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Cooperation and antagonism in information exchange in a growth scenario with two species

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HIGHLIGHTS

- We have studied the conditions for information-theoretic cooperation between two species.
- Species maximise their chances of survival by following a bet-hedging strategy.
- There is possible competition by resource constraints.
- Species can choose to communicate (cooperate) or not.
- We find distinct regimes of cooperation, non-cooperation and in-between situations.

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ABSTRACT

We consider a simple information-theoretic model of communication, in which two species of bacteria have the option of exchanging information about their environment, thereby improving their chances of survival. For this purpose, we model a system consisting of two species whose dynamics in the world are modelled by a bet-hedging strategy. It is well known that such models lend themselves to elegant information-theoretical interpretations by relating their respective long-term growth rate to the information the individual species has about its environment. We are specifically interested in modelling how this dynamics are affected when the species interact cooperatively or in an antagonistic way in a scenario with limited resources. For this purpose, we consider the exchange of environmental information between the two species in the framework of a game. Our results show that a transition from a cooperative to an antagonistic behaviour in a species results as a response to a change in the availability of resources. Species cooperate in abundance of resources, while they behave antagonistically in scarcity.

1. 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).

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

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information-theoretic terms in Kussell and Leibler (2005), Bergstrom and Lachmann (2004, 2005), Donaldson-Matasci et al. (2008, 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 its 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, and pH levels, bacteria also obtain information about their environment by detecting concentration levels of diffusable 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 diffusable 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 bioluminiscence (Miller and Bassler, 2001; Henke and Bassler, 2004).

Since the introduction of quorum sensing, other uses for diffusable 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 diffusable 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 Section 4. 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, 2012). 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, 2012). In particular, Requejo and Camacho (2011, 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. This transition is from a game equivalent to a Prisoner's Dilemma, where defection is dominant, to a Harmony Game, where cooperation dominates. In this study, we present a model from an information-theoretic perspective.

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. Where optimal strategies for communication exist, they would serve as an indication of which behaviours of a species evolution would favour. For other cases, we discuss possible modifications of the model in order to study them.

2. Model

2.1. 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 want to 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 the four equally likely states (i.e. its entropy is 2 bits) and that 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. In addition, we assume that each individual cell can measure its corresponding bit with only 85% accuracy.

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