

# Information-theoretic models of communication in biological systems

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## Abstract

This thesis aims to find general principles governing the behaviour of biological systems, with a particular emphasis in the communicational (social) aspect of these systems. Communication between biological entities plays a major role in their evolution, enabling them to exchange information about their environment and thereby improving their chances of survival. Communication also plays a pivotal role in the organisation of populations of organisms, clearly observed in social insects, but present also at least in bacteria, plants, fungi, animals and humans. It is also theorised that the genetic code is a by-product of the establishment of an innovation-sharing protocol between primitive cells [Vetsigian et al., 2006].

This thesis is mainly concerned with identifying necessary conditions for the emergence of communicational codes, and the problems that arise with their establishment. For this purpose, we introduce an information-theoretic framework where species maximise their growth rate by following a Kelly-gambling strategy to bet on environmental conditions. Information theory provides a powerful tool for abstracting away mechanisms and for focusing on hard limits of a system's dynamics which cannot be circumvented.

We begin by exploring the relation between information exchange and limited resources. We show that a transition from cooperation to antagonism in the exchange of environmental information follows from a change in the availability of resources, from abundant to scarce. We then assume a non-competitive scenario with abundance of resources, where conflicts in a population occur only at a communicational (informational) level, rather than on the physical level, such as competing for (physical) resources. However, traditional Shannon communication is non-semantic, as opposed to the semantic communication observed in biological systems, which is necessary for capturing conflicts in communication.

In the traditional use of information theory, it is assumed that every organism knows how to “interpret” the information offered by other organisms. However, this assumes that one “knows” which other organisms one observes, and thus which code they use. In our model, however, we wish to preclude that: namely, we will *do away with the assumption that the identity of the organisms who send the messages and those who receive them is known*, and the resulting usable information is therefore influenced by the universality of the code used and by which organisms an organism is “listening” to.

We introduce a model which captures semantic communication in information-theoretic terms, where organisms talk to each other in a communication network. We show that, for particular population structures, when organisms cannot identify which other organisms they talk to, the adoption of a universal code emerges as a solution for full interpretation of the shared information.

However, the evolution and establishment of universal codes for communication introduces vulnerabilities: organisms can be exploited by parasites. We define two types of parasites whose strategies have different levels of complexity and study the co-evolution of a host (the population) and a parasite by optimising their respective objective functions in stages. First, we consider a disruptive parasite (a troll) that inflicts harm in a host by minimising a population's mutual understanding, and then a more complex parasite, which manipulates the members of the population via their codes (the puppetmaster). We show emergent characterisations of both parasites, as well as which host configurations are robust against parasites and show adaptive properties.

This thesis introduces a framework which allows the study of informational properties in the host-parasite co-evolution, where the rules of the parasite's habitat, the host, are the outcome of an evolutionary process, and where these very same rules are those that allow the parasite to exploit the host.

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# Chapter 1

## Introduction

### 1.1 Motivation

In the modelling of biological systems, one major objective is to capture properties observed in nature that are emergent from the dynamics of the modelled system. Furthermore, one would like to identify the minimal set of assumptions that produces a particular phenomenon. Let us consider *quorum sensing* in bacteria: when the extracellular concentration of a specific molecule passes a certain threshold, bacterial cells switch their phenotypes in order to maximise their chances of survival (usually by coordinating behaviour on a population-wide scale) [Waters and Bassler, 2005]. This alteration of gene expression in response to a particular molecule concentration is an *evolved* property of cells, where the environment changes the internal state of the cell and vice versa.

This brief example already gives a rather abstract overview of the complexity of an organism: it needs to establish predictive rules between environmental cues (*e.g.* molecules) and its internal organisation, such that the provoked changes, in turn, produce an adequate response. The predictive rules correspond to a semantic interpretation, which is context-dependent (*i.e.* can differ with environmental conditions or among species) [Walker and Davies, 2013]. Such rules allow for effective communication between organisms, thereby increasing their predictions of their environment. However, in the same way these conventional rules can improve predictions, they can also be exploited by other organisms, for instance by communicating “false” information such that the receiver’s updated belief of the state of the environment is detrimental to its purposes [Doyle, 2010]. Therefore, some defence mechanism needs to be implemented for the long-term success of the species.

This simple picture raises several properties of interest in biological systems: first, organisms communicate to improve their chances of achieving their goals [Lachmann et al., 2000]; second, they interpret information in a semantic way (signals have a specific meaning to them) [Smith, 2000, Barbieri, 2003]; third, their evolved interpretation of information can be exploited by other organisms [Robbins, 1994, Doyle, 2010]; and finally, the resulting dynamics of the system is determined by evolution and is susceptible to further changes according to the context [Auletta et al., 2008, Walker and Davies, 2013].

These are the main properties that I intend to capture in a model of a biological system. As I mentioned in the beginning of this section, these properties should emerge, ideally, from a minimal set of assumptions over the organisms. This type of study requires the use of general models, where we want to gain insights into the possible forms of a solution for common

biological problems (in opposition to specific models, which are concerned with particular species and environments) [Parker and Smith, 1990]. I take the optimality approach to modelling, which assumes that organisms are maximising some function. The challenge is, therefore, to be able to reproduce observed outcomes in a principled manner. In this way, we can test our assumptions by determining whether there is support for the predictions of the model [Sutherland, 2005].

In this framework, I adopt an information-theoretic perspective for modelling biological systems. Information theory was originally conceived as a theory of communication [Shannon, 1948], although its potential for modelling living organisms was quickly recognised in the works of Attneave [Attneave, 1954], Ashby [Ashby, 1956] and Barlow [Barlow, 1959]. In this view, living organisms acquire information from their environment and process it in order to produce a particular response [Nemenman, 2011]. This abstract representation of an organism is very powerful, and it allows to quantify, for instance, how much information an organism needs to process in order to achieve a certain utility [Polani et al., 2006]. Furthermore, since biological sensors operate close to the theoretical optimum dictated by physics and by information theory (see [Polani, 2009] and references therein), abstracting away the constraints imposed by biological mechanisms allow us to focus purely on informational constraints (physical constraints can also be considered from an information-theoretic point of view).

This approach to modelling biological systems permits the exploration of unobserved phenomena: for a given set of assumptions, the results may show qualities that are supported in observations, or they may provide us with solutions that were not observed in nature. This expands the research in biology beyond the territory circumscribed by life-as-we-know-it, to a larger domain which Langton famously called life-as-it-could-be [Wilson and Langton, 1989]. However, we should be careful when relating these models to biological systems, since the absence of observations may be due to additional constraints that are not being considered. Another avenue that I will explore occasionally is the connection of the models I develop with different disciplines, such as economics and social sciences.

The main objective of this thesis is to develop information-theoretic models that capture the properties mentioned above: organisms can communicate (semantically) to improve their chances of survival, but at the same time they can be deceived by other organisms. The dynamics of the system are determined by evolution and are subject to further changes. As I stated, for organisms that operate close to the limit dictated by information theory, one of the main challenges is to find the constraints that capture these properties of interest. First, I explore the communicational behaviours of two species' populations competing for resources. Second, I develop a model that shows the emergence of common codes within a population, which introduces semantics in communication. Third, I study how this organisational step introduces vulnerabilities, by formalising two paradigmatic types of parasites and studying their characteristics, as well as which properties of host populations show robustness and adaptability in reaction to these parasites.

## 1.2 Research Questions

- Why do organisms communicate? How does competition for resources affect communication?
- Why do many species share common codes for communication? What are the conditions for the emergence of codes?

- How does the structure of a population influence the evolution of codes?
- Which strategies can be used to exploit communicational conventions?
- How can a host population achieve robustness, adaptability and/or immunity against parasites?

### 1.3 Contributions

- An information-theoretic model combining bet-hedging (or Kelly-gambling) and communication in a scenario with limited resources. We show a transition from cooperation to antagonism in information exchange when there is a change in resource availability from abundant to scarce.
- The development of an information-theoretic model able to capture semantic aspects of communication. The model also captures the influence that the structure of a population has on the outcome of their codes for communication.
- A framework to analyse the informational co-evolution between a host and a parasite.
- The formalisation of two types of informational parasites: a disruptive parasite (the troll), and a manipulative parasite (the puppetmaster). We show how their defined behaviours show *emergent* characteristics: for instance, the troll behaves as a contrarian, while the puppetmaster manipulates with a “dog-whistle” effect, and hides by stealing other entities’ identity.
- Identification of desired properties of a host in contact with parasites: how to achieve immunity, robustness and adaptability? We show configurations of a population that is immune to one type of parasite but vulnerable to the other; how the use of synonyms can increase robustness; and that centralised populations are more adaptable against parasites.

### 1.4 Outline

In the next chapter, we provide an overview of the technical background of the thesis’ work. This covers the several methods and frameworks used throughout the thesis. A particular method used in one of our models is described in Appendix A. Then, we present the original work of this thesis in three chapters. In each of these, we discuss other works in the literature that study the same or similar problems.

In the first of these, Chapter 3, we explore the dynamics of information exchange in a system composed of two species living in an environment with limited resources. We introduce a simple model where species have the option to share information with the other species, relating their growth rate with the information they have about the environment. Then, in Chapter 4, we take a step back and look at the necessary conditions for a species to fully interpret the information shared by other species. We present a model that captures the use of conventions for communication between organisms, and study how the structure of a population influences the evolution of communication. Chapter 5 deals with the vulnerabilities that arise when establishing conventions for communication: parasites can make use of these

to exploit other organisms to their advantage. We formally characterise two types of parasites, and study some properties of the co-evolution of host-parasite systems. Finally, in Chapter 6, we discuss our results in a general context.

# Chapter 2

## Background

### 2.1 Introduction

The main framework used throughout this thesis consists of information theory and Bayesian networks. We use Bayesian networks to model how the variables in our system (environment, organisms, etc.) are related, while we use information theory to define optimisation criteria according to which we propose the dynamics to be aligned, such as maximising or minimising mutual information quantities.

Then, we introduce the information processing view of organisms, which serves as a conceptually clear abstraction for explaining our assumptions in their modelling. By taking an optimality approach, we make, throughout the thesis, extensive use of fitness functions. The decision of what is being optimised in a biological system is usually of great controversy in biology. We briefly explain some common views/concepts of what is being optimised by Darwinian evolution.

Finally, we introduce basic game-theoretic notions that we use, by presenting a well-known social dilemma for cooperation. We conclude with a brief description of the optimisation algorithm (a genetic algorithm) utilised in this thesis in all experiments where an optimisation was carried out.

### 2.2 Bayesian Networks

#### 2.2.1 Basic concepts and notation

Bayesian networks are a framework that allows reasoning under uncertainty. They allow to describe probability distributions of variables of interest with a clear view to their statistical, and, in principle, also their causal dependencies. It provides a formalism for making quantifiable statements about these variables, relying on the rules of probability theory to manipulate values. Let us introduce the notation for probabilities that we will use in the remaining of the thesis.

For a random variable  $X$  (uppercase), its *alphabet* is the set of possible values it can take, denoted by  $\mathcal{X}$  (calligraphic). The cardinality of the alphabet is given by  $|\mathcal{X}|$ , and, for writing probability mass functions, we denote the concrete values of the alphabet using sub-indexes:  $x_1, x_2, \dots, x_{|\mathcal{X}|}$ . The probability of  $X$  having the specific value  $x \in \mathcal{X}$  will be denoted by  $\Pr(X = x)$ , unless there is no possible confusion about which variable we

are using, in which case we write  $p(x)$ . Similarly, the conditional probability is written as  $p(y | x)$  for  $\Pr(Y = y | X = x)$  when no confusion is possible. If no specific value for a variable is provided, as for instance, in  $p(X)$ , then this denotes the whole probability distribution over  $X$ . Subscripted random variables, such as  $X_i$ , denote a different variable for each index  $i$ . For sums and products over elements of an alphabet, we will write  $\sum_x$  instead of  $\sum_{x \in \mathcal{X}}$  where no confusion can arise.

### 2.2.2 Formalism

A Bayesian network is defined as a *directed acyclic graph* where each node represents a random variable, and arcs indicate the existence of direct causal influences or dependencies between the linked variables [Pearl et al., 2000]. These dependencies are quantified by conditional probabilities for each node given its parents in the network, allowing the computation of joint probabilities for any subset of variables given evidence about any other subset [Pearl et al., 2000].

Each node in the network is a random variable  $X_i$ , and its parents are denoted by  $pa(X_i)$ . How this variable depends on its parents is given by the conditional probability  $\Pr(X_i | pa(X_i))$ . The joint distribution function over the variables  $X_1, X_2, \dots, X_n$  is given by the product

$$p(x_1, x_2, \dots, x_n) = \prod_{i=1}^n \Pr(X_i = x_i | pa(X_i)) \quad (2.1)$$

Having the joint probability of any set of events allows us to answer probabilistic queries about the variables. A typical example is the following Bayesian network:

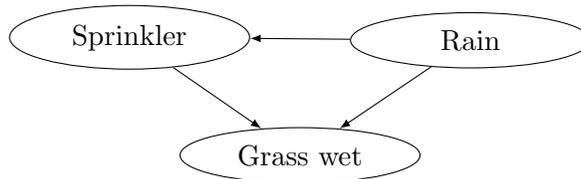


Figure 2.1: A simple Bayesian network

Let us suppose we want to investigate why the grass is wet. We know that the grass can be wet for two reasons: because it rained, or because the sprinkler was activated (or both). Also, we know that the status of the sprinkler depends on the rain. A simple Bayesian network that captures these relations is shown in Fig. 2.1. By defining the causal conditional probabilities  $p(\text{Sprinkler} | \text{Rain})$  and  $p(\text{Grasswet} | \text{Sprinkler}, \text{Rain})$ , together with  $p(\text{rain})$ , we can then answer questions such as “what is the probability that it is raining, given that the grass is wet?”. This is computed in the following way:

$$p(\text{Rain} = \text{true} | \text{Grasswet} = \text{true}) = \frac{p(\text{Rain} = \text{true}, \text{Grasswet} = \text{true})}{p(\text{GrassWet} = \text{true})} \quad (2.2)$$

## 2.3 Information Theory

Information theory was originally developed by Shannon as a theory of communication [Shannon, 1948]. The two fundamental results he introduced are (a) the entropy as the ultimate

data compression; and (b) the channel capacity as the ultimate transmission rate of communication [Cover and Thomas, 2002]. However, information theory has contributed to several fields beyond communication theory, such as physics (thermodynamics), computer science (Kolmogorov complexity) and economics (portfolio theory; Kelly-gambling). Its applications to biology are not straightforward since information theory intentionally ignores semantics.

### 2.3.1 Basic concepts

In this section we briefly introduce some basic concepts of information theory. All the definitions are taken from [Cover and Thomas, 2002], to where the reader is referred for an in-depth treatment.

#### Entropy

A measure for the uncertainty of a random variable is given by the *entropy* of that random variable. The entropy of a random variable  $X$  defined over the alphabet  $\mathcal{X}$  is given by

$$H(X) = - \sum_{x \in \mathcal{X}} p(x) \log_2 p(x) \quad (2.3)$$

For a base of the logarithm of 2, the resulting unit is *bits*, which is the one used throughout the thesis. It gives the number of bits, on average, that are required to describe it. It is always non-negative and is upper-bounded by  $\log_2 |\mathcal{X}|$ . Let us make the concept of entropy clear by an example, which we take from [Cover and Thomas, 2002]: suppose there is a horse race with eight horses, with probabilities of winning being  $(1/2, 1/4, 1/8, 1/16, 1/64, 1/64, 1/64, 1/64)$ . The entropy of the race is

$$H(X) = -\frac{1}{2} \log_2 \frac{1}{2} - \frac{1}{4} \log_2 \frac{1}{4} - \frac{1}{8} \log_2 \frac{1}{8} - \frac{1}{16} \log_2 \frac{1}{16} - 4 \frac{1}{64} \log_2 \frac{1}{64} \quad (2.4)$$

$$= 2 \text{ bits} \quad (2.5)$$

Now, let us suppose we would like to send a message indicating which horse won the race. One possibility is to send the index of the horse, but this will require 3 bits for any horse (they would be represented by 000, 001, etc.). We can do better by using shorter codes for most probable winners, and longer ones for more unlikely winners, such that, on average, we lower the number of bits used. For example, let us consider the following codes to represent the eight horses: 0, 10, 110, 1110, 111100, 111101, 111110, 111111. The average description length (weighted by probability of occurrence) is 2 bits, which is exactly the entropy. This provides a more compact way of representing the winning horses, and, actually, is the most compact one: the entropy is a lower bound for the compression of information.

The *conditional entropy* measures the uncertainty of a random variable once another random variable has been observed. For instance, let us consider a horse race where the winning horse is  $X$ , and we receive a tip about the race, represented by  $Y$  and related to the race by  $p(y | x)$ . Then, the uncertainty of the horse race considering the tip we received is given by

$$H(X | Y) = - \sum_y p(y) \sum_x p(x | y) \log_2 p(x | y) \quad (2.6)$$

The reduction in the uncertainty of the outcome of the horse race is given by  $H(X) - H(X | Y)$ , which will turn out to be exactly the mutual information between the variables (defined below). For a gambler betting all his money on repeated races, a reduction in the uncertainty of the race is directly translated in an increase in his long-term growth rate. This will be made precise using Kelly-gambling in Chapter 3, where we use it in a model of species betting on environmental conditions.

### Mutual information

*Mutual information* measures how much information, on average, the knowledge of a random variable give us about another random variable.

$$I(X ; Y) = \sum_{x,y} p(x, y) \log_2 \frac{p(x, y)}{p(x)p(y)} \quad (2.7)$$

We can also think of mutual information as the reduction in the uncertainty of a random variable due to the knowledge of another random variable:

$$I(X ; Y) = H(X) - H(X | Y) \quad (2.8)$$

The mutual information has some important properties:

- It is always non-negative:  $I(X ; Y) \geq 0$
- It is symmetric:  $I(X ; Y) = I(Y ; X)$
- It is zero if and only if the variables are independent:  
 $p(x, y) = p(x)p(y) \iff I(X ; Y) = 0.$
- It is upper-bounded by the minimum of the individual entropies  
 $I(X ; Y) \leq \min[H(X), H(Y)]$

The *conditional mutual information* is the reduction in the uncertainty of a variable due to the knowledge of another variable when a third variable is given. It is defined by

$$I(X ; Y | Z) = H(X | Z) - H(X | Y, Z) \quad (2.9)$$

Then, the mutual information for a collection of variables is given, via the chain rule for information, by

$$I(X_1, X_2, \dots, X_n ; Y) = \sum_{i=1}^n I(X_i ; Y | X_{i-1}, X_{i-2}, \dots, X_1) \quad (2.10)$$

Finally, the *Kullback-Leibler divergence* between two probability mass functions  $p(x)$  and  $q(x)$  is defined as

$$D(p || q) = \sum_{x \in \mathcal{X}} p(x) \log_2 \frac{p(x)}{q(x)} \quad (2.11)$$

When  $p(x) = 0$ , then it is assumed that  $0 \log_2 \frac{0}{q(x)} = 0$  regardless of the value of  $q(x)$ , and if  $p(x) > 0$  and  $q(x) = 0$  then  $p(x) \log_2 \frac{p(x)}{0} = \infty$ , giving  $D(p || q) = \infty$ . The Kullback-Leibler

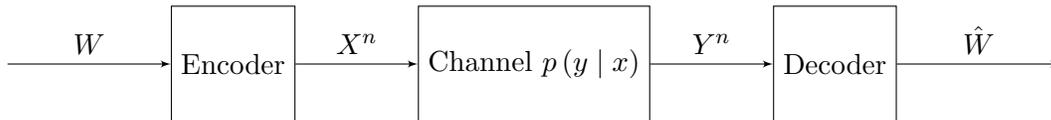


Figure 2.2: Communication system

divergence is always non-negative and is zero if and only if the probabilities  $p$  and  $q$  are equal. Sometimes it is called the Kullback-Leibler distance, although it is not a true distance since it is not symmetrical and does not satisfy the triangle inequality.

We can rewrite the mutual information using the Kullback-Leibler divergence.

$$I(X ; Y) = D(p(x, y) || p(x)p(y)) \quad (2.12)$$

The mutual information is expressed as the divergence between the joint probability and the product of the marginals. When these probabilities are equal, the divergence, and thus the mutual information, is zero.

### 2.3.2 Data-processing inequality

Let us assume the following Bayesian network:  $X \rightarrow Y \rightarrow Z$ . Then, the data-processing inequality states that  $I(X ; Y) \geq I(X ; Z)$ . Informally, it shows that no clever manipulation  $Z$  of the data  $Y$  about  $X$  can improve the inferences that can be made about  $X$  from the data  $Y$ .

For instance, let us consider again the horse race  $X$ , and a series of tips we received about it represented by  $Y$ . The information about the horse race of the tips is given by  $I(X ; Y)$ , and, the data-processing inequality tell us that we cannot make clever manipulations of the tips in order to increase that information. The only way that the information about the race can be increased is by injecting new information, as, for instance, by integrating the tip with particular knowledge from other sources and times.

### 2.3.3 Channel capacity

A central result of information theory is the *channel capacity*. It gives the maximum rate at which we can transmit information over a noisy channel.

In Fig. 2.2, we show a communication system that consists of an encoder, a channel, and a decoder. We want to transmit a message  $W$  from one point to another through a noisy channel, such that we can recover the message (i.e. such that our estimate of the message  $\hat{W}$  matches the original message). We can think of a communication channel as a system where the outputs, chosen from an alphabet  $\mathcal{Y}$ , depend probabilistically on the inputs, chosen from an alphabet  $\mathcal{X}$ . This is characterised by the conditional probability of the outputs given the inputs,  $p(y | x)$ , and the channel is said to be *memoryless* if the probability distribution of the outputs depends only on the input at that time and is conditionally independent of previous channel inputs or outputs.

The *channel capacity* of a discrete memoryless channel is defined as

$$C = \max_{p(x)} I(X ; Y) \quad (2.13)$$

The maximum is taken over all the possible input distributions  $p(x)$ . The problem with transmission of information over a channel comes when we have two different inputs giving the same output: the inputs are confusable. The idea is to choose a subset of the inputs such that there is high probability that the produced outputs are caused from only one highly likely input.

## 2.4 Information processing view

As mentioned earlier, in this thesis we are concerned with general models for biological systems. This type of system is immensely diverse, and therefore we would like to find solutions to problems in biology that hold across different organisms. A powerful abstraction for this purpose is to treat organisms as information processing units: organisms perceive their environment, they process this information, which culminates in an action [Nemenman, 2011]. The actions of the organism modify the environment, and can potentially be perceived back by the organism. This introduces a feedback cycle with intricate dynamics, and can be modelled as a perception-action loop (PAL) [Klyubin et al., 2005b]. Although we will not particularly use this model in this thesis, it will help us put into context the models we introduce later, as well as introduce and discuss some of the assumptions we make.

The perception-action loop is modelled as a Bayesian network consisting of three random variables: the environment  $E$ ; the agent’s sensors  $S$ ; and the agent’s actuators  $A$ . In Fig. 2.3 we show these variables unrolled in time. The agent perceives the environment according to the conditional probability  $p(S | E)$ , it performs an action according to its *policy*  $p(A | S)$ , and its actions influence the state of the environment according to  $p(E' | E, A)$ .

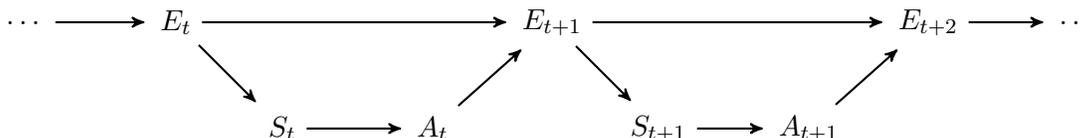


Figure 2.3: Bayesian network representing a memoryless perception-action loop

This abstraction provides a conceptually transparent and universal model for agent-centric systems. It abstracts away details about composition, mechanisms, etc. of the agent, expressing them in the form of a policy. Therefore, a policy can be as simple as a noiseless channel, or as complex as a human brain. How are all these conditional probabilities defined?

This will depend on the constraints we want to impose in the system. For instance, if we are given the conditional probabilities for sensing the environment and for updating it, which together are defining the *rules* of the world, then these constrain the system: certain states might be impossible to reach, independently of those variables whose values are not fixed. Then, what are the values of these variables?

As we have mentioned, we will take an optimality approach to modelling systems with undefined behaviour. In other words, we will specify a measure to maximise (or minimise) by letting the undefined variables of the system change. This approach is commonly used in biology to analyse evolutionary adaptations, where first we ask a question we would like to analyse, for instance “why is the sex ratio often unity?” [Parker and Smith, 1990]. The set of available actions of the organism are directly related to this question: here, we can consider a continuum from producing only female offspring to producing only male offspring. The

underlying assumption when adopting this model is that natural selection with reproduction and variation is a sufficient force to achieve optimality, although here we also consider non-Darwinian adaptations to be outcomes of optimisation processes.

The problem now is to define a criterion to choose the optimal policy  $p(A | S)$  of an organism.

### 2.4.1 Fitness function

Usually, in biology, some measure of Darwinian fitness is used [Parker and Smith, 1990]. The choice of fitness function is a significant assumption with consequences in the outcomes of a model. To illustrate this, let us imagine there is a common pasture where herdsman can place their cattle for grazing, and let us assume that the total amount of cattle is such that there is just enough re-growth of grass to maintain a constant grazing. Now, let us assume a herdsman adds an animal to its herd, which, considering our premises, would result in overgrazing. What are the consequences for that herdsman, and what are the consequences for the other herdsmen, in terms of monetary gain?

The herdsman that added the animal will have an additional sale, while all the herdsmen's cattle (including those of the abuser) will decrease in value due to malnutrition. However, from the abuser's perspective, the gains of an additional sale will normally be much higher than the cost of overgrazing, since this cost is shared among all herdsmen, while the profit is not. Therefore, if all herdsmen act in order to maximise their gains, the overgrazing will eventually deplete the grass.

This situation is famously known as *the tragedy of the commons* [Hardin, 1968], and exemplifies the difficulties of cooperation in scenarios with public goods. A similar problem is presented in the Prisoner's Dilemma [Rapoport and Chammah, 1965], which we explore later. In these situations, individual striving can lead to the breaking of the system, while cooperative behaviours can sustain it.

The point we want to make is that, if we choose as the fitness function the average gain of the herdsmen, then our optimum will be at the equilibrium point where the benefits of adding an extra animal equals the decrease in the overall gains. However, choosing a fitness function where each herdsman maximises their individual gains, then the optimal choice is to add animals up to the point of depletion. In the former choice, a cooperative behaviour is assumed, and implicitly the global effects of an agent's decisions are incorporated into the fitness function. In the latter, these effects are unknown to an actor, and a local decision needs to be made, which usually would be one in its favour, and possibly detrimental to the whole. This produces conflicts in the decision-making process, which are usually analysed using game theory.

In this thesis, we make the use of both mentioned types of fitness functions, depending on our respective purposes. For instance, we will use a fitness function that assumes cooperation to obtain a configuration which serves as a starting point to study conflicts. Conflicts are studied in two ways: through a game-theoretic analysis and by looking at adaptive responses when we consider parasites.

However, understanding the emergence of cooperation in public goods games is a major objective in biology. Fitness functions that assume cooperative behaviour within populations are said to operate at the population level. On the other hand, where organisms maximise their own fitness regardless of the others, selection operates at the individual level. Which should be the unit of selection is a controversial topic in biology [Wilson and Sober, 1994,

Nowak et al., 2010, Abbot et al., 2011], and hasn't reached a consensus to date. I will briefly review the main approaches to biological modelling in terms of the choice of a fitness function, so that later we can explain our choices in the used terminology.

### **Unit of selection**

Let us first try to clarify what is usually meant by *levels of selection*. In the process of natural selection, the units that are "selected" by nature are the ones that are better adapted to their environment, and thus have a reproductive advantage over competing units, becoming more common in their population. If we consider a population of birds, which is a group of birds, which in turn is a group of organised cells, where each cell contain many genes, then what is the *unit of selection* that we should choose in our model?

### **Gene-centric view of evolution**

The gene-centric view of evolution sees the gene as the fundamental unit of selection. This view was developed by Williams [Williams, 1966] and popularised by Dawkins [Dawkins, 1976]. They argue that evolution occurs mainly through the differential survival of competing genes, where the phenotypes that they jointly express are only to be seen as "vehicles of selection", *i.e.* they only help to propagate the genes, since phenotypes cannot themselves accumulate change. Then, a question that arises from this premise is, given that genes are selfish entities, how is it that there exist higher organisms showing altruistic behaviour (which sacrifice their own fitness in favour of the whole)?

### **Kin selection**

The concept of *kin selection* [Hamilton, 1964] can explain certain forms of altruistic behaviours while being compatible with the gene-centric view of evolution. The idea is that an agent's individual fitness can be increased by helping related individuals. In this way, the genes that are shared between these individuals gain an evolutionary advantage, since they are propagated by both individuals. There is of course a cost to helping others, and several degrees of relatedness. This is captured in Hamilton's rule for kin selection:  $rB > C$ , where  $r$  is the genetic relatedness of the interacting agents,  $B$  is the additional reproductive benefit gained by the helped agent, and  $C$  is the reproductive cost of helping the other. Where this condition holds, we expect this behaviour to be favoured by natural selection. This special way of computing an organism's fitness is called *inclusive fitness*.

### **Group selection**

The idea in group selection is that evolution acts at the level of the group, implicitly assuming that lower levels always act cooperatively within groups. According to Wilson & Sober [Wilson and Sober, 1994], a form of group selection (referred as "naïve group selection") that "uncritically assumed that natural selection evolves adaptations at upper levels of the biological hierarchy" [Wilson and Sober, 1994] was popular in the 60's, before the gene-centric view took off. It was neglected thereafter, until its revival in the form of multi-level selection.

## Multi-level selection

The theory of multi-level selection attempts to integrate the interactions among units at all levels of a hierarchy. It recognises the value of the theory of group selection, where evolution is considered at levels other than the individual, but it does not disregard conflicts at lower levels, or any levels at all [Wilson and Sober, 1994, Nowak et al., 2010]. One theory proposes that competition between populations (*i.e.* at the population level) can favour the selection of cooperative behaviour [Traulsen and Nowak, 2006].

### 2.4.2 Game Theory

Game theory was developed by von Neumann and Morgenstern for studying economic behaviour [Neumann et al., 1944]. They introduced a notion of utility which goes beyond monetary value, where quantities can be assigned to any type of outcome. Their utility theorem states that, for any rational agent, if an outcome  $X$  is preferred over another outcome  $Y$ , then there exists an utility function such that the expected value of  $X$  is larger than that of  $Y$  [Von Neumann and Morgenstern, 1947]. An agent showing *rational behaviour* is that whose preferences are consistent with the axioms of VNM-rationality [Neumann et al., 1944]. Without going into details, the axioms are *completeness*: an agent always has a preference over any pair of outcomes; *transitivity*: the preferred outcomes are consistent; *independence*: the preference between two outcomes is maintained when each outcomes is mixed equally with a third one; and *continuity*: if outcomes  $X$  is preferred to  $Y$ , and outcome  $Y$  is preferred to  $Z$ , then there exists a combination of  $X$  and  $Z$  that is indifferent from choosing outcome  $Y$ . Then, a rational agent choosing outcomes according to its preferences will behave as if it was maximising its expected utility.

A game consists in a set of two or more players, a set of actions of the players, and a defined payoff or utility for each combination of all player's actions. Games are usually described by a payoff matrix, such as the following:

|          |           | Player B  |        |
|----------|-----------|-----------|--------|
|          |           | Cooperate | Defect |
| Player A | Cooperate | -1,-1     | -3,0   |
|          | Defect    | 0,-3      | -2,-2  |

Figure 2.4: Prisoners' Dilemma

In Fig. 2.4, we show the payoff matrix for a well-known problem for cooperation: the Prisoner's Dilemma (PD) [Rapoport and Chammah, 1965]. The dilemma is depicted in the following situation: two criminals are imprisoned and put into solitary confinement with no possibility of communication with each other. The prosecutor lacks enough evidence to convict them on the principal charge, but they can convict them on a lesser charge. The prosecutor offers each prisoner a bargain: each of them can betray the other (**defect**) by testifying that the other committed the crime, or they can **cooperate** with the other by remaining silent [Poundstone, 1992].

The offers are described in the payoff matrix of Fig. 2.4: if both criminals cooperate with the prosecutor (i.e. “defect” in PD lingo), each of them get 2 years in prison (agents maximise their payoffs, but they don’t want to maximise their years in prison, hence we use negative values). If  $A$  betrays  $B$ , and  $B$  remains in silence, then  $A$  walks free and  $B$  serves 3 years in prison. Similarly, if  $B$  betrays  $A$ , and  $A$  remains in silence, then  $B$  walks free and  $A$  serves 3 years in prison. If both cooperate with each other (i.e. “cooperate” in PD lingo) by remaining in silence, they will only serve 1 year in prison.

This presents a dilemma for any of the criminals: if  $A$  cooperates, then  $B$  should defect and walk free. If  $A$  defects, then  $B$  should also defect, because serving 2 years is better than serving 3 years. From this analysis, we should conclude that both criminals will defect, getting a worse sentence than if both would cooperate. This exemplifies *strategic dominance*: defection is a dominant strategy for both players because, regardless of the action of the other player, one is always better off playing this strategy. In this case, this strategy is called *strictly dominant*, but if a player is at least equally well by playing one strategy, and better off for the rest of the strategies, no matter what the other plays, then the strategy is *weakly dominant*.

|                 |           |                 |        |
|-----------------|-----------|-----------------|--------|
|                 |           | <b>Player B</b> |        |
|                 |           | Cooperate       | Defect |
| <b>Player A</b> | Cooperate | R,R             | S,T    |
|                 | Defect    | T,S             | P,P    |

Figure 2.5: Generalised form payoff matrix for social dilemmas

The generalised form of the previous payoff matrix is shown in Fig. 2.5, which can represent different social dilemmas, depending on the values chosen for  $R$  (reward),  $P$  (punishment),  $S$  (sucker) and  $T$  (temptation). For the prisoner’s dilemma, we have that  $T > R > P > S$ . Other social dilemmas are the Snowdrift game ( $T > R > S > P$ ), where mutual cooperation is undermined by the temptation of cheating ( $T > R$ ); the Stag-hunt game ( $R > T > P > S$ ), where cooperation is undermined by the fear of being cheated ( $P > S$ ); and the Harmony game ( $R > S > T > P$ ), where cooperation is dominant. The Prisoner’s dilemma combines both the temptation to cheat and the fear of being cheated [Macy and Flache, 2002].

These games can be solved by using the concept of Nash Equilibrium (NE) [Nash et al., 1950], where, by fixing the strategies of each player, no player can improve its payoff by unilaterally deviating. For example, the Snowdrift game is an “anti-coordination” game, with two NE: one player defects and the other cooperates, and the one with opposite actions for each player. The Stag-hunt game, instead, has two NE, when both players either simultaneously cooperate or defect. The Harmony game has only one NE, with both players cooperating, and in the Prisoner’s Dilemma both players defecting is the only NE.

However, Nash equilibria relies on players with the ability to understand the game and predict the actions of other players. A solution concept better suited for biological models, which alleviates the requirements on cognition, is the evolutionarily stable strategy (ESS) [Smith, 1982]. ESS is a refined form of a NE, adding the condition that a population cannot

be invaded by a mutant agent playing a different strategy from that of the NE. In this thesis, nevertheless, we will only use the concepts of strategic dominance. Dominant strategies in games are sufficient to describe the outcomes of games, without needing to rely on NE or ESS.

## 2.5 Optimisation techniques

We argued that, when choosing an optimisation function that considers the fitness of the population, instead of having each agent maximising its own fitness, then the discussed conflicts disappear. For example, in the PD shown in Fig. 2.4, if we consider the average fitness of both players, then the optimal solution is mutual cooperation.

In cases in which we are only concerned with the final solution, then the optimisation mechanism we use is irrelevant. However, the mechanism used will have an influence on which solution is found, depending on the initial conditions and how we move through the fitness landscape. The fitness functions we consider throughout the thesis have usually a large number of local maxima, and we will use genetic algorithms (GA) for optimisation. There is no particular reason for this choice other than implementation simplicity, and we could have used any other local optimisation algorithm such as the Hill climbing algorithm for our computations. Let us note here that we are not using crossover rules in our GA, and thus these two algorithms will almost always achieve the same optimum.

Genetic algorithms, in general, consider a population of solutions, where each solution is represented as a genome. A solution can be evaluated by computing its fitness function. Given an initial population of solutions, genomes with high fitness values are selected, and mutation and/or crossover rules are applied to them probabilistically. This creates a new population, and we can repeat the process until a termination criterion is reached. The criterion can be a maximum number of generations, or, for example, no change in the fitness values for a fixed number of generations.

Although this technique is inspired on the process of natural selection, here we are only concerned with the properties of the final solution. However, since our final solutions could be many, the result of the optimisation process will be highly influenced by the parameters of the GA. This is indeed a problem but unrelated to the ability to find global optima: in general, we are interested in the properties of *all* equilibrium points, regardless whether they are local or global. Our aim when we define fitness functions for optimisation is that *all* equilibrium points share the same properties, and thus local optima are equally important to global. We will optimise via a GA in all experiments of Chapter 4 and Chapter 5.

## Chapter 3

# Cooperation and antagonism in information exchange

### 3.1 Overview

In this chapter we relate information exchange with limited resources. We lay out the Kelly-gambling model by which species bet on environmental conditions that is assumed throughout the remaining of the thesis. We show the well-known information-theoretic relation between an increase in environmental information and an increase in growth rate. Then, we introduce a game between two species where each has the option to share information with the other in a scenario with limited resources.

This chapter is based on the journal paper written by the author and Daniel Polani called “Cooperation and antagonism in information exchange in a growth scenario with two species”, which was published in the *Journal of Theoretical Biology* [Burgos and Polani, 2016b].

### 3.2 Introduction

Information is a central concept in biology. The ability of living organisms to acquire and process information about their environment is essential for their survival and reproduction. This is particularly crucial for organisms living in fluctuating environments, where they face the challenge of adapting to unpredictable circumstances. The failure of a species population to anticipate such changes could be fatal, eventually leading the species to extinction. In environments where reliable cues that a species requires to survive are present, sensing the environment may eliminate environmental uncertainty, allowing the species to adopt a suitable phenotype for the current conditions. However, when uncertainty remains in the environment, a species will follow a *bet-hedging* strategy [Slatkin, 1974, Seger and Brockmann, 1987], where it tries to maximise its long-term growth rate by adopting different phenotypes for each of the possible environmental conditions, in proportions based on the information about the environment they possess. The classic example of bet-hedging in biology is Cohen’s model of seed dormancy, where a seed germinates stochastically in different periods relative to the probability of rainfalls [Cohen, 1966].

### 3.3 Related work

The relation between information and long-term growth rate was first formalised by Kelly using the example of a horse race, where a gambler receiving side information about the race maximises its capital’s long-term growth rate by betting proportionally to the updated probabilities each horse has of winning [Kelly, 1956]. The same principle was considered in models of evolution of biological systems living in fluctuating environments [Dempster, 1955, Levins, 1962, Cohen, 1966], and the relationship between information and long-term growth rate was analysed in information-theoretic terms in [Kussell and Leibler, 2005, Bergstrom and Lachmann, 2004, Bergstrom and Lachmann, 2005, Donaldson-Matasci et al., 2008, Donaldson-Matasci and Lachmann, 2010, Rivoire and Leibler, 2011], where it is shown that an increase in environmental information of a species is translated into an increase in its long-term growth rate.

Bacteria, as many other organisms living in fluctuating environments, must constantly make adaptive decisions in order to survive [Perkins and Swain, 2009, Balázsi et al., 2011]. For instance, bacteria have the ability to switch their phenotype to a more suited one when facing a change in environmental conditions [Elowitz et al., 2002, Balaban et al., 2004, Leisner et al., 2008, Fraser and Kaern, 2009, Lopez et al., 2009]. The decision to adopt a particular phenotype is based upon its information about the environment, and when the future conditions cannot be perfectly predicted, bacteria will hedge their bets [Veening et al., 2008, Beaumont et al., 2009]. This stochastic decision-making process, where a cell adopts a phenotype with a certain probability, can be considered as the outcome of a complex internal biochemical network, and therefore as an evolvable trait [Tagkopoulos et al., 2008, Perkins and Swain, 2009, Lopez et al., 2009].

Besides sensing environmental factors such as temperature, oxygen, pH levels, etc., bacteria also obtain information about their environment by detecting concentration levels of diffusible cues released by the same bacterial species or by other species of bacteria [Fuqua et al., 1994, Surette et al., 1999, Miller and Bassler, 2001]. This process is commonly known as *quorum sensing*, although the original interpretation was more restrictive. Originally, the diffusible cues were only considered as an indicator of cell density, where a sufficiently large concentration of these cues would indicate that a quorum of cells was achieved [Fuqua et al., 1994, Surette et al., 1999]. This quorum allows bacteria to perform diverse physiological activities such as secretion of virulence factors, formation of biofilms, conjugation, sporulation and bioluminescence [Miller and Bassler, 2001, Henke and Bassler, 2004].

Since the introduction of quorum sensing, other uses for diffusible cues by bacteria have been found. For instance, in diffusion sensing, bacteria employ cues to monitor diffusion in their environment [Redfield, 2002]. Another study relates bacterial cues to pH levels in the environment, a process called diel sensing, which, due to pH fluctuations, shows a daily cycle [Decho et al., 2009]. A list of different uses for diffusible cues by bacteria can be found in [Platt and Fuqua, 2010], where they propose to utilise the term quorum sensing to refer to these processes, without restricting its meaning to a method of measuring cell density. Instead, the term should be considered as a general method to indirectly obtain information about environmental factors that influence the accumulation and perception of the cues.

Considering this, we propose a theoretical model which combines the two mentioned aspects of bacteria: bet-hedging and cell-to-cell communication, where cells exchange information about the environmental conditions on which they depend and are trying to predict. We will neither attempt to model any particular mechanism to integrate the different sources of

environmental information, nor intend to model how a cell chooses a phenotype. Instead, we will model the dynamics of bacteria cells in a generic information-theoretic framework, such that bacterial communication becomes an illustrative interpretation of a general model of growth with information exchange in a scenario with limited resources. Other interpretations of the model are discussed in Sec. 3.6. Information theory [Shannon, 1948] allows general high-level descriptions of systems, permitting to hide away irrelevant details for the purposes of a model [Polani, 2009, Nemenman, 2011]. In particular, information theory provides a natural framework to analyse cells’ decision-making processes in uncertainty where the mechanisms need not to be modelled [Mian and Rose, 2011, Waltermann and Klipp, 2011, Brennan et al., 2012, Rhee et al., 2012].

In taking this view, we focus on the emergent behaviours related to information exchange between two species of bacteria following a bet-hedging strategy in a scenario with limited resources. In our model, the consumption of resources as well as the amount of environmental information (from the same and from the other species) are density-dependent. Larger populations can potentially share more environmental information than smaller ones, increasing the long-term growth rate of recipient cells. Thus, a species can actively increase the information about the environment it could perceive in the future, by sharing information with the other species, thereby increasing its population. On the other hand, larger populations consume more resources, which affects the survival of a species’ population, and therefore the environmental information the cells in the population acquire. We analyse this trade-off through a game, where two species of bacterial cells competing for resources have the option to share all of their environmental information with the other species.

Other game-theoretical models have also considered dynamical payoffs [Tomochi and Kono, 2002, Santos et al., 2006, Lee et al., 2011, Requejo and Camacho, 2011, Requejo and Camacho, 2012]. In particular, [Requejo and Camacho, 2011, Requejo and Camacho, 2012] considered a model based on limited resources, achieving qualitatively similar results. Both in their work and ours, there is a transition in the dominant strategy resulting from a change in the availability of resources. In their work, the transition is from a game equivalent to a Prisoner’s Dilemma, where there is abundance of resources and defection is dominant, to a Harmony Game, where there is scarcity of resources and cooperation dominates. In this study, the transition is in the opposite direction: cooperation is dominant in abundance of resources and defection is dominant in scarcity. We explain this contradiction in the conclusions.

While the majority of evolutionary game-theoretical models assume species with fixed strategies during their lifetime, and then analyse the composition of the resulting population (cooperators vs. defectors), here we want to study which are the best *communication* strategies for a species based on the information it has about its context and its internal (predictive) model of the system’s dynamics.

## 3.4 Model

### 3.4.1 Overview

We consider a model where two different species of bacteria can sense complementary information about their environment and have the ability to share that information with other species. Both species follow a bet-hedging strategy, where the environmental information they obtain is translated into growth rate. Therefore, the more information about their environment they obtain, the higher their growth rate will be. We study whether the species would

communicate (cooperate) or behave antagonistically in scenarios where they both depend on a common resource for their survival.

For this purpose, we consider a minimal model that is able to capture the communication behaviour of a species. We imagine an environment that can be in one of four equally likely states (*i.e.* its entropy is 2 bits). We chose this amount of states since this accelerates computations while allowing to have two species that sense complementary bits. Each species can potentially sense only one of the two bits. In this way, species depend on each other to eliminate (approximately) their environmental uncertainty, creating a mutual interest in their survival (otherwise there is little or no incentive to communicate). In addition, we assume that each individual cell can measure its corresponding bit with only 85% accuracy. This is an arbitrary amount that leaves uncertainty in the measurement while still being valuable for prediction.

We consider two types of communication that can help bacteria obtain more information about the environment: (a) within-species communication, in which each member of the population can integrate completely the information from all other members of the population (so that even though each individual can sense the species-specific environmental bit with only 85% accuracy, several bacteria from the same species can talk to each other to obtain close to the entire bit). Thus, the total information available to an individual increases with population size; and (b) between-species communication, in which a receiver species can incorporate all the information from the individuals of the sender's species. As before, the amount of information that is available increases with the population size.

We assume that all the information shared, either within- or between-species, is fully interpretable by the receiver, and thus can always be translated into growth rate (via improving their bet-hedging strategy). This is an idealisation that allows us to focus on communication strategies rather than on the interpretation of information. Later, we discussed what is required to relax this assumption, and in the next chapter we address this problem. In order to give both species the option of not communicating with the other species, while still being able to communicate with members of its own species, we assume three different chemical languages: each species communicates through its own particular language, which cannot be understood by the other species; and we assume a joint language for between-species communication. All communication happens through an idealised non-noisy channel.

When does a species communicate with the other species? Our hypothesis is that a species will have an incentive to communicate with the other species in scenarios where competition for resources is sufficiently weak. As competition for resources between the species increases, sharing information becomes a detrimental strategy, and species will withhold information.

In the system, at each time-step, the available resources are distributed among the species such that an equal proportion of both species' populations survive. This eliminates favouritism towards a species, assuming an unstructured distribution of resources. Then, if resources are enough for both populations, then all of them survive. Of those that consumed resources, the ones that match the demands of the environmental conditions further survive and reproduce. The proportion of a population that matches the environment will depend on how much information each individual has: in the ideal case where all of them know the future environmental condition, 100% of the population that consumed resources survives and reproduce.

Then, if a species shares information with the other, the latter will increase its growth rate, since it will improve its prediction of the environmental conditions. This can be beneficial for the species that shared information, since by increasing the other species' population size, it increases the amount of environmental information that the latter can potentially share

back to the former. We note here that we are considering a system where the consequences of a species' actions can only be perceived at a later stage. However, increasing the other species' growth rate has the disadvantage that resources are depleted at a faster rate. This trade-off between environmental information and resources is what we study here through a game-theoretic scenario.

In this chapter, we characterise the relationship between resource scarcity and the evolution of communication exactly and we find that species communicate (cooperate) in abundance of resources, while they do not communicate when resources are scarce. The relative terms “abundance” and “scarce” are formally captured in our model, and we show the regimes associated to each communication behaviour for a species.

### 3.4.2 Model introduction and outline

Let us give an introduction to the model, which mainly describes the relations between the variables of the system shown in Fig. 3.1. Our system consists of populations of two species of bacterial cells,  $X$  and  $Y$ , both living in the same environment and depending on the same set of environmental conditions for survival. We assume temporarily varying conditions, and, therefore, at each time-step, one of these environmental conditions occur. We model the environmental conditions at time-step  $t$  by a random variable  $E_t$  with four states, where  $p(e_t)$  is the probability of condition  $e_t$  to occur.

Each individual cell of each species acquires information about the environment through its sensors, which are denoted  $S_{X_i t}$  for a cell  $i$  of species  $X$  at time-step  $t$ , and  $S_{Y_j t}$  for a cell  $j$  of species  $Y$  at time-step  $t$ . We denote the sensors of the *population* of species  $X$  at time-step  $t$  by the random variable  $S_{X_t}$ , and the sensors of the *population* of species  $Y$  at time-step  $t$  by  $S_{Y_t}$  (the sensor variable of a population is a function of the individual sensors, we will explain later how this is computed).

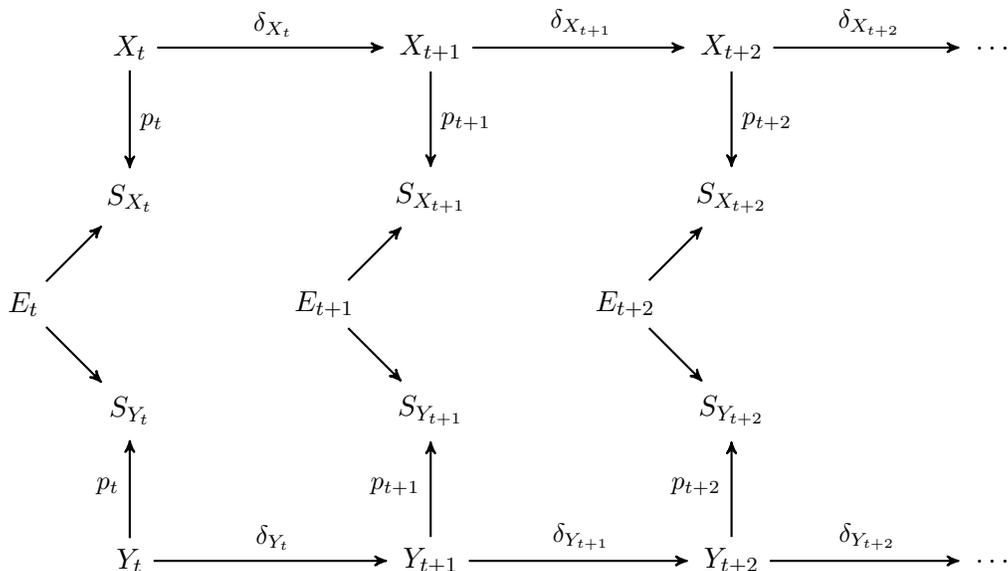


Figure 3.1: Bayesian network describing the relation between the main variables of the model.  $E_t$  denotes the environmental conditions at time-step  $t$ ,  $S_{x_t}$  ( $S_{y_t}$ ) the sensors of species  $X$  ( $Y$ ) at time-step  $t$ , and  $X_t$  ( $Y_t$ ) the population density of species  $X$  ( $Y$ ) at time-step  $t$ .

The number of individual cells of species  $X$  ( $Y$ ) that acquire environmental information at time-step  $t$  is a function of the population density  $X_t$  ( $Y_t$ ). However, only the proportion  $p_t$  of the population that consume resources (and therefore survives) is able to capture information about the environment. When resources are not sufficient for the consumption of both populations, we assume that both population densities are reduced by a proportionality factor  $p_t$ . This factor depends on the available resources (introduced later in Sec. 3.4.6), as well as on the population densities.

Now, the rate at which species  $X$  grow at time-step  $t$  is given by  $\delta_{X_t}$ , and depends on the amount of environmental information of the population at that time-step. This information can increase if, for instance, species  $Y$  shares its environmental information with  $X$ . Moreover, if species  $X$  shares back information with species  $Y$ , then species  $Y$  would have increased its growth rate by sharing information in a previous time-step. However, larger populations consume more resources, and  $Y$ 's growth rate may decrease as a consequence of sharing information. Therefore, different strategies are optimal depending on initial conditions, and this is what we will study using a game-theoretical framework.

In the following sections we explain the model in detail. The dynamics of the population are defined in Sec. 3.4.4. In Sec. 3.4.5, we explain how cells acquire information about their environment. The information is obtained from three *exclusive* sources: from environmental cues not related to bacteria (these cues infer different sensor states on bacteria, see Sec. 3.4.5); from communicated information from cells of the same species (within-species communication, see Sec. 3.4.5); and from communicated information from cells of the other species (between-species communication, see Sec. 3.4.5). In Sec. 3.4.6, we show how the environmental information each cell obtains, when a bet-hedging strategy is followed, translates into the long-term growth rate of a population. Finally, we study through a game presented in Sec. 3.4.7 the optimal communication behaviour of the species in different scenarios.

### 3.4.3 Environment

Our system consists of populations of two species of bacterial cells,  $X$  and  $Y$ , both living in the same environment and depending on the same set of environmental conditions for survival. These conditions are assumed to be independent of bacterial populations, and therefore are not affected by their consumption or production of substances in the environment. For instance, bacteria may need to adapt its phenotype to a change in temperature, or in pH levels, sugar concentration, or any combination of environmental factors. While the range of these variables may be in the continuum, we assume a partition of the range into relevant states for the organism survival.

We assume temporary varying conditions, and, therefore, at each time-step, one of these environmental conditions occur. We model the environmental conditions at time-step  $t$  by a random variable  $E_t$  with four states, where  $p(e_t)$  is the probability of condition  $e_t$  to occur. Without loss of generality, we assume  $E_t$  to be uniformly distributed. Additionally, we assume environmental conditions to be independent and identically distributed (*i.i.d.*) in time.

### 3.4.4 Population dynamics

We model the dynamics of populations of species  $X$  and  $Y$  by *logistic maps*:

$$\begin{cases} X_{t+1} = \delta_{X_t} X_t (1 - X_t) \\ Y_{t+1} = \delta_{Y_t} Y_t (1 - Y_t) \end{cases} \quad (3.1)$$

where  $X_t$  and  $Y_t$  represent the population density of species  $X$  and  $Y$  at time  $t$ , respectively. The density is the ratio of the existing population to the carrying capacity, which in our case is set to 1 for both populations.

The logistic map is a simple non-linear difference equation with complex behaviour, generally used in ecology and biology to model population growth, but also used in other research areas, such as genetics, epidemiology and economics [May, 1976]. This equation has interesting properties that makes it attractive to use, such as proportional growth at low densities and asymptotic growth at high densities. The value  $\delta_X$  and  $\delta_Y$  are the rates at which population  $X$  and  $Y$  grows, respectively, which depend on the amount of environmental information each species have obtained. For non-trivial dynamical behaviour,  $1 < \delta_X < 4$  and  $1 < \delta_Y < 4$  is required [May, 1976]. We will use values such that  $0 < \delta_X \leq 2$  and  $0 < \delta_Y \leq 2$ , assuming 2 as a reproductive limit. To define the growth rate of a species, we first need to compute how much information about the environment it acquires, which we do in the following section.

### 3.4.5 Environmental information of an individual cell

In this section we define how we compute the amount of information an individual cell obtains from each of the possible sources we are considering: its sensors, information shared by individuals of the same species, and information shared by individuals of the other species. We recall that an individual would obtain more environmental information when the density of the population of the communicating species is larger. The densities of the populations are given by Eq. 3.1.

#### Sensory information of individual cells

Each individual cell of both species sense cues from the environment. We represent the sensors of an individual cell  $i$  of species  $X$  as a random variable  $S_{X_i}$ , and the sensors of an individual cell  $j$  of species  $Y$  as a random variable  $S_{Y_j}$ . We define the conditional probabilities  $p(S_{X_i} | E)$  for every individual  $i$  of species  $X$  and  $p(S_{Y_j} | E)$  for every individual  $j$  of species  $Y$  in the system, and thus we can measure the amount of information that each individual acquires from the environment by computing the mutual information between its sensor variable and the environmental variable. These values are bounded by the entropy of the environment, which in our case is  $H(E) = 2$  bits.

In order to avoid giving an advantage to a species, we assume that all individuals of both species acquire the same amount of environmental information (this becomes important later when this amount is translated into long-term growth rate). Nevertheless, the difference between the two species is in the aspects of environmental information that they capture, as shown in the conditional probabilities Eq. 3.2 and Eq. 3.3. Individuals of species  $X$  capture information only about two states of the environment  $E$ , being unable to sense the other two states. Conversely, individuals of species  $Y$  capture information only about the two states species  $X$  cannot sense, while being unable to sense the other two states. The amount of information about the environment that an individual  $i$  of species  $X$  captures is  $I(E ; S_{X_i}) = 0.39016$  bits, the same amount as an individual  $j$  of species  $Y$ ,  $I(E ; S_{Y_j}) = 0.39016$  bits, although the intersection of the information each of them capture is  $I(S_{X_i} ; S_{Y_j}) = 0$  bits. We explain in the next sections how this assumption influences the total environmental information an individual cell can acquire, while we analyse how it affects the results obtained from our model in B.1.

$$\begin{aligned}
p(S_{X_i} | E) &:= \begin{matrix} & s_1 & s_2 \\ e_1 & \begin{pmatrix} 0.85 & 0.15 \end{pmatrix} \\ e_2 & \begin{pmatrix} 0.85 & 0.15 \end{pmatrix} \\ e_3 & \begin{pmatrix} 0.15 & 0.85 \end{pmatrix} \\ e_4 & \begin{pmatrix} 0.15 & 0.85 \end{pmatrix} \end{matrix} & (3.2) & p(S_{Y_j} | E) &:= \begin{matrix} & s_1 & s_2 \\ e_1 & \begin{pmatrix} 0.85 & 0.15 \end{pmatrix} \\ e_2 & \begin{pmatrix} 0.15 & 0.85 \end{pmatrix} \\ e_3 & \begin{pmatrix} 0.85 & 0.15 \end{pmatrix} \\ e_4 & \begin{pmatrix} 0.15 & 0.85 \end{pmatrix} \end{matrix} & (3.3)
\end{aligned}$$

### Environmental information of an individual cell obtained from within-species communication

Let us consider an individual cell  $i$  of bacterial species  $X$ . The amount of information, on average, this cell obtains from its sensors is  $I(E ; S_{X_i})$ . Now, if another cell  $j \neq i$  of species  $X$  communicates with its own species' population (as, for instance, by releasing a molecule into the extracellular environment), then, assuming cells of the same species share the same language, the information about the environment of species  $i$  increases (as well as that of the rest of the population). The total amount of information about the environment for an individual cell  $i$  of species  $X$  when another cell  $j \neq i$  communicates information is, on average,  $I(E ; S_{X_i}, S_{X_j})$ , and the increase in environmental information for cell  $i$  is  $I(E ; S_{X_j} | S_{X_i})$  (see Fig. 3.2).

The assumption about a common language that perfectly conveys the sensory state of a cell is an important one, and it allow us to simplify the model by ignoring the relationship between sensor states and output signals (which are implicitly assumed to be one-to-one in this model). A further important assumption we make regarding the population structure is that all cells perceive what other cells communicate.

As more cells communicate, the environmental information of all cells increases as shown in Fig. 3.3 (see label  $I(E ; S_{X_1}, \dots, S_{X_n})$ ), considering a carrying capacity of  $N = 15$  cells. In the same way, the amount of environmental information of cells of species  $Y$  increases with each individual exactly as it does in species  $X$  (see label  $I(E ; S_{Y_1}, \dots, S_{Y_m})$ ), with the same carrying capacity  $M$  as species  $X$ ,  $M = 15$  (this choice of value is discussed in B.1). In Fig. 3.2, we show in a different way how the environmental information of individuals increases when there is within-species communication. Each species captures exclusive bits of environmental information, and thus when individuals of the same species communicate, they can only reduce the uncertainty of one bit of environmental information.

Note that the computational complexity of the mutual information grows exponentially with the number of individual cells communicating information. Since each individual cell can be in two states, the total number of states of the whole population is  $2^{15}$  states. However, we can take advantage of the fact that the probability distribution  $p(S_{X_i} | E)$  is the same for any  $X_i \in [1, 15]$ , and thus the probability of a particular state of the population depend only on the frequencies of the states of the individuals. In this way, the total number of possible states of a population grows linearly with population size, and we can represent the states of a population conditioned on environmental conditions more efficiently, as we explain in A.1. The same reasoning is also valid for representing the population of species  $Y$ . The choice of 15 as the carrying capacity of both populations was made in order to reduce computational costs.

Finally, since both species live in the same niche, we will assume exclusive means of communication for the species, *i.e.* the chemical language used by species  $X$  and  $Y$  has no overlap.

Nevertheless, we consider a common language for between-species communication. Scenarios where bacteria use different chemical languages for within- or between-species communication are common. For instance, the bacterium *Vibrio harveyi* uses two different autoinducer signals to regulate light production and other target outputs; one mediating within-species communication, and the other between-species communication [Federle and Bassler, 2003].

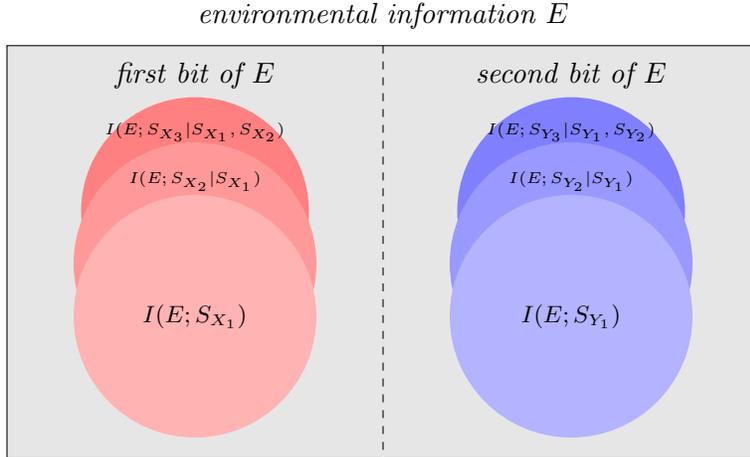


Figure 3.2: Diagram sketching the environmental information each species captures, and how this varies when there is within-species communication. Individuals of species  $X$  capture information only about the first bit of  $E$ , while individuals of species  $Y$  capture information only about the second bit of  $E$ . When, for instance, individuals of species  $X$  communicate with each other, their environmental information increases, but it only eliminates uncertainty about the first bit. In the same way, individuals of species  $Y$  communicating with each other can only increase their environmental information about the second bit of  $E$ .

### **Environmental information of an individual cell obtained from between-species communication**

In the same way as last section, individual cells also obtain information from cells of the other species. Again, we need to assume a common code between the species. However, as stated before, the chemical language used for between-species communication needs to be different from both of the within-species communication languages. Then, an individual cell  $i$  of species  $X$  acquiring communicated environmental information from cell  $j$  of species  $X$  and cell  $k$  from species  $Y$  will have an amount equal to  $I(E ; S_{X_i}, S_{X_j}, S_{Y_k})$ . In Fig. 3.3 we show the amounts of environmental information an individual cell acquires in different scenarios: with only sensory information, with within-species communication and with between-species communication.

Let us note that, since each species is specialised to capture different aspects of the environment, the contribution (from a cell’s perspective) of a first cell of the other species is significantly higher (in terms of environmental information) than that of a cell of the same species. This can be appreciated in Fig. 3.2: if we consider an individual cell 1 of species  $X$ , its environmental information is  $I(E ; S_{X_1}) = 0.39016$  bits. If cell 1 of species

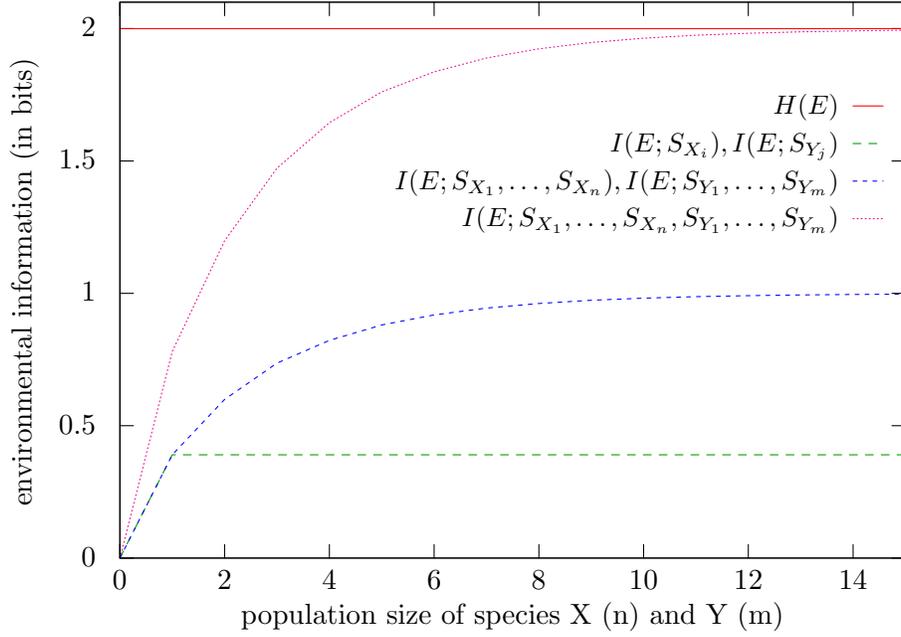


Figure 3.3: Total amount of environmental information for different scenarios:  $H(E)$  is the uncertainty of the environment,  $I(E ; S_{X_i})$  and  $I(E ; S_{Y_j})$  correspond to the case where an individual cell  $i$  of species  $X$  and an individual cell  $j$  of species  $Y$  acquire information from their sensors only, respectively.  $I(E ; S_{X_1}, \dots, S_{X_n})$  is the total amount of information of each cell of species  $X$  when  $n$  cells communicate; in the same way  $I(E ; S_{Y_1}, \dots, S_{Y_m})$  is the total amount of information of each cell of species  $Y$  when  $m$  cells communicate.  $I(E ; S_{X_1}, \dots, S_{X_n}, S_{Y_1}, \dots, S_{Y_m})$  is the total amount of environmental information each cell of both population have when  $n$  cells of species  $X$  and  $m$  cells of species  $Y$  communicate.

$Y$  communicates information, then the total amount of information for cell 1 of species  $X$  is  $I(E ; S_{X_1}, S_{Y_1}) = I(E ; S_{X_1}) + I(E ; S_{Y_1}) = 0.78032$  bits (since  $I(S_{X_1} ; S_{Y_1}) = 0$  bits); while if a cell of the same species shares information, the increase in environmental information is  $I(E ; S_{X_2} | S_{X_1}) = 0.209267$  bits, in the same way that if another cell 2 of the other species shares information, the increase is  $I(E ; S_{Y_2} | S_{Y_1}) = 0.209267$  bits.

### 3.4.6 Bet-hedging on environmental conditions

#### Long-term growth rate of a bacterial population

Bacterial cells in our system adopt one of a set of possible phenotypes at each time-step. For each possible environmental condition, we assume there is only one phenotype that meets its demands and thus allows the cell to survive. Then, cells adopting a phenotype other than the one that meets the demands of the current environmental conditions die out. This simplifying assumption will allow us to express the relationship between environmental information and

long-term growth rate in a more elegant way. We explain in Sec. 3.4.6 the consequences to our model of removing this assumption. Without loss of generality, we assume that the environmental conditions and the phenotypes are labelled from the set  $\{1, 2, 3, 4\}$ . We define the *reproduction rate*  $f$  of a bacterial cell adopting phenotype  $\varphi$  when the environmental condition  $e_t$  occur as the following function:

$$f(\varphi, e_t) = \begin{cases} 2 & \text{if } \varphi = e_t \\ 0 & \text{otherwise} \end{cases} \quad (3.4)$$

Bacterial cells are complex organisms, with intricate biochemical networks. As it is recognised in several studies, these internal networks in bacteria enable predictive behaviour in a probabilistic fashion [Libby et al., 2007, Tagkopoulos et al., 2008, Perkins and Swain, 2009]. Then, individual cells will develop one of its possible phenotypes with some probability, and we regard the probability distribution over the phenotypes as the *betting strategy*  $\pi$  of an individual cell. Which strategy do cells follow?

This part of the model is similar to the model developed in [Donaldson-Matasci and Lachmann, 2010]. If we consider a clonal population of cells, then the proportion of the population that develops a particular phenotype equals, on large populations, the probability of each cell to develop that phenotype. Considering this, we define the *growth rate* of a clonal population of bacterial cells given environmental conditions  $e_t$  as following:

$$r(f, e_t, \pi) := \sum_{\varphi} \pi(\varphi) f(\varphi, e_t) \quad (3.5)$$

In this definition, the growth rate of the population is a consequence of the betting strategy of each cell, which is the same for all cells of the population. Now, if all cells of a population are able to capture cues about the environment, then they can base their decision on the environmental cues they perceive, conditioning their strategy on them. Then, the growth rate of a clonal population of bacterial cells given environmental conditions  $e_t$  and the perceived cue  $c_t$  is defined as:

$$r(f, e_t, c_t, \pi) := \sum_{\varphi} \pi(\varphi | c_t) f(\varphi, e_t) \quad (3.6)$$

In the following sections, where we show the optimal betting strategy, we consider only one source of cues to exemplify. However, as we have explained, cells may receive information from multiple sources: from environmental cues (where, as stated, we assume these cues are not related to bacteria), from members of its own species, and from members of the other species. In Sec. 3.4.7, we show how the long-term growth rate changes for all these cases.

## Expected growth rate of a bacterial population

Which betting strategy  $\pi$  should a cell follow? The answer certainly depends on the assumptions we make about the behaviour of these organisms: in this section, we analyse the best strategy for cells that seek to maximise their population growth rate in a single generation.

In Eq. 3.6, we considered the growth rate of a population given a particular environmental condition when they perceive a particular cue. However, to analyse the possible strategies, we need to take into account all the possible environmental conditions the cells may face, in combination with all the possible cues they may perceive. The probability that a cell will face environmental conditions  $e$  together with a cue  $c$  at time-step  $t$  is given by  $p(e_t, c_t)$ . We define the *per-generation expected growth rate* of a population of bacterial cells following the betting strategy  $\pi$  as:

$$\bar{r}(f, \pi) := \sum_{e_t, c_t} p(e_t, c_t) \sum_{\varphi} \pi(\varphi | c_t) f(\varphi, e_t) \quad (3.7)$$

Since we assume that cells developing a phenotype that does not match the environment die out, and since phenotypes and environmental conditions are defined over the same set, the equation simplifies to:

$$\bar{r}(f, \pi) := \sum_{e_t, c_t} p(e_t, c_t) \pi(e_t | c_t) f(e_t, e_t) \quad (3.8)$$

However, following a strategy that maximises a cell's per-generation expected growth rate is an unlikely outcome of an evolutionary process. To see this, first we present a simple example where we do not consider (for simplicity) environmental cues: let us assume a cell can choose between two phenotypes, 1 and 2, for two possible environmental conditions, also labelled 1 and 2. The probability of each environmental condition is  $1/2$ , and we define  $f(1, 1) = 5$ ,  $f(2, 2) = 3$  and  $f(1, 2) = f(2, 1) = 0$ . In this scenario, the optimal strategy for a cell maximising its per-generation expected growth rate is to always develop phenotype 1, eventually leading to the extinction of the population once environmental conditions 2 occur.

However, if each individual develops stochastically one of its available phenotypes with non-zero probability, then for any conditions, on average, there will always be a proportion of the population that survives and reproduce, permitting the persistence and subsequent evolution of the species. For instance, if each cell in the population develops phenotype 1 with probability 0.8, and phenotype 2 with probability 0.2, then when environmental conditions 1 occur, 80% of the population (on average) survive and reproduce, while when environmental conditions 2 occur, 20% of the population (on average) survive and reproduce.

Considering that species maximising the per-generation expected growth rate eventually die out, which objective function do individual organisms seek to maximise? Several authors

have shown that a likely outcome of evolution is for organisms to maximise their *long-term growth rate* [Cohen, 1966, Slatkin, 1974, Seger and Brockmann, 1987]. The growth rate of a species over a sequence of  $n$  environments is given by:

$$G(n, f, \pi, p) := \prod_{t=1}^n r(f, e_t, c_t, \pi) \quad (3.9)$$

Here,  $e_t$  represents the environmental conditions at time-step  $t$ ,  $c_t$  is the cue received at time-step  $t$ ,  $p$  gives the joint probability  $p(e_t, c_t)$ ,  $f$  is the reproduction rate, and  $\pi$  is the betting strategy of the cell. Our goal is to find the betting strategy  $\pi$  that maximises the growth over a sequence of infinite environments, formally:

$$\max_{\pi} \lim_{n \rightarrow \infty} G(n, \hat{f}, \pi, p) \quad (3.10)$$

Since logarithm is a monotonically increasing function, then the strategy that maximises the logarithm of the growth rate will also maximise the growth rate. And, since functions of independent random variables are also independent,  $\log r(\hat{f}, e_1, c_1, \pi)$ ,  $\log r(\hat{f}, e_2, c_2, \pi)$ ,  $\dots$  are *i.i.d.*, then, first by applying the logarithm product identity and then by the weak law of large numbers, we have

$$\lim_{n \rightarrow \infty} \log G(n, \hat{f}, \pi, p) = \lim_{n \rightarrow \infty} \log \left( \prod_{t=1}^n r(\hat{f}, e_t, c_t, \pi) \right) \quad (3.11)$$

$$= \lim_{n \rightarrow \infty} \sum_{t=1}^n \log r(f, e_t, c_t, \pi) \quad (3.12)$$

$$= n E_{p(e,c)} \log r(f, e, c, \pi) \quad (3.13)$$

Here,  $E$  denotes expectation. The expected value of a random variable  $g(X)$ , where  $X \sim p$ , is given by  $E_p g(X) = \sum_x p(x) g(x)$ . The distribution of environmental conditions and cues in an infinite sequence of environments converges to the expected value, which is given by  $p(e, c)$ .

Then, we have that

$$\lim_{n \rightarrow \infty} \frac{1}{n} \log G(n, f, \pi, p) = E_{p(e,c)} \log r(f, e, c, \pi) \quad (3.14)$$

And this lead us to the definition of *long-term growth rate* of a bacterial population as

$$W(f, \pi, p) := E_{p(e,c)} \log r(f, e, c, \pi) \quad (3.15)$$

The relation between  $G$  and  $W$  is the following:

$$\lim_{n \rightarrow \infty} G(n, f, \pi, p) = 2^{nW(f, \pi, p)} \quad (3.16)$$

### Optimal long-term growth rate of a bacterial population

Which betting strategy  $\pi$  achieves the maximal long-term growth? From Eq. 3.16, we can clearly see that maximising the long-term growth rate maximises the long-term growth of a population. We define the *optimal long-term growth rate* of a bacterial population as

$$W^*(f, \pi, p) := \max_{\pi} W(f, \pi, p) \quad (3.17)$$

The long-term growth rate of a species depending on conditions  $E$ , perceiving environmental cues  $C$  with reproduction rate  $f$  is upper-bounded in the following way:

$$\begin{aligned} W(f, \pi, p) &= \sum_{e, c} p(e, c) \log \pi(e | c) f(e, e) \\ &= \sum_{e, c} p(e, c) \log \left( \frac{\pi(e | c)}{p(e | c)} p(e | c) f(e, e) \right) \\ &= \sum_e p(e) \log f(e, e) - H(E | C) - D(p(e | c) || \pi(e | c)) \\ &\leq \sum_e p(e) \log f(e, e) - H(E | C) \end{aligned} \quad (3.18)$$

with equality iff  $\pi(e | c) = p(e | c)$ . For notational convenience, we denote  $W_f^*(E | C) := W^*(f, \pi, p)$  and  $F := \sum_e p(e) \log f(e, e)$ . Now we can re-write the long-term growth rate as following:

$$W_f^*(E | C) = F - H(E | C) \quad (3.19)$$

$$= F - H(E) + I(E; C) \quad (3.20)$$

and thus we have that:

$$\lim_{n \rightarrow \infty} G^*(n, f) = 2^{nW_f^*(E | C)} \quad (3.21)$$

Equation 3.19 shows the optimal long-term growth rate for populations living in environmental conditions  $E$  perceiving environmental cues  $C$ .  $F$  is an upper bound given by the expected reproduction rate.  $H(E | C)$  is the remaining environmental uncertainty of each cell of the population given environmental cues  $C$ . Equation 3.20 shows the value of environmental cues  $C$  in the long-term growth rate, namely  $I(E ; C)$ . However, if there is at least one phenotype meeting the demands of more than one environmental conditions, then the value of  $C$  in the long-term growth rate when species follow a bet-hedging strategy is not exactly  $I(E ; C)$ , but it is bounded by this value [Donaldson-Matasci and Lachmann, 2010]. Moreover, for some non-diagonal functions of the reproduction rate  $f$ , bet-hedging is not the optimal strategy that maximises the long-term growth rate [Donaldson-Matasci and Lachmann, 2010]. Therefore, our assumption that there is only one phenotype in each species that meet the demands of each of the environmental conditions and thus survives to reproduce allows us to provide the optimal betting strategy for any case, also allowing a clear expression of the increase in long-term growth rate.

As a final remark, the value  $F$  always equals 1, and the growth rate of a population when it has no environmental information is  $2^{F-H(E)} = 2^{1-2} = 1/2$ , which means that 1/4 of the population survives and reproduces, which is the probability for an individual cell to develop a suitable phenotype by choosing one randomly. On the other hand, when the uncertainty of the environment is eliminated, let us assume by the perception of environmental cues  $C$ , then the growth rate of a population is  $2^{F-H(E|C)} = 2^{1-0} = 2$ , *i.e.* the whole population survives and reproduces, since they are all able to perfectly predict future environmental conditions.

### Growth rate of a bacterial population per time-step

We now define the growth rate  $\delta_{X_t}$  of a species  $X$  at time-step  $t$ , and the growth rate  $\delta_{Y_t}$  of species  $Y$  at time-step  $t$ . Instead of computing the growth rate of a species in one particular environment, we consider the average growth over all possible environments. The growth rate at time-step  $t$  when a species considers the information  $C$  is given by:

$$\delta_t := 2^{W_f^*(E | C)} \quad (3.22)$$

For instance, the growth rate of species  $X$  when  $n$  individuals share information only within their species is  $\delta_{X_t} = 2^{W_f^*(E | S_{X_{1t}}, \dots, S_{X_{nt}})}$ . In a similar way, the long-term growth in one time-step of species  $Y$  when  $m$  individuals share information only within their species is  $\delta_{Y_t} = 2^{W_f^*(E | S_{Y_{1t}}, \dots, S_{Y_{mt}})}$ . Here,  $n$  needs to be related to  $X_t$  (the current population density of species  $X$ ) and  $m$  needs to be related to  $Y_t$  (the current population density of species  $Y$ ).

In our model, population densities are represented by real values in the range  $[0, 1]$ , and we need to map this range to a number of individual cells to able to compute the long-term growth rate, which requires computing values  $I(E ; S_{X_{1t}}, \dots, S_{X_{nt}})$  for  $n_t$  individuals of species  $X$  and  $I(E ; S_{Y_{1t}}, \dots, S_{Y_{m_t}})$  for  $m_t$  individuals of species  $Y$ . However, only the individuals that are able to consume resources (and therefore survive) sense the environment.

The proportion of individuals that consume resources at time-step  $t$  is given by

$$p_t := \begin{cases} 1 & \text{if } R_t > X_t + Y_t \\ \frac{R_t}{X_t + Y_t} & \text{otherwise} \end{cases} \quad (3.23)$$

In Eq. 3.23, both populations survive if resources are sufficient for their consumption. However, when they are not sufficient, the proportion of each population that survives is proportional to the ratio of resources to the sum of the population densities. The dynamics of the resources is defined as follows:

$$R_{t+1} := \begin{cases} \alpha(R_t - (X_t + Y_t)) & \text{if } R_t - (X_t + Y_t) > 0 \\ 0 & \text{otherwise} \end{cases} \quad (3.24)$$

In Eq. 3.24, the resources are depleted relative to the population densities, and, if there are any left, they grow by a factor  $\alpha$ . Once resources are depleted, they remain in that state. In appendix B.3, we consider resources that are periodically replenished instead of the dynamics described above.

Now we can compute the number of individuals that sense the environment at time-step  $t$ , which is given by  $n_t = p_t \times X_t \times N$  for species  $X$  and  $m_t = p_t \times Y_t \times M$  for species  $Y$  ( $N$  and  $M$  are the assumed carrying capacity for the population of species  $X$  and  $Y$ , respectively). As stated earlier, when  $n_t$  and  $m_t$  are integers, we can represent the conditional probabilities for the populations,  $p(S_{X_t} | E)$  and  $p(S_{Y_t} | E)$ , as explained in A.1. However, when one or both of these values are not integers, we represent the conditional probabilities  $p(S_{X_t} | E)$  and  $p(S_{Y_t} | E)$  by interpolating between  $\lfloor n_t \rfloor$  and  $\lfloor n_t \rfloor + 1$  individuals for species  $X$  and between  $\lfloor m_t \rfloor$  and  $\lfloor m_t \rfloor + 1$  individuals for species  $Y$ . How we interpolate is explained in detail in A.2. Ideally, we would define a higher carrying capacity for both populations (instead of  $N = M = 15$ , the value we use in our simulations), and then we would not need to interpolate values. However, since computation costs grow exponentially, we overcome this difficulty by defining a small carrying capacity and simulating “intermediate” sizes of the population. In any case, what matters in our model is the amount of environmental information of each species, rather than the actual amount of individuals composing the population.

### 3.4.7 Game between the species

#### Introduction

In order to study the communication behaviour of the species, we set up a game where they can either share information (cooperate), or behave antagonistically. The goal of each species is to *maximise their growth rate for a local look-ahead*. We explain below why species need a look-ahead for making decisions related to communication, and how this relates to species that bet to maximise their long-term growth rate.

The game we propose here differs from traditional evolutionary game theory in that, in our model, an organism does not have an inherited (and fixed during its lifetime) strategy. Instead, we consider species whose communication behaviour depends and changes on the context.

The context of the species is composed of several variables: population densities, resource concentration, and other environmental conditions. How these variables change in time is determined by the system's dynamics. Our aim is to find optimal strategies for *communication* in different contexts, and these would serve as an indication of which communication behaviours of a species evolution would favour.

There are two important assumptions in this approach that we take: first, the species *have complete knowledge* of the current population densities and resource concentration, but their knowledge about other environmental conditions (which are relevant for their survival) depends on information that is communicated by the same/other species. Ideally, we would consider all of these factors as environmental information that a species needs to obtain by communicating (for instance, quorum sensing obtains densities estimates), but here we do not – only the survival-relevant environment state is assumed unknown to permit application of the Kelly-gambling model.

Second, the species is capable of processing the contextual information. Having complete knowledge of the former mentioned variables is not sufficient for an organism to make a decision regarding its communication behaviour. A species would need some mechanism (*e.g.* epigenetic mechanisms) that functions as a model for the dynamics of the system the species inhabits. We argue below that in order for bacteria to perceive the effects of their actions (sharing or not sharing information) in the rest of the system, at least a two-step look-ahead is necessary. In other words, the mechanism needs to be a second-order process.

Here, we are not modelling this mechanism. Instead, we are using the system's dynamics as a best case scenario for the species to make decisions. Of course, bacteria would *not* have such a detailed internal mechanism, it would be a simplified model of the dynamics that is sufficient for predicting variables of interest. However, the system's dynamics sets the limit of what is achievable in terms of optimal decisions, and when species have less information about the relevant variables, their decision-making will necessarily be worse.

Finally, in the system's dynamics, species follow a bet-hedging strategy that maximises the long-term growth rate. In the game, however, species maximise their growth rate for a defined look-ahead. There is no conflict with these assumptions: the former is a strategy related to how species bet on environmental conditions; the latter is about whether a species should share information or not. Independently of the look-ahead we are using, and under the current assumptions, species always do proportional betting.

## Species' look-ahead

For this study, we assume both species consider only a local look-ahead, and thus the horizon we will be considering in the computations is intentionally finite. For any given initial conditions  $R_t$ ,  $X_t$  and  $Y_t$ , the growth rate of a species' population at that time-step depends on the population's sensory information together with the shared information from the other species (which depends on the other species' communication strategy). Therefore, any strategy a species may take (whether it shares information with the other species or not) would not influence its immediate payoff (*i.e.* its growth rate), and hence the model does not provide an insight into how communication strategies interact with evolution. On the other hand, if we consider species with foresight, then their strategies would indirectly affect their payoffs, and here it then makes sense to analyse whether a species would share information or not.

A species that shares all of their environmental information would increase the growth rate of the other species. For instance, if species  $Y$  shares all the information it has available with species  $X$  at time-step  $t$ , then  $W_f^*(E_t | S_{X_t}, S_{Y_t}) = F_t - H(E_t) + I(E_t; S_{X_t}) + I(E_t; S_{Y_t} | S_{X_t})$ ; if it does not share any information, then  $W_f^*(E_t | S_{X_t}) = F_t - H(E_t) + I(E_t; S_{X_t})$ , which is clearly less or equal than the former value. Now, if we consider a species that maximises their growth rate at the next time-step,  $t + 1$ , then a species' payoff is, let us say for species  $X$  when species  $Y$  shares information at time-step  $t + 1$ :

$$W_f^*(E_{t+1} | S_{X_{t+1}}, S_{Y_{t+1}}) = F_{t+1} - H(E_{t+1}) + I(E_{t+1}; S_{X_{t+1}}) + I(E_{t+1}; S_{Y_{t+1}} | S_{X_{t+1}}) \quad (3.25)$$

In this equation, the terms  $S_{X_{t+1}}$  and  $S_{Y_{t+1}}$  both depend on species  $X$  and  $Y$ 's decisions at time-step  $t$ , and on species  $Y$ 's decision at time-step  $t + 1$ , but *not* on species  $X$ 's decision at time-step  $t + 1$ . Let us note  $W_{X_t}^*$  as the growth rate of species  $X$  at time-step  $t$ . While we could consider  $W_{X_{t+1}}^*$  as the value to maximise by species  $X$ , it will not reflect the consequences of the decision taken by species  $X$  at time-step  $t + 1$ . In other words, this value will be always equal for different sequences of actions (those where  $X$  shares in the last time-step, and those where  $X$  do not share in the last time-step).

On the other hand, if we consider longer (finite) decision horizons, we will incur into the same problem: the last action does not affect one's payoff. For this reason, at time-step  $t + horizon$ , we consider the payoff to be the growth rate when the other species do not share information, in a worst-case scenario for the species. In this way, all of the actions of both species influence the payoffs. Since in this study we are considering a second-order process, the minimal horizon that would show any interesting behaviour in the communication strategies is 2. For economy in the computations and simplicity, we will use this value for the horizon.

## Payoff matrix

The payoff for species  $X$  is given by

$$W_X^*(E_{t+2}|S_{X_{t+2}}) = F_{t+2} - H(E_{t+2}) + I(E_{t+2}; S_{X_{t+2}}) \quad (3.26)$$

In Eq. 3.26, the values of  $F_{t+2}$  and  $H(E_{t+2})$  are fixed. The value of  $S_{X_{t+2}}$ , however, depends on all the previous decisions taken by both species. Therefore, the payoff matrix will be composed of 16 values, since we are using a look-ahead equal to 2. This payoff matrix corresponds to the most accurate information a species could have to make a decision regarding whether it should share information or not. It is the most accurate because it is obtained from the model itself, instead of from an organism's internal approximation. An example of a payoff matrix is shown in Box 1.

To get an intuition on how the game will be played, we can imagine two opposite situations: first, with abundant resources, if a species shares information in the first time-step, it will help the other species to improve their predictions, and then the collective information of a larger population of the latter species may be “fed back” into the former species. We should note that, since resources are abundant, there is no damage for a species to share information, even if the other species do not share back. In the other case, we consider scarce resources, and then sharing information has two opposite effects: first, it increases the potential information that can be shared back, as we improve the other species' predictions on the environment, but it also decreases the total amount of available resources, which affects the information that both species capture. This trade-off between resources and environmental information is what we analyse in the following section.

### 3.5 Results

We analysed the resulting payoff matrix described above for  $250 \times 250 \times 300$  initial values (contexts) uniformly distributed in  $[0, 1] \times [0, 1] \times [0, 3]$  (the range of population density of species  $X$  times the range of population density of species  $Y$  times the range of resources' values). We look in these matrices for dominant strategies for species  $X$  (see Box 1 for strategic dominance definitions). The parameters used (those which were not yet defined) are  $\alpha = 1.05$ ,  $N = M = 15$ . In appendix B.1 we discuss the sensitivity of the parameters and the generality of the results obtained. In appendix B.2 we consider different dynamics for the resources in our simulations, where resources are replenished periodically instead of growing by a factor  $\alpha$ .

**Box 1. Strategic dominance definitions.**

The payoff matrix consists of 16 values, where each value corresponds to the growth rate of species  $X$ . Each value results from the decisions of each species of sharing or not their environmental information in two time-steps. Below is an example of a payoff matrix resulting in not sharing information being strictly dominant (see definition below) for species  $X$ , with initial values  $R = 1.0$ ,  $X = 0.304$  and  $Y = 0.392$ .

|           |        | Species Y   |             |             |             |
|-----------|--------|-------------|-------------|-------------|-------------|
|           |        | $n, n$      | $n, s$      | $s, n$      | $s, s$      |
| Species X | $n, n$ | -0.99890773 | -0.99907912 | -0.99889800 | -0.99907118 |
|           | $n, s$ | -0.99911144 | -0.99926619 | -0.99910257 | -0.99925910 |
|           | $s, n$ | -0.99891489 | -0.99908596 | -0.99890519 | -0.99907805 |
|           | $s, s$ | -0.99911738 | -0.99927174 | -0.99910854 | -0.99926468 |

We note  $s$  as the action “share information” and  $n$  as the action “do not share information”. Then, for instance,  $(n, s)$ , is a short expression of “**not** sharing in the first time-step, and sharing in the second time-step”. Let  $v, w$  be strategies in  $\{(n, n), (n, s), (s, n), (s, s)\}$ . The payoff of species  $X$  when species  $X$  plays strategy  $v$  and species  $Y$  plays strategy  $w$  is represented by  $u_x(v, w)$ .

We say a strategy  $v^* \in \{(n, n), (n, s), (s, n), (s, s)\}$  is **strictly dominant** if

$$\forall v' \in \{(n, n), (n, s), (s, n), (n, n)\}, v' \neq v^*, \text{ we have that } u_x(v^*, w) > u_x(v', w) \quad (3.27)$$

We say a strategy  $v^* \in \{(n, n), (n, s), (s, n), (s, s)\}$  is **weakly dominant** if

$$\forall v' \in \{(n, n), (n, s), (s, n), (n, n)\}, v' \neq v^*, \text{ we have that } u_x(v^*, w) \geq u_x(v', w) \quad (3.28)$$

with at least one strategy  $v'$  giving a strict inequality.

In Fig. 3.4, we show a classification of the initial values of  $R$ ,  $X$  and  $Y$  based on the resulting payoff matrices. The plots shown are the result of computing the convex hull on the classified points, and for this reason the “bottom” part of the volumes appear to be straight. This will hopefully become clear by looking at Fig. 3.5.

Figure 3.4a shows situations where there is no dominant strategy — the optimal one is conditioned on the other species’ strategy. For instance, in Table 3.1 we show an example of such payoff matrix. Here, the payoff of species  $X$  when it plays  $(n, s)$  (short for “**not** sharing in the first time-step, and sharing in the second time-step”) and species  $Y$  plays  $(s, s)$  is higher than when species  $X$  plays  $(n, n)$  while keeping  $Y$ ’s strategy the same. While this may seem counter-intuitive, since the returns (in environmental information) for species  $X$  when sharing information in the second time-step are not perceived by it due to the locality of the look-ahead, it nevertheless increases its payoff since  $Y$ ’s population mortality is increased. In Sec. 3.6 we discuss how such situations could be analysed.

For initial values where the amount of resources is higher than those of the volume of Fig. 3.4a, sharing information is weakly dominant for species  $X$ . This situation corresponds to amounts of resources such that the consumption of both populations after two time-steps

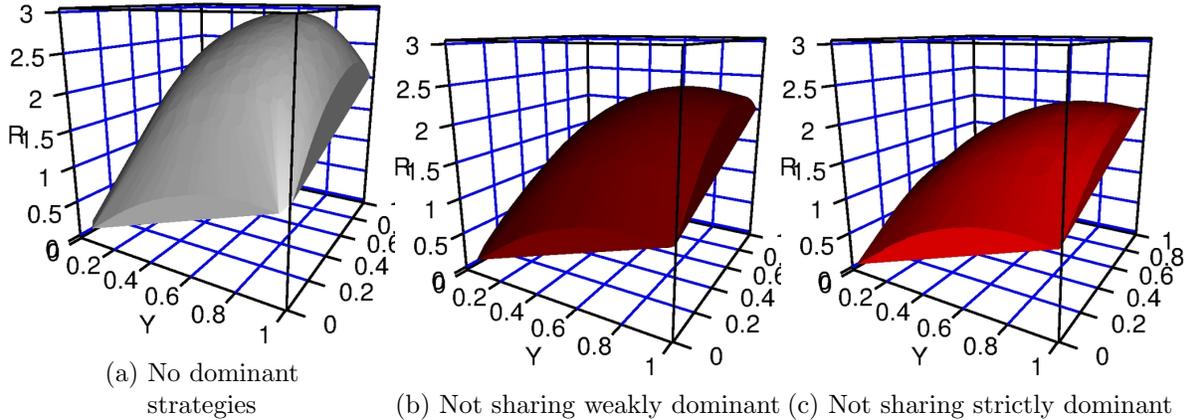


Figure 3.4: (see in colour) We analyse the payoff matrix resulting from initial values in  $\mathcal{X} \times \mathcal{Y} \times \mathcal{R}$ . We obtained five non-overlapped volumes classifying the strategies: (a) The grey volume corresponds to initial values where the optimal strategy of species  $X$  is conditioned on the strategy of species  $Y$ , and therefore there are no dominant strategies. For all points above this volume, sharing information is weakly dominant. (b) The dark-red volume corresponds to initial values where not sharing information is weakly dominant for species  $X$ . (c) The red volume corresponds to initial values where not sharing information is strictly dominant for species  $X$ . Finally, for all points below volume (c), species  $X$  will get extinct independently of its behaviour.

does not deplete them, and hence sharing information cannot hurt a species, since its growth will not be affected. Moreover, sharing information would be beneficial, in cases where the other species shares back.

For cases where the potential benefits of having extra information from the other species is always outweighed by the decrease in the populations due to the diminished resources, then not sharing information is a strictly dominant strategy (see Fig. 3.4c). In Fig. 3.4b we show the volume corresponding to initial values where not sharing is weakly dominant. This volumes “encloses” the one shown in Fig. 3.4c, where initial values can be distinguished within two types: in the first one, resources are sufficient for both species to share information only in the first time-step, and therefore, species  $X$  achieves the same payoff playing either  $(n, n)$  or  $(s, n)$  when  $Y$  plays either  $(n, n)$  or  $(s, n)$  (see Table 3.2). In these situations, the reduction of resources after the first time-step makes sharing information as damaging as the subsequent action.

For the second type of initial values, sharing information in the second time-step causes complete depletion of resources and therefore species’  $X$  subsequent extinction. A typical example of the payoff matrix for these cases is shown in Table 3.3, where we can see why the strategy  $(n, n)$  is not strictly dominant: if a species shares information in the second time-step, then species  $X$  will get extinct no matter what the other species does, obtaining the same payoff for all the other species’ options. Let us note here that a growth rate of  $-1.0$  implies the extinction of the species, since this value is a lower bound for the growth rate, and can only be achieved when the proportion of the population that acquired environmental

information is zero (which means that both populations completely die out). Finally, for all initial values of  $X$ ,  $Y$  and  $R$  below the volume shown in Fig. 3.4b, species will go extinct independently of their behaviour.

As a complement, in Fig. 3.5 we show 2D plots by fixing the amount of resources to 10 different values, in each of these values analysing  $250^2$  points uniformly distributed in  $\mathcal{X} \times \mathcal{Y}$ . The black zone corresponds to initial values of population densities in which species  $X$  go extinct regardless of its strategy. In these plots, we can more clearly visualise the described “enclosure” of the volume shown in Fig. 3.4c. Additionally, we can better appreciate the relationship between resources and population densities. Relative terms used to describe the amounts of resources such as “scarce” or “abundant” are directly correlated with the areas shown in the plots. For instance, scarce resources are in correspondence with red, dark-red and black areas; while abundant resources are in correspondence with green areas.

As resources increase in absolute values, the range of population densities for which resources are scarce gets smaller. In Fig. 3.5f, for instance, we see the red area surrounded by the dark-red areas, where values of  $X$  between the red and grey areas are those of the type exemplified by the payoff matrix shown in Table 3.2; and those between the red and the black areas are those of the type exemplified by the payoff matrix shown in Table 3.3.

The scarcity area disappears approximately when  $R \geq 2.4$ . Conversely, when resources decrease, the range of population densities for which resources are abundant also gets reduced, corresponding only to small population densities (see Fig. 3.5a and 3.5b for examples). In grey areas, resources can be considered neither scarce nor abundant. This area presents an incentive for species to coordinate behaviour. For resources values approximately of  $R > 2.8$ , then sharing information is always weakly dominant.

## 3.6 Discussion

Our theoretical model integrates two behaviours of bacteria, bet-hedging and cell-to-cell communication, which are usually studied in isolation [Perkins and Swain, 2009]. Bacterial cells follow a bet-hedging strategy, incorporating density-dependent environmental information into their decision-making process. Therefore, a cell’s communication behaviour influences the long-term growth rate of other cells. Assuming within-species communication, what can we say about the dynamics of information exchange between species?

As we have seen, environmental information is translated into long-term growth rate. Thus, cells that acquire environmental information will have an advantage over those that do not. While acquiring information (other than that which a species already has) depends solely on whether the other species shares information, the potential recipient species can actively increase the amount of information the other species may provide in the future, by sharing

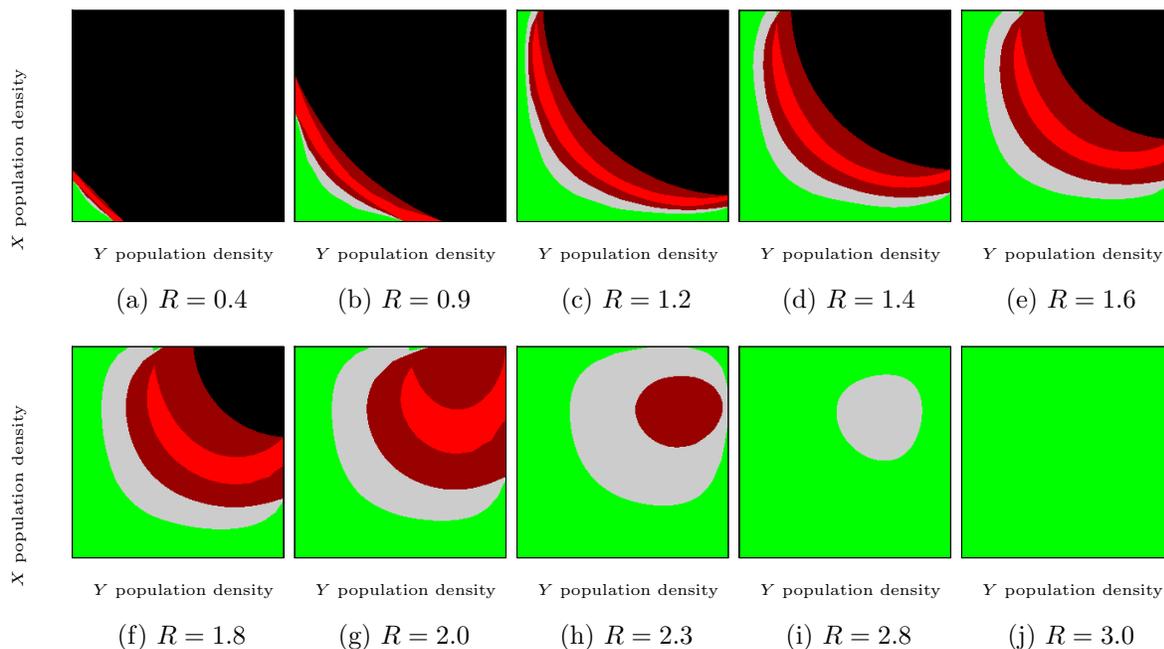


Figure 3.5: (see in colour) We analyse the payoff matrix from  $250^2$  initial values of population densities of species  $X$  and  $Y$  uniformly distributed in  $\mathcal{X} \times \mathcal{Y}$ , with the amount of resources  $R$  fixed. Green points corresponds to sharing information being a weakly dominant strategy for species  $X$ . Grey points corresponds to initial values where there is no dominant strategy for species  $X$ . Red points represent values for which not sharing information is strictly dominant for species  $X$ . Dark-red points corresponds to values where not sharing information is weakly dominant for species  $X$ . Finally, black points represent values where species  $X$  goes extinct regardless of its strategy.

information with it. The cost of this investment is zero when resources are sufficient for the consumption of both populations. Therefore, when resources are abundant, cooperative strategies between species of bacterial cells will out-compete those where none or only one of the species cooperate.

When the consumption of resources by the populations results in a reduction of resources, then the cost of sharing information is not zero any more, and it is related to the loss in the species' environmental information caused by the diminished proportion of cells perceiving the environment. In cases where a species does not share back information, the other species will always lose its investment in the first species' growth. On the other hand, when the first species does share in return, and depending on initial values, it may pay off to invest. These situations correspond to the volume shown in Fig. 3.4a, where there are no dominant strategies.

As resources become scarcer, the cost of sharing information becomes higher, and eventually the losses caused by the other species having extra information outweigh any possible benefit (volumes in Fig. 3.4b and Fig. 3.4c). In this scenario, bacterial cells developing an antagonistic behaviour will out-compete those that do not.

It becomes clear from our analysis that there is an indirect cost for sharing information which is relative to the amount of resources and to the population densities. As noted in [Lachmann et al., 2000], the immediate cost of sharing information is different from that of sharing a resource (such as food) (although there is evidence that there is a cost associated with signal production in bacteria [Keller and Surette, 2006, Diggle et al., 2007], incorporating this feature in the model would not qualitatively change the results). Namely, in the latter, the shared amount equals the losses of an organism and the gains of another, while in the former, as well as in our model, sharing information does not incur any immediate cost. However, the indirect cost of sharing information is given by the decrease in a species' environmental information, which is zero in abundance, and increases as resources become scarcer. Our model captures the relative value of resources, which dominates the species' communication behaviour.

The transition in the dominant strategy, from cooperation to antagonism, results from a change in the availability of resources: in abundance, cooperative species out-compete non-cooperative ones, while in scarcity, antagonistic species out-compete non-antagonistic ones. This is supported by the results obtained in [Requejo and Camacho, 2011, Requejo and Camacho, 2012], where there is also a transition from cooperation to defection depending on available resources. However, in this work, cooperation results (weakly) dominant in scarcity of resources, while defection is dominant in abundance. Although the results seem contradictory, the difference comes from the assumptions: for unlimited resources, cooperation, in our model, gives players an advantage, while, in their model, defection does. The model of [Requejo and Camacho, 2011] consists of a multi-agent system where the payoff of an agent when it interacts with another agent is given by

|                 |           | <b>Player B</b> |        |
|-----------------|-----------|-----------------|--------|
|                 |           | Cooperate       | Defect |
| <b>Player A</b> | Cooperate | 0               | $-E_r$ |
|                 | Defect    | $\Delta E$      | $-E_c$ |

Figure 3.6: Payoff matrix for Player A when interacting with player B

In this model, a parasitic agent will obtain from a cooperative agent a reward  $E_r$ , while paying a cost  $E_c$ . The gains obtained are given by  $\Delta E = E_r - E_c$ . Parasites always pay a fixed cost, while cooperators don't. When  $\Delta E > 0$ , this game is equivalent to a Prisoner's Dilemma. However, the rewards an agent obtains depend on limited resources, and, when they drop below the cost of defecting, then the game is transformed into a Harmony Game, where cooperation is dominant.

There are many differences between this model and ours. One is that, in their model, the cost of an interaction between two agents is fixed, while, in ours, costs are relative to a loss in growth rate. Therefore, in their model, agents will only cooperate if the benefits of cheating are lower than the costs of interacting, which happens in scarcity of resources. In our model, agents will cooperate when the costs of sharing information are zero, which happens

in abundance of resources.

The most relevant difference is what the interactions between agents are about. In their model, the agents trade resources through their actions, while, in ours, agents trade on information, which affects resources in a delayed manner. It is not clear from their model why agents would trade on a resource that is abundant: in an economy, the value of such resource is zero, which is correctly captured by our model. Then, there would be no incentive to interact. If, instead, agents trade on different resources, then their payoff matrix will need to account for this, and the model and results may be different.

Although both models capture a transition in the dominant strategies, the difference in the direction of the change is rooted in what the interactions are about. They assume that agents will interact in abundance, without a clear benefit for this, while in our model, interaction in abundance can increase a species' growth rate. The contradiction between the models arise from this assumption.

Finally, a comment regarding the complexity of the computation for bacteria of the communication strategy: contexts (initial values) where the species do not share information belong to a well-defined region that can be approximated using a threshold value. The same is valid for contexts where the species do share information. For contexts with no dominant strategies, more complicated computations are needed. One prediction that could be possible would be that simple organisms would either avoid this area because it requires more complex computation, or indeed, that even very simple organisms that operate in this region do have more complex decision-making cascades. However, we are cautious making a concrete numerical prediction, because for an experimental test a more precise understanding of the dynamics will be necessary.

### 3.6.1 Modelling bet-hedging mechanisms

In the presented model, we made a strong assumption in relation to the interpretation of the information a species obtains. Namely, we assumed that all the information communicated by one species was unambiguously interpreted by the other species, and vice versa, and they were both able to translate this information into the optimal bet-hedging strategy. However, in biological systems, information can be, for instance, ambiguous, meaningless or false, leading to the implementation of sub-optimal bet-hedging strategies.

The incorporation of a bet-hedging mechanism into the model would require explicitly modelling the actions of cells, where an action is developing into a particular phenotype. The policy of a cell would indicate how it translates the perceived information into actions. Now, in order for cells to be able to communicate, one of the following properties need to hold: either the identity of the sender is known, in which case the transmitted "message" can be fully interpreted (further assuming absence of noise in the used channel); or they would need to agree on a common language: that is, they would have identical (or similar) policies for interpreting messages, such that, no matter who the sender is, the information can still be interpreted [Burgos and Polani, 2014, Burgos and Polani, 2016b]. In other words, where

identification of the sender is not possible, then a common language is necessary in order to make sense of the information. Such framework would allow further interesting dynamics, such as parasitism, where some cells convey “false” information for the detriment of other cell’s predictions [Burgos and Polani, 2016a]. We believe that these are essential aspects to include in the study of bet-hedging mechanisms. These concepts are explored in Chapter 5.

### 3.6.2 Other interpretations of the model

Although we presented the model in a biological context, it could as well be considered in other contexts, such as economics. For instance, we could think of two software companies sharing the same market with the option to adopt two different models: open source or closed source software production. Assuming a high demand for such products, a free flow of innovations would allow higher growth rates (in terms of returns) for both companies, while, when competing for demand, a closed source model would benefit both of them.

Particularly in our model, we could consider innovations to be environmental information which is not already present in the collective information of a population. Then, if one company is more proficient than another company in developing software for a particular niche, the latter could benefit from the innovations of the former to expand its market (in our model, we assume each species is more proficient in capturing different aspects of the environment). Then, acquired innovations would be translated into higher growth rates.

It is important to note that, in our model (and under this consideration), innovations are implicitly assumed to increase with population size (see Fig. 3.3). A more truthful model should distinguish the information that is incorporated into a population (which could be redundant, innovative, or of other types), as well as how the new information is integrated with the existing information (whether it is compatible or not). Finally, our model assumes that the knowledge of *how* to perform the actions necessary to survive for certain conditions (develop a certain phenotype for bacteria, or, for a software company, produce a particular code) is available for both species or companies, and thus innovations here should be understood as new knowledge which improves the prediction of future conditions.

To consider other types of innovations, such as those that would allow the optimisation of the processes producing the actions, or even innovations that would result in new actions enabling expansion, a more comprehensive and complex model would be needed. These types of innovations allow bacteria, for example, to incorporate traits through lateral gene transfer such as antibiotic resistance, virulence attributes and metabolic properties [Ochman et al., 2000]. In the same way, software companies can integrate efficient modules performing specific tasks into their projects. As stated above, the incorporation of foreign information raises issues of redundancy and language compatibility, where reading a gene or executing a module would have to be possible, and the results of such actions would have to be integrated with the rest of the system.

In relation to this, we could also interpret our model in the framework of cellular evolution, where there is a transition from horizontal exchange of genetic material between primitive

cells (cooperation) to a stage dominated by vertical transfer (antagonism). In early stages of evolution, primitive cells would constantly exchange genetic material through horizontal gene transfer (HGT) [Woese, 2002, Woese, 2004]. These can be considered “innovations”, and would allow them to achieve higher growth rates. However, this would also present the problem we have just discussed about incorporating foreign information to a functioning system. This problem was considered in [Vetsigian et al., 2006], where they model the evolution of the genetic code accounting for universality and optimality. In their work, they consider the genetic code “not only as a protocol for encoding amino acid sequences in the genome, but also an innovation-sharing protocol” [Vetsigian et al., 2006]. While our model ignores the intricate aspects of exchange of genetic material, it offers a high level interpretation of the transition from HGT to vertical gene transfer (VGT). We discussed this interpretation in more detail in Chapter 6.

### 3.6.3 Stigmergy

As recently noted in a study of self-organisation in bacterial biofilms [Gloag et al., 2013a], bacterial communication can be considered as a type of stigmergy [Grassé, 1959], where cells modify their environment by releasing chemical signals and influence the behaviour of the cells perceiving them. This results in a coordinated collective behaviour without the necessity of a central control. In the mentioned study, the expansion in biofilms of the bacterium *Pseudomonas aeruginosa* is analysed. This bacterium has the ability to remodel its substratum to form an interconnected network of trails, which guides the transit of cells, and uses extracellular DNA to facilitate traffic flow through it [Gloag et al., 2013a, Gloag et al., 2013b].

Many distinctions have been made on the concept of stigmergy, such as sematectonic or marker-based [Wilson, 1975], quantitative or qualitative [Theraulaz and Bonabeau, 1999]. These distinctions can be considered orthogonal [Parunak, 2006], and they are important to describe in more precision the system in question: for instance, quorum sensing can be considered marker-based and quantitative, but also qualitative (bacteria recognise different chemical signals, for example in cross-species talking). Other distinctions have been proposed, one related to the duration of modifications, transient or persistent, and the other related to the structure of the population, termed broadcast or narrowcast [Heylighen, 2011].

Specifically in this study, we do not explicitly model the mentioned aspects of stigmergy, but by considering our model in the framework of stigmergy, they contribute to more accurately describe the assumptions made. First, the communication between cells is assumed to be instantaneous and transient, since in every time-step the previously shared information is not considered. Second, information is broadcasted, since every individual cell perceives the output of every other cell. Third, information is qualitative, as shown in Fig. 3.3, where the information of a population increases with population size. Finally, whether communication is marker-based or sematectonic, nothing particular is assumed in the model.

### 3.6.4 Multilevel selection

As mentioned in the introduction, we assumed in our model within-species communication in order to simplify the game-theoretic analysis. However, it would be desirable to analyse whether individual cells would share information with other cells of the same species or not by considering a communication strategy for each cell.

In this scenario, natural selection would operate at multiple levels [Wilson and Sober, 1994, Michod, 1999, Keller, 1999], where there are conflicts both at the individual level (within a species) and at the population level (between species). In our particular setting, species capture different aspects of the environment on which they depend, and we can speculate that the preference, at least initially, would be towards the other species, who contribute more to the total environmental information (see Sec. 3.4.5).

This seems contrary to kin selection [Hamilton, 1964, Smith, 1964], where individuals would prefer to cooperate with individuals of the same species (and thus maximising inclusive fitness). Instead, because of our assumption of global competition on resources, there is as much competition between kin as there is between non-kin, and since the other species provides more information about the environment, interactions with members of the other species would be preferred. Had we assumed that the contribution in environmental information from members of the same species was larger than that of the other, then the preference of cooperation would be toward kin. For the latter situation, such behaviours have been observed in the pathogen *Pseudomonas aeruginosa* [Diggle et al., 2007]. The same bacterium diminishes kin cooperation as the scale of competition becomes more local [Griffin et al., 2004]. The scale at which species compete would have a significant effect in the communication behaviour of individual cells [Griffin et al., 2004, Platt and Bever, 2009].

## 3.7 Conclusion

To conclude, we presented an information-theoretic model which integrates two aspects of bacterial behaviour, bet-hedging and cell-to-cell communication. While simple, several important aspects of communication were captured by our model: we related the communication behaviour of species to the relative availability of resources, which can be classified into three main regimes. Species would cooperate in abundance of resources, while they would behave antagonistically in scarcity. In this transition, for the situations in-between, species would have an incentive to coordinate their behaviours, adapting in response to each other's strategies.

One of the main assumptions made in this chapter is that species can fully interpret the information shared with them. In biology, organisms will have different abilities to interpret information. We address this point in the following chapter.

|           |        | Species Y   |             |             |             |
|-----------|--------|-------------|-------------|-------------|-------------|
|           |        | $n, n$      | $n, s$      | $s, n$      | $s, s$      |
| Species X | $n, n$ | -0.35204577 | -0.22381541 | -0.20745971 | -0.11033376 |
|           | $n, s$ | -0.35204577 | -0.22381541 | -0.16294896 | -0.09836764 |
|           | $s, n$ | -0.35204577 | -0.22381541 | -0.20745971 | -0.11033376 |
|           | $s, s$ | -0.35204577 | -0.23964398 | -0.16294896 | -0.15442442 |

Table 3.1: Example of a payoff matrix where there is no dominant strategy for species  $X$ . The initial values for this specific matrix where  $X = 0.5$ ,  $Y = 0.2$  and  $R = 1.8$ . Each cell contains the growth rate of species  $X$  when each species plays the correspondent sequence of actions.

|           |        | Species Y   |             |             |             |
|-----------|--------|-------------|-------------|-------------|-------------|
|           |        | $n, n$      | $n, s$      | $s, n$      | $s, s$      |
| Species X | $n, n$ | -0.46579296 | -0.31965691 | -0.27855031 | -0.25980521 |
|           | $n, s$ | -0.48390350 | -0.63747731 | -0.34778310 | -0.59688452 |
|           | $s, n$ | -0.46579296 | -0.40127033 | -0.27855031 | -0.33887903 |
|           | $s, s$ | -0.59319779 | -0.79195649 | -0.44195076 | -0.64172489 |

Table 3.2: Typical payoff matrix where not sharing information is weakly dominant for species  $X$ . The initial values for this specific matrix where  $X = 0.28$ ,  $Y = 0.76$  and  $R = 1.8$ . Each cell contains the growth rate of species  $X$  when each species plays the correspondent sequence of actions.

|           |        | Species Y   |             |             |             |
|-----------|--------|-------------|-------------|-------------|-------------|
|           |        | $n, n$      | $n, s$      | $s, n$      | $s, s$      |
| Species X | $n, n$ | -0.59296608 | -1.00000000 | -0.52533449 | -1.00000000 |
|           | $n, s$ | -1.00000000 | -1.00000000 | -1.00000000 | -1.00000000 |
|           | $s, n$ | -0.65597890 | -1.00000000 | -0.59296600 | -1.00000000 |
|           | $s, s$ | -1.00000000 | -1.00000000 | -1.00000000 | -1.00000000 |

Table 3.3: Typical payoff matrix where not sharing information is weakly dominant for species  $X$ . The initial values for this specific matrix where  $X = 0.6$ ,  $Y = 0.6$  and  $R = 1.8$ . Each cell contains the growth rate of species  $X$  when each species plays the correspondent sequence of actions.

## Chapter 4

# Evolution of communication in populations

### 4.1 Overview

In this chapter, we consider the problem of the evolution of communication within a structured population of agents. In the same way as in the previous chapter, we assume a population of agents maximising their growth rate by following a Kelly-gambling strategy. However, here, the ability of organisms to interpret information shared by others is not assumed.

The agents try to maximise their information about their environment by acquiring information from the outputs of other agents in the population. In the traditional use of information theory, it is assumed that every agent knows how to “interpret” the information offered by other agents. However, this assumes that one “knows” which other agents one observes, and thus which code they use. In our model, however, we wish to preclude that: namely, we will do away with the assumption that the identity of the agents who send the messages and those who receive them is known, and the resulting usable information is therefore influenced by the universality of the code used and by which agents an agent is “listening” to.

For this model, we assume a cooperative scenario in the population. That is, we assume that we are in the regime of abundant resources, such that communication between organisms is preferred. We postpone the analysis of conflict scenarios to first gain an understanding on the emergence of a common code in populations. We further investigate whether an agent who does not directly perceive the environment can distinguish states by observing other agents’ outputs. For this purpose, we consider a population of different types of agents “talking” about different concepts, and study whether a “blind” agent can extract new concepts by considering the agents’ outputs only.

Our hypothesis is that, in populations where agents cannot identify the source of a message, there will be an evolutionary pressure for universality in their codes.

This chapter is based on the conference paper “An informational study of the evolution of codes in different population structures” [Burgos and Polani, 2014], which won the best student paper award in the conference ALIFE 14. An extension of the paper, titled “An Informational Study of the Evolution of Codes and of Emerging Concepts in Populations of Agents” [Burgos and Polani, 2016b], was published in the *Artificial Life* journal.

## 4.2 Introduction

If we consider organisms capable of processing information, then we can argue that they must be able to internally assign meaning to the symbols they perceive in a code-based manner [Görlich et al., 2011]. For instance, bacteria perceive chemical molecules in their environment and interpret them in order to better estimate environmental conditions and (stochastically) decide their phenotype [Platt and Fuqua, 2010, Balázsi et al., 2011, Perkins and Swain, 2009]. Plants detect airborne signals released by other plants, being able to interpret them as attacks of pathogens or herbivores [Heil and Karban, 2010, Shah, 2009]. Therefore, a correspondence between environmental conditions and chemical molecules must be established. It is in this way that Barbieri characterises codes, and he proposes three fundamental characteristics for them: they connect two independent worlds; they add meaning to information; and they are community rules [Barbieri, 2003].

Codes connect two independent worlds by establishing a correspondence or mapping between them. These worlds are independent and thus there are no material constraints for establishing arbitrary mappings. The meaning of information comes exclusively from the mapping: symbols by themselves are meaningless. Finally, the third property requires that the correspondence between the two worlds constitutes an integrated system.

For instance, human languages establish a correspondence between words and objects [Barbieri, 2003]; in bacteria it is between chemical molecules and environmental and social conditions [Waters and Bassler, 2005, West et al., 2006]. Words (or chemical molecules) by themselves do not have any meaning, and each individual of a population can have its own interpretation of them, which is arbitrary to some extent. However, populations of individuals sharing the same code are ubiquitous in nature. How is it that codes come to be shared by many individuals when their constitution involve arbitrary choices for each individual? This question is what we are investigating in this chapter.

We assume a similar scenario of organisms living in a fluctuating environment to that of Chapter 3. That is, organisms will follow a bet-hedging strategy to bet on environmental conditions that maximises their long-term growth rate, where an increase in their information about the environment is translated directly into an increase in the population’s growth rate. Additionally, we assume a scenario with unlimited resources for evolution, where, as we have shown in the last chapter, sharing environmental information cannot harm a species, and those that mutually share can out-compete those that do not. The purpose of this assumption is to focus exclusively on conditions for the emergence of communication. Otherwise, as we have shown in the previous chapter, species will not share information when there is strong

competition for resources.

Those organisms obtaining additional environmental information (other than that from their sensors, which we assume does not completely eliminate environmental uncertainty) from other individuals will have an advantage over those that do not, since they would be able to better predict the future conditions. However, for individuals to be able to communicate with each other, they must be able to translate symbols into environmental conditions, where the output of these symbols is determined by an individual’s code. We consider the *code* of an individual as a mapping from its sensor states to a set of outputs.

We consider outputs (or messages) of individuals (or agents) as conventional signs. In semiotics, the science of all processes in which signs are originated, stored, communicated, and being effective [Görlich et al., 2011], two types of signs are traditionally recognised: *conventional signs* and *natural signs* [Deely, 2006]. In conventional signs there is no physical constraint on the possible mappings, they are established by conventions. Although in physical systems there can be limitations to the possible mappings that can be implemented, in this work we assume complete freedom of choice. On the other hand, in natural signs, there is always a physical link between the signifier and signified, such as smoke as a sign of fire, odours as signs of food, etc. [Barbieri, 2008].

We are not interested in the particular detailed mechanisms by which an agent implements its code, nor how the agent decodes the outputs of other agents. Instead, we focus on the theoretical limits on the amount of environmental information an agent can possibly acquire resulting from different scenarios of population structure and code distribution. The natural framework to analyse such quantities is information theory [Shannon, 1948]. However, it does not take semantic aspects into account, as it only deals with frequencies of symbols instead of what they symbolise. Codes in biology, on the other hand, add meaning to information, which makes the integration of sciences such as semiotics and information theory non-trivial [Favareau, 2007, Battail, 2009]. In Sec. 4.4, we present an information-theoretic model which incorporates the necessity of conventions by dropping from the model the usual implicit assumption of knowing the identity of the communicating units.

### 4.3 Related work

The model presented in the previous chapter implicitly assumed that individuals could fully interpret the information shared by others. For instance, when members of a population perceive a particular cue, there was an increase in the long-term growth rate equal to the mutual information between the cue and the environment. However, it is desirable that the interpretations of cues in a population are not a priori defined, mainly for two reasons: first, with common codes being typical in biology, one would like to understand in which circumstances the emergence of common codes is favoured; and second, it allows the exploration of exploitation of individuals of the population that have evolved particular interpretations of information. This last point is explored in Chapter 5, while here I review the existing literature on the evolution of communication from an artificial life perspective.

There are many models for the evolution of communication, but only a few take an information-theoretic perspective. The reason is that Shannon intentionally left out semantics from his theory of communication [Shannon, 1948], while generally in biological systems, information is useful because it has a specific meaning to the receiver. I will first introduce a useful classification of the computational methods for emergent communication, and I will briefly mention some results of similar models, with particular attention to models using information theory.

### 4.3.1 Classification of existing models

In a dated but still relevant review of the progress in the simulation of emergent communication and language [Wagner et al., 2003], the methods broadly used are classified in four categories of communication: (i) non-situated and unstructured; (ii) non-situated and structured; (iii) situated and unstructured; (iv) situated and structured. *Situated* simulations are those that place the agents in an environment, with which they interact. It is required that agents interact with the environment in “non-communicative” ways, and that they can influence it. *Non-situated* simulations consist solely of senders and receivers of signals. Then, simulations can be *structured*, where signals can be composed of other “smaller” signals; or *unstructured*, where signals are atomic.

In this thesis, we are concerned with biological systems in the situated and unstructured category. First, communication seems always to be intricately connected with tasks they need to solve (finding food, mate selection, avoiding predators, etc.) to perpetuate themselves. Models which directly reward communication are not discussed here, since we are concerned in understanding particularly the emergence of communication in an evolutionary process. Second, considering simple communication signals relaxes the complexity requirements over the organisms in consideration.

### 4.3.2 Commonalities in these models

These type of models always have prediction as the underlying objective, although in varied forms. In some of them, the agents need to distinguish properties of an object, where some properties positively affect their fitness, and other properties negatively affect their fitness. For instance, in [Cangelosi and Parisi, 1998], agents feed from mushrooms, and there are poisonous and edible ones. In [Ackley and Littman, 1994], agents need to know whether they are heading towards predators or food. Usually, agents cannot fully perceive the objects they need to predict, but they can improve them with extra information, for example that coming from a similar agent that perceives the same object in question. Then, agents have the ability to produce different signals, but initially they have no associated meaning, *i.e.* they are not related to what they need to predict. Through different scenarios and mechanisms, such as evolution or learning, such models usually establish useful associations between the conditions they need to predict and the signals they can produce [Oudeyer, 1999].

Generally, these models employ different mechanisms to control the behaviour of the agents, such as artificial neural networks, finite state machines, lookup tables, etc. This has the disadvantage of possibly introducing additional constraints on the agents, which are not directly related to their perception, making the interpretation of results harder. For example, in [Cangelosi and Parisi, 1998], they use a feed-forward neural network to control all aspects of an agent’s behaviour: movement, direction of the nearest mushroom, orientation, perceptual input of signals and emission of them. In their experimental setting, a pair of agents interact randomly, where one has full perception of the mushroom, and the other has partial or no perception at all of it. Agents have roles, where the former agent is the speaker and the latter the receiver. They found that agents achieve a relatively good consensus for signals that signify poisonous mushrooms, and signals that signify edible mushrooms. However, their experiments have not achieved perfect consensus, and it is not clear why this happened. It might be due to the experimental setting, or due to the adopted mechanisms to control the agents.

### 4.3.3 Information-theoretic models

The point is that complex settings lead to hard to understand results, and they might be adding constraints that are either unknown to the authors or not explicitly stated. Considering this, the use of information theory can alleviate these problems, by abstracting away mechanisms, and being explicit about the assumptions made. However, as I have stated, information-theoretic models do not lend themselves easily to models of “meaningful” communication. One recent study addresses this problem and defines a measure of *consistent information* between the predictions of two agents that communicate with each other [Corominas-Murtra et al., 2014].

$$X_{\Omega} \xrightarrow{P^A} X_s \xrightarrow{\Lambda} X'_s \xrightarrow{Q^B} X'_{\Omega}$$

Figure 4.1: Bayesian network representing the relationship of the variables in the model described in [Corominas-Murtra et al., 2014].

Their scenario can be illustrated by the Bayesian network shown in Fig. 4.1. There, both random variables  $X_{\Omega}$  and  $X'_{\Omega}$  take values from a finite set  $\Omega$ , and agent  $A$  codes these values using  $P^A$ , transmit them to agent  $B$  through a possibly noisy channel  $\Lambda$ , and then agent  $B$  decodes them using  $Q^B$ . They argue that maximal values of the mutual information between  $X_{\Omega}$  and  $X'_{\Omega}$  do not capture a correct reconstruction of the transmitted information. For instance, if we consider  $\Omega = \{m_1, m_2\}$ , there can be an induced mapping such that  $\Pr(X'_{\Omega} = m_1 | X_{\Omega} = m_2) = 1$  and  $\Pr(X'_{\Omega} = m_2 | X_{\Omega} = m_1) = 1$ , where the mutual information is maximised, but state  $m_1$  is “incorrectly” identified by the receiver as  $m_2$ , and state  $m_2$  is identified as state  $m_1$ . They propose a measure, which as they recognise is not an information-theoretic measure between two random variables, which captures correlations between identical labels.

Indeed, Shannon’s mutual information does not take into account the labels we use for our states, as long as they are fixed. It is assumed that all participants of a communication

process in a Shannon-like network know the probability distributions they have to operate with. In this thesis, I approach the problem of capturing semantics in information-theoretic terms, and I develop a framework where symbols acquire meaning related to environmental conditions they need to predict.

## 4.4 A model for code evolution

To introduce the model in a progressive manner, let us first consider three agents, indexed from the set  $\{1, 2, 3\}$ . Each of these agents depend on the same environmental conditions for survival, which are modelled by a random variable  $\mu$ . Agents acquire information about the environment through their sensors, which are modelled by random variables  $Y_i$ , all with values in the same set  $\mathcal{Y}$  with  $i \in \{1, 2, 3\}$ , all three conditioned on  $\mu$ . Let us assume each agent acquires the same amount and aspects of environmental information from  $\mu$ , *i.e.*  $p(Y_1 | \mu) = p(Y_2 | \mu) = p(Y_3 | \mu)$ , they are the same distributions. Let us further assume that the information each agent acquires about the environment does not eliminate its uncertainty, *i.e.*  $H(\mu | Y) > 0$ . The *code* of an agent is a mapping from its sensor states into a set of outputs, and is represented by the conditional probabilities  $p(X_1 | Y_1)$ ,  $p(X_2 | Y_2)$  and  $p(X_3 | Y_3)$  for agents 1, 2 and 3, respectively (see Fig. 4.2).

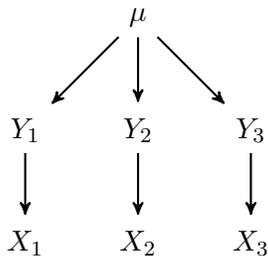


Figure 4.2: Bayesian network representing the relation between the sensor and output variables of three agents: 1, 2, and 3. The random variable  $\mu$  represents the environmental conditions.

In information theory, a *source code*  $C$  for a random variable  $X$  is a mapping from  $\mathcal{X}$  to  $\mathcal{D}^*$ , the set of finite-length strings of symbols from a  $D$ -ary alphabet [Cover and Thomas, 2002]. The codeword that corresponds to  $x$  is denoted  $C(x)$ . Our definition of a code is similar, although we are not concerned with any particular representation of the codewords. Instead, we call the result of applying a code an output, to be generic. However, sometimes we will use the term message instead of output, since we are modelling communication. Another term that we will use, particularly in the next chapter, is *encoding*, and we say that an agent encodes its perception (or its environment, depending on the model).

Source coding is used for data compression, and the entropy of a data source is the limit for its compression. However, if we transmit the compressed information from one point to another, both parties need to agree on the code in order to interpret it. The traditional use of mutual information in the model presented in Fig. 4.2 does not capture this property.

To show this, let us assume that, in the example of Fig. 4.2, agent 1 perceives only

the outputs of agents 2 and 3. One possible way of computing the information about the environment agent 1 has is to consider the mutual information between  $\mu$  and the joint distribution of the sensor of 1 and the outputs of 2 and 3:  $I(\mu ; Y_1, X_2, X_3)$ . However, by writing down this quantity, we are implicitly assuming, not only that agent 1 can interpret the outputs of both agents 2 and 3, but also that agent 1 can identify which output corresponds to 2 and which output corresponds to 3. Therefore, in this consideration, the outputs of agents 2 and 3 are uniquely identifiable as those of the particular agents by 1.

#### 4.4.1 Indistinguishable sources of messages

For this study, on the contrary, we consider an agent observing other agents' messages, but under the assumption that the source of a message cannot be identified. In this way, the total amount of information an agent can infer from the outputs of other agents will depend on to which extent it either can identify who the other agents are or can rely on them using a coding scheme that does not depend too much on their particular identity. For instance, if agents 2 and 3 both agree on the output for each of the environmental conditions, then agent 1 should be able to infer more environmental information than if they disagree on the output for each of the environmental conditions, given that agent 1 does not know which of the agents it is observing.

To model this idea, let us assume a random variable  $\Theta'$  denoting the indexed agent. This agent depends on the same environmental conditions for survival as 1, which are modelled, as above, by a random variable  $\mu$ . Agents acquire information about the environment through their sensors, which are modelled by a random variable  $Y$  conditioned on the index variable denoting the agent under consideration,  $\Theta'$ , and  $\mu$ . The amount of acquired sensory information of a specific agent  $\theta'$  about  $\mu$  is given by  $I(\mu ; Y' | \Theta' = \theta')$ . As above, the code of an agent is a stochastic mapping from its sensor states into a set of messages, and is represented by the conditional probability  $p(X' | Y', \Theta' = \theta')$  for an agent  $\theta'$  (see Fig. 4.3).

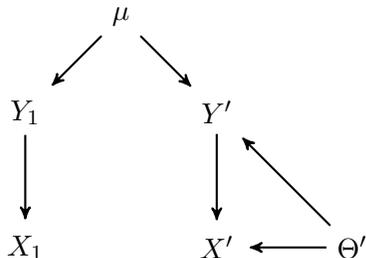


Figure 4.3: Bayesian network representing the relationships as described above (see text).

However, we want to model the fact that we do not know which agent is observed. If we do not know the value of  $\Theta'$ , then we cannot identify whose agent's output we are perceiving. In appendix C, in Sec. C.2, equations C.8 and C.9 show two examples of codes for agents 2 and 3, while their sensor states are define by the Eq. C.7 (Eq. C.6 defines the sensors states of agent 1). We compute how much information about the environment there is when agent 1 cannot identify the source of the outputs of agents 2 and 3.

If we assume  $p(\Theta' = 2) = p(\Theta' = 3) = 1/2$ , and  $p(\mu_1) = p(\mu_2) = 1/2$  and  $\epsilon = 0.01$ , then if we consider the codes shown in Eq. C.8, we have that  $I(\mu ; Y_1, X') = 0.97$  bits, where  $\Theta'$  is either 2 or 3 with equal probability. However, by setting 2 and 3 to have “opposite” codes as shown in Eq. C.9, then  $I(\mu ; Y_1, X') = 0.91$  bits, which is exactly  $I(\mu ; Y_1)$ , that is,  $I(\mu ; X' | Y_1) = 0$  bits (agent 1 cannot acquire any side information from the outputs of agents 2 and 3).

#### 4.4.2 Environmental information of a population

The model shown in Fig. 4.3 considers the environmental information of one agent only. However, measuring the average environmental information of a population will give us a good indicator of the growth rate of this population. To incorporate this option in the model shown in Fig. 4.3, we could consider the state space of  $\Theta'$  as the set  $\{\theta_1, \theta_2, \theta_3\}$ . Then, to express not only the environmental information of agent  $\theta_1$ , but the average environmental information of the whole population, we can parametrise the agent by a random variable  $\Theta$  (defined over the same state space, representing the same set of agents as  $\Theta'$ ), such that  $p(Y | \mu, \Theta) = p(Y' | \mu, \Theta')$  (*i.e.*,  $Y'$  is *i.i.d.* to  $Y$ ).

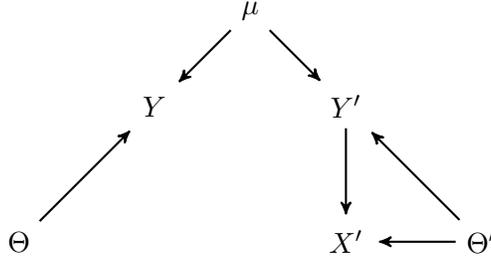


Figure 4.4: Bayesian network representing the sensor variables of a set of agents indexed by the random variable  $\Theta$ , and the sensor and output variables of a copy of the set of agents indexed by  $\Theta'$  named  $\Theta'$ .

In this way, the average environmental information of a population of the agents selected by  $\Theta$  is given by  $I(\mu ; Y, X')$  (see Fig. 4.4). Using the chain rule for information presented in Sec. 2.3, we can express this quantity as follows:

$$I(\mu ; Y, X') = I(\mu ; Y) + I(\mu ; X' | Y) \tag{4.1}$$

This decomposition of the measure shows a direct interpretation: the total environmental information corresponds to the sum of the environmental information perceived by the agents selected by  $\Theta$  (first summand) and the environmental information *added* by the messages of the agents selected by  $\Theta'$  (second summand).

This measure can be considered as the objective function to maximise in our model. We make the assumption that evolution would indeed maximise this function in the long term, since it corresponds to maximising the long-term growth rate of the population. Let us note

that, in this chapter, the considered objective functions will assume cooperative behaviour between agents, with the caveat that they are not competing for resources. In other words, those agents that favour the population’s growth rate by agreeing on their codes will be selected.

However, agents would normally not have direct access to the environmental conditions – their access is only through their noisy sensors. Then, this objective function does not give any insight about how an agent would use the information it has available in order to update its own code. For this purpose, we investigate here agents that maximise their *mutual understanding* with those agents they interact with. Although we consider this as a proxy for maximising the environmental information of the population, it does not necessarily always lead to that outcome. We discuss this in the next section. In addition, we will introduce a potentially flexible population structure, such that we can model an abstract interaction structure.

### 4.4.3 Mutual understanding

First, we introduce a copy of the codes of the agents, such that, when  $\Theta = \Theta'$ , we have that  $p(X | Y) = p(X' | Y')$ . The structure of the population is then given by  $p(\Theta, \Theta') = p(\Theta)p(\Theta')$ . However, the conditional independence of  $\Theta$  and  $\Theta'$  restricts significantly the diversity of the structures that can be represented. In such cases, the agents selected by  $\Theta$  perceive the outputs of *all* the agents selected by  $\Theta'$  (including their own clone) and vice versa. In order to model a general interaction structure between agents, we therefore consider  $p(\Theta, \Theta')$  which are not independent, as shown in the Bayesian network in Fig. 4.5, where we introduce a helper variable  $\Xi$ . This allows different agents selected by  $\Theta$  to perceive outputs exclusively from exclusive agents selected by  $\Theta'$ .

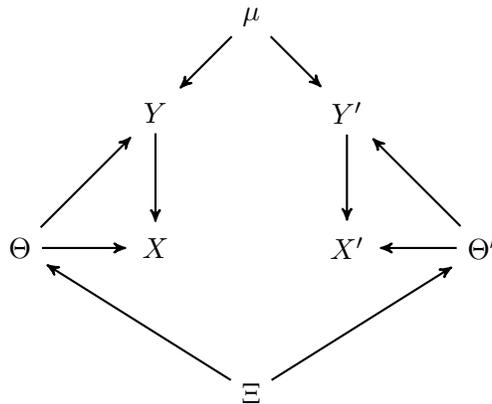


Figure 4.5: Bayesian network representing the relationship of the variables in the model of code evolution.  $p(Y' | \mu, \Theta)$  is an *i.i.d* copy of  $p(Y | \mu, \Theta')$  when  $\Theta = \Theta'$ . In the same way,  $p(X' | Y')$  is an *i.i.d*. copy of  $p(X | Y)$  when  $\Theta = \Theta'$ .  $\Theta'$  covers the same set of agents as  $\Theta$ , but its probability distribution is not necessarily the same.

We define the *mutual understanding* of a population as  $I(X ; X')$ , which takes into ac-

count the structure of the population, given by  $p(\Theta, \Theta')$ . This joint probability induces a weighted graph, where agents represent the nodes of the graph and there is an edge from agent  $\theta$  to an agent  $\theta'$  if  $p(\theta, \theta') > 0$  (which is the weight of the edge). We interpret  $p(\theta, \theta')$  as the probability of interaction between these two agents, and thus we require that  $p(\theta, \theta') = p(\theta', \theta)$  (interactions are symmetrical) and  $p(\theta, \theta) = 0$  for every agent  $\theta$  (self-interaction is excluded).

To get an intuition on the consequences of maximising the mutual understanding, we first informally analyse a few scenarios. For instance, when the interaction probability of two agents is zero, then their mutual understanding is irrelevant for the objective function. On the other hand, the ability for an agent to understand all of its sources will depend exclusively on the source's universality: this follows from its inability to identify who is talking. Then, the mutual understanding of two fully interacting subsets of agents will be maximised when all sources for each of the agents have the same code. A non-empty intersection between these two subsets implies that the mutual understanding is maximised when codes are universal between both subsets. When the intersection between them is empty (let us note that the induced graph is then bipartite), then each subset of agents is allowed to have a different code. It is important to note here that this model allows the agents to cluster into different sub-populations due to the differences in their codes. Therefore, each sub-population could have its own conventions for representing different aspects about the environment, and the conventions used can vary. Let us note that this fitness function, as well as the population's environmental information, assumes cooperative behaviour in the agents.

As we mentioned above, agents maximising their mutual understanding do not need direct access to the environment. For instance, a possible mechanism to maximise this could be for agents to update their codes such that they express the most popular output of their sources for each environmental condition. In this way, the agent relates its perception of the environment with the most popular output. Let us note that, even expressing a different output from the most popular one, it is still possible to maximise the mutual understanding, given that there is consistency across environmental conditions.

The environmental information of an agent  $\theta$  perceiving messages from the agents it interacts with is given by  $I(\mu; Y, X' | \Theta = \theta)$ . Let us note that, given that the interaction graph is symmetric, it can also be measured by  $I(\mu; Y', X | \Theta' = \theta)$ . The average environmental sensory information of the population is given by  $I(\mu; Y)$ , or equivalently,  $I(\mu; Y')$ . The average environmental information of the population when they consider their sensory perception and the messages of other agents according to the population structure is given by  $I(\mu; Y, X' | \Theta)$ , or equivalently, by  $I(\mu; Y', X | \Theta')$ . These values are bounded by  $I(\mu; Y, Y' | \Theta)$ , which corresponds to the maximum achievable average population growth rate when communication/signalling is perfect.

$$I(\mu; Y, X' | \Theta) \leq I(\mu; Y, Y' | \Theta) \tag{4.2}$$

## 4.5 Results

In this section, we put the model to test by analysing different scenarios where the mutual understanding is maximised. This objective function has a large number of local optima, and the outcomes certainly depend on our initial values and the way we traverse this landscape. However, a strength of the model is that every local optimum, which has the mutual understanding maximised, has the same property: all sources of messages for each agent has universal codes. This allows for general statements about how the assumptions lead to particular outcomes.

In all the experiments below, we assume that the conditional probabilities for sensors are defined as follows:

$$p(y | \mu, \theta) := \delta_{y,\mu}(1 - \epsilon) + \frac{\epsilon}{|\mu| - 1}(1 - \delta_{y,\mu}) \quad (4.3)$$

In this way, Eq. 4.3 introduces symmetric noise controlled by a parameter  $\epsilon$ . When  $\epsilon = 0.0$ , all agents capture unequivocally the same aspects of the environment, and  $I(Y ; Y) = H(Y)$ . However, with environmental noise, their perceptions are not related to one environmental state only, but to all of them with a peaked probability on one of them. As the noise increases, the peak value decreases, and we consider noise values until  $p(y | \mu)$  is uniformly distributed, which happens when  $\epsilon = \frac{|\mu|-1}{|\mu|}$ , giving  $I(Y ; Y') = 0$  bits.

Unless stated otherwise, we assume that  $|\mu| = |Y| = |X| = 8$ , that is, the number of states for the environment, the sensors, and outputs, is 8. The probability of the environmental states is uniformly distributed.

### 4.5.1 Well-mixed population

In the first scenario, each agent  $\theta_i$  perceives the output of every other possible agent  $\theta_j$  with the same probability, that is  $p(\theta_i, \theta_j) = 1/n(n-1)$  for every  $i, j \in [1, n]$ , where  $n$  is the population size. We consider a population of size 64, with an  $\epsilon = 0.07$ . The conditional probabilities  $p(X | Y)$  are optimised to maximise the mutual understanding. After maximisation, we obtained  $I(X ; X') = 1.67$  bits. Considering only the individual sensory input for the agents of the population, their growth rate is related to  $I(\mu ; Y) = 2.43$  bits (we say that the growth rate is “related” since, as we showed in Eq. 3.20, the actual long-term growth rate is  $F - H(\mu) + I(\mu ; Y)$ , where  $F$  is a value obtained from some fitness function). However, after maximisation of their mutual understanding, they would have improved their growth rate in an amount related to their environmental information which considers their sensory input together with their messages, given by  $I(\mu ; Y, X' | \Theta) = 2.76$  bits. In Table 4.7, we analyse different noise values, showing the benefit of communication for low/high noise scenarios.

By inspecting the resulting codes (see Fig. 4.6) we observe two properties: first, codes

are universal; and, second, agents can only distinguish 6 out of the total 8 sensory states (distinguishing all of them would certainly increase the environmental information, but not necessarily the mutual understanding). We explain why we obtain these properties below.

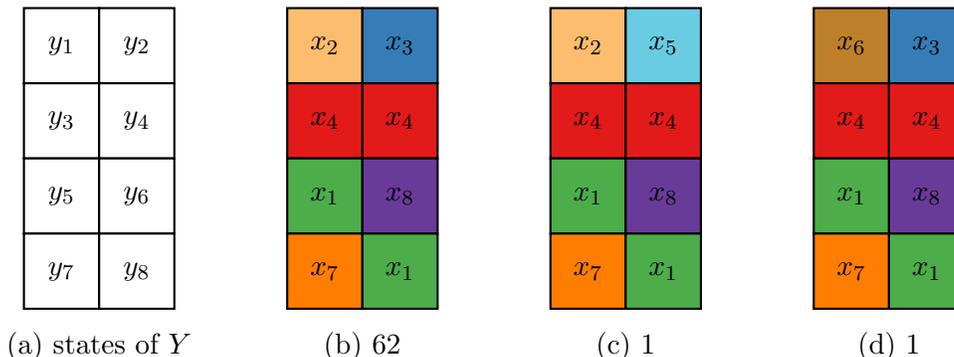


Figure 4.6: (a) Illustration of the sensory states in a grid. (b-d) Compact representation of a code  $p(X | Y)$ . For example,  $x_2$  in code (b) is in the left top corner of the grid, and so is  $y_1$  in (a). Then, this means that  $p(x_2 | y_1) = 1$ . The states  $X$  are coloured to make clear how many states a code can distinguish from  $Y$ . Below each code we show the amount of agents that adopted the code shown, which induces a partition of the sensory states.

Figure 4.6 shows three types of codes, which are represented by partitioning the sensory states according to  $p(X | Y)$ . The number of states that results from the partition is the number of states an agent can distinguish from its sensory states.

In this example, we say that the codes in the population are universal, although there are three types of codes. The reason lies in the non-semantic assumption of information theory: how we label the states of random variables is irrelevant for the computation of Shannon’s information-theoretic measures. For instance, state  $x_5$  (Fig. 4.6 (c)) denotes the same state as  $x_3$  in Fig. 4.6 (b) and (d); and, in the same way, state  $x_6$  (Fig. 4.6 (d)) denotes the same state as  $x_2$  in Fig. 4.6 (b) and (c). These are synonyms, because they have exactly the same correspondence (although stochastic in the case of noisy sensors) to the environmental states.

The question now is why the objective function settles in such an optimum. After all, a change in any code of any agent that would distinguish one more state of its sensors (7 instead of the achieved 6) would increase the mutual understanding. However, here we show that the adoption of synonyms can be disadvantageous when there is a limited set of outputs  $X$ . For example, had all agents adopted the code shown in Fig. 4.6 (b), then a change in the code of any agent that distinguishes sensory states  $y_3$  and  $y_4$  by using an unused output would increase the mutual understanding. However, this is not possible since all outputs are in use, and any update would create inconsistencies that decrease the objective function.

An inconsistency would be expressing different sensory states with the same output  $x$ . For example, the output  $x_6$  is not used in the code scheme (b) in Fig. 4.6, then we could use it such that  $p(x_6 | y_3) = 1$ . Now, agents with this updated code scheme would be able to distinguish between  $y_3$  and  $y_4$ . However, since there is one agent using this output to encode sensor state  $y_1$ , and since the population is *well-mixed*, then agents perceiving output  $x_6$  cannot distinguish whether it refers to  $y_1$  or  $y_3$ .

Let us note that increasing the available alphabet for choosing outputs alleviates this problem: the larger the set, the most likely it is that agents would be able to distinguish all of their sensor states. Typical solutions for doubling the alphabet ( $|X| = 16$ ) shows a large number of synonyms, but yet agents can distinguish all of their sensor states (results not shown).

### Noise variation

Our results have shown that a well-mixed population always leads to the emergence of a universal code for communication, assuming a cooperative scenario. Now we analyse whether these properties still hold when we vary the noise in the sensory input. Particularly, we ask if our original solution is still optimal when we vary the noise in the sensory input. If, as a result of this test, the obtained solution is still optimal, then our previous analysis is still valid independently of noise values. Let us note that the fitness landscape may change for different noise values, but our concern at this point is with the properties of optimal values, and not with the precise details of how the global optimum is reached.

| $\epsilon$ | $I(Y ; Y')$ | $I(X ; X')$ | $I(\mu ; Y)$ | $I(\mu ; Y, X'   \Theta)$ |
|------------|-------------|-------------|--------------|---------------------------|
| 0.00007    | 2.99761     | 2.50        | 2.99874      | 2.99975                   |
| 0.0007     | 2.98079     | 2.48        | 2.98969      | 2.99766                   |
| 0.007      | 2.85492     | 2.37        | 2.92018      | 2.97780                   |
| 0.07       | 2.05331     | 1.67        | 2.43756      | 2.76741                   |
| 0.14       | 1.45372     | 1.17        | 2.02273      | 2.50325                   |
| 0.28       | 0.68195     | 0.53        | 1.35849      | 1.91497                   |
| 0.56       | 0.06954     | 0.05        | 0.43829      | 0.72595                   |

Figure 4.7: Summary of further optimising the solution found in Sec. 4.5.1 by varying the value of  $\epsilon$  for the sensory input (defined in Eq. 4.3). For each  $\epsilon$  value,  $I(Y ; Y')$  is the upper bound resulting from it, and  $I(X ; X')$  is the result of further optimising the mutual understanding. In all these cases, the original solution (obtained from  $\epsilon = 0.07$ ) remained the same. We also show the average environmental sensory information of the population,  $I(\mu ; Y)$ , for each considered noise value; and the average environmental information by considering together sensors and messages, given by  $I(\mu ; Y, X' | \Theta)$ .

In Table 4.7 we show the results for further optimising the original solution (with  $\epsilon = 0.07$ ) represented in Fig. 4.6, for different  $\epsilon$  values. In all of them, the equilibrium point from the original solution did not change with the updated noise value.

### 4.5.2 Spatially-structured population

We analyse here how the structure of a population influences the outcomes in the agent’s codes. The population structure abstracts away space, and thus it allows the representation of any type of space. Here, we study the maximisation of mutual understanding for structures that “segregate” agents of the population into clusters. We consider  $c$  clusters of agents of equal size, having  $d = n/c$  agents per cluster (we consider only values of  $c$  where the remainder of the division is zero), and we specify a population structure such that there are two classes of interaction: between agents of the same cluster, and between agents of a different cluster. We index the clusters in the range  $1..c$ , and we say two clusters are neighbours if their indexes are neighbours, assuming 1 and  $c$  are also neighbours. In this way, each cluster has exactly two neighbours, and we define the population structure as shown in Eq. 4.4.

$$p(\theta_i, \theta_j) := \begin{cases} \frac{p}{c \times d \times 2 \times d} & \text{if } \theta_i \text{ and } \theta_j \text{ belong to neighbour clusters} \\ \frac{1-p}{c \times d \times (d-1)} & \text{otherwise} \end{cases} \quad (4.4)$$

Equation 4.4 defines the population structure as a function of  $p$ . The number of interactions of one agent with agents of other clusters is  $2 \times d$ , and since we have  $n = c \times d$  agents in total, the total number of interactions is  $c \times d \times 2 \times d$ . Then, the number of interactions of one agent with agents of the same cluster is  $d - 1$ , and we have  $c \times d$  agents in total, giving  $c \times d \times (d - 1)$  interactions.

When  $p = 0$ , agents interact only with agents of the same cluster; when  $p = 1$ , agents interact only with agents of neighbour clusters; and when  $p = (1 + (d - 1)/2d)^{-1}$ , agents interact with agents of neighbour clusters as well as with agents of the same cluster with equal probability. In the experiments done here, we use  $c = 8$ , which gives  $d = 8$  (the number of agents per cluster). We are interested in analysing these cases and those where agents interact “mostly” with agents of the same cluster (*e.g.*  $p = 0.15$ ); and where agents interact “mostly” with agents of neighbour clusters (*e.g.*  $p = 0.85$ ). In all experiments, we use  $\epsilon = 0.07$ . We plot the results as a graph, where nodes represent agents and are coloured according to their adopted codes (colours between different experiments are not related!), and there is an edge between nodes if the respective agents interact. Edges are in grey scale, relative to the maximum of all probabilities of interaction (black represents the maximum).

Not surprisingly, when agents interact *only* with agents of the same cluster, their adopted codes are uniform within clusters, but vary between them (see Fig. 4.8). It is possible, although unlikely, that agents in disconnected clusters develop the same code. The same outcome is achieved when agents interact mostly with agents of the same cluster, but also with agents of neighbour clusters (see Fig. 4.9). Here, a universal code among all clusters would be the optimal solution. However, the low interaction probability with other clusters does not bring enough pressure to achieve global consensus, and deviating from a cluster’s code would decrease the mutual understanding. Nevertheless, we expect the adopted codes between clusters to be “closer” to each other when there is interaction between clusters.

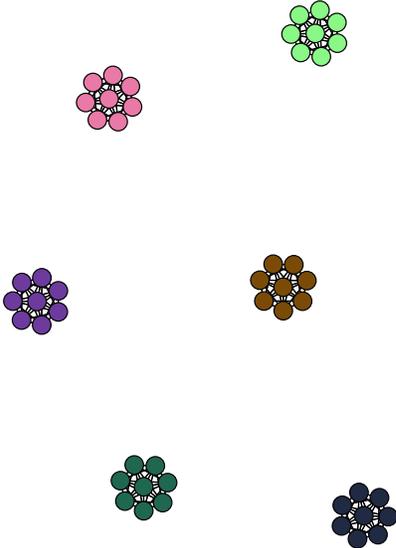


Figure 4.8: Result of codes for  $p = 0.00$ . Here, agents interact *only* with agents of the same cluster.

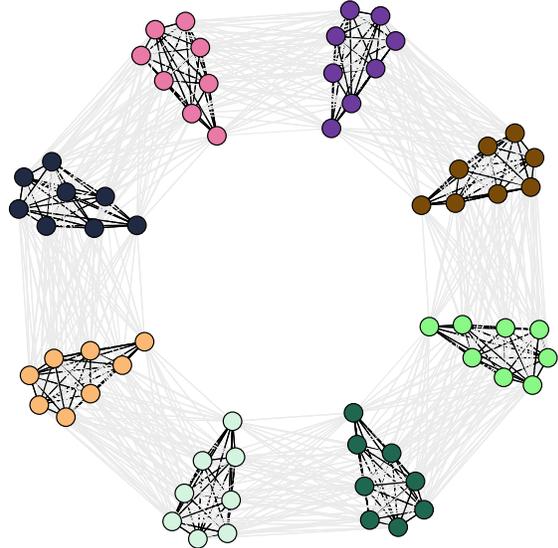


Figure 4.9: Result of codes for  $p = 0.15$ . Agents interact “mostly” with agents of the same cluster, but also with agents of neighbour clusters.

Although we do not have a distance metric between codes, we can get an idea of how close codes are by updating the population structure to a “well-mixed” one, and keeping the configuration of codes. In the extreme case were all agents agree on their codes, the mutual understanding will remain the same. However, if agents of neighbour clusters *partially* agree on how they express environmental conditions, the mutual understanding would decrease, because there will be disagreement, but not as much as if they did not agree on their codes *at all*. Our hypothesis is that, as the interaction between clusters increase, the pressure to agree on codes would be higher, favouring the agreement for expressing some environmental aspects. In Table 4.14, we show a summary of the results, which are discussed later.

We ask now what would happen if agents interact with agents of the same cluster and of neighbour clusters with the same probability. In the case where  $d = 8$ , this value corresponds to  $p = 0.69$ . Interestingly, agents belonging to the same cluster agree on their codes (see Fig. 4.10). It is not clear at first sight why this would happen, after all, any agent interacts with the same probability with 23 other agents (8 from one neighbour cluster, 8 from the other neighbour cluster, and 7 from its own cluster). Why agents do not agree on their codes among neighbours? In the case they do agree, then the only solution is universality, since agreement is needed within and between clusters. Solutions of universal codes are unlikely to happen with such structures, since early disagreements on the codes in the optimisation process can still produce an increase in the objective function. Then, once a few of these conventions are established, the possibility of full agreement between the codes is highly constrained by inconsistent ways of expressing same environmental aspects between neighbour clusters. We can test this hypothesis by “cutting” the interactions between two clusters, therefore having two of them interacting with one cluster only. The results are shown on Fig. 4.11, where we see that those clusters that have only one neighbour cluster indeed adopt the same code as their neighbours.

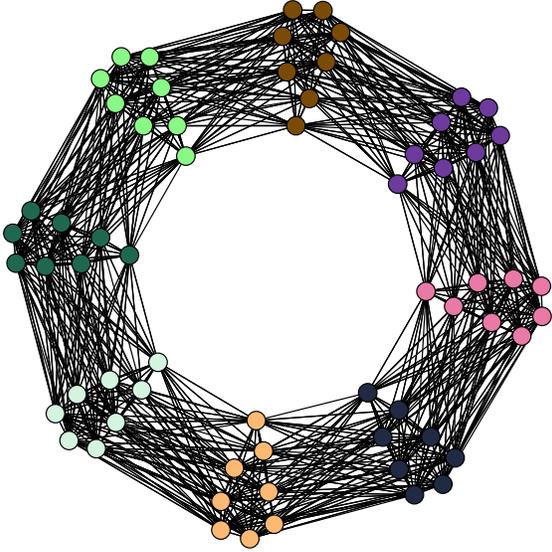


Figure 4.10: Result of codes for  $p = 0.69$ . Agents interact with agents of the same cluster and with agents from neighbour clusters with the same probability.

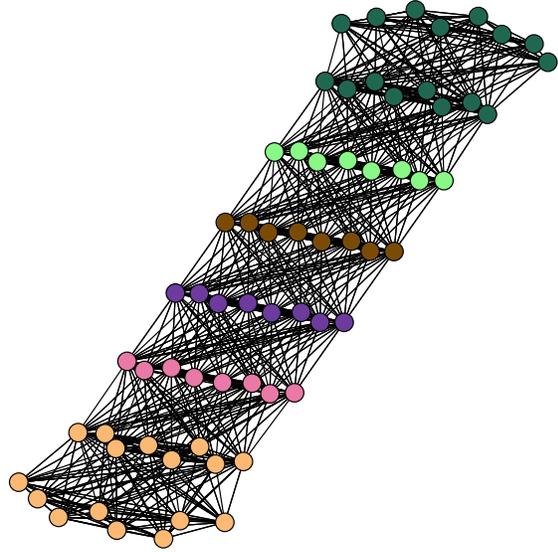


Figure 4.11: Agents interact with agents of the same cluster and with agents from neighbour clusters with the same probability, but we “cut” interactions between two clusters only.

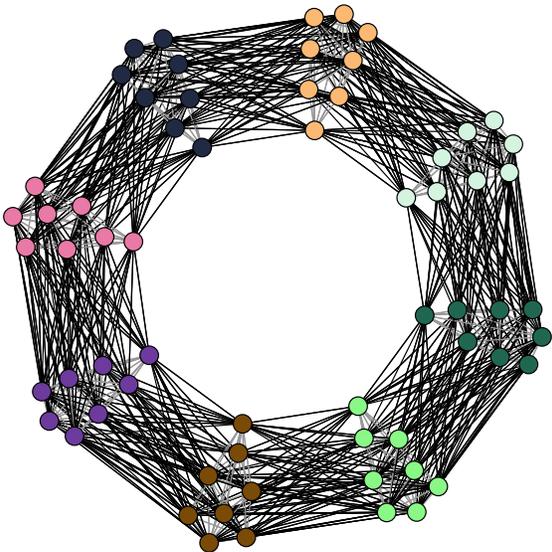


Figure 4.12: Result of codes for  $p = 0.85$ . Agents interact “mostly” with agents of neighbour clusters, but also with agents of the same cluster.

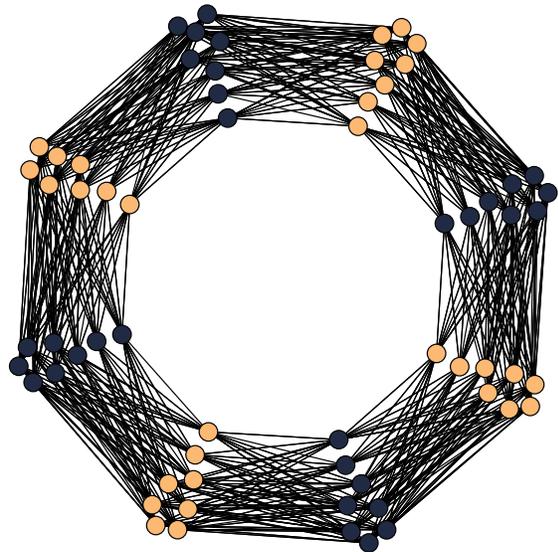


Figure 4.13: Result of codes for  $p = 1.00$ . Here, agents interact *only* with agents of neighbour clusters.

Similarly to what happens when the interaction probability is homogeneous, when agents interact mostly with agents of neighbour clusters ( $p = 0.85$ ), then they adopt common codes on a cluster basis (see Fig. 4.12). Here again, updates of codes are constrained by having to agree with two neighbour clusters. Finally, we analyse what happens when agents interact only with agents of neighbour clusters. In this case, the pressure to agree on a code is only with agents belonging to a cluster’s neighbours. Nevertheless, agents from the same cluster still agree on their codes, even if they do not interact at all (see Fig. 4.13). This is because each agent of a particular cluster is the source to agents of other clusters, and uniform sources increase the mutual understanding. In Fig. 4.13 we see that there is agreement in the adopted codes of all clusters that are neighbours of a common cluster, therefore having only two codes in the population, with agents that adopted one code interacting only with agents that have adopted the other code. This differs with the previously done experiment (shown in Fig. 4.12), where all clusters had different codes. In this experiment, the exploration of codes is less constrained, and therefore more likely to adopt the same code as your neighbour’s code.

| $p$  | $I(X ; X')$ | $I_w(X ; X')$ | $I(\mu ; Y, X'   \Theta)$ | $I_w(\mu ; Y, X'   \Theta)$ |
|------|-------------|---------------|---------------------------|-----------------------------|
| 0.00 | 2.11        | 0.10          | 2.72615                   | 2.54814                     |
| 0.15 | 1.57        | 0.07          | 2.68146                   | 2.53771                     |
| 0.35 | 1.32        | 0.31          | 2.65776                   | 2.59305                     |
| 0.69 | 1.42        | 0.97          | 2.70794                   | 2.68105                     |
| 0.85 | 1.49        | 1.23          | 2.73340                   | 2.70600                     |
| 0.95 | 1.95        | 1.30          | 2.73081                   | 2.71301                     |
| 1.00 | 2.24        | 1.24          | 2.69970                   | 2.69970                     |

Figure 4.14: Summary of optimising the mutual understanding for different values of  $p$ , determining the population structure according to Eq. 4.4. To test how “close” the evolved codes of each cluster are from each other, we change the population structure to a well-mixed one, while keeping the codes of each agent, and then we compute the mutual understanding, denoted  $I_w(X ; X')$ . We also show the average environmental information of the agents,  $I(\mu ; Y, X' | \Theta)$ , and how this changes when we change the population structure  $I_w(\mu ; Y, X' | \Theta)$ .

In Table 4.14, we show a summary of the results for different values of  $p$ . We analyse here how “close” the adopted codes of all solutions are, where closeness is given by the mutual understanding by updating the structure to a well-mixed one. In case of full disagreement between all clusters (each cluster represents a state of the environment differently than all the remaining clusters), we have that  $I_w(X ; X') = 0.00093$  (the subscript  $w$  means that the population structure was updated to a well-mixed one). Then, any increase of this value would denote at least partial agreements between the agent’s codes. With full agreement, the maximum mutual understanding is  $I_w(X ; X') = 2.05331$ . Table 4.14 shows that, in general, higher interaction probabilities between agents of different clusters results in closer codes. Closer codes enable a faster potential integration between clusters. Moreover, we see that the environmental information does not significantly decrease in those cases.

### 4.5.3 Flexible population structure

In another consideration, we let the structure co-evolve with the codes without any constraint (the probability distribution of the interaction between agents,  $p(\Xi)$ , is optimised together with the codes). In this case, agents will cluster with other agents preferring uniformity of sources. That is, an agent can incorporate another agent as a source if the latter's code does not create inconsistencies with the rest of the sources of the former. In a similar way, it can avoid interactions with agents that encode their perception with different symbols. In this optimisation process, agents that do not fit in any cluster (because of their codes) are isolated.

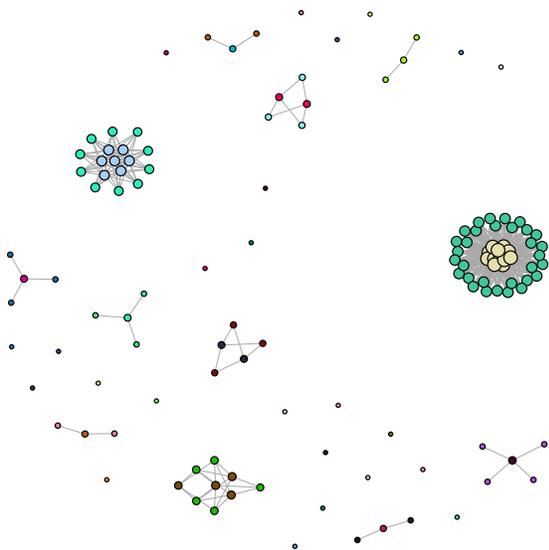


Figure 4.15: Result from maximising the mutual understanding with an evolving population structure with 128 agents.

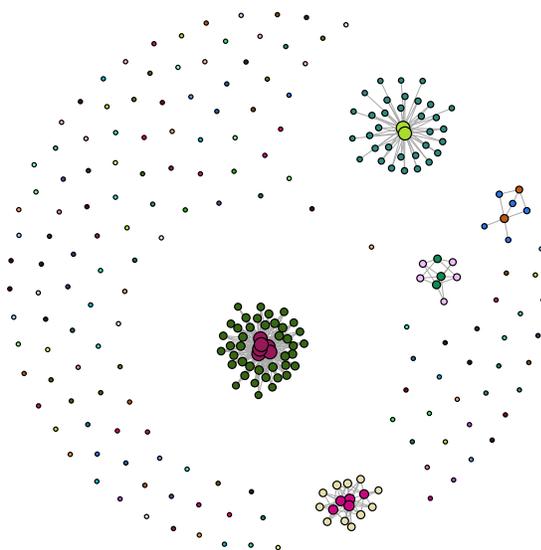


Figure 4.16: Result from maximising the mutual understanding with an evolving population structure with 256 agents.

Two examples are shown in Figs. 4.15 and 4.16. In each of them, we see that all sources of every agent have the same code, which is the condition for maximisation of the mutual understanding. However, each sub-population have two different codes, and all of the sub-populations are bipartite (agents with the same code do not interact with each other, only with agents with codes different than theirs). The reason why we have this property is that agents in the same sub-population would encode environmental conditions by using overlapping outputs, and therefore creating inconsistencies for their understanding. However, this does not always have to be the case, and it is possible to have sub-populations with uniform codes as well as bipartite ones. This could happen, for instance, where one sub-population only uses outputs that are uniquely interpretable among all agents, and other sub-populations use outputs whose meaning depends on the agent we are looking at (context dependent).

Let us compare the codes of one sub-population to understand why agents avoid interactions with agents of the same code type. The codes shown in Fig. 4.17 exemplifies this. In these codes, there are two types of differences between them: some of them correspond to synonyms, such as  $x_5$  on code (b) is a synonym of  $x_{14}$  on code (c), or  $x_9$  and  $x_8$  on code (b) are synonyms of  $x_{16}$  on code (c). These are universal synonyms in the sub-population: that

is, independently of which agent we select, they always refer to the same set of perception states, which in turn refer to the same set of environmental states (due to all of them having the same conditional probability for sensory input, as define in Eq. 4.3).

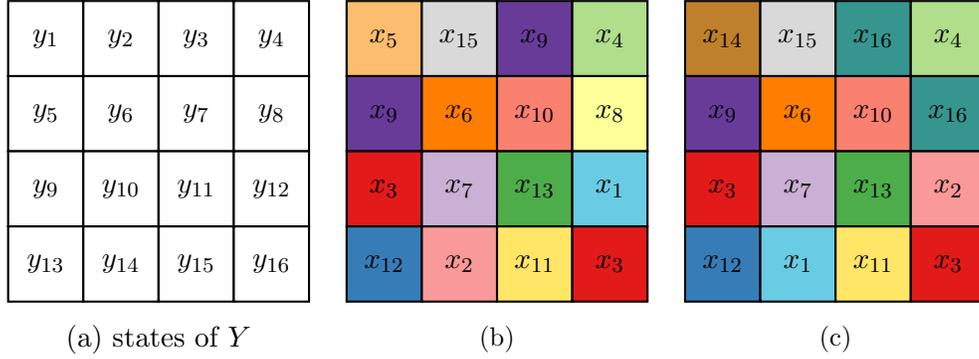


Figure 4.17: (a) Illustration of the sensory states in a grid. (b-c) Compact representation of a code  $p(X | Y)$ . For example,  $x_5$  in code (b) is in the left top corner of the grid, and so is  $y_1$  in (a). Then, this means that  $p(x_5 | y_1) = 1$ . The states  $X$  are coloured to make clear how many states a code can distinguish from  $Y$ .

On the other hand, some synonyms are context-dependent, such as  $x_1$  and  $x_2$ , which refer to perception states  $y_{12}$  and  $y_{14}$ , depending on the code of the agent. For an agent perceiving messages from agents with a code scheme like 4.17 (b), then  $x_1$  refers to the perception state  $y_{12}$ ; while, if an agent perceives messages from agents with a code scheme like 4.17 (c), then  $x_1$  refers to the perception state  $y_{14}$ .

This constrains the choice interaction partners (or sources of messages): agents cannot mix their interactions with agents of different codes, because they would be inconsistent with each other. Why agents do not interact with agents of their own type only? To answer this, let us look at what the maximisation of mutual understanding achieves: the resulting mapping  $p(x | x')$  is universal across sub-populations. Early in the optimisation of the mutual understanding, trends for this mapping are established, and changes to reverse these trends require a larger amount of updates than the ones needed for updating the structure. Therefore, bipartite sub-populations emerge as a solution to avoid inconsistencies.

#### 4.5.4 Emerging concepts in a well-mixed heterogeneous population

So far, we have only considered populations of agents that acquired the same aspects of information from  $\mu$  (*i.e.*,  $p(Y | \mu, \Theta = \theta_i) = p(Y | \mu, \Theta = \theta_j)$  for any pair of agents  $\theta_i, \theta_j$ ). Now, we consider a different scenario, where different types of agents acquire different aspects from the environmental conditions  $\mu$ . We investigate whether it is possible for an agent that does not directly perceive the environment at all (we call this type of agent “blind”) to predict conditions based solely on the outputs of other agents. We consider a well-mixed population, such that different types of agents are forced to talk to each other. Considerations with a flexible population structure are not interesting for our purposes, since in these cases, each type of agent would form a cluster disconnected from clusters of other types. This was

confirmed by simulations which are not shown here.

Let us illustrate the idea with a relatively simple scenario: we consider five types of agents (we denote the  $i$ -th type  $\phi_i$ ), where each type can only distinguish two macro-states from the environment. The environment consists of 9 states, and the probability of each state is uniformly distributed. We illustrate this environment by a  $3 \times 3$  grid, as shown in Fig. 4.18, although the square does not denote the actual structure of the environment. Then, the outputs of each type of agent will be related to the aspects of the environment they capture. For instance, for agents of type  $\phi_2$ , their outputs will be related to either environmental states such that  $p(\mu | Y = y_1) > 0$  (in this case, environmental states  $\{3, 6, 7, 8, 9\}$ ), or to those such that  $p(\mu | Y = y_2) > 0$  (states  $\{1, 2, 4, 5\}$ ) (see Fig. 4.18). We say that a population of agents has a joint *concept* of the environment if by considering its outputs of the environmental information they capture, it is possible to obtain information about the environment, *i.e.* we require that  $I(\mu ; X, X') > 0$ .

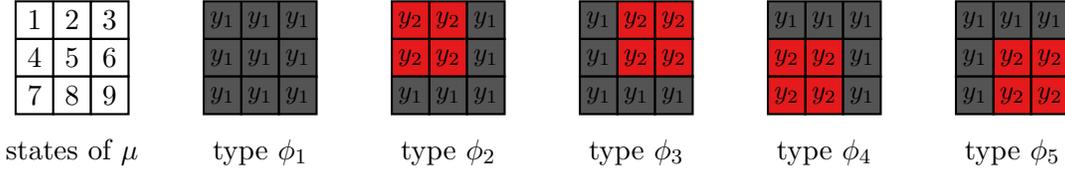


Figure 4.18: Representation of the conditional probabilities  $p(Y | \mu)$  for an agent  $\theta$  of each type. These are defined such that each type of agent can only distinguish between two environmental macro-states. For instance, the sensor of type  $\phi_2$  is defined as  $p(Y = y_2 | \mu) = 1$  if  $\mu \in \{1, 2, 4, 5\}$ , and zero otherwise, and  $p(Y = y_1 | \mu) = 1$  if  $\mu \notin \{1, 2, 4, 5\}$ , and zero otherwise. For type  $\phi_1$ , we have  $p(Y = y_1 | \mu) = 1$ .

The amount of environmental information that an agent  $\theta$  of type  $\phi_1$  (a blind agent) captures is  $I(\mu ; Y | \Theta = \theta) = 0$  bits, while all agents  $\theta$  of the other types capture  $I(\mu ; Y | \Theta = \theta) = 0.991076$  bits (note that the total entropy in  $\mu$  to be resolved is  $H(\mu) = 3.16993$  bits). Throughout this study, we considered that agents predict the environment by considering their perceptions together with the outputs of other agents. The blind agent, instead, since it is not able to capture any direct cue from  $\mu$ , we consider capable of perceiving the outputs of both of the agents selected by  $\Theta$  and  $\Theta'$ . With this relaxed consideration, we say a blind agent *has a concept* of the environment if  $I(\mu ; X, X') > 0$ , *i.e.* we consider the maximum amount of information an agent can possibly infer from the joint outputs  $X$  and  $X'$ .

Let us recall that the structure of the population is well-mixed, and thus the distribution of outputs of all agents is considered, including the blind ones, which are not able to express (via their outputs) any particular concept by themselves (for a blind agent  $\theta$ ,  $I(\mu ; X | \Theta = \theta) \leq I(\mu ; Y | \Theta = \theta) = 0$ , *i.e.*  $I(\mu ; X)$  vanishes). Therefore, whether a blind agent has some concept of the environment will depend, first, on the universality of the codes of each type of agent (agents representing the same information with different symbols may create ambiguities). Second, on the cardinality of the alphabet of  $X$  (*i.e.*  $|X|$ ) utilised by the population. A small alphabet will force agents to represent different concepts of the environment with the same symbols, while a large alphabet is likely to result in exclusive representations of concepts for each type of agent.

Taking this into account, we ask, is it possible for a blind agent to identify concepts of the environment? If so, how are these concepts related to the concepts of the individual agents (other than the blind ones)? Is the size of the available alphabet related to the quality of the concepts?

To study these questions, we performed different experiments varying the size of the alphabet  $|X|$ , where the rest of the parameters remained the same. In these experiments, we optimised the mutual understanding for a population composed of 20 agents, with 4 agents of each of the five types. In Table 4.1 we show that the cardinality of the alphabet of  $X$  affects the limit of the amount of information a blind agent can possibly infer about the environment.

| $ X $ | $I(\mu; X, X')$ |
|-------|-----------------|
| 2     | 0.34621         |
| 3     | 0.56555         |
| 4     | 0.71620         |
| 5     | 0.95467         |
| 6     | 1.08139         |
| 7     | 1.18362         |
| 8     | 1.30919         |
| 9     | 1.30919         |

Table 4.1: Results of experiments where the size of the alphabet of a population varies. The maximum amount of environmental information that a blind agent can infer is achieved with  $|X| = 8$  and remains equal for larger alphabets. As the size of the alphabet decreases, this information also decreases.

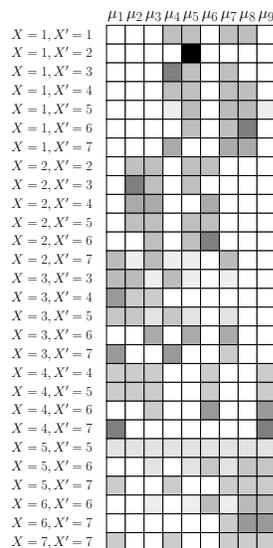


Figure 4.19: Conditional probability  $p(\mu | X, X')$  in inverse grey-scale. Each row represents a combination of values of  $X$  and  $X'$ , and each column represents a state of  $\mu$ .

Now, if we measure the uncertainty of the environment for a blind agent for each combination of outputs  $X$  and  $X'$ , we find that for some of them, it is zero. For instance, with  $|X| = 7$ , we found that when  $p(\mu = 5 | X = 1, X' = 2) = 1.0$  (see Fig. 4.19, where only combinations with  $X \leq X'$  are shown). These distributions are also valid when swapping the values of  $X$  and  $X'$ , since in the well-mixed population the structure is symmetric. Looking at the example of the conditional probability in Fig. 4.19, we can find many other concepts, although none of them —apart from the one already discussed— can uniquely identify a state of the environment. For instance, we have that  $p(\mu | X = 3, X' = 6) = 0.33$  when  $\mu \in \{3, 5, 7\}$ , which is a concept for being on a particular diagonal of the environment.

In Fig. 4.25 we show the resulting codes (which are universal for each type, including the blind one) for this particular experiment. Here, the types  $\phi_2$  and  $\phi_5$  utilise the same symbols to represent different environmental conditions. By using a small size of the alphabet for  $X$ , we force inconsistencies in the population, but these will be chosen (by evolution) such that they are minimal. In this way, we maximise the amount of information we can infer from

the outputs (although this can be a local optimum). For instance, the outputs of the blind agents (type  $\phi_1$ ) for all the experiments never overlapped that of other types (unless we use  $|X| = 2$ , where there is no choice). In other words, blind agents always choose one symbol so that they minimise the amount of utilised symbols from the whole population.

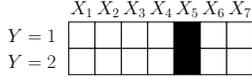


Figure 4.20: Code of type  $\phi_1$

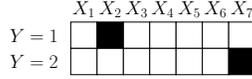


Figure 4.22: Code of type  $\phi_3$

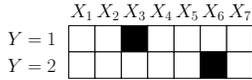


Figure 4.21: Code of type  $\phi_2$

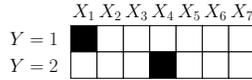


Figure 4.23: Code of type  $\phi_4$

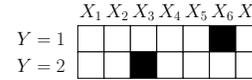


Figure 4.24: Code of type  $\phi_5$

Figure 4.25: Representation of codes  $p(X | Y, \Theta)$  by a heat-map using inverse grey-scale for the experiment with  $|X| = 7$ . For each node, the rows represent a sensor state  $y$ , while the columns represent an output state  $x$ .

In all the performed experiments, we found that for values of  $|X| \geq 6$ , the blind agent can perfectly predict the environmental state  $\mu = 5$  for at least one combination of outputs  $X$  and  $X'$ . Interestingly, this new concept, which in this particular experiment can be called the “centre” of the world or environment, cannot be obtained by looking to individual concepts only.

## 4.6 Discussion

In this chapter, we have considered populations of agents with the ability to encode their perception of the environment, through their codes, and shared this encoding with other agents according to a population structure. We proposed a model for the evolution of codes which *drops the assumption of agents knowing the identity of their communicating agents*. As a consequence, for agents to be able to interpret shared messages, they either need to rely on their universality, or they must know the identity of the source. This enables the capture of semantic communication in an information-theoretic model, a non-trivial property in such systems [Favareau, 2007, Battail, 2009].

In the evolution of codes, an important factor is the structure of the population, which determines the interactions between the agents. In well-mixed populations, we have seen that universality of codes is the only solution, since each agent needs to understand the rest of the agents. Similar results were obtained in two other studies: first, Vetsigian et al studied the evolution of the genetic code in a non-situated model [Vetsigian et al., 2006]. The genetic code was represented as a probabilistic mapping between codons and amino acids, and entities exchange their codons (subject to compatibility measures) in an Horizontal Gene Transfer (HGT) scenario. They found that a universal code emerged as a result of evolution in a well-mixed population.

Another similar study was done in [Levin, 1995]. This is also a non-situated model, where the fitness of an agent depends on its ability to predict other agent’s internal states. Each agent communicates its internal state through a code, and interprets other agent’s internal states through another code. In an evolutionary setting, they obtained a universal coding for a well-mixed population.

In another related work, [Oudeyer, 2005] explored the origins of language in a scenario consisting of artificial agents with a coupled perception and production of speech sounds. Although this work is focused on plausible mechanisms for the origin of language, it assumes the same similarity principle as we do (hearing a vocalisation increases the probability of producing similar vocalisations), arriving to the same outcome (a universal language, or code).

Our work differs from the previous studies in one crucial aspect: it is clear why a universal code for communication would increase an agent’s fitness. In our work, agents that can understand each other can incorporate side information into their Kelly-gambling strategies and improve their predictions of the environment. All other models mentioned are non-situated: agents interact with each other, but it is not specified any interaction with their environment. As a consequence, it is not clear why a universal code would give them an advantage, unless this is included in the fitness function. This is the case in the first two studies, while in [Oudeyer, 2005], the focus is on the mechanism rather than on the conceptual framework. Other works have considered similar scenarios in the evolution of languages: for instance, the naming game [Steels, 1995] and the imitation game [Boer, 2000]. However, these models assume some common conventions in order to evolve new ones.

An insight from our model that is not present in the related works is that universality follows from not being able to identify the sources of messages, and from a well-mixed population structure. The first point is not obvious, but becomes evident with the use of information-theoretic measures such as mutual information. As we explained, the traditional use of mutual information implicitly assumes that an agent knows the identity of the sender, and thus can theoretically perfectly interpret its messages. Dropping this assumption is fundamental for obtaining universal codes. The other important property is the population structure.

We have analysed different population structures in our evolutionary model. Well-mixed populations create pressure towards universal codes. On the other hand, non-interacting sub-populations would establish different conventions between them, but uniform within each sub-population. We have shown that even when the agents of each sub-population interact mostly with agents of other sub-populations, but still interact, with less frequency, with agents of its own sub-populations, then we have the same result. This is also achieved when agents *only* interact with agents of other sub-populations, but in this case homogeneity is achieved in the sources of each agent.

A particularly interesting phenomenon was observed in the experiment with a well-mixed population. There, the adoption of synonyms to express the same environmental condition (via perception states) prevented achieving a global maximum. The reason for this was the limited choice for outputs for the agents: using synonyms decreases the amount of choices

to encode the environment, and therefore not all of them can be distinguished, because the re-use of occupied outputs would create inconsistencies.

One way in which restrictions such as the one above can be alleviated is by “disconnecting” agents with dissimilar conventions. This is the case where we considered “flexible” population structures: we allowed the update of the structure simultaneously with the update of the codes. This property enhances evolution, and can potentially lead to the adoption of several different conventions within an increasingly fragmenting, or “speciating” population.

Our last scenario assumed perceptual constraints on the environmental information of each agent, as we looked at emerging concepts within a well-mixed population. This scenario was studied in [Moller and Polani, 2008], where, as well as in our study, new conceptualisations of the world emerged as a result of considering together the concepts of every agent. In both studies, the new concept was not representable individually by any agent. Differently from the mentioned study, the new concepts obtained in our study were the result of a simple similarity maximisation principle, while in the work of [Moller and Polani, 2008], concepts were obtained through the modelling of an explicit fitness function.

The type of evolution that our model captures is predominantly social. It assumes a non-competitive population of units that can improve their fitness by communicating. This is a first step for understanding the emergence of new levels of organisation, as, for instance, the emergence of the cell from the evolution of a genetic code [Woese, 2002, Woese, 2004]; the evolution of multicellularity from epigenetic codes [Jablonka, 1994]; and the evolution of societies from natural languages [Dor and Jablonka, 2001]. These are some of what are considered “major transitions” in evolution [Szathmáry et al., 1995, Szathmáry, 2015], where one fundamental property is that new ways of storing, transmitting and interpreting information are developed to give rise to a new level of organisation.

In this view, we can consider the evolution of conventional codes as a form of cultural evolution. For instance, considering the definition of culture given by [Boyd and Richerson, 1985]: “*Culture is information capable of affecting individuals’ behaviour that they acquire from other members of their species through teaching, imitation, and other forms of social transmission.*”, it could be argued that a form of cultural information is present in organisms, such as bacteria or plants. Although there is a dependence among the different dimensions on which information is transmitted in organisms (if we assume the dimensions to be, for instance, genetic, epigenetic, behavioural and symbol-based, as proposed by [Jablonka and Lamb, 2005]), our model assumes freedom of choice in one dimension, without direct influence on the others (although there is an indirect influence).

Finally, communication between individuals of a population opens up the possibility of “signal cheaters”, which could be either individuals that do not produce signals themselves but still perceive those of the others (eavesdroppers), or individuals who exploit other individual’s learned responses to symbols to their advantage (manipulators). We have ignored possible conflicts with our definition of the fitness function, which favours the fitness of the whole over the individuals. As a consequence, some individuals in our model might be sacrificed (for example, when they are isolated) to improve the population’s fitness, or their fitness may

decrease in favour of that of the population.

However, in the evolution of joint codes, there will be conflicts within a population, and the evolutionary path of a population will be greatly influenced by these conflicts and how they are resolved. For example, Krebs and Dawkins consider communication as fundamentally manipulative, where an actor will signal another organism, the reactor, in such a way that its response will benefit the former [Krebs and Dawkins, 1984]. We address possible conflicts that arise in communicating organisms in the next chapter, where we consider parasites in a population.

## 4.7 Conclusion

In the proposed model, we introduced a key assumption which allowed us to evolve, for some structures, universal codes. This assumption states that an agent cannot distinguish the sources of the outputs it perceives from other agents. Following from this, a universal code will necessarily introduce semantics by relating symbols to environmental conditions (via the internal states of the agent) for populations maximising their mutual understanding. Our model proposes an information-theoretic way of measuring the similarity within a population of codes.

In this work, we proposed, as an evolutionary principle, that agents try to maximise their side information about the environment indirectly by maximising their mutual code similarity. This behaviour produces several interesting outcomes in the code distribution of a structured population. Depending on the population structure, it captures the evolution of a universal code (well-mixed population structure), while also the evolution of different codes organised in clusters (in a freely evolving population structure).

Finally, we considered a well-mixed heterogeneous population with perceptual constraints on the agents about the environment, and showed how, just by looking at the outputs of agents, it is possible to extract concepts that relate to the environment, concepts that none of the agents of the population could individually represent.

We have postponed the study of conflicts in order to first understand how the structure of a population influences the evolution of codes. In the next chapter, we incorporate conflicts into the model, and study two forms of parasitism, as well as how populations can defend themselves against them.

# Chapter 5

## Informational parasitism

### 5.1 Overview

In this chapter, we explore how the establishment of conventional codes for communication opens up the possibility of parasitism. We first simplify the model introduced in the previous chapter such that what agents perceive from the environment is determined by their codes, instead of being fixed by their sensor variable. We then extend the model by incorporating *explicit* predictions of the population over the environment. This allows us to fix a population’s decoding, while retaining the option to change their encodings of the environment.

We study the host-parasite co-evolution in stages, by considering separate turns for optimisation of the host and of the parasite. We define two types of paradigmatic parasites, which are studied separately. We give characterisations for each of them that emerge from their behaviour. We further investigate which host properties show robustness and adaptiveness when interacting with parasites.

Part of this chapter is based on the conference paper “Information parasitism in code evolution” [Burgos and Polani, 2015], published in the Proceedings of the 15th conference on Artificial Life, although the majority of the results have not been published to this date.

### 5.2 Introduction

Codes shared among entities are ubiquitous in nature, and are not only present in biological systems, but also, at the least, in technological ones [Doyle, 2010]. For instance, the TCP/IP protocol allows the interaction of hardware and software in a code-based, “plug-and-play” fashion, as long as they both obey the protocol [Doyle, 2010]. In biology, the genetic code acts as an innovation-sharing protocol, one that allows the exchange of evolutionary innovations, for example, through horizontal gene transfer (HGT) [Woese, 2004].

However, communication protocols introduce vulnerabilities. We have shown that dropping the assumption of knowing who is the sender of information in a communication scenario forces the universality of codes in well-mixed populations. Not being able to identify the sender does not present any problems in a population of cooperative individuals, but it is this same property which creates vulnerabilities: parasitic agents, acting anonymously, can take advantage of them [Ackley and Littman, 1994, Doyle, 2010]. For instance, the chemical cues that ant colonies use to recognise nest-mates can be mimicked by slave-making workers for social integration [d’Ettorre et al., 2002]. On the Internet, one can take advantage of machine communication protocols (TCP/IP) to force target computers to perform computations on behalf of a remote node [Barabási et al., 2001], to spread viruses or to hijack machines. Once a community agree on a protocol, a law, or a set of rules on how to interpret information, then it opens itself to exploitation by malicious users.

In its broadest sense, exploitation can take two forms: manipulation, where a receiver’s response to a signal damages its success, while increasing that of the signaller; and eavesdropping, where a signaller’s success is reduced by the interception and subsequent action of an unintended receiver, and the latter benefits from this interaction. Based on this, I conceptualise a parasite as any agent that exploits any other agent or agents, damaging them in their interaction, is considered a parasite. This definition is not typical in biology, where usual requirements include nutritional dependence and utilisation of the host as an habitat [Anderson and May, 1978]. However, in this section of the thesis, I intentionally ignore such considerations (for instance, by assuming no resource competition) to focus on the informational aspects only. While these material requirements indeed play a role in communication, their inclusion would increase the complexity of the analysis, making it harder to pry apart which effect is contributed by which constraint. Most importantly, we would like to obtain a system’s dynamics (host-parasite for example) in a principled manner, with a minimal set of assumptions.

The study of informational parasitism can shed light on the evolution of biological systems in several ways: first, they improve our understanding of the properties needed for a persistent organisation, which are those that are, among other properties, robust and adaptable against parasites [Kitano, 2004]; second, they help to identify vulnerabilities in a system’s organisation, which could be used to design drugs targeting specific agents or in the context of cyber security; and third, ultimately understanding the prerequisites of parasitism can help us move towards a unified behaviour for hosts and parasites.

The host-parasite co-evolution is often characterised by Red Queen dynamics. The Red Queen Hypothesis states that organisms must constantly adapt to each other with an important point that they typically keep evolving in order to survive and be able to reproduce [van Valen, 1973]. In this dynamics, the host’s primary task consists of the identification of parasites, and the parasite’s primary task is to avoid being identified. For instance, in social insects, kin recognition is a response to the presence of parasites, but, at the same time, parasites respond to their hosts by mimicking their chemical profiles [Summers et al., 2003]. The adoption of the host’s language is fundamental to another widely observed phenomenon in this arms race: manipulation of the host by the parasite [Poulin, 2010].

We look at some aspects of the co-evolutionary arms race between host and parasite. Particularly, we would like to characterise informationally the behaviour of parasites and the consequences for the host. We put special emphasis on host's configurations that are robust and adaptable to the parasites we consider.

## 5.3 Related work

Common approaches to study host-parasite co-evolution include game theoretical models, population dynamics models, virulence models and evolutionary simulation models. I here mention some general theoretical results concerning the effects of parasitism in the evolution of a system's organisation, focusing on the emergent properties rather than on the particular methods. We focus on studies of parasitism in models that account for the evolution of communication protocols, which are mostly simulation-based studies. There are no studies of parasitism from a purely information-theoretic perspective as far as the author is concerned, and only a few that explore parasitism as a consequence of the evolved communication protocols.

### 5.3.1 Parasites in the evolution of communication

Our interest is in models where agents use communication as a mean to improve their predictions of a variable of interest. Such models naturally enable parasites to abuse the evolved protocols of communication, creating confusion in the population, and taking advantage of it. Generally, these models have a first phase of evolution, where the communication protocols are established within the population. Then, a parasite (or parasites) is introduced in the population and the consequences are studied. The reason for this two-staged evolutionary scenario is mainly that (manipulative) informational parasites are only effective if a population has evolved rules for communication. We will take a similar approach in our study.

We describe here a few results of models that studied parasitism in the context of the evolution of communication. For instance, Robbins imagined a world where female babel animals communicated with males in order to guide them to their location and be able to reproduce. His results showed that, in the presence of parasites (e.g. females that place themselves close to more mature females that already have a mutual understanding with males), communication attained more efficiency in their protocols [Robbins, 1994]. Ackley and Littman explored how the evolution of local communication protocols is vulnerable to migration, observing waves of parasites taking over most local environments, establishing new conventions, which in turn can be exploited by a new wave of parasites [Ackley and Littman, 1994]. Krakauer and Johnstone studied how the cost of signalling influence the fitness dynamics between signallers and receivers [Krakauer and Johnstone, 1995]. They found that receivers only obtain truthful information when there is a cost for producing signals, although the establishment of particular interpretations of signals by receivers also allows exploitation. The evolved dynamics showed waves of exploitation, followed by a change

in the interpretation strategy of the receivers to avoid being exploited. This in turn allowed the cycle to start over again.

Two of these studies showed Red Queen dynamics [Ackley and Littman, 1994, Krakauer and Johnstone, 1995], while in [Robbins, 1994] the result was a more efficient protocol that minimises the interaction with parasites. These are two ways in which a host population can adapt to mitigate the effects of parasites. Another possible way to achieve this is by identifying the parasites and then suppressing them, which is how immune systems protect a host population. Some parasites, then, will try to become invisible to the population to avoid detection. Let us look into some studies in this direction.

### 5.3.2 Mimicry by parasites

Franks and Noble studied the evolution of mimicry on predator-prey systems [Franks and Noble, 2002a, Franks and Noble, 2002b, Franks and Noble, 2004]. They studied two types of mimicry: Batesian mimicry, where a palatable prey mimics an unpalatable one, which presents a parasitic relationship between the two; and Müllerian mimicry, where two or more unpalatable prey species converge on appearance. In their system, each prey had a fixed palatability level, and a phenotype which evolved in time. Predators updated their experiences based on the appearance of the consumed prey, and its palatability, with some ability to generalise on appearances. In scenarios with both palatable and unpalatable species, they have shown that palatable species mimicked the unpalatable ones, where the palatable species is a parasite in relation to the unpalatable one. This happens because the palatable species is now more difficult to be identified by predators, and the traits associated with the unpalatable species by predators are no longer deadly for all cases. They also showed that the presence of Batesian mimicry decreased the number of mimicry rings (Müllerian relationships between two or more species).

Parasite's mimicry of a host is a common phenomenon in biology, and it's a fundamental property of social parasites [d'Ettorre et al., 2002, Lorenzi et al., 2014]. For instance, some social insects are chemically neutral when invading a population, such that they can avoid detection and learn the chemical profile of the population in order to manipulate them. In our model, we will give a measure of how much one can identify agents in a population, which can be used as a measure to identify parasites. Identification is directly related to mimicry: a good mimicker cannot be identified from the mimicked.

### 5.3.3 Manipulation by parasites

Poulin defines host manipulation by a parasite as any alteration in host phenotype, induced by a parasite, that has fitness benefits for the parasite [Poulin, 2010]. Studies of this phenomenon usually employ population dynamics models to study the effects of manipulation on the host [Lion et al., 2006, Fenton and Rands, 2006]. These type of models study parasitism in relation to a particular phenomenon. For instance, Lion et al. studies the influence of a parasite in

host dispersal, and Fenton and Rands study the effects of manipulation of prey in a predator-prey system. Both studies are concerned with parasitic transmission between species. In this chapter, however, we want to study parasitism in general systems, rather than in specific settings. Particularly, we would like to understand which properties a host must have for a parasite to be effective, as well as which are the emergent characteristics of a manipulative parasite. These type of properties are difficult to study in models using population dynamics. Another important property in host-parasite interactions that is of interest here is robustness and adaptability of a host population to parasites.

### 5.3.4 Robustness of hosts against parasites

Robustness is a fundamental property of systems, where their persistence depends on how well they can respond to external and internal perturbations [Kitano, 2004, Wagner, 2005, Whitacre, 2012]. Wagner argues that robustness is a pre-condition for evolvability, where neutral mutations can explore the innovation space without disrupting the general functioning [Wagner, 2005]. Robustness can be achieved by several mechanisms. Kitano proposes four of them, which are system control, alternative (fail-safe), modularity and decoupling [Kitano, 2004]. Briefly, he associates system control with negative feedback loops (maintenance of a desired state); fail-safe mechanisms with redundancy and phenotypic plasticity (diversity); modularity with isolation of perturbations from the rest of the system; and decoupling with isolation of noise and fluctuations from functional level structures and dynamics. We will focus here on literature related to fail-safe mechanisms, which is a form of adaptation.

#### Alternative (fail-safe) mechanisms

Fail-safe mechanisms maintain the functioning of a system in case of component failure. Components can be broadly classified into redundant and diverse. Redundant components provide a similar function to the system, while diverse components provide different means to maintain functioning [Kitano, 2004].

Haldane suggested that pathogens can help maintaining the genetic diversity in populations more than half a century ago [Haldane, 1949]. Now theoretical as well as experimental studies support his hypothesis [Summers et al., 2003]. In artificial systems, one early study by Hillis used co-evolving parasites as a way of avoiding local optima in evolutionary algorithms [Hillis, 1990]. He used the idea of diversity as a by-product of competitive co-evolution to “pull out” a population of solutions from a local optimum. In his experiment, parasites would attack highly frequent solutions, and an increased diversity of them would reduce the success of the parasites. Other works have extended this approach to solve search problems with rugged fitness landscapes [Paredis, 1995, Rosin and Belew, 1997, Nolfi and Floreano, 1998].

In experiments done in the digital platform Avida, where self-replicating computer programs compete for resources, the presence of parasites increased host diversity [Zaman et al., 2011]. One of the mechanisms to achieve this was to target the most frequent host pheno-

type. Another work studied how parasites lead to robust organisations in signalling networks of proteins [Salathé and Soyer, 2008]. They found that the co-evolution of these networks with parasites increased the presence of redundant proteins, although robustness was also achieved by the architecture of the networks. This means that some architectures can mitigate a parasite’s effect even in the absence of redundant proteins. Typically, in their simulations, the evolution of hosts with high fitness was preceded by an increase in structural diversity.

## 5.4 Model extension

### 5.4.1 Simplification of the model

In the model for the evolution of communication described in the previous chapter, the outputs or messages of an agent were produced according to a code which was expressed as a conditional probability from sensor states to messages. The sensor model, i.e. the probability of each sensor state of an agent conditioned on the environmental variable  $\mu$ , was given. The information about the environment which each agent obtains was given by the mutual information between the environmental variable and its sensor variable, together with the information (outputs) transmitted by other agents. These outputs would be perceived or not, according to the structure of the population. The codes, as well as the population structure, were optimised in order to maximise the mutual understanding (defined in Sec. 4.4.3) of the interacting agents of the population.

Here, instead, we further simplify the model from Chapter 4, by considering a model where the sensor states of an agent and the agent’s messages are represented by the same random variable  $X$ . That is,  $p(X | \mu, \Theta = \theta)$  gives the probability distribution of the sensor states (and, consequently, the messages) of an agent  $\theta$  given the environmental conditions  $\mu$ . We will say that this conditional probability induces an *encoding* of the environment. There are two main advantages in introducing this change: first, we are making fewer assumptions by not defining which environmental aspects each agent perceives; and secondly, we are simplifying the agents by not allowing them to perceive information directly from the environment and not sharing it.

We will further simplify the model by assuming the conditional probabilities  $p(X | \mu, \Theta)$  to be functions of  $\mu$  for each  $\Theta$ . Although this highly restricts the possible encodings, since for each value of  $\mu$  we can choose only one value of for  $X$ , the results are easier to interpret and the computations are faster. In any case, optimisations of the mutual information which are optimal would have to be functions of  $\mu$ , since otherwise they would lose information. This is simply because, in the case they are not functions of  $\mu$ , knowing  $\mu$  does not uniquely determine the value of  $X$ . Let us note that being a function of  $\mu$  can still produce non-optimal mutual information  $I(\mu ; X)$ , as, for example, when different values of  $\mu$  are mapped to the same value of  $X$ .

Agents perceive the sensor states (messages) of other agents according to the structure

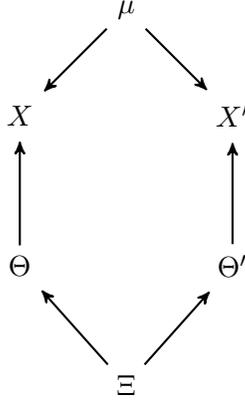


Figure 5.1: Bayesian network representing the relation of the variables in the simplified model of code evolution.  $p(X' | \mu, \Theta')$  is an *i.i.d* copy of  $p(X | \mu, \Theta)$  when we have that  $\Theta = \Theta'$ .  $\Theta$  and  $\Theta'$  selects agents from the same set, but their marginal probability distributions are not necessary the same. These two variables depend on a common variable  $\Xi$  to model more general interaction structures.

of the population interaction, which is given by  $p(\Theta, \Theta')$ . This joint probability induces a weighted graph, where agents represent the nodes of the graph and there is an edge from agent  $\theta$  to an agent  $\theta'$  if  $p(\theta, \theta') > 0$  (which is the weight of the edge). We interpret  $p(\theta, \theta')$  as the probability of interaction between these two agents. As before, we exclude self-interactions, without requiring symmetric interactions (we can have  $p(\theta, \theta') \neq p(\theta', \theta)$ ).

As we noted before, a problem of not requiring symmetric interactions in the model is that we would have two ways of measuring an agent  $\theta$ 's environmental information:  $I(\mu ; X, X' | \Theta = \theta)$  and  $I(\mu ; X, X' | \Theta' = \theta)$ . Since the interactions are not symmetrical, these values can be different. However, to analyse parasitism we will use estimations of the environment at the population level, where asymmetry is no longer an issue (this is explained in the next section). We should note here that this model is not equivalent to the one defined in the previous chapter (see Fig. 4.5). For instance, the information that an agent directly perceives from the environment cannot be “hidden” away by that agent from other agents by choosing an appropriate code, unless it is done by not interacting with them.

### 5.4.2 Modelling predictions

So far, we have not explicitly modelled predictions or bets. Here, now, we will introduce explicit “actions” or “decisions” of the agents in the form of bets. More precisely, those bets are given by the Bayes-inverse probability  $p(\mu | X, X', \Theta = \theta)$  for an agent  $\theta$ .

Our objective function is given by  $I(\mu ; X, X')$ , and, once we find a (possibly local) maximum, we interpret it as the outcome of an evolutionary process, where the encodings of agents as well as the population structure is fixed. In this equilibrium, each agent would estimate the environmental conditions by considering its own encoding together with the ones of the agents it interacts with, according to the population structure.

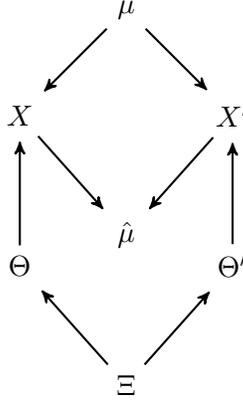


Figure 5.2: Bayesian network representing the relation of the variables in the simplified model of code evolution.  $p(X' | \mu, \Theta')$  is an *i.i.d* copy of  $p(X | \mu, \Theta)$  when we have that  $\Theta = \Theta'$ .  $\Theta$  and  $\Theta'$  selects agents from the same set, but their marginal probability distributions are not necessary the same. These two variables depend on a common variable  $\Xi$  to model more general interaction structures.

There are two ways in which we can model predictions: at the individual level or at the population level. If we consider the individual level, then each agent  $\theta$  will have its own estimation of the environment, given by  $p(\mu | X, X', \Theta = \theta)$ , and the predictions will be conditioned on the agent. However, to study parasitism, the bets on the environment are modeled at the population level. This means that the estimation of the environment is independent of the agents, or, in other words, is the same for all agents. There are several reasons to choose this option: first, as we explained, at the individual level we have two possible estimations of the environment, which is a consequence of asymmetric structures. Second, we want to study the co-evolution of a host and a parasite, and having agent-based predictions would imply different interactions with the parasite, making the analysis and display of results significantly more complicated.

The population's estimation of the environment is given by  $p(\mu | X, X')$ , i.e. by Bayesian inference on the environment, and we consider this as the evolved policy of the population for the optimal (proportional) betting on the environment. In other words, the bet is implemented by introducing a new variable whose value is determined from the predictions of the population via Bayes-inverse. We define the estimation of the environmental variable as a random variable  $\hat{\mu}$ , which is defined in the following manner:

$$p(\hat{\mu} = \mu | X, X') := p(\mu | X, X') \tag{5.1}$$

The bet  $\hat{\mu}$  is implemented by the population's prediction of the environment  $\mu$  via the Bayes-inverse probability  $p(\mu | X, X')$ . It is important to note that, while  $\hat{\mu}$  is distributed according to the Bayes-inverse of  $p(\mu | X, X')$ , it is only i.i.d., but it is not the same variable as  $\mu$ .

We will call the conditional probability defined in Eq. 5.1 the *decoding rules* of the population. The relation between all the defined random variables is shown in Fig. 5.2.

Importantly, let us note that the proposed policy has the following property:

$$I(\mu; \hat{\mu}) \leq I(\mu; X, X') \tag{5.2}$$

The inequality shown in Eq. 5.2 derives from the *data-processing inequality*, which informally states that “no clever manipulation of the data can improve the inferences that can be made from the data” [Cover and Thomas, 2002]. In our terms, the environmental information that is lost in the joint encodings of the population cannot be recovered to fully predict/reconstruct the environment.

## 5.5 Host-parasite co-evolution

To study the co-evolution of a host and a parasite, we consider a host to be a population where its environmental information  $I(\mu; \hat{\mu})$  is a local/global maximum. We want to study here how the introduction of parasitic agents affect the environmental information of the host, and how the interaction between the host and the parasite plays out. We assume hereafter that a host will always try to keep its environmental information maximised.

For this purpose, we introduce a parasite in a population which has its environmental information maximised. Such populations will have evolved ways to encode their environment, given by  $p(X | \mu, \Theta)$ , as well as their interaction structure, given by  $p(\Theta, \Theta')$ . As a consequence, the population would have evolved their rules to predict the environment, or, in other words, to decode their encodings, given by  $p(\hat{\mu} | X, X')$ .

We introduce parasites artificially rather than having them arising as a consequence of an agent’s conditions in the model, which would allow to characterise the emergence of parasites in the model. However, there are at least two disadvantages to this approach: first, it would make more difficult to analyse the interactions between an agent that is (temporarily) a parasite and a host; and, second, we would not be studying parasites that have an evolved strategy when interacting with a host. Introducing parasites artificially will allow us to test the success of different strategies, as well as to study the interactions with the host in a controlled manner.

Here, we study two types of parasites: one is a disruptive agent, which tries to minimise the mutual understanding of the overall population; and the other is a manipulative agent, which tries to maximise its influence over other agent’s actions (in our case, predictions).

To study the introduction of a parasite in a population, we will consider different stages of evolution in the host-parasite interaction. Assuming we start with a population where its environmental information is maximised, we consider the following steps:

1. Introduction of parasites in the population

## 2. Re-encoding of the environment by the population

Step 1 involves optimising a function for the parasite, which are defined later for each of the parasites we will consider. Step 2 involves the response of the population to the parasite’s attack, and here we allow the agents to update their encoding of the environment  $p(X | \mu, \Theta)$ . There are many ways in which we can allow the population to respond to the parasite: for instance, we could let the population re-structure its interactions  $p(\Theta, \Theta')$ ; we could let it update the decoding of the messages to predict the environment,  $p(\hat{\mu} | X, X')$ ; or we could let it update the encoding of the environment,  $p(\mu | X, X')$ . We will informally argue here against the first two options, and argue in favour of last option, which is to allow the agents of the population to re-encode the environment.

Let us begin considering letting the population re-structure its interactions. For an agent to choose a type of agent to interact with, it will need to be able to identify the type. For instance, agents will need to distinguish the parasite from the rest of the agents in order to avoid interactions with it. We will show that this is difficult for a host population, since parasites blend in with the host and become invisible (or hard to distinguish).

Letting the population update its predictions assumes that the rules to decode are instantly spread over the population, such that there is global agreement in the decoding rules (we recall that decoding rules are on a population basis instead of on an agent basis). On the other hand, updating the encoding of the environment can be done on an agent-by-agent basis, without the need to agree on new rules. Based on this argument, this is considered to be a “cheaper” option.

In summary, during the steps described above, we keep the decoding rules of the population,  $p(\hat{\mu} | X, X')$ , **fixed**, and we only vary the value of an agent’s encoding of the environment  $p(X | \mu, \Theta)$ , in such a way that the environmental information is back to a local/global maximum.

We will also define further steps to study this co-evolution: after the response from the population, we will let the parasite re-encode the environment without altering its interactions with the population, which will be given by  $p(\Theta, \Theta')$  after having introduced the parasite. Then, it’s the turn of the population, and so on. Although we will not show the details of the results, since until we have a better understanding of simple host-parasite interactions, would not add any insight, we will discuss them for each experiment. We formalise the steps in the following sections, where we present both types of parasites, and we study the co-evolution of a host population and each of the parasites.

## 5.6 Disinformation agents

We begin by adopting the model that characterises an informational parasite as an agent  $\pi$  that tries to minimise the mutual understanding between the agents with whom it interacts.

Here, the parasite is concentrating at abusing the host system for its own interest, but does not care about the host except for avoiding detection. However, in the context of social networks or news sources, such a parasite can be considered a *troll* or a “disinformation” (Fear Uncertainty and Doubt) agent who has direct interest in damaging the mutual understanding of the other agents of the population and/or their confidence in their knowledge of the true state of the environment.

In this characterisation, the parasite will choose its code, as well as its interactions, in such a way that the mutual understanding of the population where the parasite is introduced is minimised (see Eq. 5.3).

$$\min_{\substack{p(\pi, \Theta') \\ p(\Theta, \pi) \\ p(X | \mu, \Theta = \pi)}} I(X ; X') \quad (5.3)$$

Let us note that, in this definition, the troll does not need direct access to the environmental conditions to implement its strategy. Additionally, let us note that it by minimising the mutual understanding of the population, it will have an impact on the latter’s environmental information. In the following experiments, our objective is to show emergent properties that result from the host-parasite interaction (for a disinformation agent in this case).

### 5.6.1 Blending in with the crowd

One common characteristic of parasites is that they adopt the language of the host. There are at least two reasons for this, and they are not necessarily exclusive: first, organisms evolve to respond to specific signals and thus can only be influenced if these signals are meaningful for the recipient; and second, conveying a different set of signals from the ones used by the population makes the parasites stand out from the rest of the organisms, making them identifiable and thus vulnerable to immune response.

Our model allows us to measure how “identifiable” agents are by looking at their messages. This can be measured by the mutual information between the messages the agents produce and the agent selector:

$$I(X ; \Theta) \quad (5.4)$$

For a population with a universal encoding, this measure is zero, that is, we cannot identify the communicating agent by looking only at the message. Also, if different agents have different encodings of the environment, but the frequencies of the messages are the same, then the measure is also zero. On the other hand, if all agents produce different messages, we can perfectly identify the agent selected by  $\Theta$ . For example, if 3 agents interact with one another, and they use exclusive symbols to encode the environment, then we have

$I(X ; \Theta) = 1.58$  bit, since each agent interacts with two other agents, and they always know who is talking.

Equation 5.4 measures how much, on average, the sources of the agents can be identified by its messages. Or, if we want, it measures how universal the messages used by the sources are, being 0 when the all sources use the same messages with the same frequency. One example of this is a population with a universal encoding. This equation does not give us a direct measure of how much we can identify the parasite, but it does if we start with a population where the mutual understanding is maximised. When that condition holds, then we have that  $I(X ; \Theta) = 0$  bits, and any subsequent change must be due to the parasite. We will use this as a measure of how well a parasite blends in the population, or of how well it can be identified.

If, instead, we want to measure the universality of the sources of each agent, on average, then we need to consider the population structure. This can be done by conditioning on the other agent selector variable:

$$I(X ; \Theta \mid \Theta') \tag{5.5}$$

In this measure, we consider, on average, how much each agent selected by  $\Theta'$  can identify its sources by their messages only. By choosing a value  $\theta'$  of  $\Theta'$ , we consider only those values of  $\Theta$  where  $p(\theta, \theta') > 0$ . Therefore, if the encodings of all sources of messages, for all agents, are uniform, even if we have many types of encodings, then this measure is zero.

### 5.6.2 Contrarian behaviour

Let us start by introducing a troll into a well-mixed population of 48 agents with a universal code, with an alphabet consisting of 4 symbols, where the environmental information of the population is  $I(\mu ; \hat{\mu}) = 2$  bits. In Fig. 5.3 we show the (universal) encoding of the environment, and in Fig. 5.5 the decoding of their representation. The encodings are hand-coded for the purpose of this experiment, and the decoding rules derive from them. In this configuration, we have that  $I(X ; \Theta) = 0$  bits, and thus we cannot identify any agent in the population. The mutual understanding is  $I(X ; X') = 2$  bits, which is the maximum achievable with the current alphabet.

As a result of minimising the mutual understanding of the population by introducing a parasite, we have that it interacts with all agents of the population, but in disagreement on the encoding: the parasite always choose a different symbol than that chosen by the population to encode the environment (see Fig. 5.4).

To understand this result, let us note that the mutual understanding depends solely on  $p(X, X')$ . The parasite can only influence this joint probability by interacting with agents of the population. Since the encoding of the population is universal, the influence of the

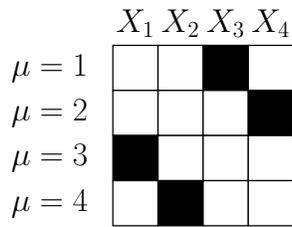


Figure 5.3:  $p(X | \mu)$ : encoding of all agents of the population

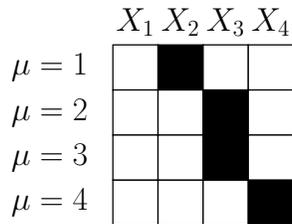


Figure 5.4:  $p(X | \mu, \Theta = \pi)$ : encoding of the parasite

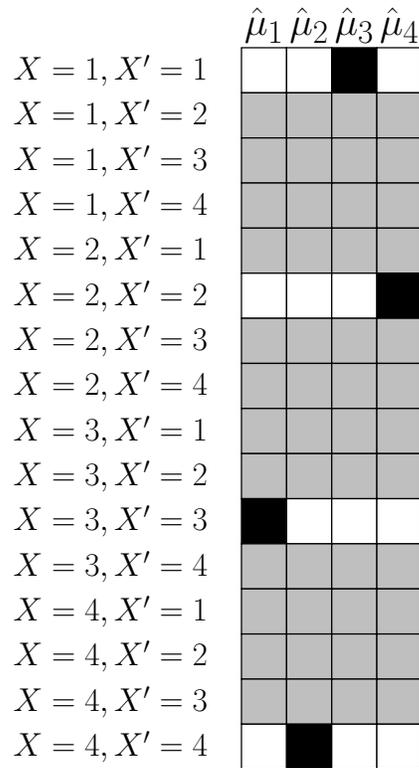


Figure 5.5:  $p(\hat{\mu} | X, X')$ : decoding rules of the population

parasite on the joint probability is increased by maximising its interactions with the agents of the population. In populations with diverse encodings, this might not hold, since the parasite’s encoding can have opposite effects on different agents regarding the mutual understanding.

The introduction of the parasite changed the probabilities for the encoding of the environment: now there are encodings for which the population doesn’t have a rule to decode them. As explained above, in these cases the population randomly chooses one environmental state. Thus, having non-zero probability on these encodings diminishes the information preserved about the environment, which in the shown example decreased to  $I(\mu ; \hat{\mu}) = 1.75$  bits, while the mutual understanding to  $I(X ; X') = 1.71$  bits. The parasite’s environmental information is  $I(\mu ; \hat{\mu} | \Theta' = \pi) = 1.85$  bits, and it slightly stands out in the population, having now  $I(X ; \Theta) = 0.01$  bits, since, although it uses the same symbols as the population, it uses them with a different frequency.

Another point to note is that there are 24 different encodings for the parasite that minimise the mutual understanding, and all of them result in the same reduction of the population’s environmental information. All these encodings have the property of being in disagreement with the population, in the sense that there is no rule on how to decode codes formed by interactions with the parasite.

Now we consider the response of the population to the introduction of the parasite: if we let the population change its interactions, including those with the parasite, then after further optimising its predictions we have that the parasite becomes isolated, reverting to the configuration prior to its introduction. However, as we explained in Sec. 5.5, we will constrain the response of the population by only allowing it to change its encoding. The population will retain the way in which it decodes the messages, but it has the ability to re-encode the environment, by using the same alphabet, in any way. Let us note that the chosen encoding of the environment by an agent determines what it perceives of the environment, and thus can be interpreted as “sensing” the environment.

We found that, for this particular example, the current encoding remained the optimal one (considering the constraints imposed). That is, no changes to the encodings of the agents increase the environmental information of the population. We explore next which conditions allow the population to improve its environmental information in response to a disruptive parasite.

### 5.6.3 Robustness and adaptability against disruptive parasites

#### Population size

One not surprising form of robustness against parasites is due to the size of the population. The larger a population, the less frequent the interactions with the parasite, and thus the less frequent agents would incorrectly predict the environmental state. Let us consider the same encodings as in the experiment of Sec. 5.6.2, as well as the same decoding rules. However,

we vary the population size between 2 and 1024 agents, without counting the parasite.

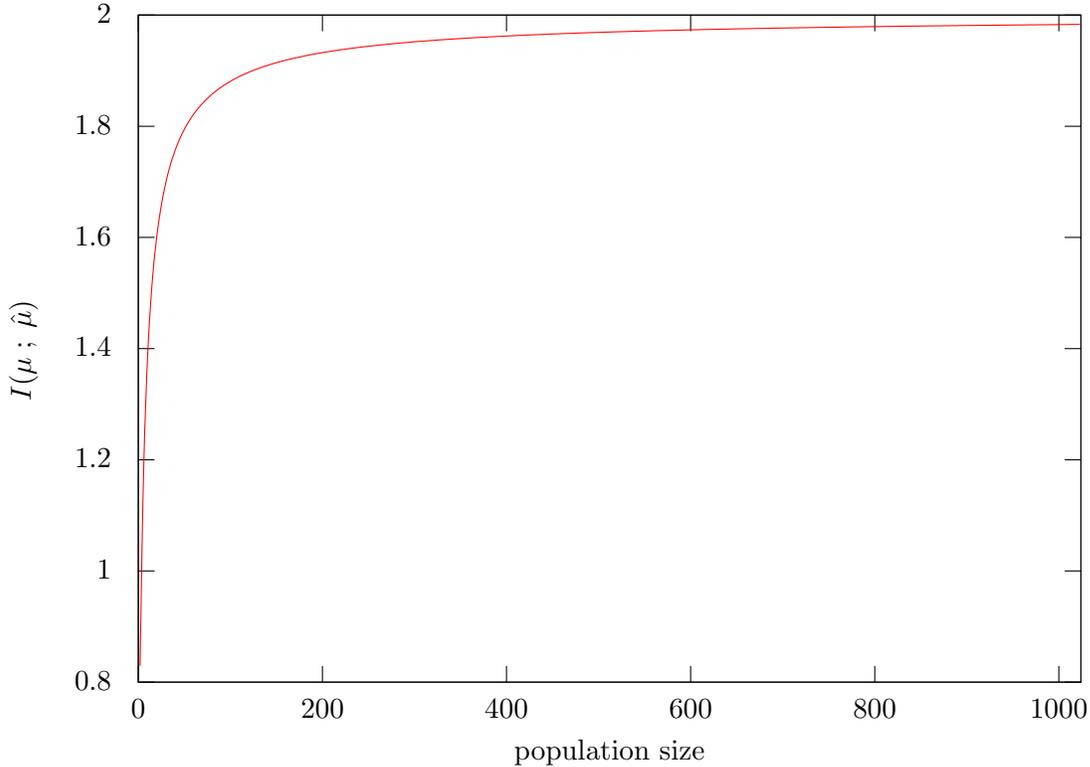


Figure 5.6: Plot of the environmental information against populations with varying size. We consider a well-mixed population with uniform encodings, with a parasite introduced as presented in Sec. 5.6.2.

In Fig. 5.6, we plot the environmental information of a well-mixed population containing a parasite when its size varies. As the population grows in size, its environmental information approaches asymptotically the maximum value of 2 bits. For well-mixed populations, small ones in size are more vulnerable, and larger populations are more resilient. However, other types of population structure with richer decoding rules allow different types of robustness. We explore this in the following subsections.

### Encoding diversity in a well-mixed population

We consider now a well-mixed population of 48 agents where we maximise the population’s environmental information by letting the codes change. The environment consists of 4 equally likely states, and we use an alphabet for encoding the environment consisting of 4 symbols. After the optimisation process, we have that the environmental information of the population is  $I(\mu; \hat{\mu}) = 2$  bits. We obtained 6 different types of codes in the population, even though there is one type that dominates (43 agents adopt this code type). This is reflected when we measure how much we can identify an agent by its messages: we have  $I(X; \Theta) = 0.051$  bits. The mutual understanding is  $I(X; X') = 1.63$  bits instead of 2 bits as when the population adopts a universal encoding.

In Fig. 5.9 we show the most popular encoding of the environment, and in Fig. 5.11 the decoding of their representation. What is interesting of this example is that the population has evolved a single interpretation for each possible combination of messages. In other words, there is a rule to interpret every possible joint messages, such that there is no unknown combination where agents must choose an environment randomly. For instance, we have  $p(\hat{\mu} = 1 | x = 1, x' = 1) = 1$ ,  $p(\hat{\mu} = 3 | x = 1, x' = 2) = 1$ , and so forth for other combinations of  $x$  and  $x'$ .

Moreover, since  $I(\mu ; \hat{\mu}) = H(\mu) = 2$  bits, the maximum possible, there are necessarily no inconsistencies when decoding the environment: that is, the possible joint encodings do not contradict each other when decoded, such that there is always certainty of which is the current environmental state. Then, since we have different ways of decoding messages into environmental states, we say that the population uses *synonyms*. For example, in the decoding rules shown in Fig. 5.11, we have three ways of expressing the environmental condition  $\mu = 2$ :  $p(\hat{\mu} = 2 | x = 1, x' = 1) = 1$ ,  $p(\hat{\mu} = 2 | x = 1, x' = 3) = 1$ , and  $p(\hat{\mu} = 2 | x = 3, x' = 1) = 1$ . These joint encodings are synonyms for  $\mu = 2$ , because we have that  $p(\mu = 2 | \hat{\mu} = 2) = 1$ .

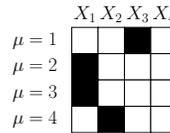
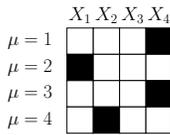
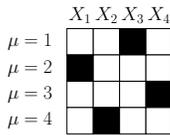


Figure 5.7: Encoding type of one agent

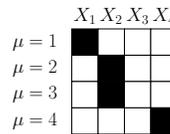


Figure 5.8: Troll encoding 1

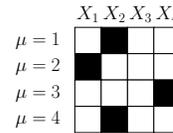
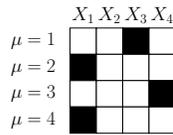
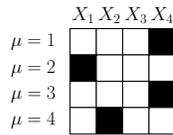


Figure 5.9: Most popular encoding

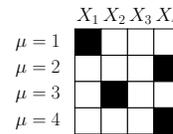


Figure 5.8: Troll encoding 1

Figure 5.10: Troll encoding 2

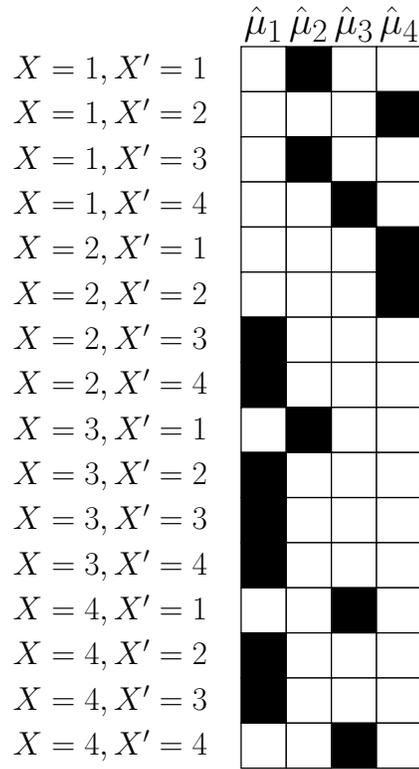


Figure 5.11:  $p(\hat{\mu} | X, X')$ : decoding rules of the population

We introduce a troll in this population, which minimises the mutual understanding. As a result, we have that the population's environmental information decreased to  $I(\mu ; \hat{\mu}) = 1.74$  bits, which is slightly less than the environmental information we obtained after introducing the parasite in the previous example. We recall that the structure of the population, well-mixed, is the same for both examples. The resulting encoding of the parasite is shown in Fig.

5.8. To check if this encoding of the parasite achieves a global minimum for the population’s mutual understanding, we run an exhaustive exploration of the parasite’s encoding. Indeed, the mentioned encoding and the one shown in Fig. 5.10 are the encodings that minimise the mutual understanding, which is  $I(X ; X') = 1.42$  bits. The parasite’s environmental information in this experiment is quite low:  $I(\mu ; \hat{\mu} | \Theta' = \pi) = 0.12$  bits (compared to 1.85 in the previous example). This is a consequence of the diversity in the encodings: the parasite perceives irregular messages producing many inconsistencies in its decoding. The graph of the population after introducing the parasite is shown in Fig. 5.12.

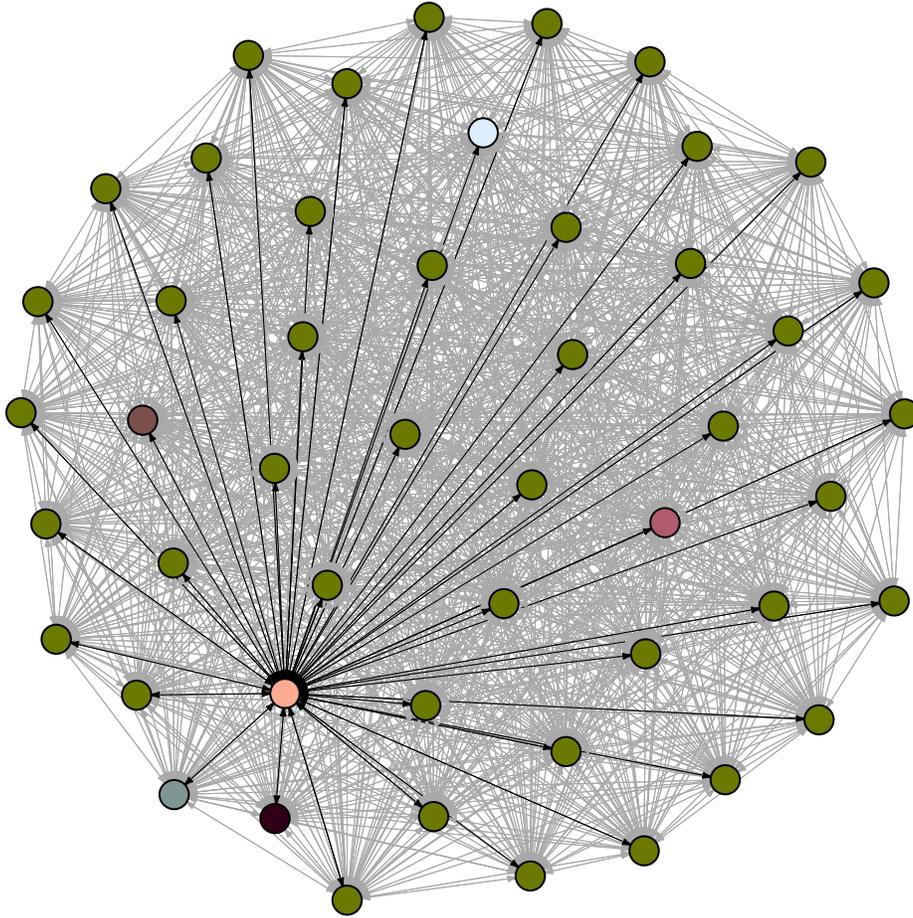


Figure 5.12: Graph of the population after introducing the parasite (in pink). The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . Each node is an agent, and its colour denotes a type of encoding. The interactions of the parasite are represented by the edges in black.

After we let the population maximise its environmental information by re-encoding the environment, the value increases to  $I(\mu ; \hat{\mu}) = 1.75$  bits. We obtain an homogeneous population where all agents adopt the most popular code, as was the case in the previous experiment we considered (Sec. 5.6.2). The graph of the population after introducing the parasite is shown in Fig. 5.13. The parasite’s information about the environment, now that all its sources are uniform, increased to  $I(\mu ; \hat{\mu} | \Theta' = \pi) = 1.85$  bits, as it was in the previous experiment. If we further allow the parasite to change its encoding, without updating its interactions, we see no further changes in the system. We can say that the parasite’s strategy is successful here,

since now its environmental information is high and the population is not able to counteract its presence.

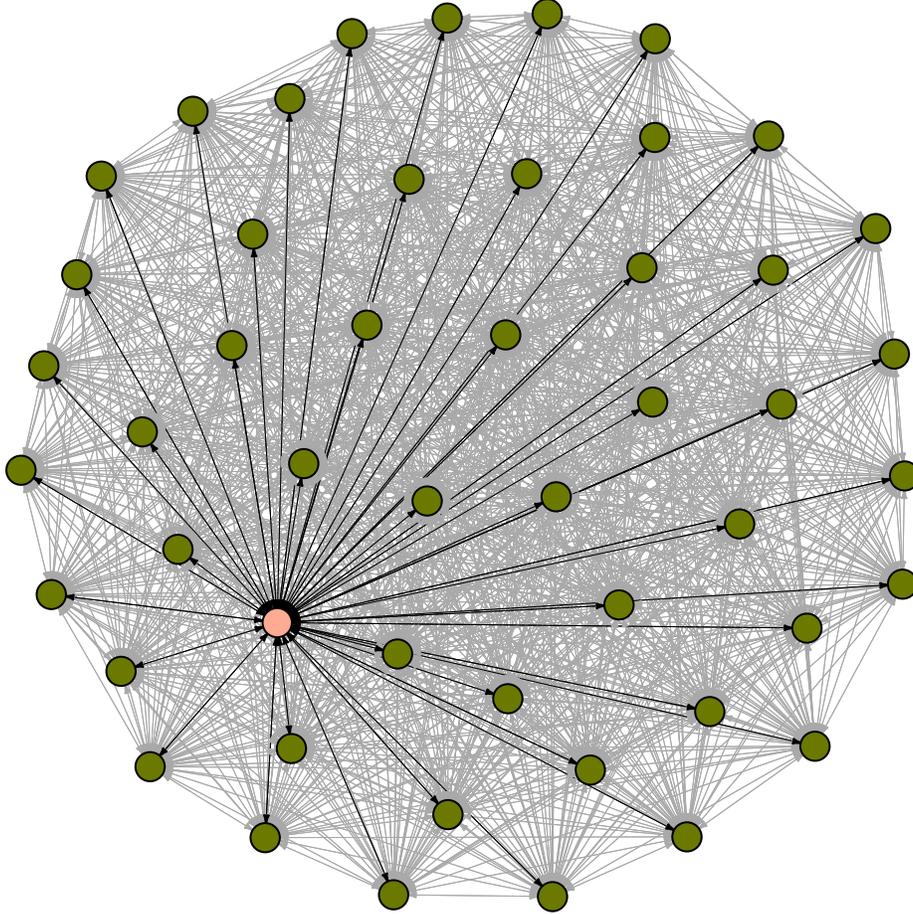


Figure 5.13: Graph of the population after the population’s response to the parasite, adopting an homogeneous encoding. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . Each node is an agent, and its colour denotes a type of encoding. The interactions of the parasite are represented by the edges in black.

We tested in this section whether the use of synonyms would increase the robustness against parasites in a well-mixed population, but this was not the case: the population’s environmental information was slightly lower. However, we could consider this population to be more robust since only two types of encodings minimise the mutual understanding, and the average environmental information of the population when introducing each parasite separately is 1.81 bits. For the previous experiment, where encodings were universal, we have that 24 parasite’s encodings minimise the mutual understanding, and the average environmental information of the population when introducing each parasite separately is 1.88 bits. For universal encodings, there are many possible parasites the population needs to defend against, while for populations using synonyms, finding the most damaging encoding for a parasite is harder.

In terms of adaptability, the population and parasite reached an equilibrium after the

population fully adopts the most popular encoding. That is, there are no further changes when we continue optimising for both the population, and then for the parasite. We explore other population structures below.

### Encoding diversity in a centralised population

We consider now a population of 48 agents where we maximise the population’s environmental information by letting the structure change. We use 48 different types of codes, where all of them use 4 different symbols to encode the environment. The environment consists of 4 equally likely states, and we use an alphabet that consists of 8 symbols to obtain a richer diversity in the encoding. After the optimisation process, we have that the environmental information of the population is  $I(\mu ; \hat{\mu}) = 2$  bits. Other measures are  $I(X ; \Theta) = 0.99$  bits and the mutual understanding,  $I(X ; X') = 0.26$  bits. The graph of the population is shown in Fig. 5.14, where we can see that the structure is highly centralised (one agent is the only source of many). This type of organisation will play a role in the response of the population after introducing the parasite.

In Fig. 5.20 we show the evolved decoding rules by the population. Although there are 4 combinations of messages where there is no rule to decode the environment, the evolved diversity to decode is much richer than in the example shown in Sec. 5.6.3. We will present only three initial encodings of the 48 of the example, and one updated encoding after the population responded to the parasite. This will suffice to convey the point of this experiment.

After introducing the parasite, we have that the population’s environmental information decreased to  $I(\mu ; \hat{\mu}) = 0.89$  bits, where initially it was 2 bits. The information about the environment of the parasite is  $I(\mu ; \hat{\mu} | \Theta' = \pi) = 0.47$  bits. The resulting interaction graph of the population is shown in Fig. 5.21. The parasite acquires a central position as a result of minimising the mutual understanding of the population, and it blends in the population, decreasing how much agents can be identified by their messages: now we have  $I(X ; \Theta) = 0.89$  bits, compared to the initial value of 0.99 bits.

Let us look at, to begin, the encoding of the central node (see Fig. 5.18), one from a peripheral node that initially solely interacts with the central node (see Fig. 5.16), and the encoding from the parasite (see Fig. 5.15). When the peripheral agent interacts with the central one, they can perfectly decode the environment (without incurring in inconsistencies with their other interactions). However, when the peripheral agent interacts with the parasite, it fails to decode the environmental state  $\mu = 2$  (having to guess randomly) and it “incorrectly” decodes  $\mu = 3$ .

There are many ways where we consider a decoding “incorrect”. For instance, if a population decodes all joint encodings to the same environment, then it retains 0 information about the environmental conditions. Another way is when there is no rule to decode joint encodings, and it needs to choose one environment randomly. The last one is when an agent has inconsistencies between its interactions. For example, an agent might be able to decode and distinguish all environmental conditions when interacting with each of two agents, but,



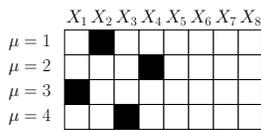


Figure 5.15: Encoding of the parasite

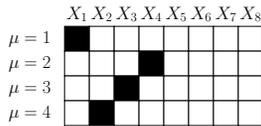


Figure 5.16: Encoding of  $\theta_p$ , a peripheral agent

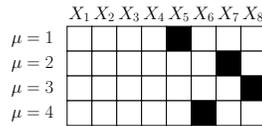


Figure 5.18: Encoding of  $\theta_c$ , the central agent

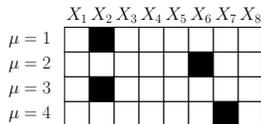


Figure 5.17: Encoding of  $\theta_p$  after Figure 5.19: responding to the parasite

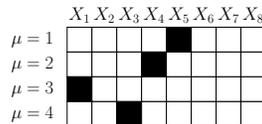


Figure 5.19: Encoding of  $\theta_c$  after Figure 5.20: responding to the parasite

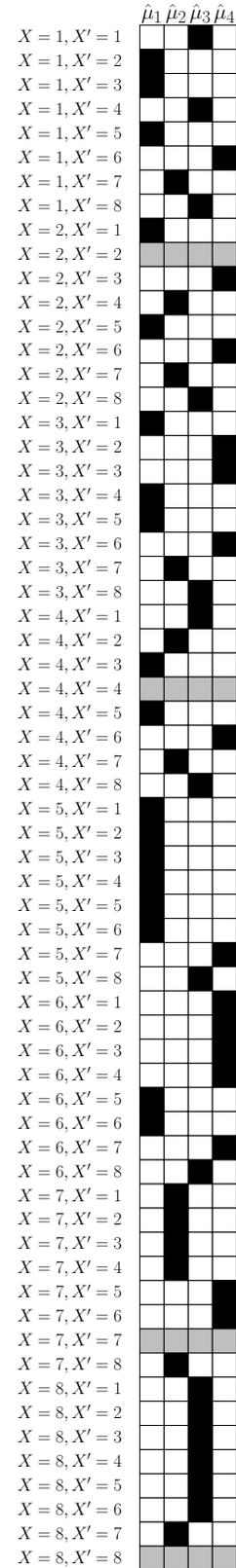


Figure 5.20:  $p(\hat{\mu} | X, X')$ : decoding rules of the population

quentially its i.i.d. copy  $p(X' | \mu, \Theta')$ , the encodings of the environment. The population keeps its evolved decoding rules. As a result, we have that the population’s environmental information is back to  $I(\mu ; \hat{\mu}) = 2$  bits, which means that re-encoding the environment, while keeping their interpretations of encodings, allows the population to fully recover from the parasite. That is, the population recovers not by avoiding the parasite (no identification possible), but by adapting to its encoding scheme, thus incorporating it to the population. As a consequence, the parasite also can always predict the environment as well. Here is where the centralised organisation of the population plays a role: for agents to re-encode the environment in such a way that, by using the evolved decoding, can distinguish all environmental states, they only need to be consistent with two agents, the central agent and the parasite.

Moreover, since the central agent, which has a very similar interaction network to the parasite, can update its encoding, then it can “imitate” the parasite’s encoding, such that now consistency is more easily reached. This is exactly what happens in the example, as shown in the updated encoding of the central agent (Fig. 5.19). The encodings are not exactly identical, differing for representing  $\mu = 1$ , although, as we argued, the evolved decoding allows the use of synonyms. Had the encodings been identical, we would have the same result.

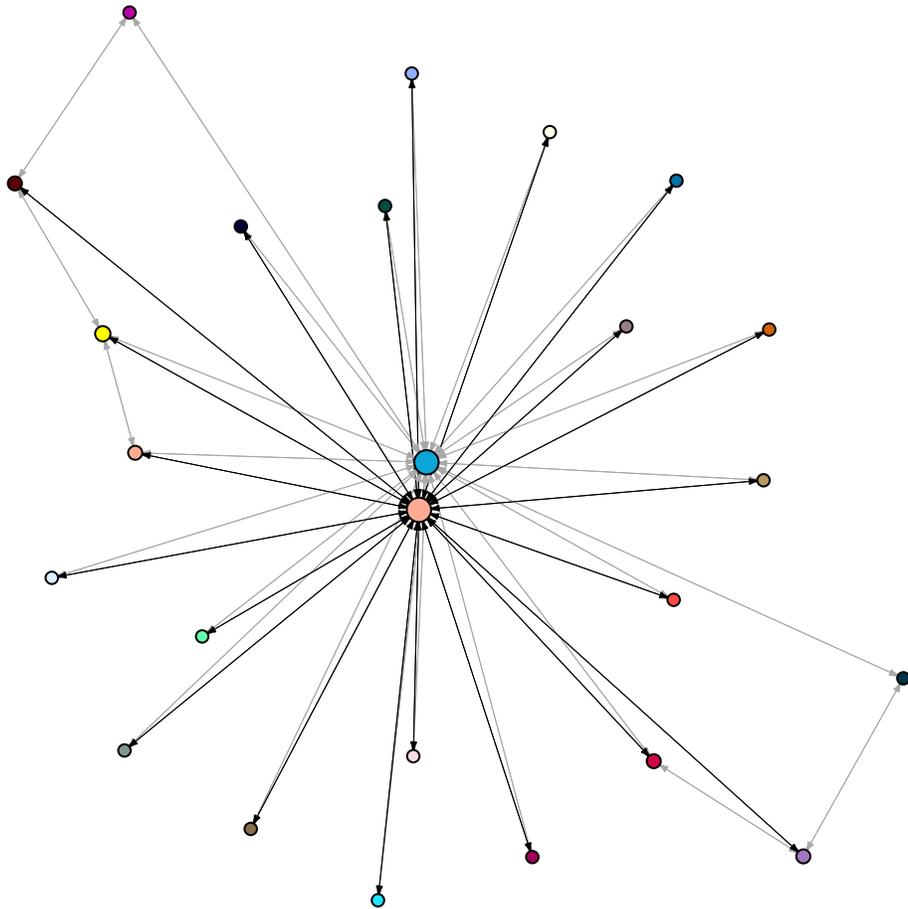


Figure 5.21: Graph of a centralised population after introducing a parasite. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . Each node is an agent, and its colour denotes a type of encoding. The interactions of the parasite are represented by the edges in black.

Let us look at the encoding of the peripheral agent after updating it (Fig. 5.17): now it is consistent with both the central agent and the parasite. The same happens to all other agents that interact with two or three agents. Centralised populations are examples of structures where most agents interact with few other agents. These have an advantage in the re-encoding process, where the update of peripheral agents' encodings are less constrained (they only need to unequivocally decode all environmental states, although by keeping consistency with the whole population).

### Encoding diversity in a decentralised population

Let us consider a population where we use the *same decoding strategy* of the previous example. However, we use different encodings and a different population structure (shown in Fig. 5.22), less centralised than the previous one, although we still have  $I(\mu ; \hat{\mu}) = 2$  bits.

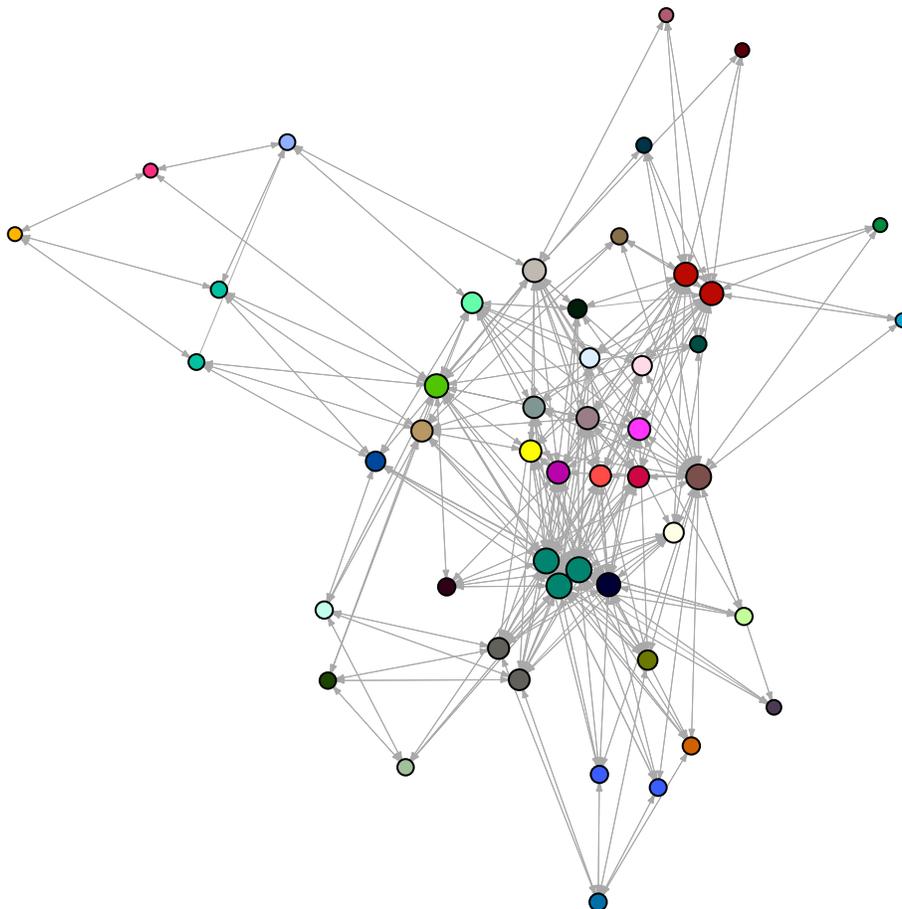


Figure 5.22: Graph of a decentralised population with maximal environmental information. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . Each node is an agent, and its colour denotes a type of encoding.

After introducing the troll in the population, we have that the environmental information is reduced to  $I(\mu ; \hat{\mu}) = 1.25$  bits (graph shown in Fig. 5.23), while for the parasite

is  $I(\mu; \hat{\mu} | \Theta' = \pi) = 0.56$  bits. When we let the population respond, the environmental information increases to  $I(\mu; \hat{\mu}) = 1.37$  bits. The reason why this population structure cannot recover well from the parasite, despite having the same decoding rules, is that here most agents interact with several agents. This constrains the options for updating the encodings, since an update has to be consistent with all of them when decoding. The parasite encounters the same problem: its environmental information is  $I(\mu; \hat{\mu} | \Theta' = \pi) = 0.69$  bits, due to the irregularities in the population.

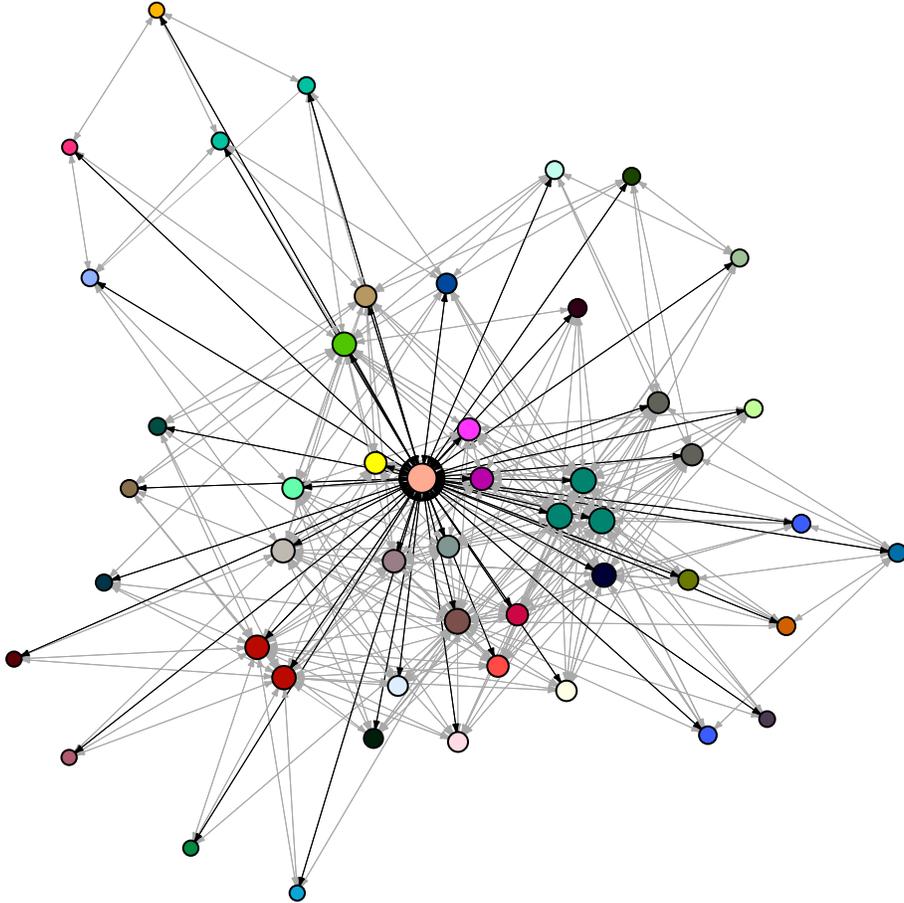


Figure 5.23: Graph of a decentralised population after introducing a parasite. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . Each node is an agent, and its colour denotes a type of encoding. The interactions of the parasite are represented by the edges in black.

### Immunity against trolls

As we have seen in Sec. 4.5.3, a bipartite interaction structure emerged in populations optimising their mutual understanding. In bipartite populations, agents with one type of encoding interact only with agents of the other type. The encodings can have different properties. For instance, as in the example of Sec. 4.5.3, we can have two types of encodings that capture the same aspects of the environment, cancelling out the noise in their perception. On the other hand, it is also possible to have two types of encodings, such that each type

complements the other in the information they perceive about the environment. In such scenarios, there are two extreme cases for the encodings: in one, the types of encoding use exclusive alphabet subsets, while, in the other, they use the same alphabet subset. For the latter case, we can have populations such that there is no mutual understanding. However, they are still able to fully predict the environment, only that one cannot predict a type's encoding by knowing the other type's encoding.

An example is shown in Fig. 5.27, where we have a bipartite population with two types of encodings, where the mutual understanding is zero. The encodings are shown in Fig. 5.24 for one type, and in Fig. 5.25 for the other. These type of populations are immune to trolls –agents that try to minimise the mutual understanding– by definition.

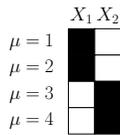


Figure 5.24: Encoding type 1

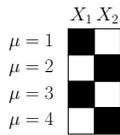


Figure 5.25: Encoding type 2

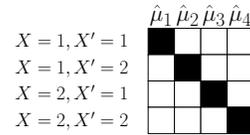


Figure 5.26:  $p(\hat{\mu} | X, X')$ : decoding rules of the population

The evolved structure shown in Fig. 5.27 is asymmetrical: we have the property that if  $p(\theta, \theta') > 0$  (meaning that agents  $\theta$  and  $\theta'$  interact), then we have that  $p(\theta', \theta) = 0$ . Since we have that interactions happen only between agents of different types, then all interactions are in one way only, from one type to the other. This is a consequence of having a small alphabet to encode the environment: there are as many possible combinations for encoding as there are environmental conditions (see Fig. 5.26). Therefore, having symmetrical interactions would reduce the amount of environmental conditions that can be distinguished. For instance, in this example, having symmetrical interactions would imply that  $p(\hat{\mu} | X = 1, X' = 2) = p(\hat{\mu} | X = 2, X' = 1)$ , leaving only two combinations of messages to represent 4 environmental states.

## 5.7 Manipulative agents

We consider another characterisation for an agent entering a population: this agent would try to maximise the influence its messages have on the predictions of the agents of a population. The *puppetmaster*, as we will call such agent, will convey messages in order to manipulate other agents. However, we don't consider a parasite that specifically manipulates to favour its agenda: we exclude this from the analysis in order to consider parasite with a simpler strategy. We look at the behaviour of a parasite with the ability to manipulate the outcome of other agent's choices in an empowerment-like quantity, and how the host can mitigate its effects.

The puppetmaster will select its code, i.e. the messages it conveys, in order to maximise its *influence* on the other agents. Formally,

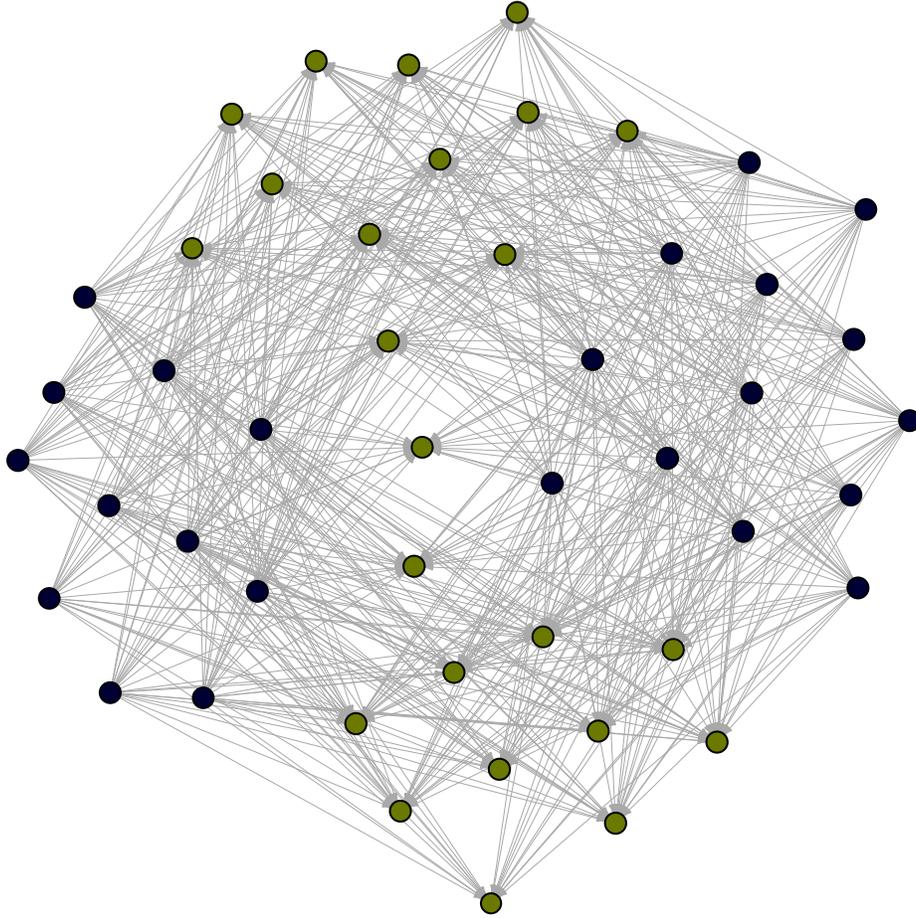


Figure 5.27: Bipartite population, where agent of one type interact only with agents of the other type. Each node is an agent, and its colour denotes a type of encoding. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ , and, in this particular case, we have that interactions are in one way only: if  $p(\theta, \theta') > 0$ , then  $p(\theta', \theta) = 0$ .

$$\max_{\substack{p(\kappa, \Theta') \\ p(\Theta, \kappa) \\ p(X | \mu, \kappa)}} I(\hat{\mu}; X' | X, \Theta' = \kappa) \quad (5.6)$$

Equation 5.6 can be interpreted as the *channel capacity* of the channel between the messages of the puppetmaster (given via its code) and the predictions of the state of the environment of the rest of the population. This behaviour is closely related to the concept of *empowerment* [Klyubin et al., 2005b], where an agent maximises its influence on the environment, but where the channel capacity is computed between the agent's actuators and sensors. Here, however, we don't require the agent itself to perceive its influence on the others.

Let us now explore this relation in more detail. Empowerment can be considered as a measure of the ability of an agent to change its environment and perceive the consequences of its actions on it. The requirement of perceiving the consequences comes because an agent

modifying its environment without perceiving any difference is a powerless agent. Empowerment is a *local*, *universal* and *task-independent* utility function for agents: it is local, because using empowerment does not rely on a long history of past experience and does not require global knowledge of the world, only a forward-cone of the future immediately ahead; it is universal, since it is applicable to any agent-world interaction; and it is task-independent because there is no specific associated goal or reward state [Klyubin et al., 2005b, Salge et al., 2014].

In the absence of specific goals, agents maximising empowerment will seek states where they maximise their options. Examples of this are having high status in a group, which allows more mating choices; or having more money, enabling one to engage in more activities [Klyubin et al., 2005a]. The maximisation of the influence over the channel between an agent’s actuators and sensors provides a natural driver for adaptive behaviour: the effects of an actuator that cannot be perceived will be selected against by evolution, if there is no gain in efficiency. In the same way, sensors that cannot detect change from an agent’s actions do not add to its survival probability and are likely to be lost during evolution to reduce metabolic cost.

The formalisation of the notion of empowerment uses the PAL (see Fig. 2.3) and information theory, and it is defined in the following way:

$$\mathfrak{E}_t = C(p(S_{t+n} | A_t)) = \max_{p(A_t)} I(A_t ; S_{t+n}) \quad (5.7)$$

Equation 5.7 defines the  $n$ -step empowerment in the unrolled PAL. It is defined as the channel capacity between the agent’s actuators at time-step  $t$  and its sensors at time-step  $t + n$ . The parameter  $n$  is usually set according to the environment of the agent: depending on the latter, a varying number of steps is needed to perceive the consequences of the actions.

An agent maximising this quantity will need a (local) forward-model of the system dynamics. That is, it will need to know, somehow, not only how its actions will affect the environment, but also how the environment will react to its actions. This might already seem impossible for a small look-ahead, but we should take into account that highly ordered environments can make this computation cheap. These can be environments, for example, where each action produces a unique reaction. Nevertheless, the agent should have this information to maximise its empowerment.

This brings us to our definition of a manipulative agent. In Eq. 5.6, the agent  $\kappa$  chooses an encoding that maximises its influence on the decisions of agents of the invaded population. In the same way as empowerment, they both compute the channel capacity. However, in our model, the channel is between the actuators of the agent and its *immediate* consequences in the environment (i.e. the population’s bets or actions); while, for empowerment, the channel is between the actuators of the agent and its perception of the environment’s reaction in a future step. The reaction could be, in our framework, the population’s re-encoding of the environmental conditions. What the puppetmaster computes can be considered a predecessor of empowerment, where the reaction/response of the environment is not taken into account.

This type of parasite can be said to be more complex than the disruptive one. A manipulative parasite has to learn the decoding rules of the population in order to manipulate, while for disruptive parasites this does not play any role. We will not model here how a parasite learns the rules of a population, and we assume they are known to it, allowing the maximisation of its influence over the population.

### 5.7.1 Behavioural characteristics

#### Dog-whistling

Let us consider the population of the experiment of Sec. 5.6.3, where a bipartite population using the same alphabet to encode the environment was immune to disruptive agents. In this population, we have that one type of agent uses, on average,  $I(\hat{\mu}; X' | X) = 1$  bit of information from the other type of agent. This opens up the possibility to influence the decisions of the agents of the population, since they rely on side information for decoding the environment.

Introducing a manipulative parasite in this population reduces the latter's environmental information to  $I(\mu; \hat{\mu}) = 1.72$  bits, while now the average side information decreased to  $I(\hat{\mu}; X' | X) = 0.84$  bits. The decrease is due to the fact that the puppetmaster's encoding differs from both types, creating inconsistencies for decoding messages. The encodings of the population are the ones shown in Fig. 5.24 and Fig. 5.25, while the decoding rules are the ones shown in Fig. 5.26. The two encodings of the puppetmaster that maximises its influence in the population's decisions, which is  $I(\hat{\mu}; X' | X, \Theta' = \kappa) = 0.07$  bits, are the one shown in Fig. 5.28 and Fig. 5.29. The parasite's environmental information is  $I(\mu; \hat{\mu} | \Theta' = \kappa) = 1.5$  bits, the loss in information being due to perceiving two types of encodings.

The puppetmaster perfectly blends in with the population, having  $I(X; \Theta) = 0$  bits in both cases, which means that it is not possible to identify the puppetmaster (or, in fact, any agent) by its messages. Having two types of agents does not matter here, since they use the same symbols with the same frequency, and the parasite does not change this.

In the graph shown in Fig. 5.30 we see that the parasite's interactions are in one direction only: it conveys information to other agents but it does not perceive any from others. This is purely because the optimisation function of the puppetmaster does not consider the effects of it perceiving information. The parasite interacts with agents of both types, since its encoding is able to affect the decisions of any type of agent. However, the agent types are affected in a different way.

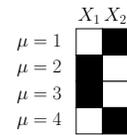


Figure 5.28: Encoding type 1

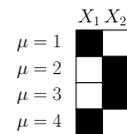


Figure 5.29: Encoding type 2

Let us consider the encoding of the parasite shown in Fig. 5.28: when it interacts with agents of the type of encoding shown in Fig. 5.24, it incorrectly decodes the states  $\mu_1$  and  $\mu_2$ . The decoding is incorrect because it is inconsistent with how agents of that type decode those states when they interact with agents of the other type. Specifically, when interacting with the parasite,  $\mu_1$  is decoded as  $\hat{\mu}_2$ , and, when interacting with agents of the other type,  $\mu_2$  is decoded as  $\hat{\mu}_1$ .

When the parasite interacts with the other type of agent (encoding shown in Fig. 5.25), this type of agent incorrectly decodes environmental states  $\mu_1$ ,  $\mu_2$  and  $\mu_3$ . Therefore, the parasite affects this type of agent more negatively than the other. When the environmental state  $\mu_3$  occurs, the parasite produces a harmless message to the former type of agent, since it is consistent with its other interactions. However, for the latter type of agent, it is detrimental. This is the “dog-whistling” effect [Albertson, 2006], where messages act as noise to only one type of agent. Here, a message is shown to have different interpretations depending on its context. It should be noted that this effect is an unintentional side effect of the puppetmaster trying to manipulate the agents. One could also (not done here) consider the framework to create intentional “dog-whistle” effects.

Optimising further the encodings of the population does not have any effect, the current configuration is the (locally) optimal one.

## Identity theft

Let us consider a similar experiment as the previous one, but this time with a larger alphabet  $\mathcal{X} = \mathcal{X}' = \{1, 2, 3, 4\}$ , with no overlap in the used symbols in the encodings by the two types of agents. One type of encoding uses the set  $\{1, 2\}$  (see Fig. 5.31) and the other uses the set  $\{3, 4\}$  (see Fig. 5.32). This is a bipartite population that can perfectly predict all environmental states, where the type of an agent can be identified by its messages: we have  $I(X ; \Theta) = 1$  bit. The decoding rules are shown in Fig. 5.34.

As a result of introducing a manipulative agent in the population, the environmental information decreased to  $I(\mu ; \hat{\mu}) = 1.92$  bits. Unlike the previous experiment, here the puppetmaster interacts only with one type of agent (see Fig. 5.35), that which can jointly be decoded according to the evolved decoding rules (Fig. 5.34). Had the parasite use an encoding that comprised the whole alphabet, it will necessarily produce codes that have no decoding rule, resulting in the agents having to guess the environment randomly. Using this type of code, formed by the interaction of the parasite and an agent of the population, would not contribute to the parasite’s influence on the actions of the agents of the population.

The parasite “adopts” the identity of the type with which it does not interact, by using the same symbols in its encoding, although the encoding is different. This motivates our characterisation of the parasite as stealing an agent’s identity: first, each type can be identified (after introducing the parasite, we have  $I(X ; \Theta) = 0.9996$  bits, since now there is one more agent of one type, and therefore the distribution of messages is not uniform), and thus, globally, agents have an identity characterised by the group they belong to. Secondly, the

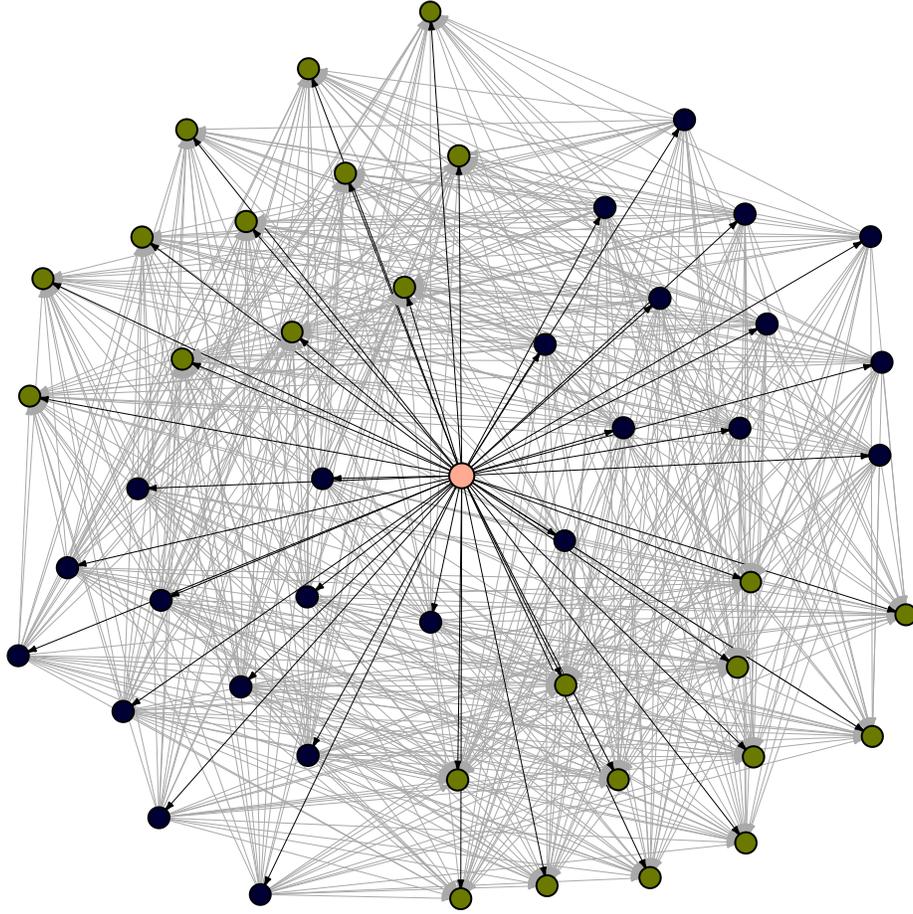


Figure 5.30: Population graph after introducing the parasite, which interacts in one direction with all agents of the population. Each node is an agent, and its colour denotes a type of encoding. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . The interactions of the parasite are represented by the edges in black.

parasite cannot be identified by the agents it interacts with. This last point is captured by conditioning the measure for identification on the other index variable: here, we have that  $I(X; \Theta' | \Theta) = 0$  bits (the parasite is selected by  $\Theta'$ , thus we measure if its sources can identify their own sources, which includes the parasite). Since the parasite perceives uniform encodings from one type of agent, its environmental information is  $I(\mu; \hat{\mu} | \Theta' = \kappa) = 2$  bits.

## 5.7.2 Robustness and adaptability against manipulative parasites

### Encoding diversity in a centralised population

We revisit the experiment of Sec. 5.6.3, only that this time we introduce a manipulative parasite instead. The initial encodings as well as the decoding rules are the same as in the mentioned experiment. In Fig. 5.36 we show the graph of the population after introducing

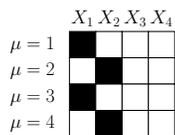


Figure 5.31: Encoding type 1

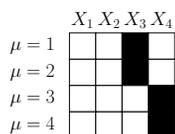


Figure 5.32: Encoding type 2

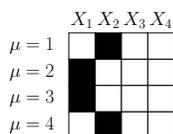


Figure 5.33: Parasite's encoding

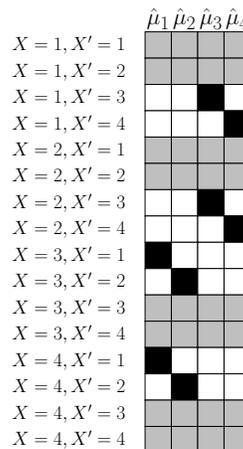


Figure 5.34:  $p(\hat{\mu} | X, X')$ : decoding rules of the population

the parasite. Here, the parasite interacts with all agents of the population, including the central agent, which was ignored by the troll when introduced in the same population. In this case, the puppetmaster is able to influence all agents of the population.

After introducing the parasite, the environmental information of the population decreases to  $I(\mu; \hat{\mu}) = 1.22$  bits, while the parasite's information about the environment is  $I(\mu; \hat{\mu} | \Theta' = \kappa) = 1.68$  bits.

In this population, we have that one agents uses, on average,  $I(\hat{\mu}; X' | X) = 1.31$  bits of information from other agents in their decisions. The central agent (let's call it  $\theta_c$ ) is the one that influences the most other agent's decisions: we have  $I(\hat{\mu}; X' | X, \Theta' = \theta_c) = 0.73$  bits, while the peripheral agent with maximal value (we call it  $\theta_p$ ) have  $I(\hat{\mu}; X' | X, \Theta' = \theta_p) = 0.02$  bits.

The puppetmaster takes influence away from the central agent, which is reflected in the values: now the parasite's influence is  $I(\hat{\mu}; X' | X, \Theta' = \kappa) = 0.58$  bits, while for the central agent it decreased to  $I(\hat{\mu}; X' | X, \Theta' = \theta_c) = 0.50$  bits. The average influence in the population is  $I(\hat{\mu}; X' | X) = 1.52$  bits.

After the population's response, the average influence in the population decreased to  $I(\hat{\mu}; X' | X) = 1.34$  bits, decreasing the influence of both the parasite and the central agent, although the former retains more than the latter. The central agent adopted the same encoding as the parasite, although the parasite's influence is higher since it reaches more agents.

In contrast to the similar experiment of Sec. 5.6.3, where after introducing a troll, the population could still re-encode the environment to retain all environmental information, here the we have after the population's response  $I(\mu; \hat{\mu}) = 1.92$  bits. What is preventing to achieve the maximum of 2 bits is the interaction between the parasite and the central

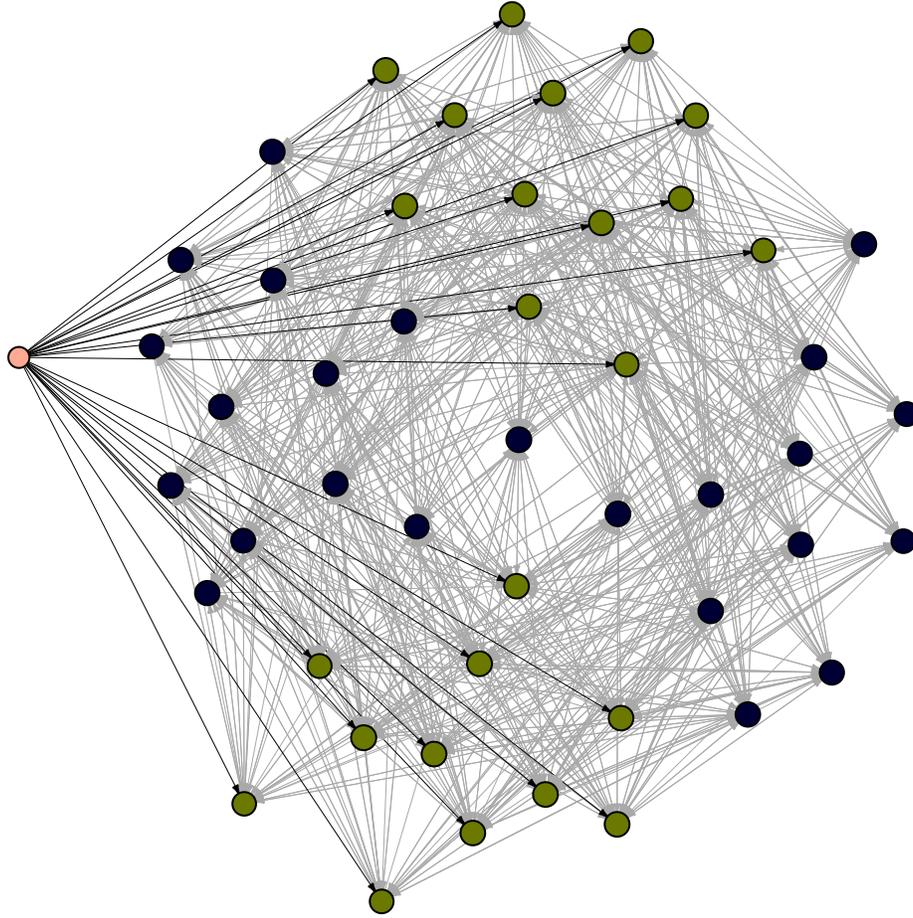


Figure 5.35: Population graph after introducing the parasite, which interacts in one direction with one type of agent only. Each node is an agent, and its colour denotes a type of encoding. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . The interactions of the parasite are represented by the edges in black.

agent: in all other interactions, the involved agents can perfectly predict the environment. The parasite's information about the environment increased to  $I(\mu; \hat{\mu} | \Theta' = \kappa) = 1.81$  bits.

Continuing with the rounds of encoding updates, we found an equilibrium for both the parasite and the population after 7 of them, with  $I(\mu; \hat{\mu}) = 1.30$  bits and  $I(\mu; \hat{\mu} | \Theta' = \kappa) = 1.23$  bits. We comment about this result later in the discussion.

### Immunity against manipulation

We re-consider here the experiment of Sec. 5.6.2, where a well-mixed population used a universal encoding. In that experiment, the amount of information coming from other agents that agents use to make predictions of the environment is 0, since they all distinguish all environmental conditions by themselves. This is captured by  $I(\hat{\mu}; X' | X) = 0$  bits.

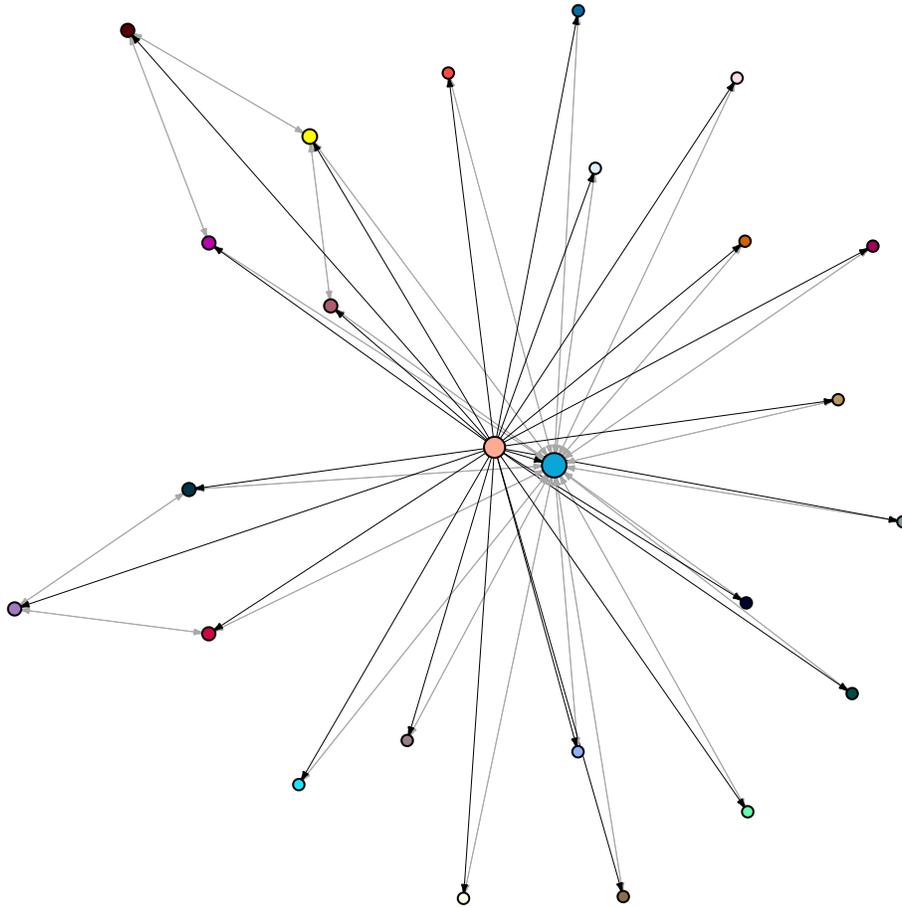


Figure 5.36: Population graph after introducing the parasite, which interacts in one direction with all agents of the population. Each node is an agent, and its colour denotes a type of encoding. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . The interactions of the parasite are represented by the edges in black.

While a troll affects this type of population, it is immune to manipulation. A manipulative parasite will maximise its influence in the decisions of the agents of the population, but, in this case, any encoding that deviates from the adopted by the population will cause the agents to choose an environment randomly. When this happens, the parasite doesn't exert any influence on the agents, since the information from the environment is completely lost. That is, the influence of the parasite through  $X'$  is lost when  $\hat{\mu}$ 's value is equiprobable distributed among its outcomes. On the other hand, having the same encoding as the population will not affect the population's decisions, since agents will predict in the same way as before introducing the parasite.

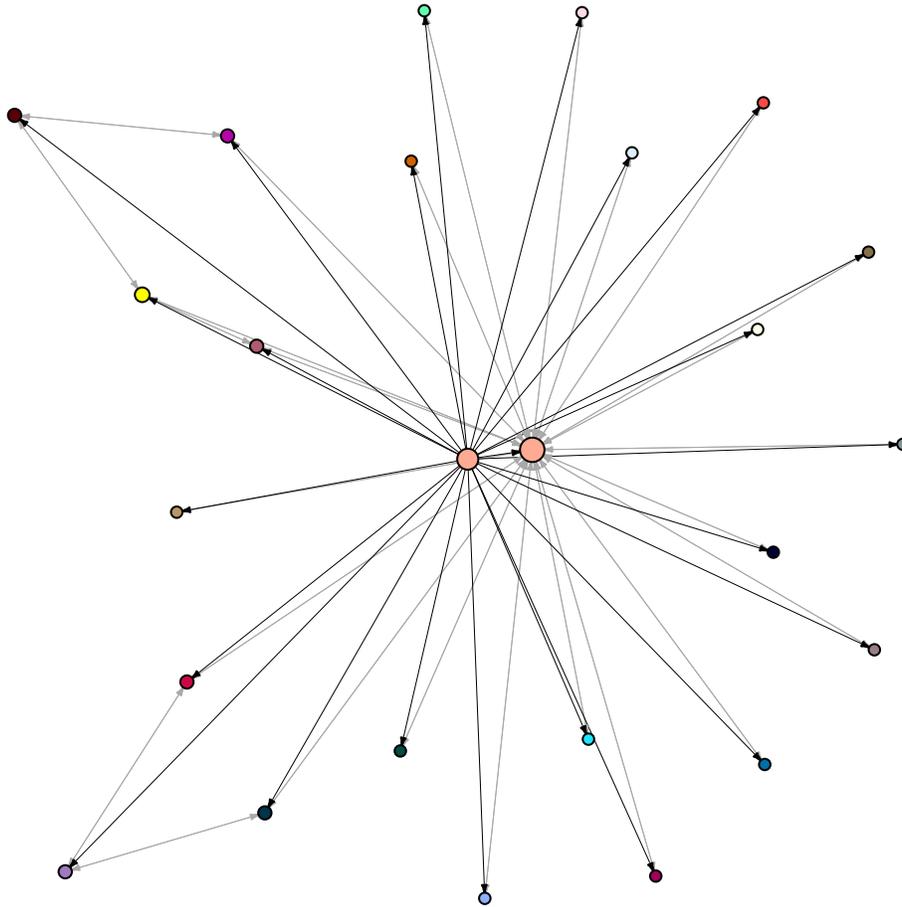


Figure 5.37: Population graph after the population’s response. The central agent has adopted the same encoding as the parasite. Each node is an agent, an its colour denotes a type of encoding. The graph is plotted from the interaction probabilities  $p(\Theta, \Theta')$ . The interactions of the parasite are represented by the edges in black.

## 5.8 Discussion

In this chapter, we have extended the model to incorporate explicit decoding rules. This allowed us to update the encodings of the environment, while keeping a fixed interpretation of them. In general, mature codes function in this way: decoding rules are well-established and would rarely change, while the information that feeds into these rules can vary. For example, genes can mutate, but the rules to translate codons into amino acids, given in the genetic code, have not been found to have changed, and may not have changed since they were widely adopted [Hinegardner and Engelberg, 1963, Woese, 2004]. We have assumed decoding rules are common over the whole population once it has found an equilibrium point with its encodings, and we do not study here how these rules change.

### 5.8.1 Parasite characterisations

We have studied two types of parasites: disruptive (trolls) and manipulative (puppetmasters). One constant characteristic of both types is that they blend in the population, sometimes to the point of being unrecognisable. Parasites are known to mimic the chemical signatures utilised by the attacked host [d’Ettorre et al., 2002, Lorenzi et al., 2014]. In this way, identification of the parasite by the population becomes harder, if not impossible. Not being able to identify who is a “friendly” agent (a nest-mate for example) and who is a “hostile” agent prevents a population to defend itself against parasites by avoidance or by attacking it.

Although interpreting our informational studies in the context of biologically relevant scenarios, the given characterisations of parasites might be transferable to the context of social networks. The main reason is that, in such an environment, we either don’t know who is sending a message or we cannot trust the claimed identity. The use of screens detaches the message from any other (e.g. physical) information about the sender, leaving only the message itself to judge its validity and/or value. This is why, for instance, fake news sources adopt common phrases and certain keywords that convey a sense of familiarity to the reader, which by-passes a simple detection alarm.

Interpreting our model in the light of social networks (rather than the biological realm), we give some examples of our characterisations. The phenomenon of “trolling” (from which we derived our naming) abound on the internet, and their behaviour can vary between aggressive, disruptive, deceptive, bullying, etc.. A particular type of troll is the contrarian, that which specifically goes to forums for discussing particular themes, where they hold different beliefs from its own. This troll will try to disrupt the forum, usually concealing its identity by the use of theme-specific keywords, but conveying a contrary view to that of the community.

For manipulative parasites, we gave two characterisations. The first one is dog-whistling, a term used in the political domain, where politicians would communicate using code words that do not stand out with a general population, but resonate strongly with a targeted part of the audience. Messages are only “heard” by some; for instance, religious code words would only have a special meaning for religious audiences [Albertson, 2006], in the same way that racial ones would only resonate with people sharing these feelings.

Our experiment showed that, for certain populations, the puppetmaster behaves just in this way: some of its messages are innocuous for a type of agent, while they generate noise in the context of the other type of agent. This behaviour is unintentional in our context, while, in politics, this is specifically desired. For this behaviour to emerge, it is necessary that different types of agent use common symbols to encode the environment. In these cases, both types will have evolved interpretations for common messages, and we have the case of messages having different interpretations depending on the recipient (or the context).

However, if each type of agent uses non-overlapping symbols to encode the environment, the puppetmaster will focus on manipulating one type only, by stealing the identity of the agent that the attacked agent interacts with. The parasite will use the same messages the attacked agent knows how to interpret, with the same frequency, but creating inconsistencies

with the recipient’s context.

Identity theft and dog-whistling (or, more generally, code words) present an interesting duality: in the former, where an agent pretends to be another agent, we have two different agents being interpreted in the same way (from the recipient’s perspective); while in the latter, we have one agent inducing two different interpretations, depending on the recipients.

## 5.8.2 Robustness and adaptability against parasites

We have also showed which properties a population may have in order to be robust against parasitic attacks. For instance, large populations are more resilient, since its numerous members provide a more solid base from which perturbations become less significant (of course, we considered only a single parasite, future more detailed studies with larger parasite proportions may lead to a disproportionately stronger influence of the parasites on the population - or vice versa).

We have also shown that populations that utilise synonyms in their decoding rules mitigate the number of encodings that damage them. In the experiment of Sec. 5.6.3, the encodings that minimise the mutual understanding were two, as oppose to the previous experiment, in Sec. 5.6.2, where there were no synonyms in the decoding rules and the encodings that minimise the mutual understanding were 24. The former presents a form of robustness, since it should be more difficult for parasites to find the right encoding for a particular population, but most importantly, a population can develop contingency strategies if it can identify the weak points. This concept is explored in the next section.

Organisms with fixed decoding rules respond to parasites via changes in their encoding of the environment, which is a form of adaptation. We showed that populations without diversity in their decoding rules (Fig. 5.5) don’t have the ability to adapt: any update in the agent’s encodings will decrease its environmental information. On the other hand, populations with diversity in their decoding rules have multiple global maxima in the fitness landscape. However, this is not sufficient to circumvent the parasite: our experiment in Sec. 5.6.3 shows that the best a well-mixed population can do in response is to adopt an homogeneous encoding. As we have explained, the population structure highly restricts the encoding updates that don’t create inconsistencies between interacting agents.

In the experiment of Sec. 5.6.3 where we considered a centralised structure, we showed that this permitted the population to fully recover form the parasite. Centralised structures have the advantage of relaxing the constraints for updating encodings such that the environmental information increases: non-central agents need to adapt to one type of agent only, since the central agent would adopt the same (or very similar) code to the parasite. We have also shown that a population with the same decoding rules but with a less centralised structure cannot go back to a global maximum.

### 5.8.3 Host-parasite co-evolution

In all the experiments where, after introducing the parasite, we continued the response steps, first by the population and then by the parasite, and then repeating these steps, we found that the co-evolution converged to an equilibrium state. In this state, further re-encoding by the population would not increase its environmental information, and further re-encoding by the parasite would not decrease the mutual understanding for the troll, or increase the influence of the puppetmaster.

This is contrary to Red Queen hypothesis, which states that organisms would have to constantly adapt to ever-evolving antagonistic organisms [van Valen, 1973]. However, Red Queen dynamics can well be the case for certain populations. One of our results showed that the population, by the use of synonyms and a centralised structure, could fully recover from a parasite. We can speculate that truly robust and adaptable populations would be in control of their weak points, facilitating a response to them. In other words, the decoding rules and the population structure can be in such a way that they would be vulnerable to certain parasite encodings, but at the same time assuring that there are paths leading to a global maximum.

This relates to the concept of “directed mutation” or “adaptive mutation” [Cairns et al., 1988, Foster, 1993], which seems contrary to the Darwinian assumption that mutations are random, and only those that are beneficial remain by the process of natural selection. The hypothesis of adaptive mutation is that, when organisms are put under stress, they would *only* produce appropriate mutations (*i.e.* mutations that are beneficial to the organism) [Cairns et al., 1988].

Our speculation can help to think about this controversial theory: if we have paths between global maxima and local minima (induced by the parasite), then it is sufficient for the population to know where the current location is in order to take action (re-encode, or “mutate”). Of course, the population must have constraints imposed to certain mutations according to the situation (there must be the concept of “taboo” paths, those which lead to only local maxima).

### 5.8.4 Immunity and the evolution of sex

Two of the presented populations had very different outcomes depending on the parasite we introduced. A well-mixed population with universal encodings is immune to manipulation, but is affected by disinformation agents, without possibility of recovering. On the other hand, a bipartite population where each type of agent uses the same symbols for their encodings is immune to trolls, but it is vulnerable to manipulation.

These are two extreme configurations of a population: in one, the messages of interacting agents are completely redundant (well-mixed population), while, in the other, the messages of interacting agents are complementary (bipartite population). When the information provided by interacting agents is redundant, then there is no possibility of manipulation. However,

when the information provided by interacting agents is complementary and necessary, then *only* in cases where both types of agents use the same symbols in their encodings, there is no room for disinformation agents.

This lead us to speculate over the evolution of sex. Thinking –consistent with the philosophy of the thesis– purely in informational terms, sexual reproduction requires to complement the information coded in genes from two types of organisms: a male and a female, where interactions are only between different types of organisms (to achieve reproduction at least). The genes of each type are encoded using the same nucleotides (Cytosine, Guanine, Adenine, Thymine). This configuration is very similar to one found in our examples, in the sense that we have a bipartite population using the same symbols to encode their environment.

Some theories put forward parasitism as the main driver in the evolution of sex [Maynard Smith et al., 1988]. Here, we show the advantages with respect to immunity that such populations have: they are immune to disruptive agents. This could be a reason why such parasites are not commonly found in biology, but are common in social contexts, where languages are more redundant. However, and as our informational models indicate, this organisation is vulnerable to manipulative parasites, which can be sex-specific or not, as we showed in the puppetmaster’s characterisation.

## 5.9 Conclusion

We have extended the model defined in the previous chapter to incorporate explicit decoding rules of a population. Then, we defined two paradigmatic types of parasites: a disruptive parasite (a troll) and a manipulative parasite (a puppetmaster), in order to study host-parasite co-evolution. We have shown that these definitions show emergent characteristics in the parasites that can be recognised in biological systems, while other characteristics are better appreciated in social networks systems. For example, the disruptive parasite shows a contrarian behaviour with the host population, while the manipulative parasite shows two dual emergent properties: identity theft and dog-whistling. In all cases, we have that the parasite blends in the host population by adopting its conventions.

We identified host properties for robustness and adaptability. For instance, we showed that the adoption of synonyms in the encoding of the environment reduces the amount of possibilities for a troll’s encoding to minimise the population’s mutual understanding. We also showed that centralised populations allow the population to re-encode their environment after being attacked by a parasite, in such a way that it fully recovers its functioning.

Finally, we showed a population immune to disruptive agents, which are those that encode different aspects of the environment using the same subset of an alphabet. However, this population is vulnerable to manipulation. On the other hand, populations immune to manipulation are vulnerable to disruption. In summary, agents cannot be immune to both disruptive and manipulative agents, unless they are communicationally isolated.

# Chapter 6

## General discussion

### 6.1 Summary

The main contribution of this thesis is the development of an information-theoretic framework that captures semantics. This allows the evolution of conventions for communication, as well as the presence of informational parasites (agents that convey false information in order to confuse/manipulate others). Only by capturing semantics is the modelling of parasitism possible, and this allowed us to explore the conditions for a population to be robust, adaptable and immune to them, from a purely informational point of view. This is of great significance, since it permits the modelling of conflicts without any a priori assumptions regarding the most desired states of either the host or the parasite.

We started by looking at the exchange of information in a model of two species competing for limited resources. We have assumed that species try to maximise their growth rate, and the optimal behaviour, under special circumstances, is to adopt a Kelly-gambling strategy. Species incorporating extra information, for instance, from other species, can improve their predictions, thereby improving their growth rate. However, with limited resources, it is not always beneficial to exchange information. We showed that there is a transition from cooperation (species share information) to indifference (species do not share information, we called this “antagonism” in Chapter 3, but now that we have defined a proper antagonist (the troll) we change terminology) when resources become scarce. We used a game-theoretical model with dynamical payoffs, which depended on several factors, but mainly on the resource density. When resources are scarce, they become valuable, and species are better off not sharing information with the other species. On the other hand, in abundance of resources, there is no competition, and sharing environmental information cannot decrease the growth rate of a species, while it may be beneficial for the sender species. In other words, a species may increase its growth rate by sharing information with the other species, but only if the latter shares back. However, there is no risk of having its growth rate decreased in any circumstance for this scenario.

We then place organisms in a cooperative scenario to focus purely on the communicational aspects of the population. That is, we assumed a scenario where there are no conflicts related to resources. Here, the more environmental information organisms have, the higher the growth rate of the population will be. However, an organism’s ability to interpret information will depend on the *universality of the codes* used by its sources in the population. This follows from dropping the assumption that an organism knows the identity of the source. This novelty allows us to *model communication in an information-theoretic way when the code is unknown to the receiver*.

We showed that, in well-mixed populations, universal representations (encodings) of the environment emerge for organisms maximising their mutual understanding, which is an information theoretic measure which does not need direct access to the environmental variable. If population structures, i.e. the selection of which agent communicates with which, are varied, this affects the evolved representations, but the main characteristic we have obtained is that, for any organism, the sources of messages are homogeneous in their representation of the environment.

The developed model enabled us to obtain a population whose structure and representations of the environment are a product of evolution. We optimised the mutual understanding and, when an equilibrium is reached, further changes in the environment representations (via their codes) of the organisms would not improve their growth rate. So far, the interpretation of shared information by an organism was implicitly computed via Bayes-inverse over the environment. Then, we incorporated in the model the way in which the population interprets encodings, by modelling **explicit decoding rules**. We assumed a “freezing” of the decoding rules once an equilibrium was reached in a population. We took this as the starting point to study conflicts in communication. This was done by introducing a parasitic agent into the population. We adopted two cornerstones of non-cooperative behaviour: namely, an agent which assumes one of two types of parasitic behaviour to maximise conflict. We studied a disruptive parasite (a troll) and a manipulative parasite (a puppetmaster), and characterised their behaviour when interacting with the population.

We also studied how the organisation of a population influences how robust and adaptive a population is against parasites. We have shown how some organisational aspects can mitigate the influence of parasites. The first one is the use of synonyms for decoding representations, which diminishes the amount of encodings a parasite can adopt that minimises the mutual understanding. The second one was adopting a centralised population structure: here, organisms are less constrained to find new encodings of the environment that will allow them to maintain their prediction accuracy. Finally, we showed two configurations of a population that are both immune to one type of parasite but not to the other. To be immune against the puppetmaster, one needs to avoid using shared information to make predictions (basically, an organism needs to be communicationally isolated). To be immune against trolls, a population can adopt a bipartite configuration, where both types of organism encode the environment using the same alphabet.

In the framework we developed, we defined an information-theoretic way of evolving a system’s dynamics. The rules of the system are established as the outcome of an evolutionary

process, and these same rules are those that allows the exploitation of the system by malicious agents.

## 6.2 Horizontal Gene Transfer and the evolution of the genetic code

One of the main inspirations for the work done in this thesis had been Carl Woese’s concepts on the evolution of the genetic code (also discussed in Sec.3.6.2 and Sec. 4.6) [Woese, 2002, Woese, 2004]. He argues against the reductionist approach widely adopted by biologists in the second half of the 20th century, where “the organism was stripped from its environment, separated from its history [...] and shredded into parts to be studied mostly in isolation” [Woese, 2004]. Instead, he proposes to put the emphasis on holistic, “nonlinear”, emergent biology, and to consider the emergence of the genetic code with non-Darwinian dynamics. This means putting aside theories that explain the universality of the code either as following from common descent or as a “frozen accident” [Vetsigian et al., 2006].

Woese imagines that, in the remote evolutionary past of the RNA world, there must have been an evolutionary saltation where the capacity to represent symbolically amino acid sequences developed. This would bring about new levels of organisation facilitated by the ability to communicate innovations. This is a common theme in the major evolutionary transitions [Szathmáry et al., 1995], where each of them came about with new types of information storage, use and transmission. In these transitions, lower-level units form the medium, a complex, sophisticated network of interactions, on which the new level of organisation comes into existence [Woese, 2004]. Examples of these are the origin of the genetic code in prokaryotic cells, eukaryotic cells, multicellularity, and societies with natural languages [Szathmáry, 2015].

Considering the evolution of the genetic code in primitive cells, there are two factors of strong influence: horizontal gene transfer (HGT) and the constraints imposed by a primitive translation apparatus of primitive cells (protocells) [Woese, 2004]. Different translation apparatus among the information sharing protocells will produce, for any given gene, not a unique protein, but a family of related protein sequences, a “statistical protein” [Vetsigian et al., 2006].

We wish to argue that these concepts relate to the models developed in this thesis. Our first model sets the stage for the evolution of a code: it states that an organism’s growth rate would not decrease if it shares information in a scenario of abundance of resources. In such a scenario, cooperative organisms (those that share information) would have an advantage over those that do not. On the other hand, in scarce resources communication does not give an advantage, and therefore a common code would not be evolved.

In our second model, we looked specifically at the evolution of codes. Although our model is intentionally kept general, here we draw parallels with the concepts of cellular evolution. We can assume that a protocell, like any organism, lives in an environment and thus will have some perception of it. This allows them, for instance, to express an adequate protein

for the corresponding environmental state, that is, to prepare themselves to survive in those conditions. We further assume that the proteins are expressed via a code that is particular to each protocell. This is a symbolic representation of the protein, for instance, by a nucleic acid sequence.

The genetic code then plays a dual role in evolution: it is both a protocol for encoding amino acid sequences, and an innovation-sharing protocol [Vetsigian et al., 2006]. We give protocells the possibility of sharing this encoding with other protocells according to a population structure, which in the simplest case is well-mixed. In the first model, an organism encodes the environment (it is actually its perception of the environment that is encoded, but let us assume for simplicity that it directly encodes the environment, which we assume to define its perception in its raw form) via a conditional probability, the code. At the same time, the organism has the ability to interpret encodings that are shared by other organisms. We have not made any assumptions regarding how an organism decodes shared encodings, the only assumption we made is that the shared encoding is interpreted contextually by the recipient. Specifically, the context of the recipient comprises all of the protocells that share their encoding with it.

Protocells receiving messages from other protocells can potentially increase their certainty about the environmental state, which would translate into an increase in their growth rate. How much information an organism can extract from a message, averaging over all of its sources, will depend on the universality of the sources' codes. Universal codes among sources allows a protocell to have one interpretation for each message, and is the *only solution* for maximising the information about the environment when the sources cannot be identified. However, if the sources of a recipient cell have heterogeneous encodings of the environment, then this will produce a distribution of proteins when decoded. In these cases, adapting a cell's decoding mechanism in favour of popular codes gives the advantage of having the "correct" interpretation "most of the time". This is a way in which the genetic code of donor cells can indirectly affect the genetic code of the recipient.

A way of increasing this trend is for organisms to assort into communities that share related codes. This was the case in the experiment where we allowed updates of the population structure. Also, codes that can distinguish more environmental states will be favoured, since they would provide higher growth rates, creating a positive feedback in the popularity of better codes during evolution. This stage of evolution, which is in essence communal and not individual [Woese, 2004], ends when the optimisation of the codes is achieved.

For this model, we did not explicitly include the translation rules of the encodings. Instead, the decoding was implicit in the model via the Bayesian inverse probability of the environment given an organism's own encoding together with shared encodings. This assumes a best case scenario for interpreting information without knowing the identities of the sources. Once the optimisation is complete, we fixed the decoding by explicitly modelling the Bayesian inverse probability.

We have postponed the analysis of parasitism until we incorporated explicit decoding rules into the model. However, one of the defined parasites, the troll, does not even make use of the

decoding rules of the invaded population. This type of parasite can be present in all stages of evolution of the genetic code, although in early stages, when the mutual understanding is low, it will be inefficient. On the other hand, for the puppetmaster, manipulation requires a certain degree of universality in the decoding rules. Having many sub-populations, each with their own decoding rules, will make more difficult, if not impossible, for the parasite to manipulate all organisms of a population. We didn't model the learning of the rules, and instead it was incorporated in the optimisation function.

Parasitism in the context of the evolution of the genetic code must have played a major role. The evolution of the genetic code would not only have been driven by agreement in how to encode their common environment, but also by "choosing" an encoding that is robust and adaptable. We explored these interactions in a simplified manner in order to validate the parasite definitions. We showed which parasite characteristics arise, sometimes depending on the context. For instance, both parasites blended in the invaded population, which makes them indistinguishable from other members of the population. The troll behaves like a contrarian, while we showed that the puppetmaster "steal identities", if there are any, or make use of the dog-whistling effect. The emerging characteristics highlight the social aspect in the evolution of codes, and are by no means exhaustive.

We have also shown that the evolved structures of the population, as well as the use of synonyms in the decoding rules, can enhance the population's adaptation in the presence of parasites. For instance, we showed that centralised populations can incorporate parasites without decreasing their growth rate. We have also showed which configurations are immune to different parasites, although the one immune to disruption is vulnerable to manipulation and vice versa.

To summarise, we have taken a measured step with a minimal information-theoretic model that captures some aspects of the evolution of the genetic code. Some of these are a consensus-driven representations of the environment highly influenced by the population structure, the establishment via evolution of a semantic interpretation of information, and the vulnerabilities this creates to parasitic agents.

### 6.3 Conclusions and future work

This thesis has focussed on the social aspects of biological systems, with a particular emphasis on communication between organisms. In retrospective, one of the most important contributions of this thesis has been the development of a model, in an information-theoretic framework, where entities are able to communicate with each other without assuming a priori a shared code between them. The key insight which allowed to capture this idea in a model is that organisms do not know the identity of who is talking, thus not being able to choose a suitable interpretation for the message.

An organism that cannot identify sources of messages is forced to interpret all of its sources in the same way. The interpretation of the messages was explicitly included in our

latest model, although we considered the same interpretation for each member of the population. We have assumed this to simplify our study of parasitism. However, it is possible to consider agent-centric decoding rules. In this case, each agent/organism would have its own way of interpreting messages. One may think that, a priori, this would add difficulty to a parasite's strategy, since now not every organism would respond in the same way to the parasite's messages. This could be a possible avenue for studying vulnerabilities and robustness in systems. The vulnerabilities can be identified by introducing a parasite in the system: now, the parasite would "choose" more carefully its interactions, since it will not be able to troll/manipulate all agents effectively, because they respond to different "stimuli".

We have formally defined in Chapter 5 a manipulative parasite that optimises a function similar to empowerment. We mentioned that this function, unlike empowerment, does not consider the reaction of the population to the agent's actions. In other words, our parasite maximises its influence over the decisions of the population's agents, but not over what the parasite would perceive once the population reacts to it by re-encoding the environment. The puppetmaster's optimisation function does not consider how the population reacts to its actions, but, for being able to do this, one may need particular properties in the population.

In order for a simple parasite to compute an empowerment-like function, the ways in which the environment, the population in this case, reacts, needs to be constrained to a few attractors. In our model, letting the population respond can lead to possibly many attractors. It is difficult to contemplate a parasite with the ability to relate its actions to one or several of the many outcomes of a population's response. The environment would need to be simplified first, in the sense that a population's possible responses are unique or a few, to allow such computation.

Whether a simplification of the environment would result by following a simple manipulation strategy as the one defined was inconclusive in our experiments. We have seen in the example where we introduced the puppetmaster in a centralised population that, after several rounds of optimisation, an equilibrium was found. Here, neither a re-encoding of the population will improve their environmental information, nor a re-encoding of the parasite will improve its influence in the population's predictions. This is indeed a simplified environment, but one that does not allow further evolution.

We should recall that we used toy environments of small uncertainty in the experiments. Environments with more states and more uncertainty may produce more interesting results, but are expensive to optimise. In any case, an interesting aspect to capture in the experiments would be the Red Queen dynamics, which none of ours did. The simplest case of such dynamics would be to have two attractors, and having the population go back and forth between them, avoiding the parasite, in a cat-and-mouse type of dynamics.

Another consideration is the role that metabolic cost, or information processing cost, would play in the evolution of organisms or agents. Agents capable of distinguishing more environmental information by themselves would realise more costly encodings. On the other hand, this cost can be avoided by reading other agents already processing the needed information for making predictions. This suggests that agents will try to maximise their en-

vironmental information, while minimising their information processing cost. Considering this, we can imagine that in early stages of an evolutionary process, where organisms have not yet developed communication protocols and live in isolation rather than in a community, there would be a pressure on agents to capture most of the information they need about the environment by themselves.

This follows from the unlikelihood of evolving, at first instance, a “division of labour” type of configuration in an unstructured population, where all interacting agents capture different aspects of the environment, and read from the other agents the information they lack. As a consequence, at first stages we would have agents capturing the information they need, possibly having a high overlap, if they depend on common environmental condition, in the captured aspects among them. Once we have this, agents can proceed to reduce their information-processing cost by taking advantage of reading other agents. Thus, this first set of agents can be considered the “building blocks” of a (yet) undetermined process. For the next generation of agents, one could picture agents capturing the information they cannot obtain by reading the others. Therefore, an agent can minimise its information processing cost by maximising the information contained in a coarse-grained description of the information provided by the agents it interacts with.

The described phenomenon suggests a hierarchical organisation of the system, and its study could shed light on the topic of major evolutionary transitions [Szathmáry et al., 1995], where the building blocks provide the lower-level units forming the medium in which a higher level of organisation could emerge [Woese, 2004].

# Appendix A

## Method of types

### A.1 Efficient representation of the states of a population

In a population of  $n$  individuals, where each of them can take 2 states, the number of possible states that the population can take is  $2^n$ . Let  $s_1, \dots, s_n$  be the states of individuals  $1, \dots, n$ , where  $s_i \in \mathcal{S}$  is the state of individual  $i$ , with  $1 \leq i \leq n$ . The probability of the population to be in state  $s_1, \dots, s_n$  given some environmental conditions  $e$  is given by  $p(s_1, \dots, s_n|e) = p(s_1|e) \dots p(s_n|e)$ . Considering that conditional probabilities among individuals of the same species are equal (see Eq. 3.2 and 3.3), then  $p(s_1, \dots, s_n|e)$  depend solely on the number of occurrences of each state in  $\mathcal{S}$ . For instance, if  $\mathcal{S} = \{0, 1\}$ , then  $p(0, 0, 1|e) = p(0, 1, 0|e) = p(1, 0, 0|e) = p(0|e)^2 p(1|e)$ <sup>1</sup>. In this way, the number of states of the population grows linearly with population size (see [Cover and Thomas, 2002] for a proof). Below, we show how to compute  $\Pr(S|E)$  (where  $S$  represents the state of the population as a unit) by using the fact that individuals are indistinguishable.

Let  $s_1, \dots, s_n$  (or alternatively  $\mathbf{s}$ ) be a sequence of  $n$  states, where  $s_i \in \mathcal{S}$  is the state of individual  $i$  of species  $X$ , with  $1 \leq i \leq n$ . The *type*  $P_{\mathbf{s}}$  of a sequence  $\mathbf{s}$  is a probability distribution given by  $P_{\mathbf{s}}(a) = N(a|\mathbf{s})/n$  for all  $a \in \mathcal{S}$ , where  $N(a|\mathbf{s})$  is the number of times state  $a$  occurs in the sequence  $\mathbf{s}$ . The *type class* of a type  $P$  is defined as the set

$$T(P) = \{\mathbf{s} \in \mathcal{S}^n : P_{\mathbf{s}} = P\}$$

and the size of  $T(P)$  is the number of ways of arranging  $N(s_1|\mathbf{s}), \dots, N(s_{|\mathcal{S}|}|\mathbf{s})$  individuals in a sequence, which is

$$|T(P)| = \binom{n}{N(s_1|\mathbf{s}_x), \dots, N(s_{|\mathcal{S}|}|\mathbf{s}_x)} = \frac{n!}{N(s_1|\mathbf{s}_x)! \times \dots \times N(s_{|\mathcal{S}|}|\mathbf{s}_x)!}$$

Since  $s_1, \dots, s_n$  given some environmental conditions  $e$  are drawn *i.i.d* according to Eq. 3.2 for species  $X$  and according to Eq. 3.3 for species  $Y$ , the probability of  $\mathbf{s}$  depends only on its type and is given by

$$p(\mathbf{s} | e) = 2^{-n(H(P_{\mathbf{s}}) + D(P_{\mathbf{s}} || Pr(S_i|e)))} \quad (\text{A.1})$$

(see [Cover and Thomas, 2002] for a proof). However, we are interested in the probability of types of sequences rather than sequences:

$$p(P_{\mathbf{s}} | e) = |T(P_{\mathbf{s}})| 2^{-n(H(P_{\mathbf{s}}) + D(P_{\mathbf{s}} || Pr(S_i|e)))} \quad (\text{A.2})$$

The number of states of the random variable  $S$  representing a population of  $n$  individuals is given by the cardinal of the set of types,

$$|\mathcal{P}_n| = \left( \binom{|\mathcal{S}|}{n} \right) = \binom{n + |\mathcal{S}| - 1}{n}$$

which is the number of  $n$ -multisubsets of the set  $\mathcal{S}$ , *i.e.* the total number of combinations of the states of  $n$  individual random variables, where each one can take any state of  $\mathcal{S}$ , counting permutations only once. In our case, where  $\mathcal{S} = \{0, 1\}$ , the number of states of the random variable  $S$  is  $n + 1$ .

## A.2 Interpolation of conditional probabilities

Population densities in our model are represented by a value in the range  $[0, 1]$ , and this value is mapped to the actual number of individuals in the population, for instance for species  $X$  this value is  $n = p_t \times X_t \times 15$ . If  $n$  is an integer, then we proceed as explained in appendix A.1. For other cases, let us assume the states of  $\lfloor n \rfloor$  individuals are represented in a sequence  $\mathbf{s}^{\lfloor n \rfloor}$ , where each state is in  $\mathcal{S}$ . As our model requires conditional probabilities for continuous sequences, we define a surrogate sequence which adds a proportion  $\lambda$  of state  $b \in \mathcal{S}$  to sequence  $\mathbf{s}^{\lfloor n \rfloor}$  as  $\mathbf{s}'(\mathbf{s}^{\lfloor n \rfloor}, b, \lambda)$ , which we denote  $\mathbf{s}'$  for shortness when the arguments can be deduced from context. Thus, we have  $|\mathbf{s}^{\lfloor n \rfloor}| \leq |\mathbf{s}'| \leq |\mathbf{s}^{\lfloor n+1 \rfloor}|$ , or equivalently  $\lfloor n \rfloor \leq |\mathbf{s}'| \leq \lfloor n+1 \rfloor$ . We define the type of a sequence when adding a proportion  $\lambda$  of state  $b$  to the sequence  $\mathbf{s}^{\lfloor n \rfloor}$  as

$$P_{\mathbf{s}'(\mathbf{s}^{\lfloor n \rfloor}, b, \lambda)}(a) = \begin{cases} \frac{N(a|\mathbf{s}^{\lfloor n \rfloor}) + \lambda}{\lfloor n \rfloor + \lambda} & a \in \mathcal{S}, a = b \\ \frac{N(a|\mathbf{s}^{\lfloor n \rfloor})}{\lfloor n \rfloor + \lambda} & a \in \mathcal{S}, a \neq b \end{cases} \quad (\text{A.3})$$

For  $\lambda = 0$  one has  $P_{\mathbf{s}'} = P_{\mathbf{s}^{\lfloor n \rfloor}}$ , and for  $\lambda = 1$  one has  $P_{\mathbf{s}'} = P_{\mathbf{s}^{\lfloor n+1 \rfloor}}$ .

We should note that when  $0 < \lambda < 1$ , the total number of states of the population is  $|\mathcal{S}| \times |\mathcal{P}_n|$ . Let us illustrate the states of a population when  $0 < \lambda < 1$  for a population that consists of two individuals, where each individual can be in a state 0 or 1. The possible states of this population are 3: 00, 01, and 11 (with type size 1, 2, 1, respectively). Now, if we add a proportion  $0 < \lambda < 1$  of a state to each possible state of the population, then we multiply by  $|\mathcal{S}|$  the number of states (before shrinking when  $\lambda = 1$ , see Fig. A.1).

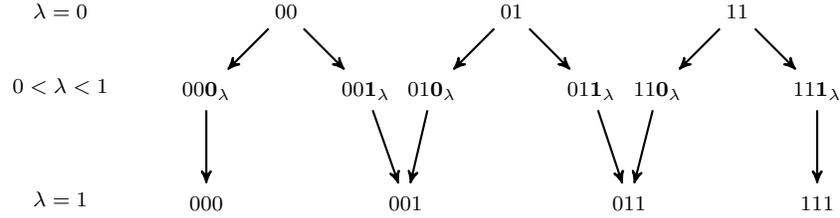


Figure A.1: States of a population in the transition from two to three individuals. We denote a sequence  $\mathbf{s}'(\mathbf{s}, b, \lambda)$  as  $\mathbf{s}\mathbf{b}_\lambda$  for shortness. For instance,  $(00,1,\lambda)$  is denoted  $00\mathbf{1}_\lambda$ .

We could consider the type size of each sequence by

$$|T(P_{\mathbf{s}'(\mathbf{s}^{\lfloor n \rfloor}, b, \lambda)})| := \binom{\lfloor n \rfloor + \lambda}{N(s_1 | \mathbf{s}_\mathbf{x}), \dots, N(s_b | \mathbf{s}_\mathbf{x}) + \lambda, \dots, N(s_{|\mathcal{S}|} | \mathbf{s}_\mathbf{x})}$$

where the factorial is approximated by using the gamma function  $\Gamma(x) = \int_0^\infty t^{x-1} e^{-t} dt$ , with  $(\lfloor n \rfloor + \lambda)! = \Gamma(\lfloor n \rfloor + \lambda + 1)$ . However, when counting the unique ways of arranging the states, for instance,  $00\mathbf{1}_\lambda$  and  $01\mathbf{0}_\lambda$ , we would not be considering the overlap between these two states. In other words, we would be counting more than once some sequences. This depends on the sequences and the value of  $\lambda$ , for example  $000_\lambda$  and  $00\mathbf{1}_\lambda$  fully overlap when  $\lambda = 0$ , but there is no overlap when  $\lambda = 1$ . On the other hand,  $00\mathbf{1}_\lambda$  and  $01\mathbf{0}_\lambda$  do not overlap when  $\lambda = 0$ , but fully overlap when  $\lambda = 1$ .

Then, some sequences (such as  $00\mathbf{1}_\lambda$  and  $01\mathbf{0}_\lambda$ ) are always counted twice, independently of the value of  $\lambda$ : they either overlap with one sequence or the other (this is because we are considering  $|\mathcal{S}| = 2$ ). However, the sequences  $000_\lambda$  and  $111_\lambda$  (those such that  $|T(P_{000_\lambda})| = T(P_{111_\lambda})| = 1$ ) are counted twice when  $\lambda = 0$ , but only once when  $\lambda = 1$ . In Fig. A.2 we show some values of the sizes of types as  $\lambda$  increases.

Taking this into account, we approximate the conditional probability by

$$p(P_{\mathbf{s}'(\mathbf{s}^{\lfloor n \rfloor}, b, \lambda)} | e) = \begin{cases} \frac{1+\lambda}{|\mathcal{S}|} 2^{-(\lfloor n \rfloor + \lambda)} (H(P_{\mathbf{s}'}) + D(P_{\mathbf{s}'} || Pr(S'|E))) & \text{if } |T(P_{\mathbf{s}'})| = 1 \\ \frac{|T(P_{\mathbf{s}'})|}{|\mathcal{S}|} 2^{-(\lfloor n \rfloor + \lambda)} (H(P_{\mathbf{s}'}) + D(P_{\mathbf{s}'} || p(S'|E))) & \text{otherwise} \end{cases} \quad (\text{A.4})$$

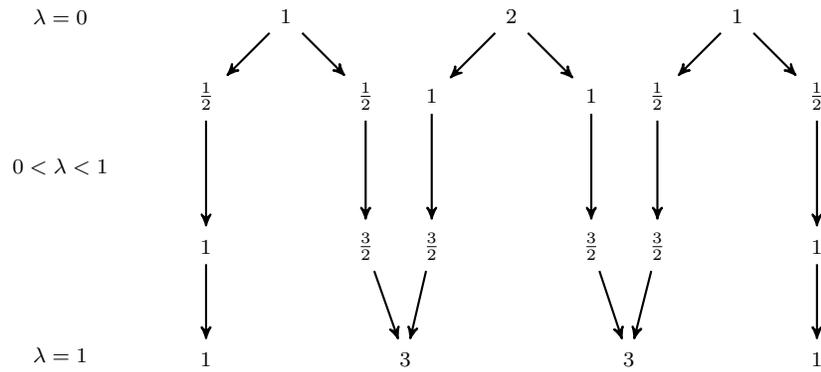


Figure A.2: Sizes of types for sequences in the transition from two to three individuals in a population. The sizes are corresponded with the sequences shown in Fig. A.1, and the values when  $0 < \lambda < 1$  show how they change from  $\lambda = 0$  to  $\lambda = 1$ .

# Appendix B

## Sensitivity analysis

### B.1 Parameters sensitivity and results generality

The parameter settings used in Sec. 3.5 were specially chosen to show the transition from cooperation to antagonism in species sharing environmental information. These were  $\alpha = 1.05$ ,  $N = M = 15$ , together with the conditional probabilities shown in Eq. 3.2 and Eq. 3.3. Here, we analyse the sensitivity of the parameters by introducing changes in each one of them and showing how this affects the results. Instead of computing the dominant strategies for the same subset of  $\mathcal{X} \times \mathcal{Y} \times \mathcal{R}$  (as we have done in Sec. 3.5), we show results for a fixed value of resources,  $R = 1.8$ , which clearly shows all the possible volumes (see Fig. 3.5f).

| Parameter          | Description  |
|--------------------|--|
| $\Pr(S_{x_i}   E)$ | This conditional probability defines the amount of information that an individual cell $i$ of species $X$ captures from sensing the environment. |
| $\Pr(S_{y_j}   E)$ | This conditional probability defines the amount of information that an individual cell $j$ of species $Y$ captures from sensing the environment. |
| $N$                | Carrying capacity of the population of species $X$ .   |
| $M$                | Carrying capacity of the population of species $Y$ .   |
| $\alpha$           | Growth rate of resources.  |

Table B.1: List of parameters used by the model with their description.

In Table B.1, we show the used parameters by the model with their descriptions. First, let us consider parameter  $\alpha$ , the growth rate of resources. In Fig. B.1b, we show the results we obtain when we change to  $\alpha = 1.25$ , instead of its original value,  $\alpha = 1.05$ , whose results are shown in Fig. B.1a. This change extends the volume where sharing information is weakly

dominant such that it includes initial values with relatively lower resources, while the other volumes will be shifted in such a way that they are composed of initial values with lower values for resources. Additionally, the amount of initial values composing the other volumes is smaller. The reason for this is that, since resources grow at a higher rate, higher populations can be supported, and thus the regime in which antagonism is dominant is reduced.

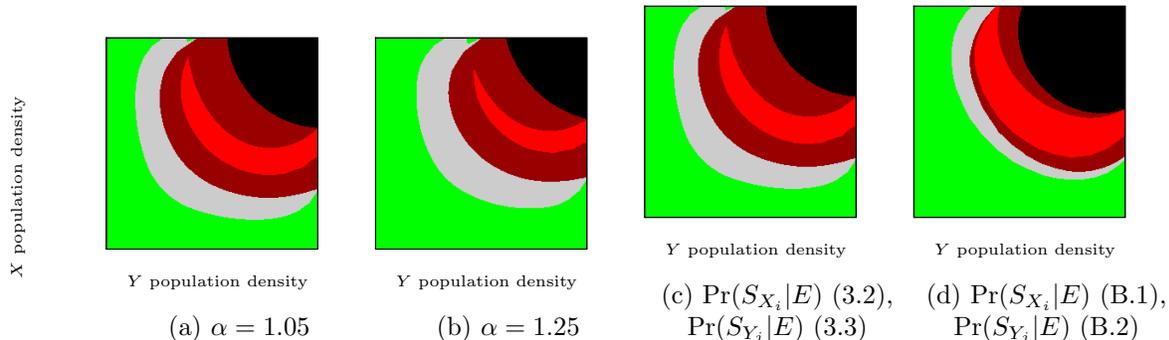


Figure B.1: (see in colour) We analyse the payoff matrix from  $250^2$  initial values of population densities of species  $X$  and  $Y$  uniformly distributed in  $\mathcal{X} \times \mathcal{Y}$ , with the amount of resources  $R = 1.8$  fixed. See Fig. 3.5 for an explanation of what colors represent. Each subcaption shows the parameter whose effect is being exemplified.

Let us consider now the conditional probabilities  $\Pr(S_{X_i}|E)$  and  $\Pr(S_{Y_j}|E)$ . They determine how much environmental information each individual captures,  $I(E; S_{X_i}) = I(E; S_{Y_j}) = 0.39016$  bits, which is a low amount of the total environmental uncertainty,  $H(E) = 2$  bits. Together with  $N$  and  $M$ , the conditional probabilities determine the different curves shown in Fig. 3.3. A property of the defined conditional probabilities is that populations achieve a fast increase in environmental information when population densities are low, with small increases for high population densities. Lower values of  $I(E; S_{X_i})$  and  $I(E; S_{Y_j})$  would have a slower growth for low population densities, and species will not acquire high amounts of environmental information for high population densities (see Fig. B.2 for an example).

Therefore, the two conditional probabilities together with  $N$  and  $M$  will define the total environmental information when species communicate. This amount is  $I(E; S_{X_1}, \dots, S_{X_n}, S_{Y_1}, \dots, S_{Y_m})$  (see the curve in Fig. 3.3 and in Fig. B.2), and the gain in environmental information for a species receiving the shared information from the other species (assuming equal population densities) is the difference between the two mentioned curves. This difference is high for our chosen conditional probabilities since the species were meant to capture different aspects of the environment (see Fig. 3.2 and 3.3), but if the aspects of the environment that species capture intersect, then this difference decreases (see, for instance, Fig. B.2).

In Fig. B.1c and Fig. B.1d, we show how changing the conditional probabilities  $\Pr(S_{x_i}|E)$  and  $\Pr(S_{Y_j}|E)$  affect the results. Instead of the probabilities defined in Eq. 3.2 and in Eq.

3.3, we used the ones defined in Eq. B.1 and in Eq. B.2, where the intersection of the acquired environmental information from sensors between two individuals of different species is  $I(S_{X_i}; S_{Y_j}) = 0.151452$  bits, while the amount of environmental information each individual captures is roughly the same as before,  $I(E; S_{X_i}) = I(E; S_{Y_j}) = 0.389767$  bits. However, how the amount of environmental information changes in relation to the population densities is different from the original definitions, as shown in Fig. B.2.

In this case, a species by itself is able to capture more information about the environment (roughly 1.5 bits while before it was close to 1 bit). Therefore, higher populations will consume more resources than before even when they do not exchange information, and, as a consequence, the area where species always get extinct (the black area) now includes initial conditions where before they could survive by not sharing information (see Fig. B.1c and B.1d, initial conditions that were dark red are now black). Similarly, the area where not sharing information is strictly dominant now also contains initial values that originally were classified as not sharing weakly dominant. The reason for this is the same as mentioned: species by themselves capture more information than before, and therefore the consumption of resources is higher even when species share information only in the first time-step (such situations are exemplified in Table 3.2). Another consequence of the defined conditional probabilities is that the area where species cooperate was slightly extended. This happens because the amounts of consumed resources for high population densities decreased in comparison to our original parameters, since high population densities now possess less environmental information.

To summarise, changes in the parameters can extend or reduce the initial conditions where species cooperate, and they also can extend or reduce the initial conditions where species get extinct independently of their strategies. These changes also affect the initial conditions where there is no dominant strategy, where not sharing is strictly dominant, and where not sharing is weakly dominant. However, in the results there is always a transition from cooperative strategies to antagonistic strategies, and the parameters we chose are ones that clearly show it.

## B.2 Different dynamics for resources

In the model, we defined a dynamics for resources such that they grow at a rate of  $\alpha$  unless they are exhausted, in which case they remain in that state. Here, we consider a periodic replenishment of resources which is independent of the current amount available for bacteria. The dynamics are shown in the following equation:

$$R_{t+1} := R_t - (X_t + Y_t) + \beta \tag{B.3}$$

In this equation, resources are consumed proportionally to the sum of the population densities, and they are replenished by an amount  $\beta$ . We would like to test whether this change affects the observed transition from cooperation to antagonism in information exchange. For this purpose, we re-run the experiments of Sec. 3.5, but instead of using Eq. 3.24 in the

model, we use the one defined in this section, Eq. B.3, with a value  $\beta = 0.05$  (this value has been chosen particularly to show the transition of regimes from cooperation to antagonism).

The plots shown in Fig. B.3 are very similar to the ones shown in Fig. 3.5, the latter corresponding to the figures obtained from the original simulations. The difference that stands out between the two experiments happens for population densities close to their carrying capacity. In the original simulations, such population densities went extinct independently of their actions. In the current consideration, not sharing information is weakly dominant. Before, large populations would exhaust resources, and, since they were never replenished, both species would die out. Now, resources are may be fully consumed, but they would be replenished in any case.

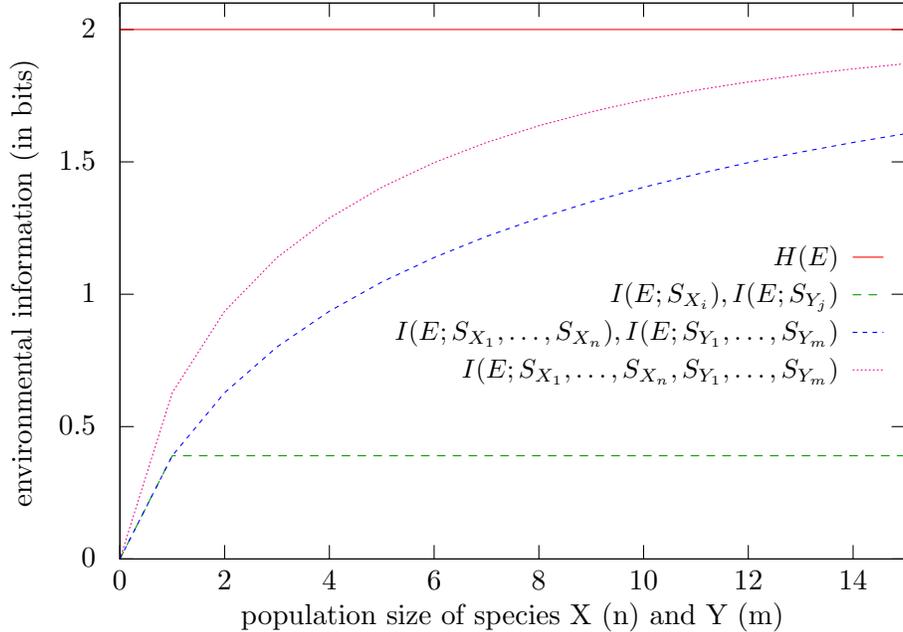


Figure B.2: Total amount of environmental information for different scenarios (using conditional probabilities B.1 and B.2):  $I(E; S_{X_i})$  and  $I(E; S_{Y_j})$  correspond to the case where an individual cell  $i$  of species  $X$  and an individual cell  $j$  of species  $Y$  acquire information from their sensors only, respectively.  $I(E; S_{X_1}, \dots, S_{X_n})$  is the total amount of information of each cell of species  $X$  when  $n$  cells communicate; in the same way  $I(E; S_{Y_1}, \dots, S_{Y_m})$  is the total amount of information of each cell of species  $Y$  when  $m$  cells communicate.  $I(E; S_{X_1}, \dots, S_{X_n}, S_{Y_1}, \dots, S_{Y_m})$  is the total amount of environmental information each cell of both population have when  $n$  cells of species  $X$  and  $m$  cells of species  $Y$  communicate. Finally,  $H(E)$  is the uncertainty of the environment.

$$\Pr(S_{X_i} | E) := \begin{matrix} & s_1 & s_2 \\ e_1 & \begin{pmatrix} 0.95 & 0.05 \end{pmatrix} \\ e_2 & \begin{pmatrix} 0.65 & 0.35 \end{pmatrix} \\ e_3 & \begin{pmatrix} 0.35 & 0.65 \end{pmatrix} \\ e_4 & \begin{pmatrix} 0.05 & 0.95 \end{pmatrix} \end{matrix} \quad (\text{B.1})$$

$$\Pr(S_{Y_i} | E) := \begin{matrix} & s_1 & s_2 \\ e_1 & \begin{pmatrix} 0.05 & 0.95 \end{pmatrix} \\ e_2 & \begin{pmatrix} 0.35 & 0.65 \end{pmatrix} \\ e_3 & \begin{pmatrix} 0.65 & 0.35 \end{pmatrix} \\ e_4 & \begin{pmatrix} 0.95 & 0.05 \end{pmatrix} \end{matrix} \quad (\text{B.2})$$

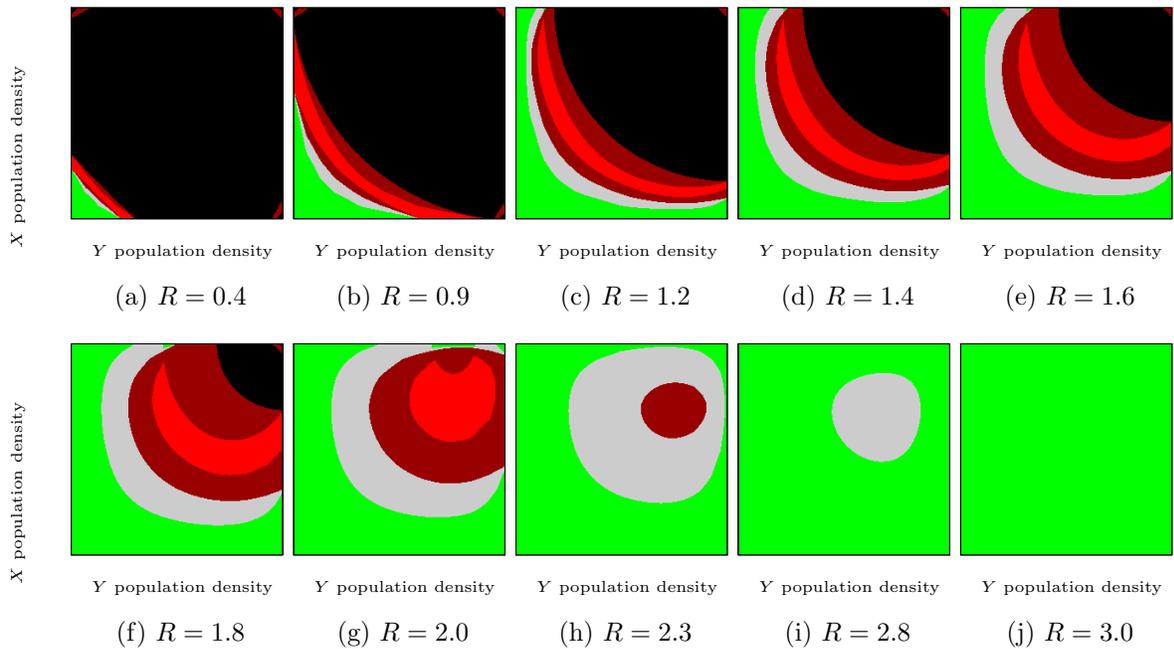


Figure B.3: (see in colour) We analyse the payoff matrix from  $250^2$  initial values of population densities of species  $X$  and  $Y$  uniformly distributed in  $\mathcal{X} \times \mathcal{Y}$ , with the amount of resources  $R$  fixed. Green points corresponds to sharing information being a weakly dominant strategy for species  $X$ . Grey points corresponds to initial values where there is no dominant strategy for species  $X$ . Red points represent values for which not sharing information is strictly dominant for species  $X$ . Dark-red points corresponds to values where not sharing information is weakly dominant for species  $X$ . Finally, black points represent values where species  $X$  goes extinct regardless of its strategy.

# Appendix C

## Numeric computations

### C.1 Environmental information computations

In this section, we show the computations for the mutual information values shown in Sec. 3.4.5. The conditional probabilities for the species' sensors are the ones defined in Eq. 3.2 and Eq. 3.3. The mutual information  $I(E ; S_{X_1})$  depends solely on the joint probability distribution  $p(e, s_x)$ , which is computed by

$$p(e, s_x) = p(s_x | e)p(e) \tag{C.1}$$

For example,

$$\begin{aligned} p(e_1, s_{x_1}) &= p(s_{x_1} | e_1)p(e_1) = 0.85 \times 0.25 = 0.2125 \\ p(e_1, s_{x_2}) &= p(s_{x_2} | e_1)p(e_1) = 0.15 \times 0.25 = 0.0375 \end{aligned}$$

The environmental probability  $p(E)$  is uniformly distributed, and  $p(s_x)$  is computed by

$$p(s_x) = \sum_e p(s_x | e)p(e) \tag{C.2}$$

Then,

$$\begin{aligned}
p(s_{x_1}) &= \sum_e p(s_{x_1} | e) p(e) \\
&= 2 \times (0.85 \times 0.25 + 0.15 \times 0.25) \\
&= 0.5 \\
p(s_{x_2}) &= \sum_e p(s_{x_2} | e) p(e) \\
&= 2 \times (0.15 \times 0.25 + 0.85 \times 0.25) \\
&= 0.5
\end{aligned}$$

In a similar way, we have that  $p(s_{y_1}) = p(s_{y_2}) = 0.5$ . The computation of the mutual information between the environmental variable and the sensor variable of one individual cell of species  $X$  is computed by

$$\begin{aligned}
I(E ; S_{X_1}) &= \sum_{e, s_x} p(e, s_x) \log_2 \left( \frac{p(e, s_x)}{p(e)p(s_x)} \right) \\
&= p(e_1, s_{x_1}) \log_2 \left( \frac{p(e_1, s_{x_1})}{p(e_1)p(s_{x_1})} \right) + p(e_2, s_{x_1}) \log_2 \left( \frac{p(e_2, s_{x_1})}{p(e_2)p(s_{x_1})} \right) \\
&\quad + p(e_3, s_{x_1}) \log_2 \left( \frac{p(e_3, s_{x_1})}{p(e_3)p(s_{x_1})} \right) + p(e_4, s_{x_1}) \log_2 \left( \frac{p(e_4, s_{x_1})}{p(e_4)p(s_{x_1})} \right) \\
&\quad + p(e_1, s_{x_2}) \log_2 \left( \frac{p(e_1, s_{x_2})}{p(e_1)p(s_{x_2})} \right) + p(e_2, s_{x_2}) \log_2 \left( \frac{p(e_2, s_{x_2})}{p(e_2)p(s_{x_2})} \right) \\
&\quad + p(e_3, s_{x_2}) \log_2 \left( \frac{p(e_3, s_{x_2})}{p(e_3)p(s_{x_2})} \right) + p(e_4, s_{x_2}) \log_2 \left( \frac{p(e_4, s_{x_2})}{p(e_4)p(s_{x_2})} \right) \\
&= 0.2125 \log_2 \left( \frac{0.2125}{0.25 \times 0.5} \right) + 0.0375 \log_2 \left( \frac{0.0375}{0.25 \times 0.5} \right) \\
&\quad + 0.2125 \log_2 \left( \frac{0.2125}{0.25 \times 0.5} \right) + 0.0375 \log_2 \left( \frac{0.0375}{0.25 \times 0.5} \right) \\
&\quad + 0.0375 \log_2 \left( \frac{0.0375}{0.25 \times 0.5} \right) + 0.2125 \log_2 \left( \frac{0.2125}{0.25 \times 0.5} \right) \\
&\quad + 0.0375 \log_2 \left( \frac{0.0375}{0.25 \times 0.5} \right) + 0.2125 \log_2 \left( \frac{0.2125}{0.25 \times 0.5} \right) \\
&= 0.2125 \log_2 (1.7) + 0.0375 \log_2 (0.3) \\
&\quad + 0.2125 \log_2 (1.7) + 0.0375 \log_2 (0.3) \\
&\quad + 0.0375 \log_2 (0.3) + 0.2125 \log_2 (1.7) \\
&\quad + 0.0375 \log_2 (0.3) + 0.2125 \log_2 (1.7) \\
&= 4 \times (0.2125 \times 0.765534746363 + 0.0375 \times -1.73696559417) \\
&= 0.390159695
\end{aligned}$$

In a similar way, we have that  $I(E ; S_{Y_1}) = 0.390159695$ . The joint probability of sensors

of an individual of species  $X$  and an individual of species  $Y$  are given by

$$p(s_x, s_y) = \sum_e p(s_x | e) p(s_y | e) p(e) \quad (\text{C.3})$$

Because of our definitions of the conditional probabilities  $p(s_x | e)$  and  $p(s_y | e)$ , we have the property that  $p(s_x, s_y) = p(s_x)p(s_y)$ , and thus we have

$$I(S_{X_1} ; S_{Y_1}) = D(p(s_x, s_y) || p(s_x)p(s_y)) = 0 \quad (\text{C.4})$$

Now, let us compute the mutual information about the environment when individuals from different species share their information:

$$I(E ; S_{X_1}, S_{Y_1}) = I(E ; S_{X_1}) + I(E ; S_{Y_1} | S_{X_1}) \quad (\text{C.5})$$

We know the value of  $I(E ; S_{X_1})$ , thus we just need to compute the following conditional mutual information:

$$\begin{aligned}
I(E; S_{Y_1} | S_{X_1}) &= \sum_{e, s_x, s_y} p(e, s_x, s_y) \log_2 \left( \frac{p(e, s_y | s_x)}{p(e | s_x) p(s_y | s_x)} \right) \\
&= p(e_1, s_{x_1}, s_{y_1}) \log_2 \left( \frac{p(e_1, s_{y_1} | s_{x_1})}{p(e_1 | s_{x_1}) p(s_{y_1} | s_{x_1})} \right) + p(e_2, s_{x_1}, s_{y_1}) \log_2 \left( \frac{p(e_2, s_{y_1} | s_{x_1})}{p(e_2 | s_{x_1}) p(s_{y_1} | s_{x_1})} \right) \\
&+ p(e_3, s_{x_1}, s_{y_1}) \log_2 \left( \frac{p(e_3, s_{y_1} | s_{x_1})}{p(e_3 | s_{x_1}) p(s_{y_1} | s_{x_1})} \right) + p(e_4, s_{x_1}, s_{y_1}) \log_2 \left( \frac{p(e_4, s_{y_1} | s_{x_1})}{p(e_4 | s_{x_1}) p(s_{y_1} | s_{x_1})} \right) \\
&+ p(e_1, s_{x_2}, s_{y_1}) \log_2 \left( \frac{p(e_1, s_{y_1} | s_{x_2})}{p(e_1 | s_{x_2}) p(s_{y_1} | s_{x_2})} \right) + p(e_2, s_{x_2}, s_{y_1}) \log_2 \left( \frac{p(e_2, s_{y_1} | s_{x_2})}{p(e_2 | s_{x_2}) p(s_{y_1} | s_{x_2})} \right) \\
&+ p(e_3, s_{x_2}, s_{y_1}) \log_2 \left( \frac{p(e_3, s_{y_1} | s_{x_2})}{p(e_3 | s_{x_2}) p(s_{y_1} | s_{x_2})} \right) + p(e_4, s_{x_2}, s_{y_1}) \log_2 \left( \frac{p(e_4, s_{y_1} | s_{x_2})}{p(e_4 | s_{x_2}) p(s_{y_1} | s_{x_2})} \right) \\
&+ p(e_1, s_{x_1}, s_{y_2}) \log_2 \left( \frac{p(e_1, s_{y_2} | s_{x_1})}{p(e_1 | s_{x_1}) p(s_{y_2} | s_{x_1})} \right) + p(e_2, s_{x_1}, s_{y_2}) \log_2 \left( \frac{p(e_2, s_{y_2} | s_{x_1})}{p(e_2 | s_{x_1}) p(s_{y_2} | s_{x_1})} \right) \\
&+ p(e_3, s_{x_1}, s_{y_2}) \log_2 \left( \frac{p(e_3, s_{y_2} | s_{x_1})}{p(e_3 | s_{x_1}) p(s_{y_2} | s_{x_1})} \right) + p(e_4, s_{x_1}, s_{y_2}) \log_2 \left( \frac{p(e_4, s_{y_2} | s_{x_1})}{p(e_4 | s_{x_1}) p(s_{y_2} | s_{x_1})} \right) \\
&+ p(e_1, s_{x_2}, s_{y_2}) \log_2 \left( \frac{p(e_1, s_{y_2} | s_{x_2})}{p(e_1 | s_{x_2}) p(s_{y_2} | s_{x_2})} \right) + p(e_2, s_{x_2}, s_{y_2}) \log_2 \left( \frac{p(e_2, s_{y_2} | s_{x_2})}{p(e_2 | s_{x_2}) p(s_{y_2} | s_{x_2})} \right) \\
&+ p(e_3, s_{x_2}, s_{y_2}) \log_2 \left( \frac{p(e_3, s_{y_2} | s_{x_2})}{p(e_3 | s_{x_2}) p(s_{y_2} | s_{x_2})} \right) + p(e_4, s_{x_2}, s_{y_2}) \log_2 \left( \frac{p(e_4, s_{y_2} | s_{x_2})}{p(e_4 | s_{x_2}) p(s_{y_2} | s_{x_2})} \right) \\
&= 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.5} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.5} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.5} \right) + 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.5} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.5} \right) + 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.5} \right) \\
&+ 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.5} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.5} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.5} \right) + 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.5} \right) \\
&+ 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.5} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.5} \right) \\
&+ 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.5} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.5} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.5} \right) + 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.5} \right) \\
&= 4 \times 0.031875 \log_2 (0.3) + 4 \times 0.031875 \log_2 (1.7) \\
&+ 4 \times 0.005625 \log_2 (0.3) + 4 \times 0.180625 \log_2 (1.7) \\
&= 4 * (-0.055365778 - 0.009770431 + 0.02440142 + 0.138274714) \\
&= 0.390159698
\end{aligned}$$

Then, we have

$$\begin{aligned} I(E ; S_{X_1}, S_{Y_1}) &= I(E ; S_{X_1}) + I(E ; S_{Y_1} | S_{X_1}) \\ &= 0.390159 + 0.390159 \\ &= 0.780318 \end{aligned}$$

Finally, we show the increase in environmental information when we consider two individual cells from the same species:

$$\begin{aligned}
I(E ; S_{X_2} | S_{X_1}) &= \sum_{e, s_x, s_{x'}} p(e, s_x, s_{x'}) \log_2 \left( \frac{p(e, s_{x'} | s_x)}{p(e | s_x) p(s_{x'} | s_x)} \right) \\
&= p(e_1, s_{x_1}, s_{x'_1}) \log_2 \left( \frac{p(e_1, s_{x'_1} | s_{x_1})}{p(e_1 | s_{x_1}) p(s_{x'_1} | s_{x_1})} \right) + p(e_2, s_{x_1}, s_{x'_1}) \log_2 \left( \frac{p(e_2, s_{x'_1} | s_{x_1})}{p(e_2 | s_{x_1}) p(s_{x'_1} | s_{x_1})} \right) \\
&+ p(e_3, s_{x_1}, s_{x'_1}) \log_2 \left( \frac{p(e_3, s_{x'_1} | s_{x_1})}{p(e_1 | s_{x_1}) p(s_{x'_1} | s_{x_1})} \right) + p(e_4, s_{x_1}, s_{x'_1}) \log_2 \left( \frac{p(e_4, s_{x'_1} | s_{x_1})}{p(e_2 | s_{x_1}) p(s_{x'_1} | s_{x_1})} \right) \\
&+ p(e_1, s_{x_1}, s_{x'_2}) \log_2 \left( \frac{p(e_1, s_{x'_2} | s_{x_1})}{p(e_1 | s_{x_1}) p(s_{x'_2} | s_{x_1})} \right) + p(e_2, s_{x_1}, s_{x'_2}) \log_2 \left( \frac{p(e_2, s_{x'_2} | s_{x_1})}{p(e_2 | s_{x_1}) p(s_{x'_2} | s_{x_1})} \right) \\
&+ p(e_3, s_{x_1}, s_{x'_2}) \log_2 \left( \frac{p(e_3, s_{x'_2} | s_{x_1})}{p(e_1 | s_{x_1}) p(s_{x'_2} | s_{x_1})} \right) + p(e_4, s_{x_1}, s_{x'_2}) \log_2 \left( \frac{p(e_4, s_{x'_2} | s_{x_1})}{p(e_2 | s_{x_1}) p(s_{x'_2} | s_{x_1})} \right) \\
&+ p(e_1, s_{x_2}, s_{x'_1}) \log_2 \left( \frac{p(e_1, s_{x'_1} | s_{x_2})}{p(e_1 | s_{x_2}) p(s_{x'_1} | s_{x_2})} \right) + p(e_2, s_{x_2}, s_{x'_1}) \log_2 \left( \frac{p(e_2, s_{x'_1} | s_{x_2})}{p(e_2 | s_{x_2}) p(s_{x'_1} | s_{x_2})} \right) \\
&+ p(e_3, s_{x_2}, s_{x'_1}) \log_2 \left( \frac{p(e_3, s_{x'_1} | s_{x_2})}{p(e_1 | s_{x_2}) p(s_{x'_1} | s_{x_2})} \right) + p(e_4, s_{x_2}, s_{x'_1}) \log_2 \left( \frac{p(e_4, s_{x'_1} | s_{x_2})}{p(e_2 | s_{x_2}) p(s_{x'_1} | s_{x_2})} \right) \\
&+ p(e_1, s_{x_2}, s_{x'_2}) \log_2 \left( \frac{p(e_1, s_{x'_2} | s_{x_2})}{p(e_1 | s_{x_2}) p(s_{x'_2} | s_{x_2})} \right) + p(e_2, s_{x_2}, s_{x'_2}) \log_2 \left( \frac{p(e_2, s_{x'_2} | s_{x_2})}{p(e_2 | s_{x_2}) p(s_{x'_2} | s_{x_2})} \right) \\
&+ p(e_3, s_{x_2}, s_{x'_2}) \log_2 \left( \frac{p(e_3, s_{x'_2} | s_{x_2})}{p(e_1 | s_{x_2}) p(s_{x'_2} | s_{x_2})} \right) + p(e_4, s_{x_2}, s_{x'_2}) \log_2 \left( \frac{p(e_4, s_{x'_2} | s_{x_2})}{p(e_2 | s_{x_2}) p(s_{x'_2} | s_{x_2})} \right) \\
&= 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.745} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.255} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.255} \right) + 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.745} \right) \\
&+ 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.745} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.255} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.255} \right) + 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.745} \right) \\
&+ 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.745} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.255} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.255} \right) + 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.745} \right) \\
&+ 0.005625 \log_2 \left( \frac{0.01125}{0.075 \times 0.745} \right) + 0.031875 \log_2 \left( \frac{0.06375}{0.075 \times 0.255} \right) \\
&+ 0.031875 \log_2 \left( \frac{0.06375}{0.425 \times 0.255} \right) + 0.180625 \log_2 \left( \frac{0.36125}{0.425 \times 0.745} \right) \\
&= 4 \times 0.031875 \log_2 (3.333333333) + 4 \times 0.031875 \log_2 (0.588235294) \\
&+ 4 \times 0.005625 \log_2 (0.201342282) + 4 \times 0.180625 \log_2 (1.140939597) \\
&= 4 * (0.0553658 - 0.0244014 - 0.0130066 + 0.0343589) \\
&= 0.209267
\end{aligned}$$

## C.2 Indistinguishable sources of messages computations

In this section, we show the computations for the mutual information values shown in Sec. 4.4.1. We assume  $p(\mu = 1) = p(\mu = 2) = \frac{1}{2}$ , that  $\Theta'$  can take values from the set  $\{2, 3\}$ , and that  $p(\Theta' = 2) = p(\Theta' = 3) = \frac{1}{2}$ , and  $\epsilon = 0.01$ . The rest of the probabilities are defined as follows:

$$\Pr(Y_1 | \mu) := \begin{matrix} y_1 & y_2 \\ \mu_1 & \begin{pmatrix} 1 - \epsilon & \epsilon \\ \epsilon & 1 - \epsilon \end{pmatrix} \\ \mu_2 & \end{matrix} \quad (\text{C.6})$$

$$\Pr(Y' | \mu, \Theta') := \begin{matrix} y'_1 & y'_2 \\ \theta'_2, \mu_1 & \begin{pmatrix} 1 - \epsilon & \epsilon \\ \epsilon & 1 - \epsilon \end{pmatrix} \\ \theta'_2, \mu_2 & \\ \theta'_3, \mu_1 & \begin{pmatrix} 1 - \epsilon & \epsilon \\ \epsilon & 1 - \epsilon \end{pmatrix} \\ \theta'_3, \mu_2 & \end{matrix} \quad (\text{C.7})$$

$$\Pr(X' | Y', \Theta') := \begin{matrix} x'_1 & x'_2 \\ \theta'_2, y'_1 & \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \\ \theta'_2, y'_2 & \\ \theta'_3, y'_1 & \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \\ \theta'_3, y'_2 & \end{matrix} \quad (\text{C.8})$$

$$\Pr(X' | Y', \Theta') := \begin{matrix} x'_1 & x'_2 \\ \theta'_2, y'_1 & \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \\ \theta'_2, y'_2 & \\ \theta'_3, y'_1 & \begin{pmatrix} 0 & 1 \\ 0 & 1 \end{pmatrix} \\ \theta'_3, y'_2 & \begin{pmatrix} 1 & 0 \\ 1 & 0 \end{pmatrix} \end{matrix} \quad (\text{C.9})$$

We want to compute the following mutual information:

$$I(\mu ; Y_1, X') = \sum_{\mu, y, x'} p(\mu, y, x') \log_2 \left( \frac{p(\mu, y, x')}{p(\mu)p(y, x')} \right)$$

For this, we need to compute the following joint probabilities:

$$p(\mu, y, x') = \sum_{y', \theta'} p(x' | y', \theta') p(\theta') p(y' | \mu, \theta') p(y | \mu) p(\mu) \quad (\text{C.10})$$

$$p(y, x') = \sum_{y', \theta', \mu} p(x' | y', \theta') p(\theta') p(y' | \mu, \theta') p(y | \mu) p(\mu) \quad (\text{C.11})$$

The mutual information between the environmental variable and the sensors of individual 1, together with messages of individuals 2 and 3, which are produced according to the coding scheme in Eq. C.8, is given by:

$$\begin{aligned}
I(\mu; Y_1, X') &= \sum_{\mu, y, x'} p(\mu, y, x') \log_2 \left( \frac{p(\mu, y, x')}{p(\mu)p(y, x')} \right) \\
&= p(\mu_1, y_1, x'_1) \log_2 \left( \frac{p(\mu_1, y_1, x'_1)}{p(\mu_1)p(y_1, x'_1)} \right) + p(\mu_1, y_1, x'_2) \log_2 \left( \frac{p(\mu_1, y_1, x'_2)}{p(\mu_1)p(y_1, x'_2)} \right) \\
&\quad + p(\mu_1, y_2, x'_1) \log_2 \left( \frac{p(\mu_1, y_2, x'_1)}{p(\mu_1)p(y_2, x'_1)} \right) + p(\mu_1, y_2, x'_2) \log_2 \left( \frac{p(\mu_1, y_2, x'_2)}{p(\mu_1)p(y_2, x'_2)} \right) \\
&\quad + p(\mu_2, y_1, x'_1) \log_2 \left( \frac{p(\mu_2, y_1, x'_1)}{p(\mu_2)p(y_1, x'_1)} \right) + p(\mu_2, y_1, x'_2) \log_2 \left( \frac{p(\mu_2, y_1, x'_2)}{p(\mu_2)p(y_1, x'_2)} \right) \\
&\quad + p(\mu_2, y_2, x'_1) \log_2 \left( \frac{p(\mu_2, y_2, x'_1)}{p(\mu_2)p(y_2, x'_1)} \right) + p(\mu_2, y_2, x'_2) \log_2 \left( \frac{p(\mu_2, y_2, x'_2)}{p(\mu_2)p(y_2, x'_2)} \right) \\
&= 0.49005 \log_2 \left( \frac{0.49005}{0.5 \times 0.4901} \right) + 0.00495 \log_2 \left( \frac{0.00495}{0.5 \times 0.0099} \right) \\
&\quad + 0.00495 \log_2 \left( \frac{0.00495}{0.5 \times 0.0099} \right) + 0.00005 \log_2 \left( \frac{0.00005}{0.5 \times 0.4901} \right) \\
&\quad + 0.00005 \log_2 \left( \frac{0.00005}{0.5 \times 0.4901} \right) + 0.00495 \log_2 \left( \frac{0.00495}{0.5 \times 0.0099} \right) \\
&\quad + 0.00495 \log_2 \left( \frac{0.00495}{0.5 \times 0.0099} \right) + 0.49005 \log_2 \left( \frac{0.49005}{0.5 \times 0.4901} \right) \\
&= 0.489977869 + 0 + 0 - 0.000612943 - 0.000612943 + 0 + 0 + 0.489977869 \\
&= 0.978729852
\end{aligned}$$

Now, we compute the same mutual information, but this time using the coding scheme defined in Eq. C.9:

$$\begin{aligned}
I(\mu; Y_1, X') &= \sum_{\mu, y, x'} p(\mu, y, x') \log_2 \left( \frac{p(\mu, y, x')}{p(\mu)p(y, x')} \right) \\
&= p(\mu_1, y_1, x'_1) \log_2 \left( \frac{p(\mu_1, y_1, x'_1)}{p(\mu_1)p(y_1, x'_1)} \right) + p(\mu_1, y_1, x'_2) \log_2 \left( \frac{p(\mu_1, y_1, x'_2)}{p(\mu_1)p(y_1, x'_2)} \right) \\
&+ p(\mu_1, y_2, x'_1) \log_2 \left( \frac{p(\mu_1, y_2, x'_1)}{p(\mu_1)p(y_2, x'_1)} \right) + p(\mu_1, y_2, x'_2) \log_2 \left( \frac{p(\mu_1, y_2, x'_2)}{p(\mu_1)p(y_2, x'_2)} \right) \\
&+ p(\mu_2, y_1, x'_1) \log_2 \left( \frac{p(\mu_2, y_1, x'_1)}{p(\mu_2)p(y_1, x'_1)} \right) + p(\mu_2, y_1, x'_2) \log_2 \left( \frac{p(\mu_2, y_1, x'_2)}{p(\mu_2)p(y_1, x'_2)} \right) \\
&+ p(\mu_2, y_2, x'_1) \log_2 \left( \frac{p(\mu_2, y_2, x'_1)}{p(\mu_2)p(y_2, x'_1)} \right) + p(\mu_2, y_2, x'_2) \log_2 \left( \frac{p(\mu_2, y_2, x'_2)}{p(\mu_2)p(y_2, x'_2)} \right) \\
&= 0.2475 \log_2 \left( \frac{0.2475}{0.5 \times 0.25} \right) + 0.2475 \log_2 \left( \frac{0.2475}{0.5 \times 0.25} \right) \\
&+ 0.0025 \log_2 \left( \frac{0.0025}{0.5 \times 0.25} \right) + 0.0025 \log_2 \left( \frac{0.0025}{0.5 \times 0.25} \right) \\
&+ 0.0025 \log_2 \left( \frac{0.0025}{0.5 \times 0.25} \right) + 0.0025 \log_2 \left( \frac{0.0025}{0.5 \times 0.25} \right) \\
&+ 0.2475 \log_2 \left( \frac{0.2475}{0.5 \times 0.25} \right) + 0.2475 \log_2 \left( \frac{0.2475}{0.5 \times 0.25} \right) \\
&= 4 * 0.243911357 - 4 * 0.01410964 \\
&= 0.919206868
\end{aligned}$$

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