differing base pairs in a molecular sequence). Given similar measures of cultural properties, the same algorithms can be used to infer cultural phylogenies, eg. board games [53] or folk tales [54].

Where sufficient data is available, theories and models – including phylogenetic trees created in any way – can be compared by how consistent they are with the data. This does require a well-defined measure of consistency of different models and theories.

Following the Bayesian interpretation of probability theory, probabilities quantify uncertainty in propositions and hypotheses. As such, it makes sense to talk about the probability of non-repeating events, even those in the past, or the truth of a hypothesis [140]. Probability theory thus provides a language to express consistency with given data quantitatively. In addition to then choosing one model that maximises consistency with the data, Bayesian methods enable researchers to specify a model that incorporates uncertainty, and to infer results that include a well-defined measure of confidence.

An important property of probabilities is given by a theorem named after Thomas Bayes (1702–1761), stating that

$$P(M|D) = \frac{P(D|M)P(M)}{P(D)} \tag{7.1}$$

In the context of reconstructing evolutionary histories, this theorem states how to obtain the *posterior probability* $P(M|D)$, the specific measure of consistency, of a model M, which implements some hypotheses, after taking the data D into account. It states that $P(M|D)$ is can be calculated using other quantities.

The first required quantity is the *likelihood* $P(D|M)$ of the model, *i. e.* the probability that this model produces the given data. There are computational methods, such as approximate Bayesian computation, to obtain good estimates of $P(D|M)$ when direct calculation is not feasible. In many cases, including those given in this chapter, $P(D|M)$ can however be calculated directly.

The second quantity needed is the *prior probability* $P(M)$, an a-priori estimate how consistent the model is with other knowledge. If the choice of $P(M)$ does not reflect background knowledge appropriately, the conclusions from the Bayesian inference process can be misleading .

Equation (7.1) involves a third quantity, the *marginal likelihood* $P(D)$. While $P(D)$ is very hard to estimate, it only depends on the data and is thus a normalising constant across all models M.

This framework is applicable to stochastic modelling of a variety of cases. For example, Kandler and Shennan [141] use stochastic modelling on an analysis of cultural artefacts, namely archaeological pottery finds from the neolithic Linear Pottery Culture. They show that it is much more consistent with the data to assume that rare stylistic variants are copied more frequently, than to assume that all variants have equal chance to be copied, or even that frequent variants are copied over-proportionally.

One particular application of Bayesian inference is however very present in both evolutionary biology and linguistics. Given a specific phylogenetic tree structure with branch lengths and a substitution model, it is mathematically straightforward to calculate the probability that it gives rise to the real sequence data, and therefore the (unnormalised, up to the factor $P(D)$) probability of the tree under the data. The calculations for any general tree can not be expressed in explicit terms, so inferences about derived statistics are not possible through analytical methods. Furthermore, the space of all possible trees with all possible branch lengths is however unfeasibly large. It is thus also impossible to generate trees at random and expect to get reasonable insight into the models with high posterior probability.

Instead, there are algorithms (in concept going back to an article by Metropolis *et al.* [142]) that randomly walk the parameter space, making steps towards those configurations that are more probable more often. This generates a Markov chain which can be used for Monte Carlo sampling, because its stable state distribution is precisely the posterior distribution of the parameters.

Today, standard tools [143–145] take prior distributions of model parameters such as tree shapes, change rates and population sizes, and use Markov chain Monte Carlo (MCMC) sampling to generate a representation of the model's posterior distribution, under consideration of observed facts. An overview of the history of Bayesian inference for biological phylogenies can be found in [146]. Few of these algorithms and models do specifically rely on sequences of four particular nucleotides, and can therefore be applied to other evolutionary processes, such as the evolution of language [147].

7.1 Reconstructing language evolution

Gray and Atkinson [148] showed that Bayesian methods can indeed be used to give arguments to long-standing linguistic debates. The publication led to a wave of indignation among professional linguists, because the article's results claimed to settle a famous controversy in Indo-European linguistics, but unfortunately the conclusions lay counter to the majority opinion in the academic field.

The debate concerns the origin of the proto-Indo-European (PIE) language, which is the reconstructed common ancestor of most European and many south Asian languages.

Conflicting hypotheses exist concerning both *when* and *where* original PIE speakers were located. The two main contestants are the following. Either PIE was the language spoken around the 4th millennium BCE by peoples in the Pontic-Caspian steppe, who were the first to domesticate the horse [149, 150]. Alternatively, PIE is assumed to have been spoken in Neolithic times (ca. 7000 BCE) in Anatolia, associating the expansion of Indo-European languages with a different technological advantage, namely the neolithic revolution of the spread of agriculture [151].

Traditionally, linguists reconstruct ancestral languages through the *comparative method*. Given two languages that are supposed to be related by descent from a common ancestor, similar words and morphemes – sub-word constituents of meaning – in the two languages are assembled and compared. If the differences can be explained by systematic sound changes from a postulated common ancestor, the words are considered *cognates*, and the genetic relationship between the languages is established. The first set of such sound changes explaining the rise of a present language from an ancestral one was found by Rasmus Christian Rask (1787–1832) and Jacob Grimm (1785–1863). It is widely known as Grimm's Law, and describes how fricatives ("f", "th", German "ch") in the Germanic languages developed from stops ("b", "d", "g") in a common ancestral language with Latin, explaining cognates such as (en.) "father" and (lat.) "pater". There are some attempts to use algorithmic methods [152] to make the process of cognacy judgement and ancestral reconstruction more explicit, better reproducible or less laborious. But the majority of trusted cognacy judgements come from experts in diachronic linguistics, who study and compare the development of languages through time. Knowledge about likely and unlikely sound changes, shifts in meanings, or the effects of internal morphological changes and language contact is not easily codified and highly relevant in the application of the comparative method. Cognacy judgements thus require enormous linguistic expertise.

Swadesh [153] suggested the idea of *glottochronology*. As explained by Lees [154], the method works as follows.

> If (1) the morpheme inventory of a language, or a definable portion of it, is observed over a span of time, and if (2) the individual members of the inventory at a given time are identified as cognates of members at some previous time, and if (3) some statable [*sic*] regularity can be found in the time-rate at which members disappear from the inventory to be replaced by new items, then the number of items in a certain subset which are present at any one time can be used as a measure of time elapsed since some previous time-point for which a similar count is available.

The truth of each of these three premises has however been doubted. Swadesh originally presented a list of 225 meanings, and revised and changed the list of what he considered the core vocabulary, the definable portion of language available in every language. But he did review this list over time, to arrive at a shorter list of 100 entries. A later analysis of Arabic dialects [155] doubts that even the 100-word list Swadesh arrived at later is a well-defined portion of language. The clear identification of cognates is also doubtful, because the underlying linguistic expertise makes results not easily reproducible. The most well-known criticism, e. g. due to Bergsland and Vogt [156], is however casting doubt on the fact that fundamental vocabulary does change regularly. Instead, detailed data analysis has shown vastly different rates of change.

Dating languages according to a purely linguistic basis is therefore hard [157]. Additionally, the reconstruction of ancient language relies on reconstructions of later languages. Instead, linguistics can establish relative dates, for example by establishing when a word was borrowed from or to another language, or by establishing what sound changes have affected a word for an innovation. For example, words for wheeled transport can be reconstructed for PIE, establishing that PIE was spoken after the invention of the wheel. While not all linguists accept the validity of these reconstructions, this is widely seen as evidence for the Steppe hypothesis [158].

In their paper, Gray and Atkinson [148] use a more complex glottochronological model. Because the model infers variable rates, the core criticism against the premise (3) does not apply, and the Indo-European languages as well-studied and closely related languages make the points raised against premises (1) and (2) less relevant. Their results support the Anatolian hypothesis. Because both the method and the result run counter to the majority opinion of linguists, it is no surprise that a large number of linguists criticised the prominent article. Interestingly, we find that much of the criticism focuses on the underlying data and the results obtained. The actual Bayesian methodology and the internal assumptions of the model are far less prominently examined, although from a modelling perspective their critique might prove far more insightful. Similar models have since been used to investigate the origins of other language families [159, 160]. Methods for more detailed analyses, eg. by including geographical [161] or deeper linguistic evidence [158] have been applied to the Indo-European phylogeny, improving phylogenetic models to correspond better to linguistic evidence.

However, so far, computational phylogeny of languages is most often inferred from lexical data. That is, the data is based only on individual words, instead of also incorporating grammatical (or even semantic or pragmatic) information. It is heavily criticised for this in the linguistics literature [157]. Beyond lexical data, the comparative method can to a large extent also reconstruct morphemes, and thus morphological aspects of grammar. For those cases where cognate morphemes can be established, handling them would be very similar to handling cognate words. However, when we go beyond vocabulary, functions which in some languages may be taken by bound morphemes may be expressed through separate words or even syntactical structures in other languages[1]

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[1] For example, possessive expressions use the bound genitive morpheme "-'s" in English, whereas French uses the separate word "de", and in Hungarian, the possessor is not marked at all. *cf.* [162]

As a consequence, this type of evidence cannot easily be described in terms of finite-valued features (as it is eg. for enumerating the groups of cognates representing a lexical meaning). This makes grammatical reconstruction difficult to formalise in computational models.

Typological information, *i. e.* data about structural and functional features, appears so far not to have been used in Bayesian inference studies. There are two reasons for this. On the one hand, compared to lexical change, it is far less obvious how typological change proceeds in languages [163]. On the other hand, the phylogenesis of typological features appears to be different from the lexical phylogenesis. Many languages are postulated to retain typological features of a substrate language, which was of lower prestige or power than and therefore replaced by a superstrate language [47].

In the following, we will discuss the methodology of using computational tools to reconstruct language phylogenies in some more detail, before focusing on the specific application of the evolution of typological features.

7.2 Phylogenies of Languages with Beast 2

BEAST 2 [143] is an extensible open source application for Bayesian inference of phylogenetic trees. The core of the software includes an implementation of Monte Carlo sampling of a Markov chain (MCMC), which is constructed in such a way that its steady state distribution is the posterior distribution $P(M|D)$ of the models considered. It contains the operators, priors and likelihood functions necessary for various inference tasks of phylogenetic trees from biological sequence data. In addition to functionality specific for biological data, Beast 2 also contains more generic models, such as classes and methods for a binary covarion model of character change. The precise family of models which Beast analyses is defined through a template-based XML format, which can also be generated by the separate application BEAUti. A package management system allows the community to write new models, operators, functions and so on. These extensions can be independently published and directly installed into the system, without requiring a new release of the core application. An in-depth introduction to the software and its use has been compiled by Drummond and Bouckaert [164].

The generic models of Beast, and similar programs by other authors, can be applied to appropriately preprocessed linguistic data. Genetic information persists in the form of a well-structured physical entity, the DNA, which can be represented as a linear sequence of four different characters (the four nucleobases cytosine (C), guanine (G), adenine (A), and thymine (T)) By contrast, the sequential structure of linguistic data when considering spoken or written corpora has long-distance structures and a much higher complexity than strands of the DNA. This structure is unsuitable for current models of evolution. Any reduction to the presence and absence of certain features is however a vast simplification, losing a large amount of potentially relevant information.

In most data-driven studies of the phylogeny of languages, going back to Swadesh [153], the traits the analysis is based on are an encoding of the presence or absence of words of a certain cognate type for each language [158–161, 165]. This includes a recent article by Chang *et al.* [158], in which the authors argue for a specific encoding which takes the (possibly reconstructed) meaning of the considered word into account. The article goes into more detail concerning the implications of modelling choices, and carefully compares the results of a few different modifications to the model.

In addition to providing linguistic and theoretical evidence for their model choices, Chang *et al.* have published their configuration files for the predecessor of Beast 2, thus allowing us to reproduce their results. We build upon their lexical-data based study.

We have translated the configuration file for their B3 model to Beast 2, and implemented the `BranchLengthPrior` class necessary for the ancestry constraints they introduce.

The model presented in [158] is as follows. The data is given in a trait matrix. Each entry of the matrix encodes the presence (1) or absence (0) of a word from a cognate class with a specific meaning for some language. If the underlying data set, taken from the cognacy database IELex by Dunn [166], does not contain a word for some pair of language and meaning, all corresponding cognacy cells are marked as unknown (?). Words tagged in IELex as known loan words are encoded as absent (0) in the trait matrix. If a language contains words of the same meaning in different cognacy classes, all of them are marked as present (1), as shown in Table 7.1.

Trait	X	Y	Z		X	Y	Z
English	feather				1	0	0
Friulian	pene	plume			1	1	0
Spanish		pluma		→	0	1	0
Greek	ftero				1	0	0
Persian			par		0	0	1
Hittite					?	?	?

Table 7.1: Words from IELEX for ‘feather’ (left), coded as a trait matrix (right). The competing forms in Friulian result in an overloaded slot. The lack of a form in Hittite yields an empty slot; each corresponding cell, marked ‘?’, is a hidden cell. *Reproduced from Chang et al. [158]*

The phylogeny is assumed to be a binary tree. Established knowledge of the phylogeny of Indo-European languages, such as Latin as the most recent common ancestor of the Romance languages and no other language, are encoded through hard constraints on the shape of the tree.

The model assumes that trait data is generated along the tree according to a binary covarion model, a continuous time Markov chain in which characters randomly switch between periods of stability and of change. The rates of change are assumed to be

$$\rho_{ij} = \rho_0 s_i b_j \tag{7.2}$$

where ρ_0 is a primary parameter of the model, s_i is gamma-distributed over the cognacy-meaning classes (columns of the matrix) with mean 1, and b_j follows a log-normal distribution over branches of the tree. The model therefore also infers the posterior distributions of these parameters.

Where the age of an ancestral language is known, a prior on this date is included in the model. This serves to infer the clock for the model. Otherwise, any rescaling of the base rate ρ_0 and the branch lengths in the tree by reciprocal factors would yield an equivalent tree.

The tree is assumed to follow a coalescent prior with a population parameterised through a Bayesian skyline plot. A coalescent tree prior [167] assumes a certain distribution of trees. The distribution is consistent with assuming that the population evolves according to a generalization of the Wright-Fisher model [31], in which the population of each generation is drawn randomly from the previous generation. The skyline plot [168] is one method of inferring the population size along the tree in a Bayesian way. The model by Chang *et al.* uses a stepwise function in the skyline plot [169], while Beast2 natively only supports linear interpolation for skyline plots. We therefore deviate from their reference in how population sizes are estimated[2].

Reproducing the study with this modification, we obtain the maximum clade credibility tree shown in Fig. 7.1. A clade is the set of a most recent common ancestor and all its descendants. The maximum clade credibility tree is the tree such that the product of the posterior probabilities of all its clades is maximal. That is, each node x in the tree is scored by the probability that, in a random tree drawn from the posterior distribution, the descendants of x and all their most recent common ancestors form a clade.

The posterior distribution of root height is shown below in Fig. 7.2b. The change in the tree prior leads to a wider spread of the posterior distribution for the age of the tree root compared to the corresponding distribution given in [158], but while the 95% estimate for the root height goes significantly up, the median of our posterior is actually lower than given by Chang *et al.*

The posterior distribution for the root height from our replication of [158] is given in Fig. 7.2b.

Having introduced the reference model and methodology which we use to reconstruct language evolution, we now add a way of including non-lexical data into models for

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[2] Two further issues in the translation from classical BEAST to Beast 2 are marked in the XML file. They do however concern operators, which, while affecting the short-term behaviour of the Markov chain, have no influence on its limit behaviour, as long as the same states can be reached.

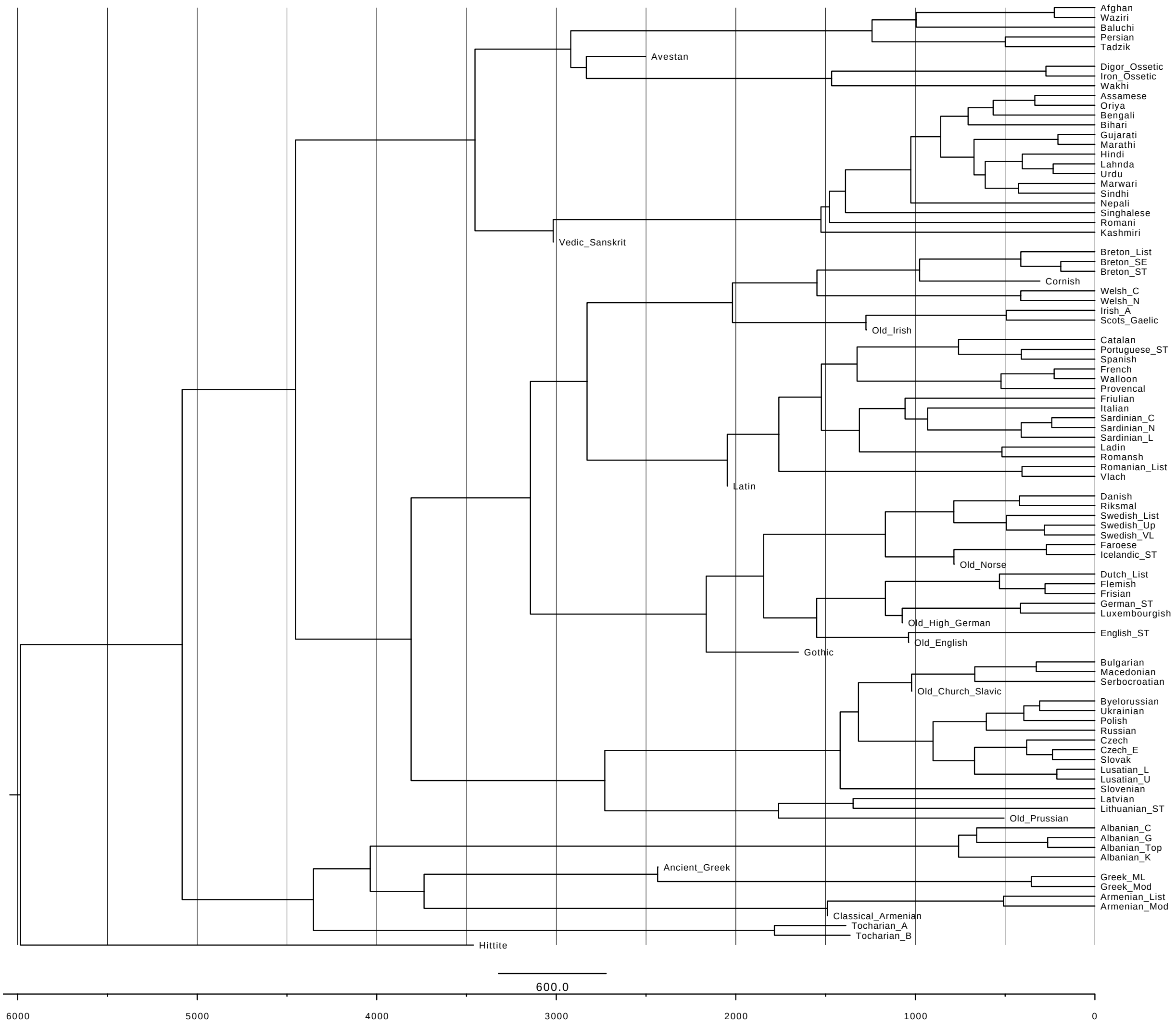


Figure 7.1: Maximum clade credibility tree from a replication of Chang *et al.* [158, B3] with linear Bayesian skyline prior for population sizes along the coalescent tree.

the reconstruction of language trees. We present a Beast extension for non-independent evolutionary traits, and use it in a preliminary analysis of a simple model of the evolution of word order.

7.3 The evolution of Typological Features

The similarity between cognate words, induced by slow, systematic sound changes, allows linguists to classify languages into genera, families and macro-families by reconstructed common ancestry. There is however an orthogonal way of language classification, which uses the formal characteristics they share. The field of linguistics engaged in this outlook is known as *typology* [163, 170].

Among all possible characteristics that could be studied, there are formal properties shared by all languages. For example, all languages have constituents fulfilling the roles of subject (S), verb (V) and object (O). Statements of this nature are referred to as *absolute universals*. These constituents could *a priori* appear in any of 6 different orders. It is however the case that most languages have a single dominant order of these three constituents. Additionally, some of those dominant constituent orders are much rarer among the languages of the world than others [171]. The fact that SOV and SVO are far more frequent than any other possibilities of constituent order is a *statistical universal*. In addition to these two types of universals, there are *implicational universals*. For example, every language in which the verb is the first constituent in the dominant word order has prepositions (such as "*in* 2010"), not postpositions (such as "five years *ago*") [163]. This universal has no known exceptions, but it does not say anything about languages that do not have the verb as first constituent.

These formal traits of languages are obviously relatively stable, but subject to change. In fact, Greenberg [172] argues that synchronic regularities – implicational as well as statistical universals about languages at a fixed point in time – can be explained as artefacts of absolute universals about language change. By extension, the exceptional cases for merely statistical universals can often be explicitly understood as languages that are currently in the process of transition from one more likely state to another.

The structural constraints given in linguistic universals is therefore very helpful in understanding fundamentals about human language. On the other hand, this implies strong correlations between typological features of languages, raising a methodological obstacle for the computational analysis of the evolution of typological characters.

Just as in the case of cognacy judgement, typological classification requires linguistic expertise. The World Atlas of Language Structures (WALS) [173] is a database of typological features collated by 55 experts under the curation of Dryer and Haspelmath of the Max Planck Institute for Evolutionary Anthropology in Leipzig. While it is far from complete and beyond doubt [174], it provides a good knowledge base in particular for well-studied features of common languages. WALS has been used in the past to study the speed and structure of typological innovation with consideration of reticulate phylogeny by Greenhill *et al.* [175]. But that study did not use Bayesian inference on the typological features, and furthermore did not take the correlation of characters into account in their model.

In this section, we will employ a method based on the reversible jump Monte Carlo method introduced by Huelsenbeck, Larget, and Alfaro [176] and extended to study correlated characters by Pagel and Meade [177]. In pursuit of establishing the viability of this method for the study of the evolution of typological features, we want to concentrate on a logically obvious "universal". Specifically, we base our analysis on the dominant order of the constituents S, V and O in Indo-European languages.

We encode the dominant word order in three features. The first feature contains the order of subject and verb, and can take the values *SO*, *OS*, or *SO?* for "No dominant order of S and O". Missing data is encoded as - and denotes that this slot should not be used in the inference, and is thus different from *SO?*. Similarly, the second feature encodes the order of verb and object as *OV*, *VO*, *VO?* or -. The third feature specifies the full constituent order, and takes one of the values *SVO*, *SOV*, *VSO* or *SVO?*, or denotes that the value is missing from WALS.

The other three possible word orders, where O comes before S, are not attested in the Indo-European languages. This is not surprising, because the scarcity of OS languages is a strong statistical universal. The logical implication between the third feature and the first two features will allow us to evaluate the consistency of the method without having to rely on a linguistic universals result which might accidentally be statistical with exceptions in the history of Indo-European.

7.4 Model and Data

WALS contains data on 176 Indo-European languages and dialects. Of these entries, 69 contain data on the order of SVO, SV and OV, and a few additional languages have entries for SV and OV, or OV only. This list is not in direct correspondence with the 97 languages given in the B3 Model given by Chang *et al.* [158], even after accounting for different names for the same language in both. Among other things, WALS only includes recent languages, while the cognacy data set used in [158] includes attested words from extinct languages. The WALS chapter by Dryer accompanying the data [171] does however remark on the word order in some ancient languages. For those languages where the relevant data was given in WALS [171, 173], we took the data given there. For all other cases, the corresponding data was encoded as missing.

In the resulting matrix, 19 languages of the 97 languages are missing all three entries, one language has no entry for the SOV order, but is known to be SV and OV otherwise, and 22 languages lack entries for SV and OV.

We cannot assume that the frequencies we observe in the recent languages are representative of the general frequency of these typologies among all languages, or even in the tree of the given Indo-European languages. The true distribution is therefore another unknown parameter, which needs to be estimated. In absence of other influences such as sampling bias, the observed frequencies would derive from the true underlying distribution of typologies naturally through a multinomial distribution. A conjugate prior of the multinomial likelihood is a Dirichlet distribution. This means that for a Dirichlet prior on the parameters of the multinomial distribution, the posterior probability will again be Dirichlet distributed. We thus assume that the frequencies of the different compound traits follow a Dirichlet prior. From the data points present, we obtain the parameter values of this prior as $\alpha_i = n_i + 1$, where n_i is the observed frequency of compound trait i. Because some $\alpha_i \neq 1$, this results in a non-flat Dirichlet prior.

We assume that, as a combination of the three traits goes along a branch, it can instantaneously switch to a neighbouring state, where only one of the three traits differs, according to a constant rate. This implies the existence of some self-inconsistent states. We will comment on this below in Section 7.6. The instantaneous transition matrix is therefore a sparse 36×36 matrix with 7 off-diagonal entries in each row. These entries are parameters of the evolutionary model.

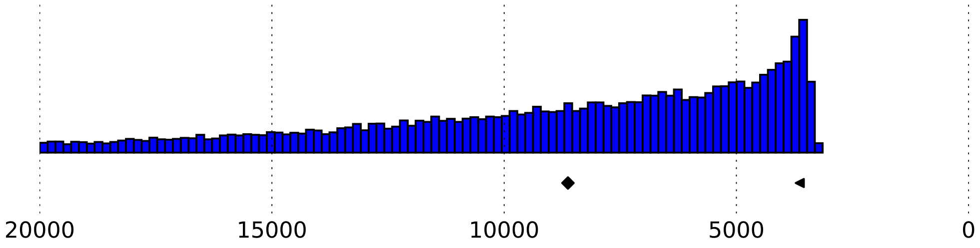
Using a technique similar to that employed by Pagel and Meade [177], we reduce the number of possible rate parameters. The jumps between different groupings of the rates will however be automatically reversible, because we continue to track the unused parameters, their prior probabilities etc. Making the ansatz that the system has essentially 4 logically consistent states, we assume that all transitions are of one of three types. Either (1) a transition governs the rate between two of these consistent states. There can a priori be 12 different rates of this type, from each consistent state to each other consistent state, or (2) a transition is consistency-regenerating, that is, it leads from an inconsistent state towards a consistent state at high rate, or (3) it occurs at 0 rate. We therefore reduce the maximum number of different rate parameters to $4 \cdot 3 + 2 = 14$, one of which is fixed to be zero. Individual rates are assumed to be uniformly distributed over these 14 rate classes.

Typological features are assumed to be more stable than cognates. This means that understanding the evolution of typological features may expand the depth to which we can make inferences about ancestral languages.

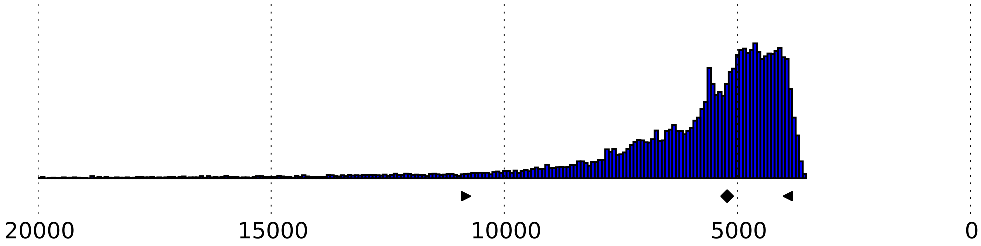
Past research has shown that word order features may be among the most stable linguistic features [175]. According to their analysis, word order properties are about twice as stable as basic vocabulary items. In our augmentation of [158], we therefore choose a similar gamma prior for typological substitution rates to that for word-meaning substitution rates. But to reflect the higher stability, we increase the rate parameter β of the gamma distribution of typological rates by a factor of 2. The mean of the typological substitution rate prior is therefore half the mean of the word substitution rate prior. This prior applies to the 13 rate categories (bar the last category, which is constant 0), not weighted by the number of rates assigned to each category.

7.5 Results

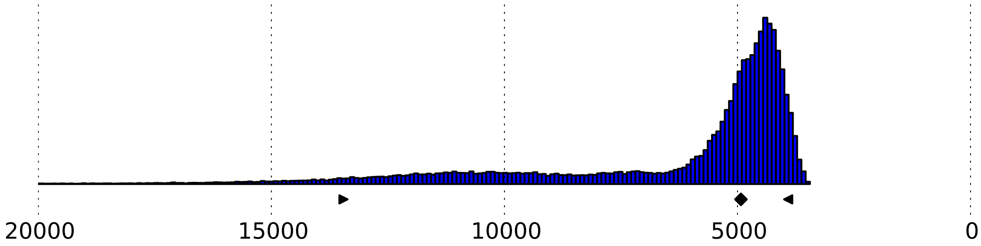
Our model adds an alignment with 189 data points (each specifying a value out of 3 or 4) to the model, as well as prior distributions obtained from the structure of the same



(a) Prior distribution of root heights.



(b) Posterior distribution of root heights without evolution of typological features.



(c) Posterior distribution of root heights with evolution of typological features.

Figure 7.2: Distributions for the age of the most recent common ancestor of the supplied Indo-European languages in a replication of Chang *et al.* [158, B3] with linear Bayesian skyline prior for population sizes along the coalescent tree. Symbols mark the 5%, 50% and 95% quantiles.

underlying data set combined with other prior knowledge that is already contained in the model. It attempts to infer 288 more posterior distributions (252 rates and 36 frequencies to be estimated) than the reference model.

We obtain the posterior distribution of the root height, *i. e.* for the age of Proto-Indoeuropean, which is shown in Fig. 7.2c. Most of the weight of the posterior is concentrated on ages less than 5000 years. This is in contrast with both the results reported by Chang *et al.* [158] and our replication thereof, and even further away from the prior distribution, which has its median at 8903 years in the past, than either of these. On the other hand, the distribution has a longer tail, with notable probabilities up to 13000 years in the past.

The mean of the estimated frequencies of the compound typological states is shown in Fig. 7.4b. The model does follow the prior in assigning higher probabilities to the states

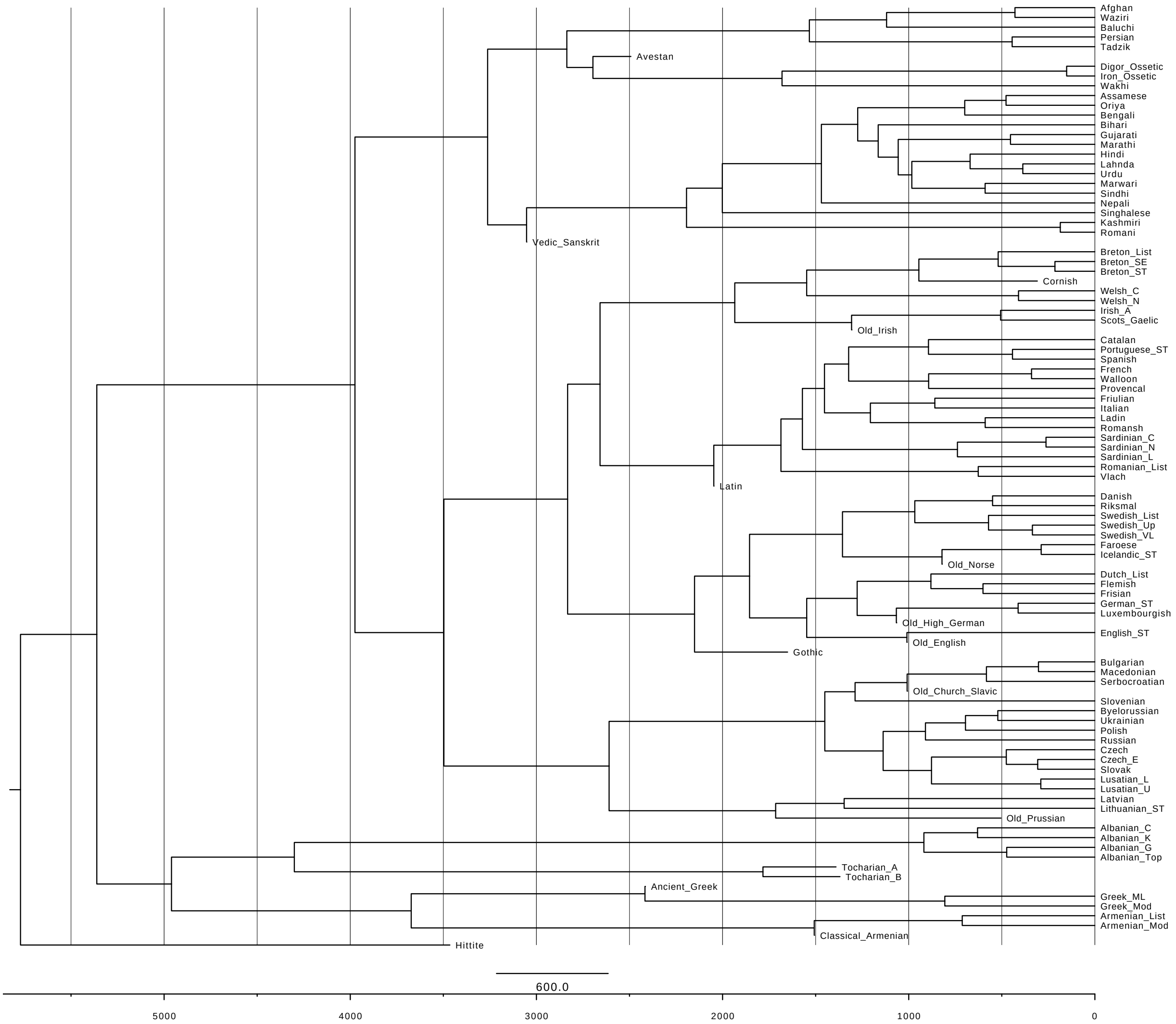


Figure 7.3: As Fig. 7.1, but with evolution of typological features.

observed more often. In addition, we see that the impossible mixed states, in particular $SOV/VS/OV$ and $SVO/SV/OV$, have become more rare. The actual real states $VSO/VS/VO$, $SVO/SV/VO$, $SOV/SV/OV$, and the plausible combinations with “No dominant order” on the other hand are more frequent in the posterior than in the prior. A miscoded combination of $SVO/VS/VO$ present in WALS has decreased in probability, whereas another one, $SVO/None/VO$ is assigned a higher probability under the posterior than under the prior. While the order of subject and verb can be deduced from the general dominant word order, the latter combination is a much more reasonable mistake than the former.

We therefore conclude that the model was able to deduce the structure of the underlying data to a large enough extent to warrant a closer look at the posterior probabilities deduced for the rates of change. We observe that more than 165, or roughly two thirds of the rate parameters are in the 0 class less than 3% of the time, while the other 87 parameters were assumed to be 0 at various times, most of them in ca. 1/3 of all Monte Carlo steps.

The maximum likelihood rate matrix (Fig. 7.5a) shows a wide spread of rates. Many of the high transition rates ($\rho > 2 \cdot 10^{-5}$), which are depicted in Fig. 7.5b, lead to one of the consistent states.

One transition that is frequently observed in the data is from SOV to SVO, as seen in the Romance languages, as well as from Sanskrit to Kashmiri. There are two shortest paths for this complete transition in our model. Either $SOV/SV/OV$ switches to $SOV/SV/VO$ first before relaxing to $SVO/SV/VO$, or the global reordering towards $SVO/SV/OV$ occurs first. For the maximum likelihood matrix, we see that the former path (via $SOV/SV/VO$) happens at a rate of $3.27 \cdot 10^{-6}$ transitions per year, while the other path is more than three times as likely, at $1.01 \cdot 10^{-5}$ transitions per year. The path in which the transition $SOV \to SVO$ occurs first is generally more probable than the path where $OV \to VO$ occurs first. The posterior distribution assigns 90% probability to a quotient of rates of ≈ 2.4, and low probabilities to some other rates, including to the one in the maximum likelihood.

For the maximum likelihood matrix, we sort the paths from SOV to SVO by their cumulative rate (*i. e.* $\frac{1}{1/r_1+\ldots+1/r_n}$ for the rates r_i of the intermediate steps) Four other (not disjoint) transition paths are more likely than the path via $SOV/SV/VO$. All of these involve states that describe “No dominant order” for at least one of the components, as shown in Fig. 7.5d. None of these paths leaves the SV plane. It is however noteworthy that two of these paths also make use of a high rate between the inconsistent states $VSO/SV/OV$ and $VSO/SV/VO$. This is not an exception, similar transitions occur for many other likely states of the Markov chain, as well.

In general, we see that the correlated substitution model is able to recover some features of the logical structure underlying the evolution of word order as a typological feature. In the mean, rates of change take values of less than 10^{-4} transitions per year, usually closer to 10^{-6}, showing that word-order typologies are indeed well-preserved under language evolution.

7.6 Discussion

We have applied a model originally developed for the evolution of correlated morphological characters of species to a logically necessary typological universal, and seen that the model can infer relevant features of the universal from scarce and partially miscoded data. Inferred transition rates show that word order features are typically persistent over long time, with changes happening over time scales of 10000s of years.

In view of apparent logical inconsistency of intermediate states, the model may seem to falsify itself *a priori*. [3] There are however obvious miscategorisations in WALS. The fact that it is hard to classify languages even according to such fundamental properties as basic word order shows that transient states, such as assumed in this model, may exist in reality and could be found by observant historical linguists. Given that we predict that the change $SOV \rightarrow SVO$ occurs before the change $OV \rightarrow VO$ in more than 2/3 of such transitions, we suggest that this hypothesis might be tested by considering sentences in late Latin without subject pronoun, to see whether they retain the object-verb order for longer than comparable sentences with a subject.

While typological features change only very slowly, the model does nonetheless predict a lower median age of the Proto-Indoeuropean language than a model incorporating purely lexical data [158]. It is possible that this discrepancy comes from us still overestimating the rate of change of typological features: if the prior distribution assumes rates of change that are too high, the expected times between changes will be shorter, which leads to a younger root age of the inferred tree for the same data. To resolve this and adjust the prior, we would need more evidence about the speed of language typology evolution from other sources. The core of the posterior distribution under inclusion of the typology of dominant word order is much narrower than for the same model excluding structural data. While the posterior shows a longer tail for the age of PIE, this can be understood as overfitting the high parameter count, such that the behaviour of the prior distribution of root height has as stronger influence on the posterior. The analysis therefore shows that typological data will be helpful in constructing and dating phylogenies of languages.

In addition to typological data, a there is a second property of language evolution that is still widely neglected in computational attempts to reconstruct phylogenies of languages. Language evolution is in many cases highly non-vertical. Specifically, borrowed words are ubiquitous in languages around the globe. More generally, language contact [47] is an important topic in linguistics [178]. But true reticulate phylogenies lead to artefacts and therefore incorrect inference when models assume a tree structure. For example, the tree obtained will depend on an (explicit or implicit) weighting of the data chosen, and included borrowings will lead to artificially long branches, because the expected time for the corresponding innovation is far longer than the time the borrowing takes.

Bayesian methods for inference of phylogenetic *networks* (as opposed to trees) are, however, still in their infancy. Such methods are being developed, eg. for the application to strains of bacteria and viruses that show high recombination, or for other organisms where hybridisation is a suspected relevant evolutionary event, but there are conceptional challenges. The space of reticulate phylogenies is far larger than the space of phylogenetic trees, because the latter are a special case of the former. Networks have more free parameter values. Likelihood functions are therefore more complex to calculate, and need

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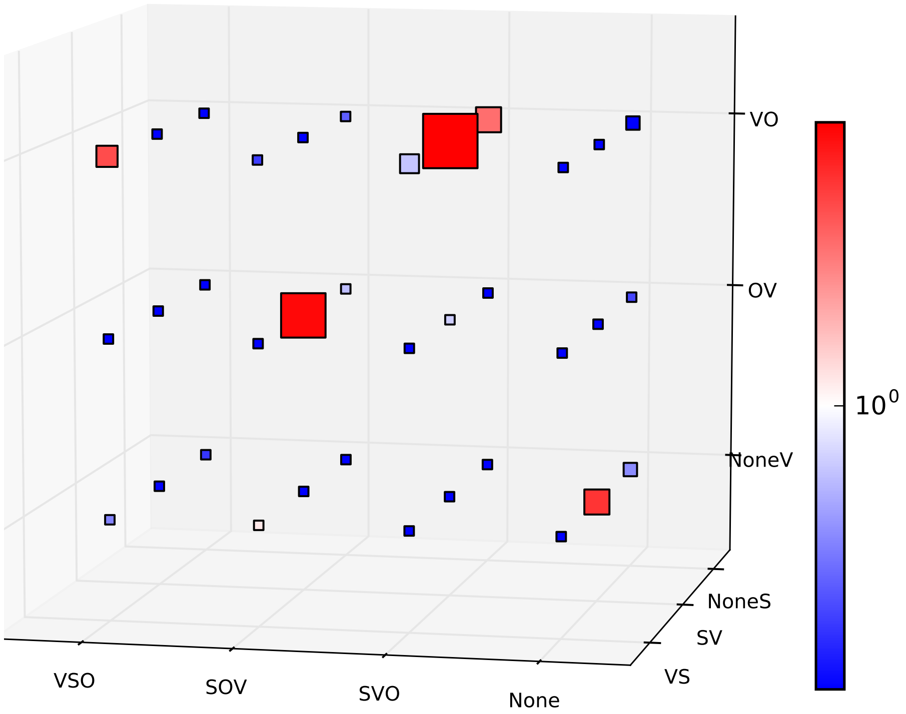
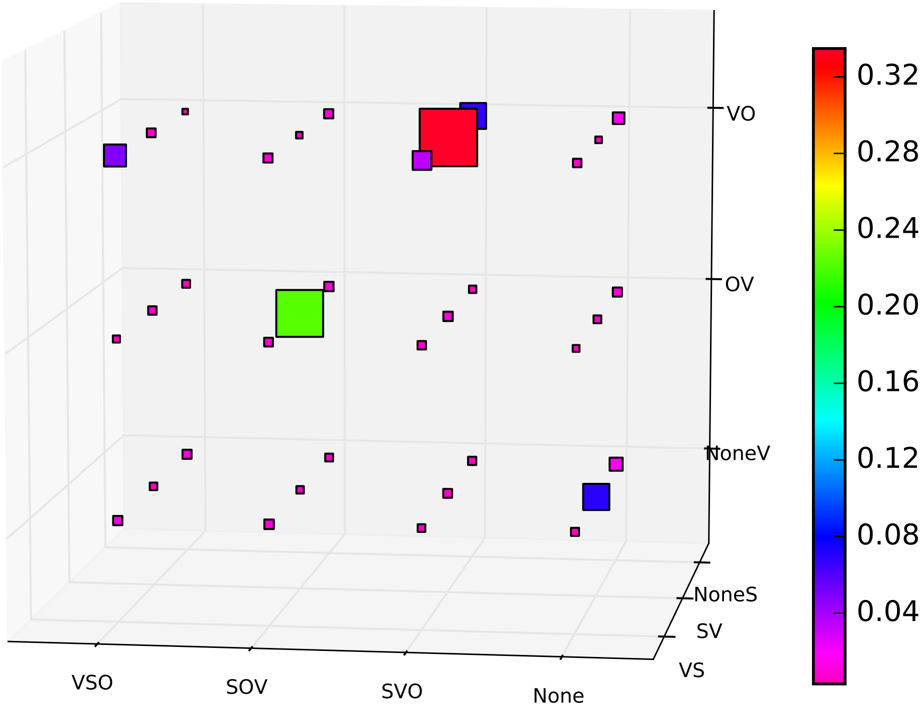
[3] It will thus no doubt contribute to the ongoing debate in the field, where both computational modellers and historical linguists each accuse the other of lack of science.

to be constructed to avoid over-fitting. Maximum-likelihood methods, such as presented by Yu et al. [179], avoid some of this complexity, but cannot give insight into the uncertainty of the results. There are methods for Bayesian inference of reticulate phylogenies [180, 181], but they generally require the use of data such as genomic sequences that is not applicable for linguistic data.

Future work should therefore investigate how methods for reticulate phylogenies can be applied to the evolution of language, or develop new such methods. In combination, typological and network-based methods should also be able to answer other hard questions of the evolution of language, such as discerning whether special features of Germanic languages can be explained by contact between Indo-European languages from different branches, between an Indo-European superstrate replacing an older substrate, or something else.

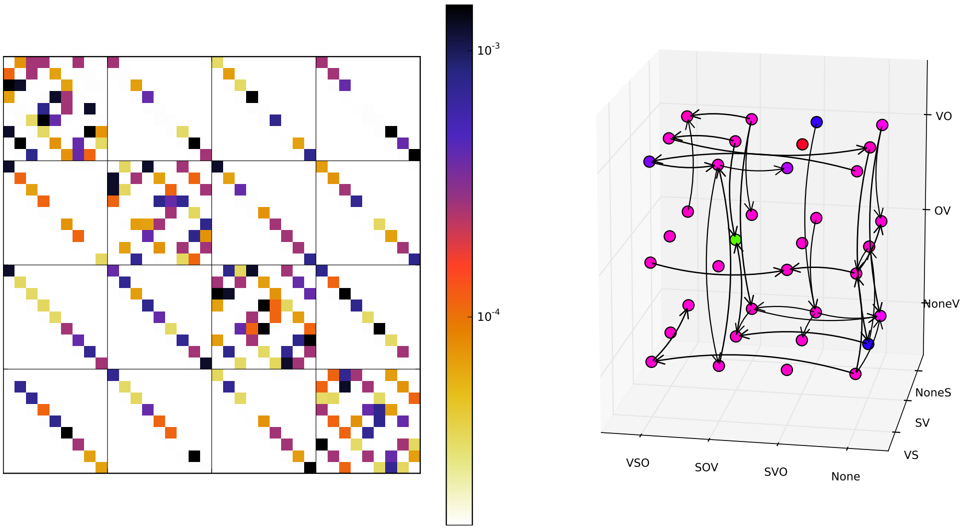


(a) Mean of the of the Dirichlet prior (1+observed cases according to WALS, normalised to sum to 1). Colour marks the relative change to (b), red means the MCMC assigns a higher probability than the prior.



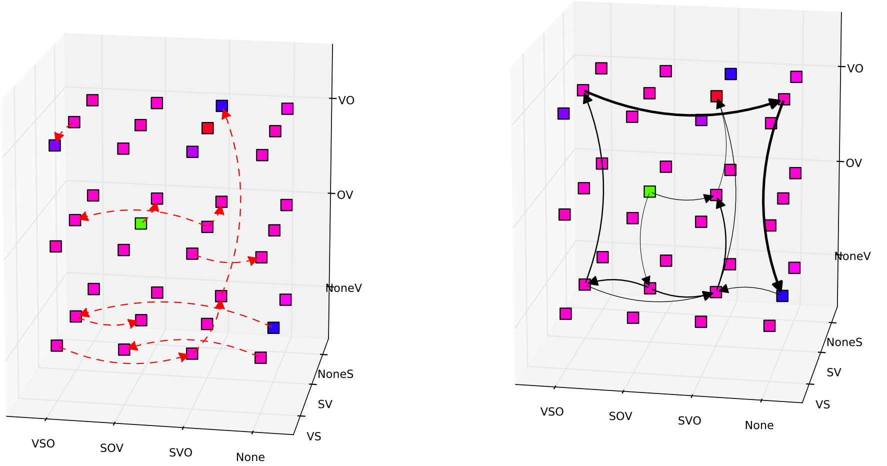
(b) Mean of the posterior distribution generated by the MCMC. Colours also denote frequency.

Figure 7.4: Distribution of compound typologies of Indo-European languages. The area of the dots is proportional to the frequency of the corresponding state.



(a) Maximum Likelihood rate matrix

(b) The top 40 highest transition rates in the maximum likelihood matrix



(c) The transition rates set to 0 in the maximum likelihood matrix

(d) The transition rates of the most likely paths from $SOV/SV/OV$ to $SOV/SV/VO$ according to the maximum likelihood matrix

Figure 7.5: Maximum likelihood transition rates matrix for typological features. All arrows are unidirectional and go counter-clockwise, so there is eg. no high transition rate from $SOV/SV/OV$ to $SOV/SV/None$, and the rate from $SOV/None/None$ to $SVO/None/None$ is positive. Colours as given in Fig. 7.4b

Chapter 8

Discussion

In this thesis, we have investigated two questions from evolutionary anthropology. We have contributed insight to the puzzle of cooperation and punishment and the evolution of languages, using methods and computational models from theoretical biology. In the process, we have investigated the assumptions and components underlying these models, and identified problems and further applications of stochastic computer simulations in this theoretical field.

We have applied computational modelling to four specific questions from the fields of socioecology and diachronic linguistics. Our main contributions and results are as follows.

- In Section 2.2.2, we have considered an abstract game theoretic model of grammatical typology proposed by Komarova, Niyogi, and Nowak [41]. Our results show that a dominant language is more resilient to learning errors and more frequent when selection primarily weeds out maladapted individuals, instead of promoting well-adapted ones.
- In Chapter 4, we have replicated previous results showing that group selection can support cooperation, and extended prior knowledge by showing that this also holds for across-group selection of individual agents, even for populations incorporating high randomness.
- In Section 5.1 and Chapter 6, we have seen that institutional punishers cannot emerge in the public goods game with punishment from supported peer punishers. Instead, pool punishment is a more complicated strategy that pre-supposes a fundamental difference in the payoff structure to the standard D, C, P set of strategies.
- In Chapter 7, we have used Bayesian computational models for phylogenetic inference from linguistic data. We have shown that the inference method can make use of highly correlated typological information, without *a priori* knowledge about the underlying linguistic universals.

8.1 Challenges of theoretical anthropology

In the process of this endeavour, we have encountered three major challenges that we would like to summarise in the following. These challenges concern (1) cultural differences in communicating methodology and results between mathematical and computational modellers on one side and anthropologists and linguists on the other side, (2) lack of attention to the "moving parts" in models of evolutionary game theory, and (3) a large number of variations and ad-hoc modifications between models of similar scope, which are passed without comment, often simplifying the mathematical analysis – and making it difficult for the reader to distinguish between changes leading to profound new results and those highlighting the lack of robustness.

8.1.1 Bridging between mathematics and anthropology

The ideal model would of course span the whole range between first principles and detailed real-world data, while still being simple enough to be understood and manipulated by the researcher. This is obviously unfeasible. Theoretical models can therefore generally be justified from one of two perspectives. Of course, no model is entirely one or the other, but this dichotomy is well able to illustrate some of the problems in the dialogue.

Either models show the implicit consequences of first principles. In this *top-down* approach, models tend to be abstract. The toolbox of evolutionary theory can outline what theoretical mechanisms are necessary or sufficient for the evolutionary emergence or stability of anthropological properties. But relating the outcomes of top-down models, as general propositions, to specific real-world anthropological situations is hard, because it may be disputable how the circumstances in reality relate to assumptions or parameters of the model.

Alternatively, models are built upwards from available data. In that case, the goal is to construct and check hypotheses that explain the available data in the best possible way. The purpose of the computational model is then to specify the hypothesis formally without ambiguity, and to generate the quantities necessary to ascertain how well the data fits the model. As such, a *bottom-up* model requires very good understanding of the data and its genesis.

Different measures of quality apply to top-down and bottom-up models. Where detailed models are checked against their consistency with data, be it through a direct Bayesian approach or through other statistical methods, top-down models need to be tested in terms of robustness of the results under small changes in assumptions. If a model is robust, the conclusions drawn from it hold approximately even if the reality of the underlying assumptions are not met exactly.

In both cases, simpler models are considered to have a higher explanatory value. This constitutes another reason for *initially* concentrating on lexical data in computational phylogeny models: If phylogenies can be robustly inferred using a smaller model with simpler data, other data can be assumed independent and be used to infer additional results. But a main criterion for quality in either case is the consistency with prior knowledge.

Anthropological and linguistic theories are based on the observation of real people and their cultures and languages, and as such they are generally bottom-up models in the sense given above. Researchers in these fields traditionally do not use mathematical formalisms or computer descriptions to capture the theories formally. Academics are only slowly beginning to consider mathematical, statistical and computational tools.

Nonetheless, other fields have greatly benefited from increased use of quantitative and mathematical methods to formalise and quantify hypotheses. We therefore concur with McMahon and McMahon [182] and the fundamental tenet in their book “Language classification by numbers”,

> ‘in which the authors suggest that using quantitative methods to test hypotheses and represent results may be a useful addition to comparative historical linguistics’

and assert that the same applies to anthropology.

We assume that this late adoption of numerical methods in anthropology is due to the complex but profoundly human nature of of the system studied, and not due to an inherent fundamental difference in the epistemology and philosophy of knowledge between human culture and (for example) ecology as a field of study.

8.1.2 The structure of models in evolutionary game theory

Both theoretical biology and evolutionary linguistics use computational top-down and bottom-up models. Formal theoretical bottom-up models in anthropology appear to be much rarer. This makes it even more important to consider the “first principles”, the general underlying assumptions, considered in top-down models of cooperation. In this work, we have identified components of these evolutionary game theory models. For some of these components, one or two different choices appear to make up the vast majority of models considered.

Firstly, a model describes an evolving population. This population has a structure that specifies who interacts with whom. In the simplest case, this is given by a complete graph. In many cases, the core interaction to be studied, *i. e.* the population structure relevant for the game, is the same as the reproduction population structure. The literature on evolutionary games in structured populations is ample (reviews can be found in [20, 89, 109]), but most models assume a static population of constant size. Only as of now do researchers extend their studies to dynamic populations. It has meanwhile been shown that population dynamics and different types of competition are relevant to the evolutionary dynamics of the model [32, 93, 94, 120, 183–185].

Secondly, a model must specify a game which characterises the interaction between individuals in a population. Interactions are characterised in terms of decisions for the individuals and numerical values ("payoffs") characterising the benefit or detriment of possible outcomes of the interaction. The core interaction to be studied by the model is given in terms of a game, which defines the payoffs for combinations of strategies actualised by the players. Formally [15], a game is specified by a set of players P, a pure-strategy set S_n for each player $n \in P$, and a payoff function $\pi : \prod_n S_n \mapsto \mathbb{R}^P$. Specifics of the game may vary without much comment, and the in- or exclusion of strategies may influence the behaviour through the implicit changes in the mutation matrix in addition to the explicitly intended changes.

But as a third component, the model develops in time according to some updating rule. Usual choices here are variants of the birth process and the link dynamics rule. Specific implementations vary however widely, in particular with respect to the transition from payoff to selection probabilities. As we have shown, even the subtle choice between BP, LD and DP can have a stark influence on the evolutionary dynamics of a model, and the choice between cutoff fitness and exponential fitness has a strong influence on the evolutionary dynamics, in particular for link dynamics. In the literature, an even wider range of translations from fitness to transition probabilities is given, often without further comment or consideration. Examples for constant population structures include

$$p(i \to j) \propto f_0 + \pi_j \tag{8.1}$$
$$p(i \to j) = \frac{1}{2}(1 + d_i - d_j) \tag{8.2}$$
$$p(i \to j) = \frac{1}{2} + \frac{w}{2}\frac{\pi_j - \pi_i}{\max_{kl}(\pi_k - \pi_l)} \tag{8.3}$$

where d_j is the frequency of defectors in the community j, in [42], [114] and [34] respectively. For variable population size, Huang, Hauert, and Traulsen [185] present an updating rule similar to the death process with constant birth rates and death depending on payoffs, while Powers and Lehmann [32] implement variable population sizes according to strategy-dependent growth rates, with death governed by a multi-strategy generalisation of the Beverton-Holt competition model. Given the high number of different 1-strategy competition models known in the literature already [183], updating rules for variable population sizes will require even more justification and analysis of robustness than those in constant populations.

8.1.3 Ad-Hoc simplifications

While there are a small number of frequently chosen options in evolutionary models, the literature also contains many examples of less prevalent variants that are applied without discussion about how the outcomes differ. Of particular note are modifications that simplify the mathematical analysis, while it is unclear that they do not oversimplify the model or alter the results obtained otherwise.

We have frequently argued in this thesis that one such simplification is the assumption of low mutation rates. When mutation rates are negligible, many models can be analysed explicitly by considering only those states where the population is homogeneous, and taking the fixation probabilities as transition probabilities between states, in particular where coexisting strategies or finite time spans are considered.

Another frequent example of ad-hoc simplifications is the use of average payoffs in models with high stochasticity, in particular with a link dynamics updating rule or exponential fitness functions, as seen in [27, 81, 107, 108]. Because the exponential function is convex, the mean of fitnesses derived from individual payoffs will be larger than the fitness derived from a mean payoff. This ad-hoc simplification will therefore put strategies relying on stochasticity, such as mixed strategies, at a disadvantage, compared to how they would fare if each individual action would be generated separately and give rise to an individual fitness. When mixed strategies are a focus of investigations (such as in [27]), the effect of this simplification must be considered very carefully.

In this thesis, we have pointed out and explicitly investigated two further opaque variations in models. We have shown that a "migration-like process that causes behaviours to diffuse from one group to another"[114] becomes a group-selection–like process for stronger selection between communities. We have also shown that pool punishment implicitly assumes the presence of a deeper institutional structure, which cannot easily be approximated by other strategies.

If theoretical biology wants to come to dialogue with anthropology, the justification for the models must change. Instead of relying on models that are easy to analyse mathematically, we must start justifying model choices from real-world principles, and include data that reflects the breadth of humanity [103, 186].

8.2 Further work

We have identified some badly justified choices in studies trying to solve the large and complicated puzzle of the evolution of cooperation. While some of our investigation aims to point out and fill these gaps, there are particularities which we have consciously or implicitly neglected. We do not consider exponential fitness the optimal solution for translating payoffs into fitnesses, and consider further investigations necessary in this domain.

The rise in computational power makes populations with demographic fluctuations accessible for stochastic simulations. These models have even more parameters that could be tweaked than constant populations, and make a careful decision for or against models of reproduction and competition even more important.

In view of reconstructing the evolution of typological characters in linguistics, the methodology is also still in need of improvement. The number of estimated transition rates, while lower than in a fully-connected model, is still very large, and without inner structure. A better model would explicitly infer the dependency structure of features. In that case, the model could be given a prior for this structure, and infer linguistic universals explicitly.

Beyond methodological questions, our research points to questions of a more contentual nature. In the models considered in this thesis, punishment reduces the fitness of the punished, and costs represent a significant risk to the punisher, either directly or in terms of the cost of maintaining an institution. In addition to these two types of punishment based on individual choice, economists and anthropologists have identified a number of other punishment models. The possible punishments have a wide range. While bad-mouthing does require models of reputation, as has been implemented eg. in [13, 23, 28], other forms of punishment such as ostracism (eg. by affecting individual migration in a community-structured model) could already be implemented in models of the same basic structure as considered here. In general, not all types of punishments should be expected to directly influence the fecundity of the punished.

On the other side, punishers can take many different forms. Punishers are not necessarily peers with a personal choice to contribute individually or institutionally to the punishment of wrong-doers. Other options range from leaders punishing inferiors [138, 187] to external individuals taking over the punishment for the victims (third party punishers or hired guns [28, 136, 188]). But in all such cases, the punishers would need to compete and co-evolve with other individuals (which is not the case in pool punishment, as we have seen), and to increase explanatory value, comparability and transitions between different such punishment systems would be desirable.

While we have shown that the model by Pagel and Meade [177] can be applied successfully to typological characters, the model needs improving to be capable of coping with larger numbers of potentially correlated features. In particular, explicitly considering the structure of pairwise dependencies in a Bayesian manner will reduce the complexity of matrix calculations, and thus allow it to be applied to matters of interest. It could then be used to try to understand other synchronic linguistic universals from an evolutionary perspective.

In addition to Bayesian methods concentrating on lexical data, linguists have criticised them for not considering borrowings and other ways of network structures. Implementing Bayesian inference of phylogenetic networks should therefore be a high priority for computational modellers intending to contribute to linguistic phylogeny. Such methods would not only overcome concerns directly pertaining to the over-simplification of this fundamental structure of the model. Instead, phylogenetic networks would also alleviate criticism about not sufficiently pre-processed lexical data, because a reticulate phylogeny would implicitly infer which lexical items are related by descent from a common ancestral language, and which ones are borrowed. But the highlight of network-structured genealogies would be in conjunction with non-lexical data, where it could be used to infer profound truths about language contact in general, and specific instances of it in our cultural history.

Lastly, we hope that future work will be able to bridge the gulf still gaping in this interdisciplinary field. Formal models of humanity, based on Darwinian concepts and methods subsequently developed in theoretical biology, should be able to propel anthropology further from being a small and esoteric field to a quantitative empirical science that gives core insight into current economical, philosophical, and cultural questions, influencing policy-making in a direction apt for humanity in general.

8.3 Conclusions

In this thesis, we have constructed a computational model to investigate the transition from peer to pool punishment in a system where cooperation is an available strategy. We have found that institutional punishment is more complex as a strategy than peer punishment or taxpaying. The choices in constructing the model were weighed against possible alternatives. We have studied alternative population structures in the context of the basic public goods game, and have found that different updating rules affect the qualitative evolutionary outcome in a theoretical model of the evolution of language.

We have constructed a Markov chain Monte Carlo model for the inference of the genealogical tree of Indo-European languages from linguistic data. In addition to lexical data, we have incorporated typological evidence, which had not been done before in a Bayesian context.

Having thus met the objectives of this thesis, we have seen that both numerical simulations and Bayesian inference models, which originate from theoretical biology, have a place in application to anthropological questions. Because cultural evolution is fundamentally Darwinian [9], and the algorithms are fundamentally founded only on assumptions of heredity and variability, and apply biological knowledge only in a later specialisation, the same methods can be fundamentally applied to theoretical anthropology.

This does however not mean that all models are equally well suited for this task. For Bayesian inference models, probability gives an explicit numerical measure for the quality of a model, expressing the consistency of the presented hypotheses with the data. The consistency of the presented hypotheses with previous evidence is expressed in terms of prior probability distributions, which need to be carefully chosen to accurately represent prior knowledge. The overall quality of an inference model is therefore not how well its conclusions concur with prior research, but instead how well the priors (including the invariant model choices, which effectively assume a prior of 1) represent the actual prior knowledge.

This extends somewhat to top-down models testing abstract hypotheses in the absence of comparable data. Here, as well as in the case of other difficult to estimate priors, the quality of the conclusions of a model depends on the robustness of those conclusions under variation of the model. It is thus necessary to be aware of the points of variation of a model, to be able to estimate, if not investigate, how it will influence the results obtained.

The biggest hurdle for mathematical models is thus a lack of cross-expertise on both sides of the gulf. Researchers coming from a theoretical modelling background lack the deep anthropological expertise to judge the adequacy of their (explicit or implicit) priors, while anthropologists and linguists may lack the mathematical insight to critique those aspects of a model that are least consistent with their expertise, and are instead often forced to criticise the results of the model.

There are accusations on both sides over lack of scientific rigour. Profound, hard acquired expertise makes it difficult to present results in a manner that is easily quantifiable or explicable to someone not immersed in the field, so scientists favouring quantitative methods criticise anthropologist for a lack of reproducibility. Models on the other allow researchers to specify hypotheses unambiguously and without having to rely on implicit knowledge, but require the data to be equally formal, introducing a sampling bias in favour of easily quantifiable data. Data-driven studies then make use of computers specifically because computers are far more efficient and less error-prone in manipulating big amounts of data. Because not every small step is tracked by a human mind, these models draw criticism for being opaque.

Both directions of criticism are easily misunderstood and taken as offensive, because they stem from fundamentally different traditions of understanding and verifying results. Nonetheless, the bridge across the gulf is under construction, with researchers on both sides initiating collaborations and learning from each other. We hope that this thesis contributes its fair share to this effort.

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