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# Game of Coordination for Bacterial Pattern Formation: A Finite Automata Modelling

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**Abstract.** Bacterial colonies in nature are often required to evolve under harsh and hostile environmental growth conditions. In order to do so, bacteria work as a social formation and employ intricate communication capabilities to exchange information and interact cooperatively to form highly complex colonies, equipped with higher capabilities for adaptation to the environmental challenges. These colonies that could be observed as intricate spatial patterns are essentially the manifestation of bacterial self-organization resulting from such cooperative behavior. The information required by the bacteria for giving rise to the observed self-organized complex pattern formation is generated through cooperative interactions, depending on and in response to the available growth conditions. Bacterial self-organization and colony formation, thus, appears as an instance of a social network, essentially created through communicative interactions.

In this paper, we use concepts from game theory and informatics to describe the emergence of self-organization and consequent pattern formation through communicative cooperation in *Bacillus subtilis* colonies. The emergence of cooperative regime is modelled as an Assurance game, with the bacterial colonies as individual players. The game is played iteratively through cooperative communication, and mediated by exchange of information about the local environment between the different bacterial colonies comprising the system. The iteration causes the interactive system to grow and produce beautiful complex spatial patterns signaling the emergence of self-organization.

As a formal description of the game, we model the emergence of this cooperative behavior as finite deterministic automata, whose transition function is informed by the Assurance game pay-off.

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**Index to information contained in this paper**

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## 1. Introduction

Interacting groups of motile organisms form complex systems that offer a rich repository for studying and learning about various interesting facets of complexity. These organisms may exhibit characteristic patterns of self-organized collective behavior, forming spatial aggregation. Microorganisms communicate and cooperate to perform a wide range of multicellular behaviors such as dispersal, nutrient acquisition, bio-film formation and quorum sensing [26, 41, 62].

In this paper, we study an interacting colony of bacteria as a typification of complexity. A single bacterium can be treated as a complex molecule, which interacts with its environment, communicates with other individuals, replicates and undergoes evolution and mutation. These interactions include competition for nutrients, cooperation by providing public goods essential for the formation and maintenance of the biofilm, communication through the secretion and detection of extracellular substances [25]. When millions of bacteria act collectively as a group (as is the case in any bacterial colony), a large variety of different, fascinating spatial patterns emerge as a result of games played by the individual bacteria colony with its neighbours as well as with the environment. These patterns are the emergent result of local interactions (interactions within the neighbourhood of each individual colony) through exchange and processing of information over discrete time, and environmental conditions. The self-organization in the colonies that is manifest as the emergent phenomenon can be viewed as being programmed by both the particular way the bacteria in question interact, as well as by the particular way these bacteria respond to environmental signals [6, 11, 35].

In nature, bacterial colonies may often experience hostile, challenging environmental conditions that may not offer optimal factors for growth and evolution of the colonies. Evolving populations of bacteria (and therefore bacterial colonies) carry and mediate information via games played by them locally. Each colony would receive a finite set of input information or signals from its neighbours (and therefore, as well as the environment) in the form of the strategies played by the neighbouring colony in the game. This input set is the determinant for the strategies that the focal colony would play in response. Strategies in the game would decide the pay-offs for the colonies (the players) playing the game. The pay-offs would determine the transition of the focal colony to the next state in discrete time step, producing a final set of states (the next generation). The behavior of bacterial colonies could therefore be mimicked by finite state machines.

To cope with environmental stress, these aggregations of colonies or finite state machines which essentially form the complex system, through the mechanism of information processing develop extensive cooperative behavior. These cooperative behaviors could be modelled as pay-offs of games played between the colonies mentioned in the above paragraph, to share available resources usefully via transmission of information between them, and evolve. These stressed bacterial colonies exhibit emergence and self-organization, two of the essential signatures of a complex system, and produce fascinating spatially complex patterns of aggregations, manifesting the complexity of information transfer and processing [7,8,17,36,41,55].

Our objective in this paper is to model the cooperative behavior of such stressed bacterial colonies which emerges as a collective manifestation of information processing by the interacting bacterial colonies, by using deterministic finite automata (DFA).

## 2. Background for Modelling

The growth of bacterial colonies in harsh, challenging environment could be modelled as an instance of management of commons. In the present context, such a management regime addresses three very critical issues: producing a public good by wetting the surface hardened by chemical stress, regulating proper appropriation of the limited nutrient by the growing colonies and preventing public 'bad' by avoiding the effect of antibiotic-induced stress. Such a regime may encourage emergence of cooperation among the colonies competing for the constrained resources for growth. Thus the situation as is in this work, may be viewed as a problem of resource appropriation through coordination among the colonies.

We apply game theory to model the above bacterial behavior leading to coordinated cooperation among the colonies. The spatial patterns observed are the manifestation of emergent phenomena, which are in turn the consequence of essentially non-linear interactions among the individual bacteria colonies, as well as with their immediate environment.

Assurance game, a generic name for the Stag Hunt game, best represents the present situation. In the modelling of the cooperative behavior, we assume that each bacterial colony is a player in the game, and thus accrues a quantum of pay-off depending on its own as well as its co-player's strategies. The game is iterated over time-steps for a countable number of steps to produce the emergence of complex spatial patterns of bacterial colonies.

Further, in Assurance game, a minimal cost must be contributed by all players if they are to receive any benefit from their own action. Thus, such a game would best capture the essence of coordinated, social cooperation as observed in the experiments we conducted, and also since Assurance game properly describes such behaviors especially in the context of biological communities [46,47,48,54].

To construct a rudimentary model of the interactions and consequent bacterial evolution, we assume that the Assurance game progresses by exchange of information between the colonies. Each bacterial colony receives a finite number of input information from its neighbor at each time step at a given state, and makes a transition to an unambiguously determined next state at the next time step. With this assumption, we design deterministic finite automata (DFA) to model the discrete growth dynamics of the stressed bacterial colonies [32,33,37]. We propose that the colonies exchange information using a context free grammar, which is obtained via the automata.

With the above agenda, we pose our research problem as:
*What are the DFA and the corresponding grammar that model the growth dynamics and pattern formation in a system of stressed bacterial colonies over discrete time?*

To address the problem, we make the following assumptions [6]:

1. The environment is a two-dimensional matrix, which represents the medium. The resources necessary for growth of bacterial population are locally (within a neighborhood) constrained.

2. Growth of bacterial colony is an orderly increase in the quantity of bacterial constituents.
3. The agent's fitness, which we define as a linear function of the pay-off received by the agent in a game, is the determinant of the agent's growth.
4. Availability of an appropriate biochemical and biophysical environment is the necessary condition for the bacteria to propagate. The biochemical environment is the environment of the nutrition, and is made available as the culture medium; the biophysical environment is supplied by the agar concentration that forms the substrate for the bacteria population to grow.
5. In a single time step each agent consumes a fixed amount of nutrients to grow.
6. The ability to reproduce depends on the amount of free space available in the agent neighborhood.
7. The game provides the pay-off to each agent for computing its fitness, and growth determined by the fitness, is contingent upon the game played by the agent at the instant of discrete time.

Let an *n*-player Assurance game in the strategic form be given by $G(\Theta, \Sigma, \Pi)$, where $\Theta = \{\Theta_i\}$ is the set of players, with $i \in \Im = \{1, 2, ..., n\}$ a finite index set and $n \geq 2$, $\Sigma = \{\Sigma_i\}$ where $\Sigma_i$ is the pure strategy set for each player $\Theta_i$, with $\sigma = (\sigma_1, \sigma_2, ..., \sigma_n)$ where $\sigma_i \in \Sigma_i$ for $i \in \Im$ is a pure strategy profile of the game and $\Pi = \{\Pi_i\}$, the set of pay-off functions $\Pi_i : S \rightarrow \Re \ \forall i \in \Im$ where $S$ is the set of strategy profiles, give the player's von Neumann-Morgenstern utility $\Pi_i(\sigma)$ for every profile.

Let the game be repeated in periods of discrete time $t \in N$. Note that each strategy $\sigma_i$ in this game $G$ is a member of the standard basis for the simplex $\Lambda = \left\{ \hat{p} = (p_1, p_2, ..., p_n)^T \in \Re : p_i \geq 0, i \in N, \sum_{i=1}^{n} p_i = 1 \right\}$, which is the simplex for all strategies (pure as well as mixed) in the game *G*.

Let the evolving population of bacterial colonies play the game *G*, iterated over time steps of *t*, with $t \in N$ .Assume that for each player $\Theta_i, i \in \Im$, the strategy set $\Sigma_i = \{C, D\}$ comprises two pure strategies called cooperate *(C)* and defect *(D)*.

For building the model, let us adopt a bottom-up approach, and first discuss the game with *n*=2. Thetwo-player Assurance game is described by the following pay-off matrix:

$$\begin{array}{ccc} & \mathbf{C} & \mathbf{D} \\ \mathbf{C} & R,R & S,T \\ \mathbf{D} & T,S & P,P \end{array}$$

with the row player being the first player $\Theta_1$, and the column player being the second, $\Theta_2$

If both the players play *C*, then each obtains a reward *R* as the pay-off for cooperating. If both play *D* instead, each obtains a punishment *P* for defecting, as the pay-off. If one player plays *C* while the other plays *D*, then the one playing *D* obtains a pay-off of temptation (to defect) *T* while the one playing *C* gets a pay-off of sucker's, *S*. The game $G$ is then defined by the constraint on the pay-offs as: $R > T > P > S$ .It is thus obvious that in Assurance game, the dominant strategy is *C*. The important point to note is that the net pay-off accruing to a player when the individual free-rides on the public good provided by the other player is smaller than the net pay-off that the free-rider would receive by cooperating.

We may assign arbitrary numerical values to the pay-offs obtained by the players to describe $G$ by the following pay-off matrix:

| | **C** | **D** |
|---|---|---|
| **C** | 8,8 | 1,6 |
| **D** | 6,1 | 2,2 |

However, it may be noted that even in this situation of two Assurance game players interacting, one of the players may have a greater interest in playing *C* than the other. With the above pay-off matrix, the simplex $\Lambda$ for $G$ would then be depicted as:

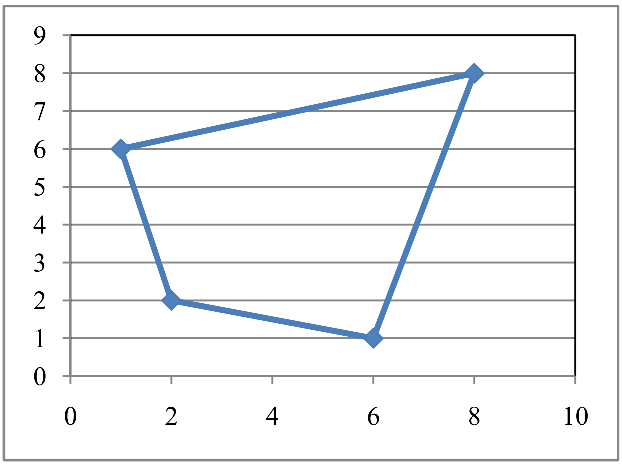
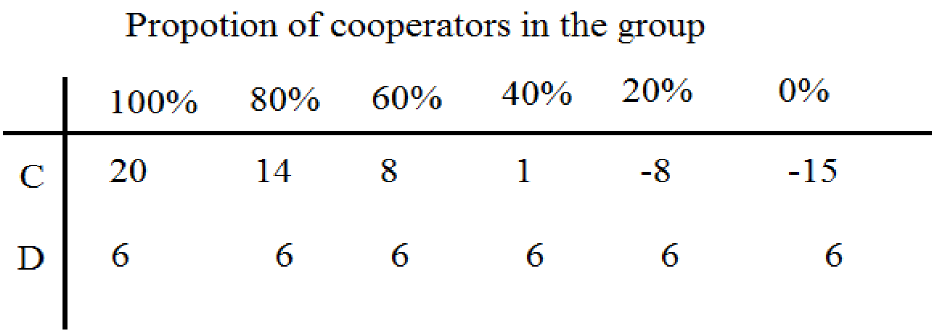


**Figure1. Simplex for Assurance game with n=2**

The simplex $\Lambda$ thus defines the area within which the orbits resulting from repeated and iterated play of $G$ over steps of $t$ (generations) would remain confined [1,14,39,43,52,53].

Players with Assurance game pay-off structure (implying that it has no incentive to free-ride on other player's cost) would therefore, for reasons argued above, like best to cooperate with their co-players and would not want to be exploited by free-riders. This requires a trust mechanism to be in place that would assure the Assurance game players of mutual intentions and interests of cooperation. Such a mechanism then would take care of the uncertainty surrounding the behavior of the players and its resultant effect on the emergence of cooperation through coordinated effort among the players [4].In this work, we assume that there exists a mechanism of pre-play signalling between the bacterial colonies declaring their intentions for mutual cooperation.

To obtain an understanding about the interactions between growing bacterial colonies that leads the emergence of complex spatial patterns, we next study theAssurance game for *n*=*n*, with *n* significantly large. The game is played between Assurance game players. For analyzing this *n*-player Assurance game, consider the pay-off matrix adopted from [4]:



Propotion of cooperators in the group

| | 100% | 80% | 60% | 40% | 20% | 0% |
|---|---|---|---|---|---|---|
| C | 20 | 14 | 8 | 1 | -8 | -15 |
| D | 6 | 6 | 6 | 6 | 6 | 6 |

The matrix shows pay-offs obtained by an individual player while playing against co-players who cooperate. As could be observed from the matrix, the pay-offs from cooperation and defection for each player depends on the proportion of players who actually play *C* or play *D* in the entire population. It can be noticed on the one hand that the pay-offs for an individual player playing *C* varies directly and monotonically with the proportion of co-operators in the population. On the other hand, the pay-offs obtained by the individual by playing *D* remains constant irrespective of the proportion of players choosing to defect. This implies that whether an Assurance game player would cooperate or would it defect, depends on its expectations of the likely behavior of the co-players. If it expects that at least 60 % of its co-players in the population would play C, only then will it choose to play C. Else, it would obtain a higher pay-off by choosing to play *D.*

The above reasoning shows that for cooperation to prevail in such a growing bacterial population through an *n*-player Assurance game, a significant determinant is that the players develop a confidence about the expected behaviour of their co-players. In our modelling of the bacterial growth, we assume that such a message would be transmitted as a signal – both pre-play, as also during the play.

The above discussions point to the fact that under stressed conditions when the environment is not favorable for growth, bacterial colonies interact through coordination game to cooperate, by employing communication to overcome the constraints to their growth. Such signaling lead to evolution of cooperative sharing of resources as public good, within and between the stressed colonies, and the emergence of such self-organization is manifested through beautiful complex spatial patterns [5,9,10,15,16,18,23,25,29,34,42,44,49,51,57].

During such an iterated play of strategies, instead of obtaining a static equilibrium solution, the focus shifts to adopting the best available strategy dynamically, expressed in terms of a fitness score, a measure of the success of each strategy with respect to the other strategies, in the play of *G*. The bacteria colonies, during the play of *G,* seek to optimize the fitness of their respective strategies and evolve by adopting the most successful strategy in their strategy profile [2,3,46,47,48,54,55]. The spatial complexity, manifested as fascinating spatial patterns, which emerge as an effect of the pay-offs obtained by the colonies (players) in this game by adopting different cooperative strategies, are the pay-offs obtained by the players in the iterative game, and are essentially the macroscopic emergent structures resulting from the microscopic bacterial interactions via the iterated game $G$ in this complex system dynamics [19, 20, 21, 22, 24, 31, 39, 45, 49, 50, 59].

## 3. Experimental Observations

The experiments to observe bacterial growth dynamics and colony formation under favorable as well as stressed conditions were conducted following strict protocol given in [8] to obtain reproducible results.

In the following paragraphs, we describe the observations of the experiment, subjecting the growth of bacterial colonies to three different sets of chemically induced stresses, and the following section, describe the corresponding inferences that were drawn.

- *Peptone stress:* To observe the competition of bacterial colonies for common resource [12], we inoculated simultaneously the two colonies of *Bacillus subtilis* on an agar plate at approximately equidistant from the plate’s centre. The initial growth of both colonies is same as for a single isolated colony, and results in two clusters of bacterial colonies.After a well-definedperiod of time, it is observed that the growth of each of the two colonies in the direction of each other gets halted, and a region of clear demarcation between boundaries of the growing clusters is formed, without any colony occupying this region, and hence we call it a region of no occupancy.We found that the size of this unoccupied region is inversely related to the peptone concentration, and is almost independent of agar concentrations, as presented in Fig 2.

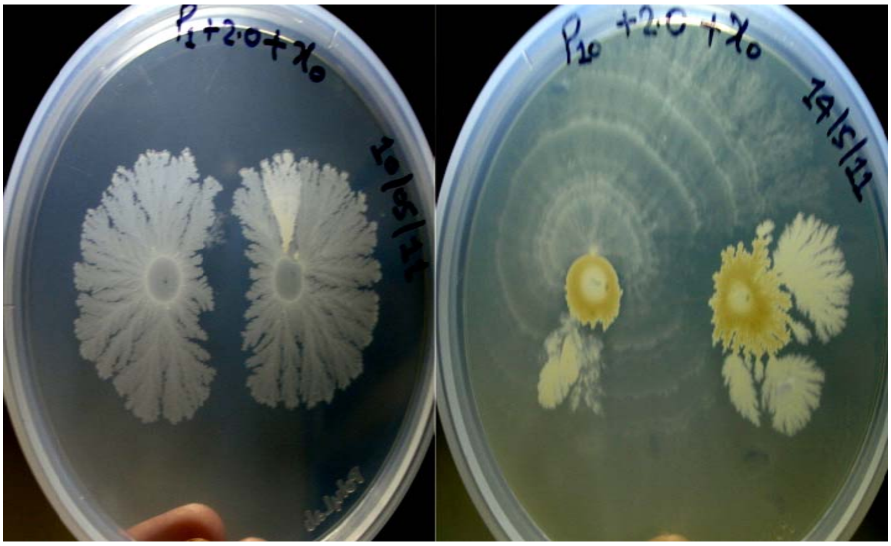


**Figure 2. Left photograph with poor nutrient (peptone: 2g/l) and right photograph with rich nutrient (peptone: 10 g/l) with same agar (2.0%) and no antibiotic.**

**Figure 3. Left photograph with poor nutrient (peptone: 1g/l) and right photograph with rich nutrient (peptone: 10 g/l) with identical concentration of agar (1.5%) and no antibiotic.**

We further observethat at normal and identical agar concentration in absence of any antibiotic stress in the environment, at low level of peptone the growing cluster of colonies exhibits a pattern of dense branching, while with higher peptone levels, the cluster exhibits a compact structure, as shown in Fig 3.

- *Agar stress:* High quantity agar results into hard surface, thus affecting the motility of bacteria. Motility, in turn, affects their efficiency of communication, and hence their growth. Literature suggests certain mechanisms bacterial colonies may employ to cope with such environmental stress as this, via distributed information processing and cooperation [6,10,13,28,60].The resultant growth patterns as observed in our laboratory are depicted in Figure3 below.

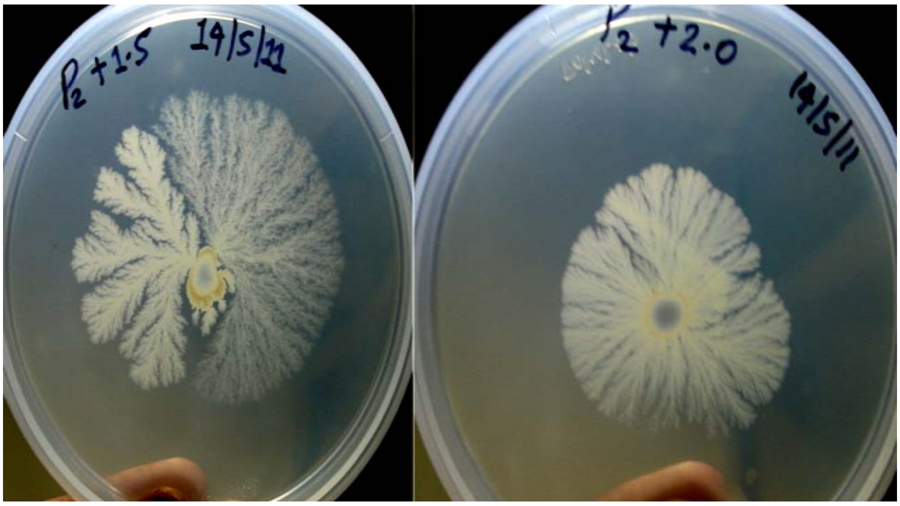


**Figure 4.Left photograph with normal agar (1.5%) and right photograph with high agar (2%) with same peptone (2 g/l) and no antibiotic.**

- *Antibiotic stress:* Septrin (co-trimoxazole), used as anantibiotic stress in the experiment, inhibits the bacterial DNA synthesis and thus it affects the bacterial growth and multiplicity [30]. We allowed the system to be stressed by varying concentrations of peptone and agar, and obtained the growth patterns both, in the absence and in presence of Septrin in the Petri dish. The results are depicted by Figures 4a –4c below:

**Figure 5a. Peptone 10g/l, agar 2.0%, with no antibiotic**

**Figure 5b. Peptone 5g/l, agar 1.5%, antibiotic 3µg/ml**

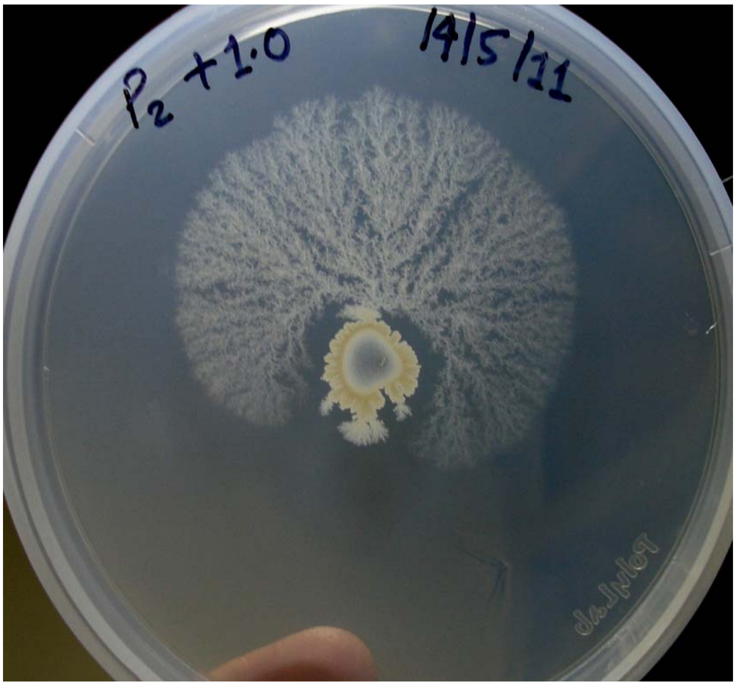


**Figure 5c.Peptone 2g/l, agar 1.0%, antibiotic 3µg/ml**

## 4. Inferences and Discussion

It would be apparent from the photographs of the previous section, that the emergent patterns of bacterial colonies present some amount of diversity in their appearances. Hence, in what follows, we present a pattern-specific discussion of the four prominently observed patterns emerging due to the interaction between bacterial colonies constrained to grow in stressed environment. We give names to the four observed types.

### *1. Dense branching*

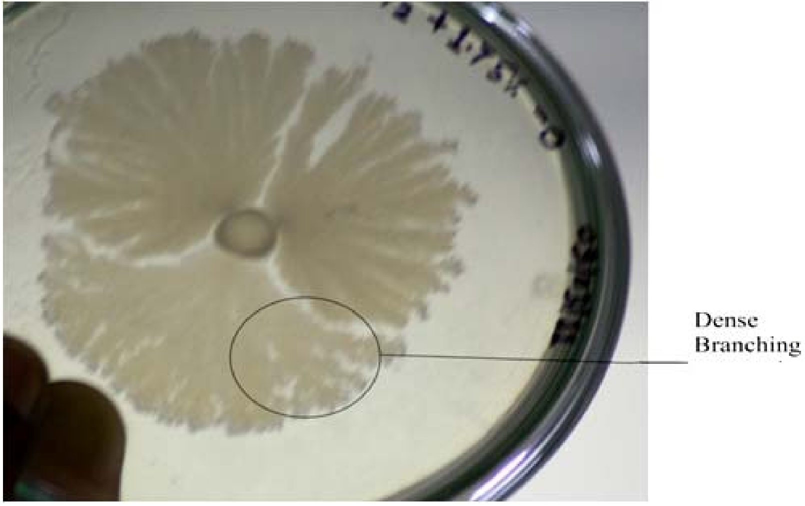


**Figure 6. Dense branching pattern**

The pattern we have called dense branching structure (DBS) and illustrated in Figure6 is observed when the bacterial colonies are grown under poor nutrient (low peptone concentration) and normal agar concentration. We propose that such a pattern gets generated when a small proportion of the interacting colonies collectively secrete an anti-bacterial compound to compete for limited resource (nutrient) with the rest of the players, rather than contributing their efforts in the cost for coordinating and thus sharing the resource. We have, based on the argument as above, propose that the strategy used to reach this state from the initial state is ($C_{80}$, $D_{20}$), that is, 80% of the bacterial colonies comprising the population of players are cooperating and the remaining 20% refrain from cooperating, and tend to free-ride on the efforts invested by the cooperators.

### *2. Meagerly spaced branching*

The next type of patterns observed is named meagerly spaced branching (MSB), because of a low density of colonies present in the formation, as depicted in Figure7.

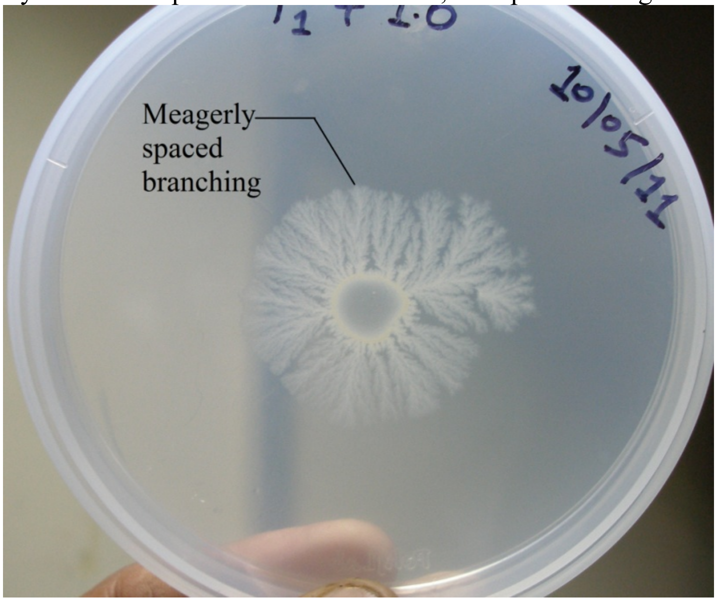


**Figure 7. Meagerly spaced branching pattern**

This pattern appeared when the colonies were subjected to poor nutrient level combined with high agar concentration (thus a hard surface). In such a constrained growth environment, we propose that 60% of the colonies coordinate through cooperation to cope with hard surface, and thus survive and 40% of the colonies defect with others to compete for limited resource, and in this extreme harsh substrate condition, may perish in the act. Following the above reasoning, we inferred that MSB patterns forms when the strategy used by the player population is ($C_{60}$, $D_{40}$).

### *3. Sparse branching*

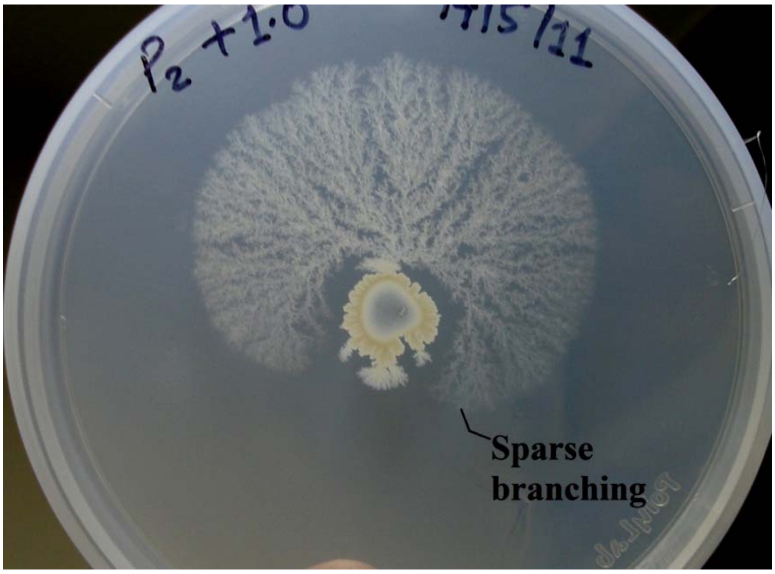


**Figure 8. Sparse branching pattern**

The type we have called sparse branching (SB), depicted in Figure8 is observed when the bacterial colonies are constrained to grow in normal peptone and normal or high agar concentration, in an environment containing antibiotic stress. Presence of antibiotic may affect the DNA synthesis and hence the growth of a significant proportion of the colonies. Therefore, a considerable proportion of the colonies is disabled from participating in the iterated game, and subsequently withdraws from the game. It is thus reasonable to infer that SB type of pattern emerges when the population of bacterial colonies uses the strategy **($C_{60}$, W),** that is, the proportion of colonies that cooperate is 60%, while 40% of the population withdraws from the game.

### *4. Compact structure*

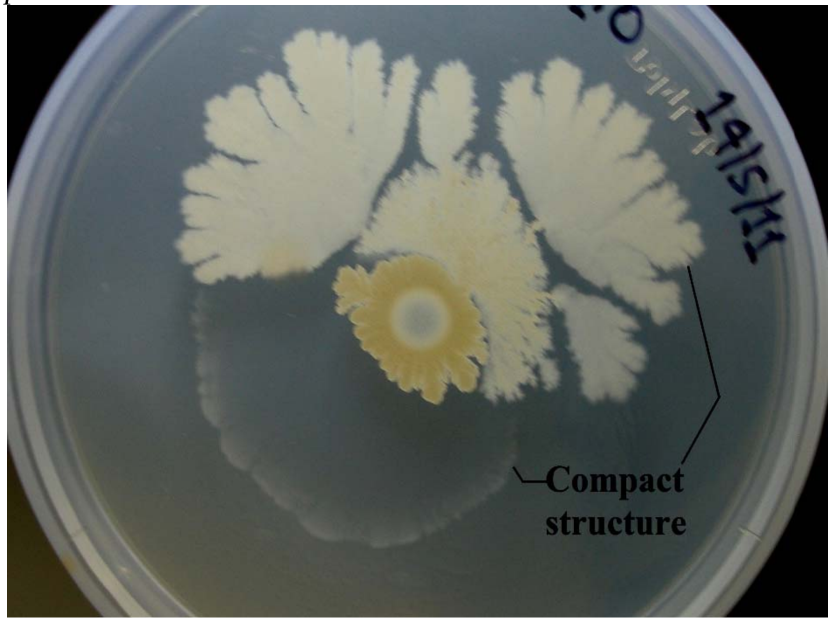


**Figure 9. Compact structure pattern**

Compact structures (CS) depicted in Figure9 emerge from bacterial colony interactions when the environment though has normal nutrient concentration, but high agar concentration, thereby hardening the surface considerably and affecting the motility of the colonies.We infer from the observation that underthe given constraint, the bacterial colonies collectively produce surface wetting fluid to cope with hard surface. We propose in this scenario that the bacterial colonies cooperate with one another without any free-riding, in order to grow by negotiating the hard surface through coordinated effort. We thus propose that the colonies use the strategy pair($C_{100}$, $D_0$) to establish cooperation and coordination throughout the population.

## 5. Modelling

In this section we describe a modelling of the interactions described above, among the bacterial colonies and their growth over discrete time steps, which eventually results into the complex patterns that are formed in Petri dish. With the assumptionthat the bacterial colonies play an n-player Assurance game iterated over a very large number of generations over time $t \in N$ , we provide a graph of a DFA that captures in essence the observed pattern formations that emerge due to the game.

The pay-off received by each strategy in the bacterial game described aboveis an expression of the fitnessof that strategy (and hence of the player using that strategy), when by fitness of a strategy we understand a quantity that is a function of the pay-off and is a measure for the success or performance of the strategy. The success of a strategy, in turn, may be expressed as a function of the survival, fecundity and area occupied by the bacterial colony [27, 38, 40, 61]. We infer from our observations that the space (area) covered by a given stressed colony is proportional to the pay-off to the strategies adopted by it (therefore the fitness of the colony), and the observed complex patterns are an expression of this fitness, aggregated for all colonies playing the game [5, 6, 9, 51].

To model the growth dynamics of the stressed bacterial colonies based on the inferences drawn from the experimental observations as discussed in the preceding paragraphs, we develop a discrete dynamical system using automatic structures. For this purpose, we design deterministic finite automata whose state transition function is informed by the pay-off of the colonies received in the Assurance game [24].

Let the DFA that models the growth dynamics of the bacterial colonies leading to the emergence of patterns be $\Delta(Q, \Sigma, q, \delta, h)$, where $Q$ is the set of states, $\Sigma$ is the alphabet, the set of input symbols or letters, $q \in Q$ is the initial state, $\delta$ is the transition function that prescribes the mapping of the automaton from one state to the next in time steps of $t \in N$ , $h$ is the set of final states, the theorems in a Turing machine[32,33,37,58].We list the objects comprising $\Delta$ in the following paragraphs:

$Q$ comprises the following states, which represent the different pay-offs that the players would receive on their respective strategic moves:

- Initial state (I)
- Compact structure (CS)
- Dense branching (DB)
- Meagerly spaced branching (MSB)
- Sparse branching (SB)
- Dead state (DS)

The alphabet $\Sigma = \{a, b, c, d, e\}$ comprises the letters (inputs for the automata), which are the strategies used by the players in playing *G*, and given by the following table in table:

| Strategy | Corresponding letter in $\Sigma$ |
|---|---|
| $C_{100}$, $D_0$ | *a* |
| $C_{80}$, $D_{20}$ | *b* |
| $C_{60}$, $D_{40}$ | *c* |
| $C_{60}$, W | *d* |
| $C_{<60}$, $D_{>40}$ | *e* |

**Table 1. Strategy coding**

In Table 1, Iis the initial state, representing the initial state of the growth of the bacterial colonies when they are inoculated in the Petri dish, at the given conditions. The transition function $\delta$ is described by the following matrix:

| **Letter** $\rightarrow$<br>**State** $\downarrow$ | *a* | *b* | *c* | *d* | *e* |
|---|---|---|---|---|---|
| **I** | CS | DB | MSB | SB | DS |
| **CS** | CS | DB | MSB | SB | DS |
| **DB** | CS | DB | MSB | SB | DS |
| **MSB** | CS | DB | MSB | SB | DS |
| **SB** | CS | DB | MSB | SB | DS |
| **DS** | DS | DS | DS | DS | DS |

**Table 2. Transitions of $\Delta$ to various states**

We have named the final state as DS as, after iteration through a finite number of generations, the growth of bacteria is stopped (dead configuration). Table 2 gives the graph corresponding to $\Delta$:

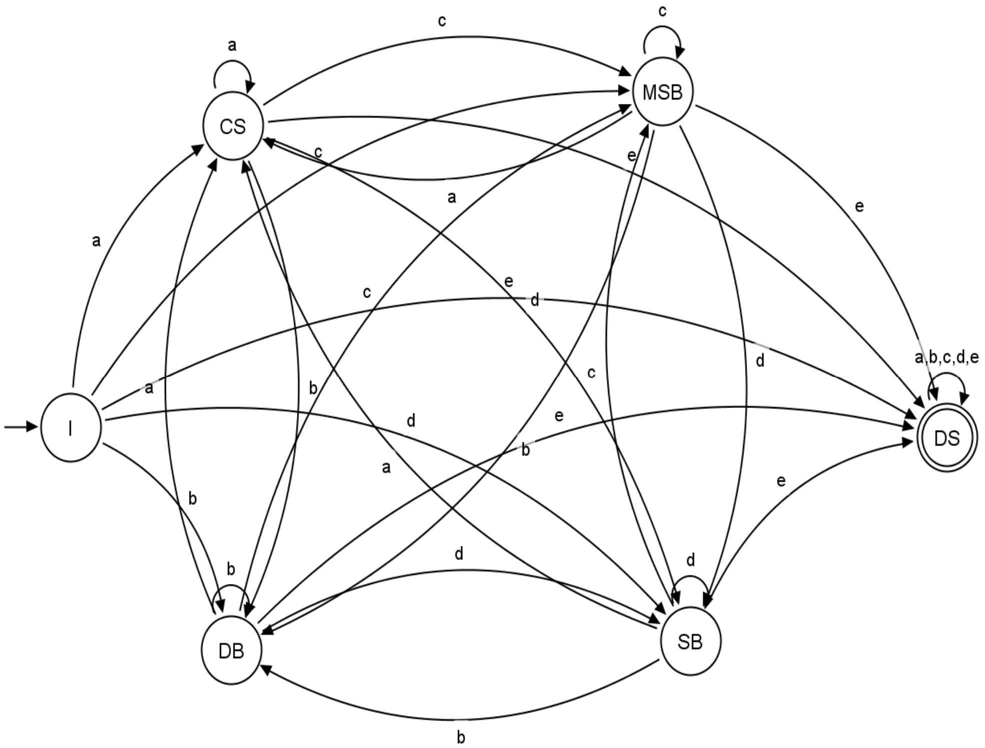


**Figure10. DFA for bacterial growth dynamics**

The above model of DFA would generate a standard context free grammar (CFG), which would, in essence, be determined by the transition function $\delta$ . Let the non-terminals in the DFA be denoted by $V$ . $V$ comprises the following states:

I: Initial state
J: Compact state
K: Dense branching state
L: Meagerly spaced branching state
M: Sparse branching state
D: Dead state

Corresponding to such a set of non-terminal states, the context free grammar (CFG) could be written as

→ I→ aJ|bK|cL|dM|eD
J→ aJ|bK|cL|dM|eD
K→ aJ|bK|cL|dM|eD
L→ aJ|bK|cL|dM|eD
M→ aJ|bK|cL|dM|eD
* D→ aD|bD|cD|dD|eD| $\varepsilon$

D is the final state of the automata, which, for the sake of identification, is prefixed by an asterisk sign.

## 6. Conclusion

The experimental and theoretical discussions presented in this paper pertain to a modelling of the complexity that emerges due to iterated play of Assurance game of coordination, by the bacterial colonies subjected to grow in harsh environmental conditions. Growth of the colonies under such chemical stresses as we have induced in the environment in form of nutrient depletion, augmentation of hardness of substratum and antibiotic material, resulted in complex, often fractal like pattern formation. We have obtained a deterministic finite automata model for the game of coordination played by the bacterial colonies subjected to such a constrained growth scenario giving rise to the beautiful complex patterns observed. The context free grammar that emerges consequently, describes the transition rules that govern the growth of the colonies in space and time, by surviving the harsh environmental conditions that prevail.

We are, however, aware of the rather narrow sense and scope of such a model, as the DFA would accept only regular languages, implying only restricted transitions. We still undertake this task because of the fundamental character of such an exercise, with a hope that the work might serve the purpose of a rudimentary model for further investigations in this direction in the future.

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