



# Instability in bacterial populations and the curvature tensor



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## HIGHLIGHTS

- Pattern formation in bacterial populations.
- Mobility of bacteria and diffusive processes.
- A decrease of bacterial motility with density can promote separation into bulk phases of two coexisting densities.
- The singularity of the scalar curvature as instability criterion for nonequilibrium systems.

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## ABSTRACT

In the geometry associated with equilibrium thermodynamics the scalar curvature  $R_S$  is a measure of the volume of correlation, and therefore the singularities of  $R_S$  indicates the system instabilities. We explore the use of a similar approach to study instabilities in non-equilibrium systems and we choose as a test example, a colony of bacteria. In this regard we follow the proposal made by Obata et al. of using the curvature tensor for studying system instabilities. Bacterial colonies are often found in nature in concentrated biofilms, or other colony types, which can grow into spectacular patterns visible under the microscope. For instance, it is known that a decrease of bacterial motility with density can promote separation into bulk phases of two coexisting densities; this is opposed to the logistic law for birth and death that allows only a single uniform density to be stable. Although this homogeneous configuration is stable in the absence of bacterial interactions, without logistic growth, a density-dependent swim speed  $v(\rho)$  leads to phase separation via a spinodal instability. Thus we relate the singularities in the curvature tensor  $R$  to the spinodal instability, that is the appearance of regions of different densities of bacteria.

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## 1. Introduction

In the laboratory, bacteria such as *Escherichia coli* and *Salmonella typhimurium* form regular geometric patterns when they reproduce and grow on a Petri dish containing a gel such as agar. These patterns range from simple concentric rings to elaborate ordered or amorphous arrangements of dots [1,2]. Their formation results from collective behavior driven by interactions between the bacteria, such as chemotactic aggregation [3], competition for food [4] or changes in phenotypes according to density [5]. The question as to whether general mechanisms lie behind this diversity of microscopic pathways to patterning remains open.

Although in principle one would like a similarly detailed mechanism for each system in which such patterns can form, it is also important to ask whether more general explanations can be found by studying the process at a coarse-grained level.

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This does not abandon the search for a mechanism, but aims to subsume the complex, system-specific microscopic details into a small number of effective parameters that control the macroscopic behavior.

We follow a description on intermediate scales between the microscopic dynamics of bacteria and the macroscopic scale of the patterns. In effect we are “averaging out” all specific microscopic aspects, such as the motion of chemoattractants or steric interactions, and retaining only a coarse-grained dependence of the bacterial motility on density. Here we focus on the net effect of all such interactions on the swim speed  $v(\rho)$ , which we assume to decrease with density  $\rho$ .

The logistic population dynamics alone would cause a bacterial density evolution toward a uniform one,  $\rho(\mathbf{r}) = \rho_0$  ( $\mathbf{r}$  represents the position). Although this homogeneous configuration is stable in the absence of bacterial interactions without logistic growth, a density-dependent swim speed  $v(\rho)$  leads to phase separation via a spinodal instability [6]. That is, the system is separated into a bacteria-rich and a bacteria-poor phase. We use the term “spinodal” due to the similarity with binary decomposition of immiscible fluids.

Furthermore, the Riemann geometry of the state of thermodynamics parameters has been used to study phase transitions, particularly through the visualization of the singularities of the scalar curvature  $R_s$  [7]. In this sense, the method of Riemann geometry is fruitful in equilibrium thermodynamics and we expect that differential–geometrical methods become important in non-equilibrium processes. Following this, we think the problem of mobility as a diffusive process with an effective diffusion coefficient  $D_e(\rho)$ . With effective diffusion coefficient we mean that the process can still be described by a classical diffusion equation. This effective coefficient has two contributions,  $D(\rho)$  due to Brownian motion and  $\bar{D}(\rho)$  associated to the mobility of the bacteria [8].

Considering the problem as a diffusive process in the regime without logistic growth, and following the work of Obata et al. [9], we can construct a two-dimensional manifold characterized by coordinates  $(\mu, \sigma)$ , where  $\sigma$  is now associated with effective diffusion coefficient  $D_e(\rho)$ . Under these assumptions, we study the non-equilibrium instabilities and find that our results are consistent with those found by other authors [8].

This work will be ordered as follows. Section 2 is split into three parts, the first one will be devoted to a brief presentation of general aspects of statistical differential manifolds. In the second one, we will study the particular case of the diffusion process, and the last one, we will analyze the mobility in the context of a diffusive process. In Section 3, we will present our conclusions.

## 2. Diffusion and two-dimensional manifold

In Part A of this section, we briefly review the information geometrical theory [10] that is used to geometrically analyze a family of probability density functions (PDF) for its application to non-equilibrium processes. In Part 2.2, we will connect the geometric aspects to the problem of diffusion. Finally, Part 2.3 will be dedicated to discussion of the problem of mobility in terms of an effective diffusion coefficient.

### 2.1. General aspects on statistical manifold

Let  $p(x, \theta)$  be a PDF described by a random variable  $x$  and parameters  $\theta = (\theta^1, \theta^2, \dots, \theta^n)$  that characterize a system. A set of PDFs

$$S = \{p(x, \theta), \theta \in \Omega \subset \mathbb{R}^n\} \quad (1)$$

becomes an  $n$ -dimensional statistical manifold having  $\theta^i$  coordinates. According to information geometrical theory, we can make a metric tensor  $g_{ik}(\theta)$ :

$$g_{ik}(\theta) = E[\partial_i l(x, \theta) \partial_k l(x, \theta)] = -E[\partial_i \partial_k l(x, \theta)] \quad (2)$$

where  $l(x, \theta) = \ln p(x, \theta)$  and  $E[\cdot]$  means the expectation operation with respect to  $p(x, \theta)$ .

The Christoffel connection coefficients are given by

$$\Gamma_{ijk}(\theta) = \frac{1}{2} (\partial_k g_{ij}(\theta) + \partial_j g_{ik}(\theta) - \partial_i g_{jk}(\theta)). \quad (3)$$

The curvature tensor  $R$  gives a measure of the curvature of the manifold. In the case  $R = 0$ , the manifold is said to be flat. In this sense, the covariant component  $R_{ijkl}$  plays an important role in the analysis of the curvature of the manifold:

$$\begin{aligned} R_{ijkl} &= g_{im} R_{jkl}^m \\ &= \partial_k \Gamma_{ijl} - \partial_l \Gamma_{ijk} - \Gamma_{mik} \Gamma_{jl}^m + \Gamma_{mil} \Gamma_{jk}^m \end{aligned} \quad (4)$$

with

$$\Gamma_{jk}^i = \frac{1}{2} g^{li} (\partial_k g_{lj} + \partial_j g_{lk} - \partial_l g_{jk}) \quad (5)$$

and

$$\Gamma_{ij}^l = \Gamma_{ijk} g^{lk} \quad (6)$$

where  $g^{ij}$  denotes the inverse of the metric tensor  $g_{ij}$ .

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