



## The mathematical theory of endosymbiosis I

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### ABSTRACT

This work presents a new model of the evolutionary process formulated by the Serial Endosymbiosis Theory represented by a succession of stages involving different metabolic and ecological interactions among populations of bacteria considering both the population dynamics and production processes of these populations. In such an approach we make use of systems of differential equations known as Volterra–Hamilton systems as well as some geometric concepts involving KCC Theory and the Projective Geometry of Berwald Spaces and also correct a statement of M. Matsumoto in the literature on this topic. We also recount in some detail previous work comparing production stability of Endosymbiosis Theory with that of Ancestral Commune Theory.

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### 1. Introduction

According to the Ancestral Commune Theory of Carl Woese, life started as a loose conglomerate of many types of proto-cells, some 4000 MYBP. A billion years later trading loose bits of RNA and DNA between these precursors gave way to Darwinian natural selection. An anaerobic thermophile bacterium was present in the primordial soup and possessed a nuclear genome. This evolved prokaryote was subsequently parasitized by a bacterium that had a flagellum for swimming and could process oxygen for its energy. It is called a mitochondrion, while the symbiocosm is called a eukaryote. It is the common ancestor of all creatures except the prokaryotes themselves. This theory has been fully validated via molecular genetics and is credited to Lynn Margulis. It is therefore obvious that the most ancient symbiocosm is the eukaryote cell. For plant species, one has the chloroplasts as well as mitochondria, both of which occur in variable small numbers across the plant and animal species spectrum. Using the Volterra–Hamilton method we have compared the evolutionary theories of Woese and Margulis and because we treated both within a single logical framework, in spite of the fact that the communes of proto-cells in Woese's theory predate the evolved eukaryote symbiocosm, sensible comparison was achieved. We are now going to recount the detailed mathematical material.

Using the Volterra–Hamilton systems as a *logical method* we have compared (see [1] for recent advances in endosymbiosis) the evolutionary theories of Carl Woese and Lynn Margulis and found the former suffers from robust instability while the later is robustly stable in its production processes [2,3].

$N^i$  = density of  $i$ -th bacterial population, assumed to satisfy classical logistic dynamics

$$\frac{dN^i}{dt} = \lambda N^i (1 - \alpha_{(i)} N^i),$$

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with pre-symbiont condition (all lambdas equal),  $i = 1, 2, \dots, n$  and repeated indices are summed except if there is a parenthesis. Since our model will describe ecology and chemical production (in the form of modular bits of RNA), we introduce the Volterra production equation

$$\frac{dx^i}{dt} = k_{(i)}N^i.$$

We require that, for either model, our evolved system has the form

$$\frac{d^2x^i}{ds^2} + G_{jk}^i \frac{dx^j}{ds} \frac{dx^k}{ds} = 0,$$

where the  $n^3$  coefficients are constants or involve  $x^i$ . This class of dynamical systems will encompass both the primeval and the evolved systems, and serve for modeling either Margulis' or Woese' theories.

In order to accommodate our ergonomics, i.e., division of labour, we require the production parameter to be given by the cost of production functional,  $ds = F(x, dx) > 0$ . Moreover,  $F$  is to be positively homogeneous of degree 1 in  $dx = (dx^1, \dots, dx^n)$ , that is, for any positive constant  $c$ ,

$$F\left(x, c \frac{dx}{dt}\right) = c F\left(x, \frac{dx}{dt}\right),$$

so that  $ds/dt$ , the rate of production in the symbiocosm, depends on individual bacterial rates  $dx^i/dt$  through the cost  $F(x, dx/dt)$ . The arc-length  $s = \int_{t_0}^t F(x, dx/dt)dt$  represents the total production of the symbiocosm in the interval  $(t_2 - t_1)$  along a given curve  $x(t) = (x^1(t), \dots, x^n(t))$ . The homogeneity of  $F$  means that, if all the individual rates  $dx^i/dt$  are magnified by a factor of  $c$ , then  $ds/dt$  is so magnified. This forces  $s$  to be independent of the time measure.

We have to introduce the expression  $H_s = (1/2)F^2(x, dx/dt)$ , which yields Euler–Lagrange equations. Note that  $H_s$  is therefore positively homogeneous of degree 2 in  $dx/dt$ , thus, multiplying each  $dx^i/dt$  by a positive constant  $c$  implies that  $H_s$  is multiplied by  $c^2$ . Furthermore,  $H_s$  defines two classes of systems, namely, the Riemannian class, where  $H_s$  is quadratic in  $dx/dt$ , and the Finsler (non-Riemannian) class, where  $H_s$  is not quadratic, but is homogeneous of degree 2 in  $dx/dt$ . Here are two examples, one for each class. For the former, quadratic case, we may have

$$H_s = \frac{1}{2} e^{2\alpha_i x^i} \left[ \left(\frac{dx^1}{dt}\right)^2 + \dots + \left(\frac{dx^n}{dt}\right)^2 \right],$$

while for the latter, non-quadratic but homogeneous case, we have

$$H_s = \frac{1}{2} e^{2\phi(x)} \frac{(dx^2/dt)^{2+2/\lambda}}{(dx^1/dt)^{2/\lambda}},$$

where we have taken  $n = 2$ ,  $\lambda$  is a positive constant and  $\phi(x)$  is an arbitrary polynomial on  $x^1$  and  $x^2$ . We will see in the following sections that the former applies to Woese's theory, while the latter applies to Margulis' theory.

To solve the problem we need to use the techniques of Finsler geometry. Our main result is that, for  $H_s$  given as above, with  $\phi(x) = -\alpha_1 x^1 + (\lambda + 1)\alpha_2 x^2 + \nu_3 x^1 x^2$ , and  $\lambda > 0$ ,  $\alpha_i > 0$  and  $\nu_3$  non-zero, the Euler–Lagrange equations are

$$\begin{cases} \frac{dy^1}{ds} + \lambda(\alpha_1 - \nu_3 x^2) \cdot (y^1)^2 = 0, \\ \frac{dy^2}{ds} + \lambda \left( \alpha_2 + \frac{\nu_3}{\lambda + 1} x^1 \right) \cdot (y^2)^2 = 0. \end{cases} \tag{1}$$

Note that, if  $\nu_3 = 0$ , then the original double logistic system is obtained.<sup>1</sup> Moreover, Liapunov stability of this system is completely determined by the sign of the curvature (see [Appendices](#)):

$$K = \frac{\lambda^2}{\lambda + 1} \nu_3 \left(\frac{y^1}{y^2}\right)^{1+2/\lambda} \cdot \exp(-2[-\alpha_1 x^1 + (\lambda + 1)\alpha_2 x^2 + \nu_3 x^1 x^2]).$$

If  $\nu_3 > 0$ , then stability results, while the reverse is true for  $\nu_3 < 0$ . Geodesics of 2-dimension positively curved spaces, such as a sphere, will remain close generally in  $x$ -space, the system being, therefore, stable, while for those with a negative or zero curvature, as a trumpet surface or a plane, respectively, will not, yielding unstable systems. The parameter  $\nu_3$  is called the exchange parameter. Thus, Margulis # 1 has stable production. Index # 1 indicates the parasite and # 2, the host [4–7].

In the Ancestral Commune model we disallow explicit  $x^i$  in the coefficients, but allow the number of species to be large. This is our model of a loose conglomerate of diverse bacterial species. Neither do we allow the coefficients to depend on

<sup>1</sup> Where  $ds = e^{\lambda t} dt$  must be employed to transform to real time  $t$  from parameter  $s$ .

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