CONTINUOUS AND DISCRETE MODELS OF COOPERATION IN COMPLEX BACTERIAL COLONIES

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We study the effect of discreteness on various models for patterning in bacterial colonies. In a bacterial colony with branching pattern, there are discrete entities – bacteria – which are only two orders of magnitude smaller than the elements of the macroscopic pattern. We present two types of models. The first is the Communicating Walkers model, a hybrid model composed of both continuous fields and discrete entities – walkers, which are coarse-graining of the bacteria. Models of the second type are systems of reaction diffusion equations, where the branching of the pattern is due to non-constant diffusion coefficient of the bacterial field. The diffusion coefficient represents the effect of self-generated lubrication fluid on the bacterial movement. We implement the discreteness of the biological system by introducing a cutoff in the growth term at low bacterial densities. We demonstrate that the cutoff does not improve the models in any way. Its only effect is to decrease the effective surface tension of the front, making it more sensitive to anisotropy. We compare the models by introducing food chemotaxis and repulsive chemotactic signaling into the models. We find that the growth dynamics of the Communication Walkers model and the growth dynamics of the Non-Linear diffusion model are affected in the same manner. From such similarities and from the insensitivity of the Communication Walkers model to implicit anisotropy we conclude that the increased discreteness, introduced be the coarse-graining of the walkers, is small enough to be neglected.

Keywords. bacteria, bacterial colonies, bacterial communication, chemotaxis, discreteness cutoff, non-linear diffusion, random-walk, reaction-diffusion equations, signaling chemotaxis.
1 Introduction

The endless array of patterns and shapes in nature has long been a source of joy and wonder to layman and scientists alike [1, 2, 3, 4, 5]. During the last decade, there were exciting developments in the understanding of pattern determination in non-living systems [6, 7, 8, 4]. The attention of many researchers is now shifting towards living systems, in a hope to use these new insights for the study of pattern forming processes in living systems [9, and references therein]. Bacterial colonies offer a suitable subject for such research. In some senses they are similar enough to non-living systems so as their study can benefit from the knowledge about non-living systems, yet their building blocks (bacteria) are complex enough to ensure ever so new surprises.

In figure 1 we show representative branching patterns of bacterial colonies. These colonies are made up of about $10^{10}$ bacteria of the type *Paenibacillus dendritiformis* var. *dendron* (see [10, 11] for first reference in the literature and [12] for identification). For other studies of branching bacterial patterns see [13, 14, 15, 16, 17]. Each colony is grown in a standard petri-dish on a thin layer of agar (semi-solid jelly). The bacteria cannot move on the dry surface and cooperatively they produce a layer of lubrication fluid in which they swim (Fig. 2). Bacterial swimming is a random-walk-like movement, in which the bacteria propel themselves in nearly straight runs separated by brief tumbling. The bacteria consume nutrient from the media, nutrient which are given in limited supply. The growth of a colony is limited by the diffusion of nutrients towards the colony – the bacterial reproduction rate that determines the growth rate of the colony is limited by the level of nutrients available for the cells. Note, however, that a single bacterium put alone on the agar can reproduce, grow in numbers and make a new colony.

Bacterial colonies entangle entities in many length scales: the colony as a whole is the range of several cm; the individual branches are of width in the range of mm and less; the individual bacteria are in the range of µm, so is the width of the colony’s boundary; and chemicals in the agar such as the constitutes of the nutrient are on the molecular length scale.

Kessler and Levine [18] studied discrete pattern forming systems, using reaction-diffusion models with linear diffusion and various growth terms. They showed that the ability of the system to form two-dimensional patterns depend on the derivative of the growth term (reaction term) at zero densities.
With a negative derivative, the system can form branching patterns; with a positive derivative, the system can form only compact patterns with circular envelope. They accounted for the discreteness of the system by introducing a low-densities-cutoff in the growth term. Doing so to a growth term with positive derivative at zero can introduce bumps to the pattern, which is a manifestation of a diffusive instability in the two-dimensional front (the first step towards branching pattern).

We present here three models for growth of the bacterial colonies. The first is the Communicating Walkers model (Sec. 2) which includes discrete entities to describe the bacteria, continuous fields to describe chemicals in the agar and an explicit free boundary for the colony’s edge. The second model is a continuous one, a reaction-diffusion model that couples the bacterial movement to a field of lubrication fluid (Sec. 3). The diffusion coefficients of the bacterial field and the lubrication field depend on the lubrication fluid, resulting in a spontaneous formation of a sharp boundary to the colony. The third model tries to simplify the former model and dispose of the lubrication field by introducing a density-dependent diffusion of the bacterial field (Sec. 4). We discuss the effect of a cutoff in the growth term in the two continuous models. We then turn our attention to various features of the observed bacterial patterns and see similarities in the different models’ ability to reproduce these features (Sec. 5).

2 The Communicating Walkers Model: An Hybrid Model

The Communicating Walkers model [19] was inspired by the diffusion-transition scheme used to study solidification from supersaturated solutions [20, 21, 22]. The former is a hybridization of the “continuous” and “atomistic” approaches used in the study of non-living systems. The diffusion of the chemicals is handled by solving a continuous diffusion equation (including sources and sinks) on a tridiagonal lattice with a lattice constant $a_0$. The bacterial cells are represented by walkers allowing a more detailed description. In a typical experiment there are $10^9 - 10^{10}$ cells in a petri-dish at the end of the growth. Hence it is impractical to incorporate into the model each and every cell. Instead, each of the walkers represents about $10^4 - 10^5$ cells so that we work with $10^4 - 10^6$ walkers in one numerical “experiment”.

The walkers perform an off-lattice random walk on a plane within an envelope representing the boundary of the wetting fluid. This envelope is de-
fined on the same triangular lattice where the diffusion equations are solved. To incorporate the swimming of the bacteria into the model, at each time step each of the active walkers (motile and metabolizing, as described below) moves a step of size \( d < a_0 \) at a random angle \( \Theta \). Starting from location \( \vec{r}_i \), it attempts to move to a new location \( \vec{r}'_i \) given by:

\[
\vec{r}'_i = \vec{r}_i + d(\cos \Theta, \sin \Theta).
\] (1)

If \( \vec{r}'_i \) is outside the envelope, the walker does not move. A counter on the segment of the envelope which would have been crossed by the movement \( \vec{r}_i \rightarrow \vec{r}'_i \) is increased by one. When the segment counter reaches a specified number of hits \( N_c \), the envelope propagates one lattice step and an additional lattice cell is added to the colony. This requirement of \( N_c \) hits represent the colony propagation through wetting of unoccupied areas by the bacteria. Note that \( N_c \) is related to the agar dryness, as more wetting fluid must be produced (more “collisions” are needed) to push the envelope on a harder substrate.

Motivated by the presence of a maximal growth rate of the bacteria even for optimal conditions, each walker in the model consumes food at a constant rate \( \Omega_c \) if sufficient food is available. We represent the metabolic state of the \( i \)-th walker by an ‘internal energy’ \( E_i \). The rate of change of the internal energy is given by

\[
\frac{dE_i}{dt} = \kappa C_{\text{consumed}} - \frac{E_m}{\tau_R},
\] (2)

where \( \kappa \) is a conversion factor from food to internal energy (\( \kappa \approx 5 \cdot 10^3 \text{cal/g} \)) and \( E_m \) represent the total energy loss for all processes over the reproduction time \( \tau_R \), excluding energy loss for cell division. \( C_{\text{consumed}} \) is \( C_{\text{consumed}} \equiv \min(\Omega_C, \Omega'_C) \), where \( \Omega'_C \) is the maximal rate of food consumption as limited by the locally available food \([23]\). When sufficient food is available, \( E_i \) increases until it reaches a threshold energy. Upon reaching this threshold, the walker divides into two. When a walker is starved for long interval of time, \( E_i \) drops to zero and the walker “freezes”. This “freezing” represents entering a pre-spore state (starting the process of sporulation, see section [3]).

We represent the diffusion of nutrients by solving the diffusion equation for a single agent whose concentration is denoted by \( n(\vec{r}, t) \):

\[
\frac{\partial n}{\partial t} = D_n \nabla^2 C - bC_{\text{consumed}},
\] (3)
where the last term includes the consumption of food by the walkers ($b$ is their density). The equation is solved on the tridiagonal lattice. The simulations are started with inoculum of walkers at the center and a uniform distribution of the nutrient.

Results of numerical simulations of the model are shown in figure 3. As in the case of real bacterial colonies, the patterns are compact at high nutrient levels and become fractal with decreasing food level. For a given nutrient level, the patterns are more ramified as the agar concentration increases. The results shown in figure 3 do capture some features of the experimentally observed patterns. However, at this stage the model does not account for some critical features, such as the ability of the bacteria to develop organized patterns at very low nutrient levels. Ben-Jacob et al. [24, 25, 26, 5] suggested that chemotactic signaling must be included in the model to produce these features (see section 5).

3 A Layer of Lubrication

The Lubricating Bacteria model is a reaction-diffusion model for the bacterial colonies [27]. This model includes four coupled fields. One field describes the bacterial density $b(\vec{x}, t)$, the second describe the height of lubrication layer in which the bacteria swim $l(\vec{x}, t)$, third field describes the nutrients $n(\vec{x}, t)$ and the fourth field is the stationary bacteria that “freeze” and begin to sporulate $s(\vec{x}, t)$ (see section 5).

The dynamics of the bacterial field $b$ consists of two parts; a diffusion term which is coupled to the lubrication field and a reaction part which contains terms for reproduction and death. Following the same arguments presented for the Communicating Walkers model, we get a reaction term of the form $(\kappa b \min(\Omega, n) - E_{m} b / \tau_{R})$. Assuming that nutrient is always the factor limiting the bacterial growth we get, upon rescaling, the growth term $bn - \mu b$ ($\mu$ constant).

We now turn to the bacterial movement. In a uniform layer of liquid, bacterial swimming is a random walk with variable step length and can be approximated by diffusion. The layer of lubrication is not uniform, and its height affects the bacterial movement. An increase in the amount of lubrication decreases the friction between the bacteria and the agar surface. The term ‘friction’ is used here in a very loose manner to represent the total effect of any force or process that slows down the bacteria. As the bacterial
motion is over-damped, the local speed of the bacteria is proportional to
the self-generated propulsion force divided by the friction. It can be shown
that variation of the speed leads to variation of the diffusion coefficient, with
the diffusion coefficient proportional to the speed to the power of two. We
assume that the friction is inversely related to the local lubrication height
through some power law: friction $\sim l^{\gamma}$ and $\gamma < 0$. The bacterial flux is:

$$\vec{J}_b = -D_b l^{-2\gamma} \nabla b$$  \hspace{1cm} (4)$$

The lubrication field $l$ is the local height of the lubrication fluid on the
agar surface. Its dynamics is given by:

$$\frac{\partial l}{\partial t} = -\nabla \cdot \vec{J}_l + \Gamma b n (l_{\text{max}} - l) - \lambda l$$  \hspace{1cm} (5)$$
where $\vec{J}_l$ is the fluid flux (to be discussed), $\Gamma$ is the production rate and $\lambda$
is the absorption rate of the fluid by the agar. $\lambda$ is inversely related to the
agar dryness.

The fluid production is assumed to depend on the bacterial density. As
the production of lubrication probably demands substantial energy, it also
depends on the nutrient’s level. We assume the simplest case where the
production depends linearly on the concentrations of both the bacteria and
the nutrients.

The lubrication fluid flows by diffusion and by convection caused by bacte-
rial motion. A simple description of the convection is that as each bacterium
moves, it drags along with it the fluid surrounding it.

$$\vec{J}_l = -D_l \eta \nabla l + j \vec{J}_b$$  \hspace{1cm} (6)$$
where $D_l$ is a lubrication diffusion constant, $\vec{J}_b$ is the bacterial flux and $j$
is the amount of fluid dragged by each bacterium. The diffusion term of the
fluid depends on the height of the fluid to the power $\eta > 0$ (the nonlinearity
in the diffusion of the lubrication, a very complex fluid, is motivated by
hydrodynamics of simple fluids). The nonlinearity causes the fluid to have
a sharp boundary at the front of the colony, as is observed in the bacterial
colonies (Fig. 4).

The complete model for the bacterial colony is:

$$\frac{\partial b}{\partial t} = D_b \nabla \cdot (l^{-2\gamma} \nabla b) + bn - \mu b$$  \hspace{1cm} (7)$$
\[ \frac{\partial n}{\partial t} = D_n \nabla^2 n - bn \]
\[ \frac{\partial l}{\partial t} = \nabla \cdot (D_l l^\eta \nabla l + jD_b l^{-2\gamma} \nabla b) + \Gamma bn(l_{\text{max}} - l) - \lambda l \]
\[ \frac{\partial s}{\partial t} = \mu b \]

The second term in the equation for \( b \) represents the reproduction of the bacteria. The reproduction depends on the local amount of nutrient and it reduces this amount. The third term in the equation for \( b \) represents the process of bacterial “freezing”. For the initial condition, we set \( n \) to have uniform distribution of level \( n_0 \), \( b \) to have compact support at the center, and the other fields to be zero everywhere.

Preliminary results show that the model can reproduce branching patterns, similar to the bacterial colonies (Fig. 5). At low values of absorption rate, the model exhibits dense fingers. At higher absorption rates the model exhibits finer branches. We also obtain finer branches if we change other parameters that effectively decrease the amount of lubrication. We can relate these conditions to high agar concentration.

We can now check the effect of bacterial discreteness on the observed colonial patterns. Following Kessler and Levine [18], we introduce the discreteness of the system into the continuous model by repressing the growth term at low bacterial densities (“half a bacterium cannot reproduce”). The growth term is multiplied by a Heaviside step function \( \Theta(b - \beta) \), where \( \beta \) is the threshold density for growth. In figure 6 we show the effect of various values of \( \beta \) on the pattern. High cutoff values make the model more sensitive to the implicit anisotropy of the underlying tridiagonal lattice used in the simulation. The result is dendritic growth with marked 6-fold symmetry of the pattern. Increased values of cutoff also decrease the maximal values of \( b \) reached in the simulations (and the total area occupied by the colony).

The reason for the pattern turning dendritic is as follows: the difference between tip-splitting growth and dendritic growth is the relative strength of the effect of anisotropy and an effective surface tension [4]. In the Lubricating Bacteria model there is no explicit anisotropy and no explicit surface tension. The implicit anisotropy is related to the underlying lattice, and the effective surface tension is related to the width of the front. The cutoff prevents the growth at the outer parts of the front, thus making it thinner, reduces the effective surface tension and enables the implicit anisotropy to express itself.
We stress that it is possible to find a range of parameters in which the
growth patterns resemble the bacterial patterns, in spite a high value of
cutoff. Yet the cutoff does not improve the model in any sense, it introduces
an additional parameter, and it slows the numerical simulation. We believe
that the well-defined boundary makes the cutoff (as a representation of the
bacterial discreteness) unnecessary.

4 Non-Linear Diffusion

It is possible to introduce a simplified model, where the fluid field is not
included, and is replaced by a density-dependent diffusion coefficient for the
bacteria $D_b \sim b^k$ \cite{28}. Such a term can be justified by a few assumptions
about the dynamics at low bacterial and low lubrication density:

– The production of lubricant is proportional to the bacterial density to the
  power $\alpha > 0$ ($\alpha = 1$ in the previous mode).

– There is a sink in the equation for the time evolution of the lubrication
  field, e.g. absorption of the lubricant into the agar. This sink is proportional
to the lubrication density to the power $\beta > 0$ ($\beta = 1$ in the previous mode).

– Over the bacterial length scale, the two processes above are much faster
  than the diffusion process, so the lubrication density is proportional to the
  bacterial density to the power of $\beta/\alpha$.

– The friction is proportional to the lubrication density to the power $\gamma < 0$.

Given the above assumptions, the lubrication field can be removed from
the dynamics and be replaced by a density dependent diffusion coefficient.
This coefficient is proportional to the bacterial density to the power $k \equiv
-2\gamma\beta/\alpha > 0$

A model of this type is offered by Kitsunezaki\cite{30}:

\begin{align}
\frac{\partial b}{\partial t} &= \nabla(D_0 b^k \nabla b) + nb - \mu b \\
\frac{\partial n}{\partial t} &= \nabla^2 n - bn \\
\frac{\partial s}{\partial t} &= \mu b
\end{align}

(8) 

(9) 

(10)

For $k > 0$ the 1D model gives rise to a front “wall”, with compact support
(i.e. $b = 0$ outside a finite domain). For $k > 1$ this wall has an infinite
slope. The model exhibits branching patterns for suitable parameter values
and initial conditions, as depicted in Fig. 7. Increasing the initial nutrient level makes the colonies more dense, similarly to what happens in the other models.

As in the Lubricating Bacteria model, adding the “Kessler and Levine correction” to the model, i.e. making the growth term disappear for $b < \beta$, does not seem to make the patterns “better”, or closer to the experimental observations (Fig. 8). The apparent increased sensitivity to the implicit anisotropy results from the narrowed front, which decreases the effective surface tension.

5 Chemotaxis

So far, we have tested the models for they ability to reproduce macroscopic patterns and microscopic dynamics of the bacterial colonies. All succeeded equally well, reproducing some aspects of the microscopic dynamics and the patterns in some range of nutrient level and agar concentration, but so can do other models [27, and reference there in]. We will now extend the Communicating Walkers model and the Non-Linear Diffusion model to test for their success in describing other aspects of the bacterial colonies involving chemotaxis and chemotactic signaling (which are believed to by used by the bacteria [24, 23, 20, 4]). Chemotaxis means changes in the movement of the cell in response to a gradient of certain chemical field [30, 31, 32, 33]. The movement is biased along the gradient either in the gradient direction or in the opposite direction. Usually chemotactic response means a response to an externally produced field, like in the case of chemotaxis towards food. However, the chemotactic response can be also to a field produced directly or indirectly by the bacterial cells. We will refer to this case as chemotactic signaling. The bacteria sense the local concentration $r$ of a chemical via membrane receptors binding the chemical’s molecules [30, 32]. It is crucial to note that when estimating gradients of chemicals, the cells actually measure changes in the receptors’ occupancy and not in the concentration itself. When put in continuous equations [34, 27], this indirect measurement translates to measuring the gradient

$$\frac{\partial}{\partial x} \frac{r}{(K + r)} = \frac{K}{(K + r)^2} \frac{\partial r}{\partial x}. \quad (11)$$
where $K$ is a constant whose value depends on the receptors’ affinity, the speed in which the bacterium processes the signal from the receptor, etc. This means that the chemical gradient times a factor $K/(K+r)^2$ is measured, and it is known as the “receptor law” [34].

When modeling chemotaxis performed by walkers, it is possible to modulate the periods between tumbling (without changing the speed) in the same way the bacteria do. It can be shown that step length modulation has the same mean effect as keeping the step length constant and biasing the direction of the steps (higher probability to move in the preferred direction). As this later approach is numerically simpler, this is the one implemented in the Communicating Walkers model.

In a continuous model, we incorporate the effect of chemotaxis by introducing a chemotactic flux $\vec{J}_{\text{chem}}$:

$$
\vec{J}_{\text{chem}} \equiv \zeta(\sigma)\chi(r)\nabla r
$$

(12)

$\chi(r)\nabla r$ is the gradient sensed by the cell (with $\chi(r)$ having the units of 1 over chemical’s concentration). $\chi(r)$ is usually taken to be either constant or the “receptor law”. $\zeta(\sigma)$ is the bacterial response to the sensed gradient (having the same units as a diffusion coefficient). In the Non-Linear Diffusion model the bacterial diffusion is $D_b = D_0 b^k$, and the bacterial response to chemotaxis is $\zeta(b) = \zeta_0 b (D_0 b^k) = \zeta_0 D_0 b^{k+1}$. $\zeta_0$ is a constant, positive for attractive chemotaxis and negative for repulsive chemotaxis.

Ben-Jacob et al. argued [24, 25, 26, 5] that for the colonial adaptive self-organization the bacteria employ three kinds of chemotactic responses, each dominant in different regime of the morphology diagram. One response is the food chemotaxis mentioned above. It is expected to be dominant for only a range of nutrient levels (see the “receptor law” below). The two other kinds of chemotactic responses are signaling chemotaxis. One is long-range repulsive chemotaxis. The repelling chemical is secreted by starved bacteria at the inner parts of the colony. The second signal is a short-range attractive chemotaxis. The length scale of each signal is determined by the diffusion constant of the chemical agent and the rate of its spontaneous decomposition.

**Amplification of diffusive Instability Due to Nutrients Chemotaxis:** In non-living systems, more ramified patterns (lower fractal dimension) are observed for lower growth velocity. Based on growth velocity as function of nutrient level and based on growth dynamics, Ben-Jacob et al. [19] concluded that in the case of bacterial colonies there is a need for mechanism
that can both increase the growth velocity and maintain, or even decrease, the fractal dimension. They suggested food chemotaxis to be the required mechanism. It provides an outward drift to the cellular movements; thus, it should increase the rate of envelope propagation. At the same time, being a response to an external field it should also amplify the basic diffusion instability of the nutrient field. Hence, it can support faster growth velocity together with a ramified pattern of low fractal dimension.

The above hypothesis was tested in the Communicating Walkers model and in the Non-Linear Diffusion model. In figures 9 and 10 it is shown that as expected, the inclusion of food chemotaxis in both models led to a considerable increase of the growth velocity without significant change in the fractal dimension of the pattern.

*Repulsive chemotactic signaling:* We focus now on the formation of the fine radial branching patterns at low nutrient levels. From the study of non-living systems, it is known that in the same manner that an external diffusion field leads to the diffusion instability, an internal diffusion field will stabilize the growth. It is natural to assume that some sort of chemotactic agent produces such a field. To regulate the organization of the branches, it must be a long-range signal. To result in radial branches it must be a repulsive chemical produced by cells at the inner parts of the colony. The most probable candidates are the bacteria entering a pre-spore stage.

If nutrient is deficient for a long enough time, bacterial cells may enter a special stationary state – a state of a spore – which enables them to survive much longer without food. While the spores themselves do not emit any chemicals (as they have no metabolism), the pre-spores (sporulating cells) do not move and emit a very wide range of waste materials, some of which unique to the sporulating cell. These emitted chemicals might be used by other cells as a signal carrying information about the conditions at the location of the pre-spores. Ben-Jacob *et al.* [19, 35, 25] suggested that such materials are repelling the bacteria ('repulsive chemotactic signaling') as if they escape a dangerous location.

The equation describing the dynamics of the chemorepellent contains terms for diffusion, production by pre-spores, decomposition by active bacteria and spontaneous decomposition:

$$\frac{\partial r}{\partial t} = D_r \nabla^2 r + \Gamma_r s - \Omega_r br - \lambda_r r$$  \hspace{1cm} (13)
where $D_r$ is the diffusion coefficient of the chemorepellent, $\Gamma_r$ is the emission rate of repellent by pre-spores, $\Omega_r$ is the decomposition rate of the repellent by active bacteria, and $\lambda_r$ is the rate of self decomposition of the repellent. In the Communicating Walkers model $b$ and $s$ are replaced by active and inactive walkers, respectively.

In figures 9 and 10 the effect of repulsive chemotactic signaling is shown. In the presence of repulsive chemotaxis the patterns in both models become much denser with a smooth circular envelope, while the branches are thinner and radially oriented.

6 Conclusions

We show here a pattern forming system, bacterial colony, whose discrete elements, the bacteria, are big enough to raise the question of modeling discrete systems. We study two types of models. The Communicating Walkers model has explicit discrete units to represent the bacteria. The ratio between the walkers’ size and the pattern’s size is even bigger than the ratio in the bacterial colony. The second type of models is continuous reaction-diffusion equations. Non-linear diffusion causes a sharp boundary to appear in these models. Following Kessler and Levine [18], we account for the discreteness of the bacteria by including a cutoff in the bacterial growth term. The cutoff does not improve the models’ descriptive power. The main effect of such cutoff is to decrease the width of the colony’s front, making the growth pattern more sensitive to effects such as implicit anisotropy. We conclude that the presence of a boundary cancels the need for explicit treatment of discreteness.

In order to assess the similarity between the discrete Communicating Walkers model and the continuous Non-Linear Diffusion model, we incorporate food chemotaxis and repulsive chemotactic signaling into the models (both are expected to exist in the bacterial colonies). Both models respond to such changes in the same way, exhibiting altered patterns and altered dynamics, similar to those observed in the bacterial colonies. From this similarity we conclude that to some extent inferences from one model can be applied to the other. Specifically we focus on insensitivity of the Communicating Walkers model to implicit anisotropy and on the sensitivity a cutoff imposes on the continuous models. From the two facts combined we conclude that the magnified discreteness in the Communicating Walkers model is still small enough to be neglected.
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Figure Captions

Fig. 1: Observed branching patterns of colonies of *Paenibacillus dendritiformis* var. *dendron* grown on 2% agar concentration. The nutrient level is, from left to right, 0.25 gram peptone per liter, 0.5g/l and 5g/l. The colony on the right has wide branches, much wider than the gaps between them, can be seen. The pattern in the middle is less ordered, fractal-like pattern, similar to patterns seen in electro-chemical deposition and DLA simulations [8, 4]. As the nutrient level is further decreased the pattern become denser again, with pronounced circular envelope (on the left).

Fig. 2: Closer look on a branch of a bacterial colony. The left figure shows the lubrication fluid in which the bacteria are immersed. On the right, the individual bacteria can be seen. Each dot in the branch is a $1 \times 2\mu m$ bacterium. The dots outside the branch are not bacteria but deformations of the agar.

Fig. 3: Colonial pattern of the Communicating Walkers model. Here $N_c = 20$ and $n_0$ is 6, 8, 10 and 30 from left to right respectively.

Fig. 4: Closer look on simulated colonies. On the right: a tip of a branch in the Communicating Walkers model. The boundary of the branch and walkers can be seen. On the left: lubrication at a tip of a branch in the Lubricating Bacteria model.
Fig. 5: Growth patterns of the Lubricating Bacteria model, for different values of initial nutrient level $n_0$. The apparent (though weak) 6-fold anisotropy is due to the underlying tridiagonal lattice.

Fig. 6: The effect of a cutoff on the growth patterns in the Lubricating Bacteria model. Aside from the cutoff, the conditions are the same as in the middle pattern of figure 5, where the maximal value of $b$ was about 0.025. The values of the cutoff $\beta$ are, from left to right, $10^{-6}$, $10^{-5}$ and $3 \cdot 10^{-5}$. The 6-fold symmetry is due to anisotropy of the underlying lattice which is enhanced by the cutoff.

Fig. 7: Growth patterns of the Kitsunezaki model, for different values of initial nutrient level $n_0$. Parameters are: $D_0 = 0.1$, $k = 1$, $\mu = 0.15$. The apparent 6-fold symmetry is due to the underlying tridiagonal lattice.

Fig. 8: Growth patterns of the Kitsunezaki model, with a cutoff correction. Cutoff value $\beta = 0.1$, all other parameters as in Fig. 7, right pattern. The apparent 6-fold symmetry is due to the underlying tridiagonal lattice.

Fig. 9: The effect of chemotaxis on growth in the Communicating Walkers model. On the left: chemotaxis towards food is added to the model. The conditions are the same as in figure 3, second from right pattern. The pattern is essentially unchanged by food chemotaxis, but the growth velocity is almost doubled. On the right: repulsive chemotactic signaling is added to the model. The conditions are the same as in figure 3, left pattern. The pattern is of fine radial branches with circular envelope, like in figure 1, left pattern.

Fig. 10: Growth patterns of the Non-Linear Diffusion model with food chemotaxis (left) and repulsive chemotactic signaling (right) included. $\chi_0 f = 3, \chi_0 r = 1, D_r = 1, \Gamma_r = 0.25, \Omega_r = 0, \Lambda_r = 0.001$. Other parameters are the same as in figure 7. The apparent 6-fold symmetry is due to the underlying tridiagonal lattice.
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