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Resonance for Life: Metabolism and Social Interactions in Bacterial Communities

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Abstract: The description of the organization of microorganisms in terms of emergent "social" interactions has long been a fascinating and challenging subject, in both biology and sociology. In these organisms, the role of the individual is far less dominant than that of the community, which operates as a sort of superorganism. The coordination is achieved through a communication mechanism known as quorum sensing. Quorum sensing coordinates and regulates various biological aspects of a microbial community, such as the expression of pathogenicity factors, biofilm formation, and the production of secondary metabolites, among others. These processes rely on the coordinated behavior of the entire bacterial population, enabling them to adapt and thrive withing a specific ecological niche under its unique biological, physical and chemical conditions. Finally, quorum sensing also allows the community to control the development of potentially harmful individuals, thus preserving the cooperativeness of the community. This study uses an agent-based quorum sensing model to explore the relationship between metabolic functions and social behavior in bacteria. In particular, we identify two metabolic parameters whose variations provide a broad panorama of possible social characteristics. Furthermore, the proposed QS model allows us to reproduce, at least qualitatively, some experimental results regarding the competition between some strains with different social characteristics. Finally, we examine how an ideal polyculture responds to variations in the metabolic characteristics of its components. Specifically, we identify a particularly stable condition in which the components cooperate to maximize the overall health of the colony. We refer to this state as resonance for life.

Keywords: sociomicrobiology; quorum sensing; cooperation; agent-based model

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1. Introduction

The social behavior of microbes presents many fascinating aspects and has become the focus of increasingly in-depth studies. It is no coincidence that the term sociomicrobiology was coined in 2005 by Parsek and Greenberg [1] as the "investigation of any group-behaviors of microbes".

Social behavior implies an individual and a society as distinct entities. However, in this field, questions regarding the concept arise, such as how do we define an individual if it lacks self-awareness, and what constitutes conscious behavior at this level?

Cooperation, mutualism, and cheating are behaviors we typically associate with evolved organisms, from an anthropocentric perspective. We often perceive these beings as entities capable of making individual choices about their destiny. However, a more objective study—particularly of bacteria—suggests that the colony, rather than the individual, is the key functional. The colony acts as a kind of "super-individual", sustaining its components, producing defenses against enemies, mitigating defects, and acquiring resources. All this occurs without a conscious awareness, but instead through genetic programming and communication mechanisms that regulate gene expression across vast distances within the colony. As the theory of complex networks suggests, these mechanisms must be hierarchical [2,3] to ensure an effective response to external threats, preserving the colony's deeper structural integrity.

The communication mechanism does not induce cooperation in a social sense but rather facilitates structural and functional aggregation. In bacterial studies, this process is known as quorum sensing (QS), as it is identified with the mechanism by which bacteria sense their population density (quorum) and accordingly, the community as a whole coordinates its gene expression, thus producing public goods (e.g., toxins, enzymes, light, and so on), making the colony grow, protecting themselves from enemies or adverse environmental conditions [4–11]. In this perspective, QS also introduces cooperative behavior in the colony. Furthermore, various studies suggest an active role of QS in regulating behavioral anomalies [12–16].

Regarding the QS circuit in particular, it has been extensively detailed and reviewed in several seminal papers such as [5–7]. Here, we summarize key findings: 1. QS has been identified in both Gram-negative and Gram-positive bacteria. 2. In Gram-negative bacteria it was first discovered in *V. fischeri* and *V. harveyi* [5] and involves at least two regulatory proteins responsible for the biosynthesis and reception of autoinducers (small inorganic molecules) [5]. In analogy with *V. fischeri*, these proteins are called LuxI-like (inducer) and LuxR-like (receptor). As bacterial population density increases, so does the concentration of autoinducers. Once a critical threshold is reached, the LuxR-like protein detects them and activates gene transcription. 3. In Gram-positive bacteria, autoinducers are small peptides, and the QS circuit is more complex than in Gram-negative bacteria, because the sensing mechanism involves two-component adaptive response proteins [5].

In a study conducted a few years ago, Bruger and collaborators [12–14] analyzed the behavior of different mutants of *Vibrio harveyi*, a bacterium well known for its bioluminescence (most famously observed in *milky seas* phenomenon [17]). Due to its widespread presence, *V. harveyi* serves as a model organism for bacteria studies. In particular, the authors of [12] engineered mutants with defects in the QS circuit. They examined the natural wild-type (WT) strain (BB120) alongside the two following mutants: one lacking the *luxR* gene, which encodes the master regulator LuxR (Δ*luxR*), and another, deprived of the *luxO* and *luxU* (Δ*luxOU*) genes. The first mutant, which reproduced poorly and did not produce public goods (PGs), was classified as a defector. The second mutant was defined as an unconditional cooperator (UC), because it gave priority to the production of PGs over the generation of offspring. In [12], several experiments were performed to understand if, and under which conditions, Δ*luxR* strains (defectors) were able to compete with WT and Δ*luxOU* (UC) strains. Finally, it was reported that the WT strain was able to counteract the growth of both defectors and UCs, while UCs were easily outcompeted by defectors. The authors of [12] concluded that the QS, fully functional only in the WT, is the key mechanism that allows the colony to regulate the spread of both mutant types.

In this paper, using a previously developed QS theoretical/computational model, we draw inspiration from the studies conducted by [12] to explore a possible metabolic framework for social behaviors. Specifically, we propose a metabolism-based *behavioral* phase diagram, i.e., a continuous behavioral landscape, within which the most common social traits observed in bacteria can be identified. By analyzing this diagram alongside the public goods (PGs) produced by an ideal colony, we also investigate the competitive dynamics of the various social types. Finally, and in agreement with the main conclusions of [12], we highlight how the competition between organisms with vastly different social behaviors can lead to a condition of serendipity, where both contenders maximize their outcomes by utilizing each other's resources.

2. Materials and Methods

2.1. Materials

As mentioned in the Introduction, quorum sensing (QS) is a coordination mechanism among bacteria, mediated by the production and detection of signaling molecules called autoinducers (AIs) [5]. A functional QS circuit equips each bacterium with genes encoding both AIs and their corresponding receptors. Once released into the environment, AIs can be detected by all bacteria capable of sensing them, potentially over any distance. However, coordination effects only become significant when the bacterial population reaches a critical size. To replicate this phenomenon, we introduced a long-range communication mechanism driven by the number of bacteria.

The analysis is conducted at a coarse-grained level, using a system of agents that move freely on a square grid, with movement restricted to the eight nearest neighbors. In addition to moving, agents can replicate, with the duplicate occupying one of the adjacent positions.

Each agent is defined by a set of parameters that determines its phenotype and by the sensing charge, Q. Here, Q represents the source of interactions between the agents. While real bacteria possess a surface electric charge [18], Q does not necessarily describe this property. Instead, in this context, it is more closely related to the agent's size. Thus, each agent should be considered an aggregate of bacteria. Initially, agents are randomly distributed in a two-dimensional space, with Q set to 1. They then spread or multiply based on the specific metabolic characteristics.

The metabolic features that characterize a single agent include the maximum lifespan, τ_{max}, measured in iteration steps and set to 10; the minimum size required for reproduction, Q_{min}, set to 2; the assimilation rate, σ; and the productivity index, α. Each agent has an internal clock (τ) that increments with each iteration in which reproduction does not occur ($\tau \rightarrow \tau + 1$). When an agent reproduces, its aging resets ($\tau \rightarrow 0$). If τ reaches τ_{max}, the agent disappears.

2.2. Methods

The model is implemented by an initial cluster of agents within a confined space, where the positions are evenly distributed in a regular pattern (grid). Each agent can occupy only a single position, and each position can host only one agent. Depending on their specific metabolic characteristics, agents can produce offspring until they fill the space or, unable to reproduce, continue to explore the landscape. In the first scenario, colony growth halts when resources are depleted, while in the second, the agents gradually die of old age. The outcome is determined by metabolic parameters, allowing for an exploration of parameter space to study the different evolutionary trajectories. Specifically, we analyze growth performance as a function of two key parameters, assimilation rate and productivity index, while keeping other parameters constant.

The model described here applies to an ideal bacterial colony implementing quorum sensing (QS). It has previously been used to describe bioluminescence in *Vibrio harveyi* and its dependence on three different types of autoinducers [19–21], but the results are broadly applicable to any form of bacterial growth.

The stochastic procedure follows five steps. The first four steps are mainly concerned with the development of the colony and the fifth step focuses on the production of public goods. All steps depend on the two fundamental parameters, σ and α, assimilation rate and productivity index, respectively [21]. The amount of public goods produced is calculated as the information that percolates through the colony and is measured by a network of random resistors associated with the network of interactions between the agents [19,20].

1. Calculation of the energy, E, and potential, V, of each agent. It is performed according to the following formula:

$$E_a = Q_a \sum_{b \neq a} \frac{Q_b}{D_{a,b}} = Q_a V_a \quad (1)$$

where $D_{a,b}$ is the geometrical distance between the nodes a, b.

2. Establishing connections between nodes. Each agent creates a link with other agents that have a lower potential. This step constructs the network.

3. Distribution of the resources (sensing charges) among the agents. This occurs with a higher probability; the higher the total energy, the closer the energy of the agents involved, and the lower the productivity index. Through the links, resources (sensing charges) are transferred and assimilated with the assigned assimilation rate σ (σ is in the range [0,1]) [19].

4. Reproduction/migration. Each agent with a charge higher than $Q_{\min}$ divides itself in equal parts (binary fission), and the daughter agent occupies the lowest potential position among the eight nearest neighbors. Agents with a charge lower than $Q_{\min}$ move to the lowest potential position among the eight nearest neighbors. A larger than 1 value of the *fitness* of the colony indicates that the initial nucleus of agents has grown [21].

5. Production of public goods. When a link is established, it is assigned an effective resistance [19]. This resistance measures the difficulty of transferring information between agents, and depends on factors such as distance, $D_{a,b}$, and the propensity to produce public goods (α); it increases as this propensity decreases. Additionally, the resistance value decreases as the amount of charge distributed across the landscape and the productivity index increases.

An ideal pair of contacts is positioned at the ends of the grid, and a potential difference is applied across them. The resulting current serves as a measure of the network's connectivity and the amount of charge present in the landscape. We associate this current with the quantity of public goods that the colony can produce [19].

The single resistance $r_{a,b}$ is given by the formula:

$$r_{a,b} = \frac{D_{a,b}}{\alpha}\left[r_0(1 - h_{ab}) + r_1 h_{ab}\right] \quad (2)$$

where $\frac{r_0}{r_1} = 1000$ is an arbitrary input variable, and h_{ab} is a sigmoidal function of the sensing charge whose codomain is the range [0,1] [20,21].

Simulations are performed on a 20 × 20 grid, and the results are mediated over sixty realizations, where each realization simulates the development of a single colony.

3. Results

3.1. Metabolic Origin of the Social Behaviors

In the considered model, the competition between the assimilation rate (σ) and the productivity index (α) determines the distribution of charges carried by individual agents. By focusing on these two parameters, we computed a growth phase diagram (see Figure 1), which represents the probability of colony growth as a function of σ and α. Moving from bottom to top or from right to left, the probability of reproduction decreases, eventually disappearing completely. In Figure 1, this behavior is depicted using a color scale from blue to red (low to high reproduction). The white region highlights the combinations of (σ, α) that prevent colony development.

Within this diagram, we can identify various social traits, as suggested by studies like [10,12–14]. Dormant agents, for example, are agents that can only migrate. They move toward positions of minimum potential, where the likelihood of receiving a charge is higher. This corresponds to a long lifespan state (determined by τ_{max}) that simulates the quiescent condition adopted by some microorganisms when the environmental conditions are too harsh [10].

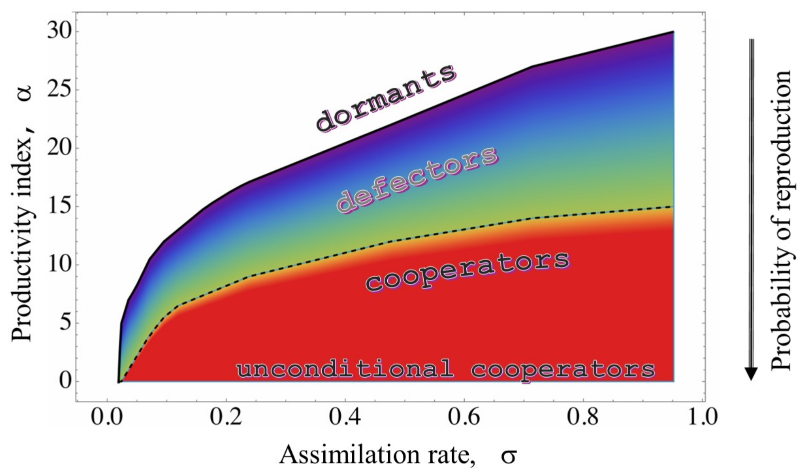

Figure 1. Colony growth phase diagram showing the probability of reproduction as calculated by our simulations. The color scale goes from blue (very low % of colonies able to reproduce) to red (maximal probability of reproduction). White indicates that reproduction does not occur. The dotted mid line highlights the conditions where the probability of reproduction is 97%. Different regions are qualitatively labeled by the corresponding social trait of agents that may be classified as dormants, defectors, cooperators, or unconditional cooperators.

To understand the behavior of agents in the plane (σ, α) in a more quantitative way, we examine the production of public goods (PG) by varying α or σ separately. In Figure 2, we present the system's response in terms of productivity, lifespan, and the percentage of ungrown colonies, for varying σ at a fixed productivity index ($\alpha = 10$). This is equivalent to following a horizontal line in Figure 1.

We observe that there is a minimum value of σ (here, $\sigma = 0.02$), below which no colony development occurs and no PG production is obtained; here, we have the dormants. As σ increases, PG production also increases, and eventually saturates at a maximum value that depends on α. In this regime, all initial configurations result in a fully developed and highly productive colony. Conversely, one observes that the colony's survival time decreases as the metabolic rate increases, due to the rapid consumption of resources.

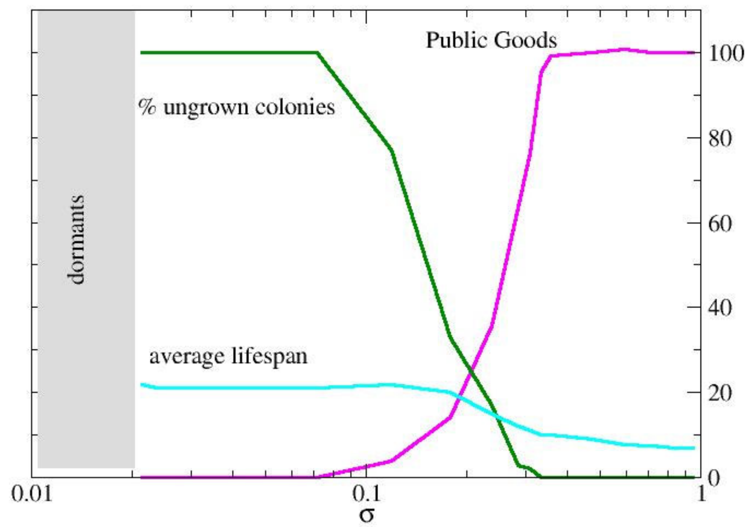

Figure 2. Colony development at the assigned production index, $\alpha = 10$, and variable assimilation rate. The production of public goods, the % of ungrown colonies, and the average lifespan are shown as a wide range of values of the assimilation rate, σ.

In Figure 3, we show the effects of varying α on agents with a fixed σ (represented by a vertical line in the phase diagram in Figure 1). In this case, the PG curve is bell-shaped, while both the average lifespan and the percentage of ungrown colonies maintain the saturation-like behavior observed in Figure 2. Specifically, as the demand for productivity increases, fewer colonies can develop, and their survival time increases because they consume fewer resources.

Figures 1–3 provide an interpretative framework for understanding the social behaviors in metabolic terms. Specifically, we can consider the ideal operating condition (wild type) where σ and α are tuned to maximize both the production of PGs and the ability to produce offspring as well. This condition corresponds to the central region of the PGs curve in Figure 3. The social trait that should be associated with this condition is that of cooperators.

To the left of this region, we find colonies that develop rapidly, producing the maximum amount of PGs required by the productivity index. These colonies can be identified as unconditional cooperators (UCs) [12]. To the right of this region, we find colonies that develop at a progressively lower rate. In each case, the PGs yield is lower than the amount required by the productivity index. These colonies should be identified as *defectors* [12].

This mapping of the (α, σ) plane to specific "social" traits can be compared with experimental results in Ref. [12]. For example, in [12] it is observed that the Δ*luxR* (defector) reproduces at a rate equal to about 4% of that of the wild type. Referring to Figure 3, this corresponds, approximately, to the pair ($\alpha = 15$, $\sigma = 0.7$), while the wild type, if represented by a single pair, would be the point ($\alpha = 7$, $\sigma = 0.7$). More generally, the various manifestations of the social traits highlighted in Ref. [12] can be linked to specific bacterial growth and productivity characteristics (single points in the (α, σ) plane). On the other hand, the picture is obviously more general and includes the continuous variety of metabolic responses highlighted in Figure 1 and Table 1. In this sense, the growth phase diagram can be considered a behavioral (social) phase diagram.

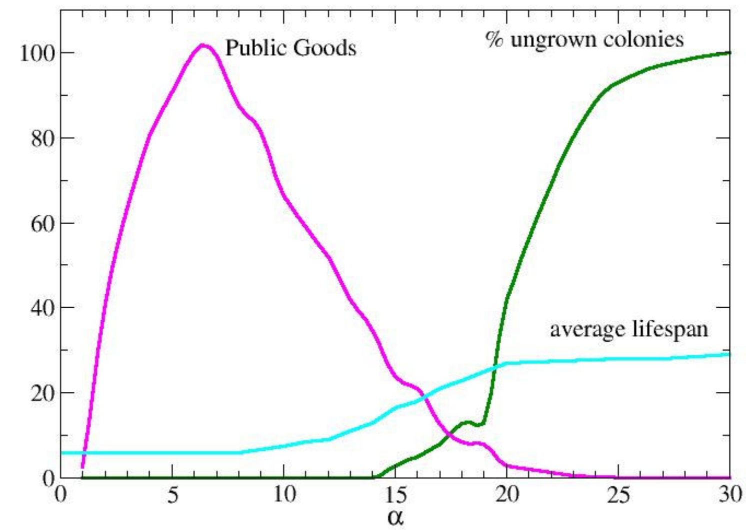

Figure 3. Colony development at the assigned assimilation rate, σ = 0.7. The production of public goods, the % of ungrown colonies, and the average lifespan are reported for the different values of the productivity index, α.

Table 1. Bacterial social traits. Summary of the main social traits seen in this article and their declination in terms of probability of reproduction. As described in the text, due to the continuity of the phase diagram, the classification is qualitative.

Social Trait	Probability of Reproduction	PG Production
dormant	0	Zero
cooperators	1	Maximal
unconditional cooperators	≤1	From modest to high
defectors	< 1	From modest to low

3.2. QS Mediation Between Different Behaviors

As found in the literature, see, e.g., [22–26], quorum sensing (QS) plays a crucial role in managing the well-being of a bacterial colony. This may happen by a sort of mediation between the different behaviors that could potentially harm it. In our model, QS is parametrized by the two variables, α and σ. Our main assumption is that QS mediation may be implemented by averaging the productivity index α.

Specifically, when two different types of agents with different α values develop on the same landscape (grid), we simulate two different kinds of agents with the original assimilation rates σ and a common, averaged α.

The ability to mediate between the two different productivity demands creates a broad range of outcomes. To narrow this down, we will focus on two distinct cases: 1. agents with an equal metabolism but a different productivity index (α) and 2. agents with an equal productivity but a different metabolism (σ).

1. In the case of two different types of agents with identical values of σ but different values of α, the proposal to use an average productivity index for both leads to a single type of agent with production characteristics that intermediate between the original types. This represents a new homogeneous colony that is able to mimic, at least qualitatively, the competition results observed in [12], where defeaters and unconditional cooperators can

coexist with the wild type (WT), preserving their fitness. Furthermore, looking at Figure 3, it is clear that both the defeaters (to the right of the maximum of the PGs curve) and UC (to the left of the maximum of the PGs curve) gain in the production of public goods when mixed with the WT (central region of the PGs curve), because averaging over α shifts both towards the maximum of the PGs curve.

As a final comment, this QS mediation is somehow reminiscent of a horizontal gene transfer, a phenomenon common in bacteria and of significant clinical interest, as it underpins the development of antibiotic resistance [27].

2. A more general situation would involve competition between the agents with differences in both of the considered metabolic parameters. This creates a very broad range of possible outcomes, so we choose to focus on the case of agents differing in assimilation rate σ (and having the same productivity index α), setting one of the two competitors at the highest possible value, $\sigma = 1$, and varying σ for the other. As we remarked previously, for each value of α, changing σ explores a horizontal line in the phase diagram in Figure 1, covering multiple "social" regions. To clarify the discussion, we will refer to the competitor with the highest assimilation rate as the "host" and the other as the "intruder," even though they both have the same initial concentration.

As a general result, for each value of α, the interaction between the two competitors exhibits different phases.

Phase 1 The intruder has a very low assimilation rate and cannot spread, while the host quickly fills all the empty positions. The average lifespan of the colony is close to that of the host and much shorter than that of the intruder.

Phase 2: The intruder has an intermediate assimilation rate and begins to spread (fitness between 1 and 2). Note that an intruder with these metabolic parameters, when grown in a monoculture, is in a dormant state. However, in polyculture, due to the high number of charges produced by the host, the intruder can reproduce. This moderate competition allows the host to slow down its growth, resulting in a colony with a relatively high lifespan, longer than that of either the host or the intruder in the monoculture; we call this condition resonance for life because it represents a condition of perfect coexistence of the two species. Note that this condition holds for a very wide range of productivity indices, in particular until α is so large that even the strain with the maximum metabolism cannot reproduce.

Phase 3: As the assimilation rate of the intruder increases, it becomes capable of competing on equal terms with the host, increasing its fitness. This, in turn, reduces the colony's lifespan due to faster resource consumption.

Phase 4: Both the host and the intruder develop in the landscape with equal capacity, and the lifespan of both competitors tends to converge to the same value. In Figure 4, we present these results in terms of the normalized mean lifespan of the colony. This is the ratio of the colony's lifespan to that of the intruder (which has a longer lifespan than the host) and represents the colony's gain in lifespan.

The data were calculated for three different values of the productivity index: $\alpha = 10^{-4}$, where the host is in the UC state; $\alpha = 10$, where it is in the cooperative (WT) state; and $\alpha = 20$, where it is in the defector state. The behaviors are very similar, and to make the figure more readable, only the initial part of Phase 4 is reported (where the curve tends to 1).

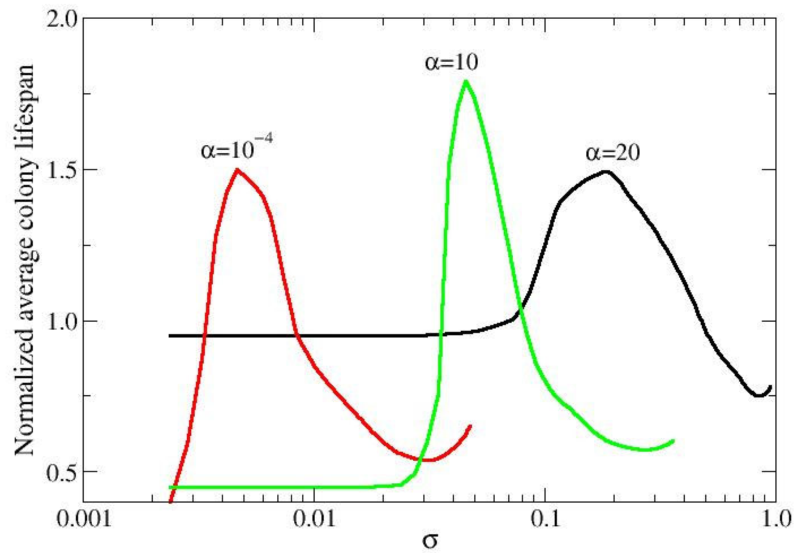

Figure 4. Resonance for life. A pair of strains with different values of assimilation rate can evolve in the same landscape with assigned productivity index, α, thus forming a colony. One of the strains (host) has the maximum assimilation rate, σ′ = 1, the other strain (intruder) has assimilation rate σ. The survival time of the colony follows a bell-shaped curve, and eventually becomes longer than that of each individual competitors. We name this condition "resonance for life". Further increasing σ has the effect of decreasing the survival time. The three curves (with low, medium, and high productivity index α) correspond to 3 different "social behaviors" of the host. Phases 1, 2, 3 discussed in the text are reported.

4. Conclusions

The concept of self-consciousness, typical of evolved individuals, driving them, among other things, to organize into societies, is not equally applicable to less evolved living beings such as bacteria. However, these organisms are known to form very well-organized societies. In this case, although there is no form of individual self-consciousness, quorum sensing is a form of collective self-awareness that supports and organizes the colony. It develops alongside the colony and is an expression of it, as it manifests with the increase in colony size. At the same time, it serves as the colony's generator, overseeing cell growth and the production of public goods.

Therefore, having a theoretical model of QS can be a valuable tool for predicting the behavior of bacterial colonies in all aspects of their evolution. As highlighted in [28], a general theoretical model may be considered imprecise or overly broad unless its parameters are finely tuned to align with the specific biological model under study. In the present research, social behaviors and metabolic characteristics of a generic bacterial system are correlated, yielding a continuous spectrum of correspondences. Within this spectrum, we can also identify several social behaviors reported in the literature.

Finally, this model allows for the exploration of ideal polycultures composed of two different types of bacteria. The results show, as a particular case, the formation of a monoculture with intermediate characteristics between the two initial types, similar to what occurs in horizontal gene transfer. Another significant finding is the emergence of a condition where both competitors derive an advantage (in terms of fitness or lifespan) from the presence of the other. This condition arises only when specific combinations of metabolic parameters are met. Finally, this model does not aim to capture the complexity of the QS mechanism, which encompasses many additional aspects, also of considerable ecological interest, as partially referenced in the bibliography of this article. However, its novelty lies in the ability to simultaneously describe both colony evolution and PG production, which is used here to outline the various social behaviors in an ideal homogeneous or heterogeneous bacterial colonies.

As a final comment, we emphasize the extraordinary ability of microorganisms to organize themselves into highly efficient structures, capable of reacting to changing environmental conditions and seizing opportunities to exploit or contain elements with different metabolic characteristics. Any model or prediction that can be developed is confirmed by what natural evolution has already explored and refined. This, too, is not surprising; it is in fact one of the fundamental principles of Darwin's theory of the struggle for life.

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