

Reply to comments

Reply to the commentaries on “Evolutionary dynamics of RNA-like replicator systems: A bioinformatic approach to the origin of life”

Nobuto Takeuchi^{a,*}, Paulien Hogeweg^b

^a National Center for Biotechnology Information, National Library of Medicine, National Institutes of Health, 8600 Rockville Pike, Bethesda, MD 20894, USA

^b Theoretical Biology and Bioinformatics Group, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands

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1. Introduction

Our paper [1] reviews computational studies on prebiotic evolution. In particular, it seeks to address how a system of simple RNA-like replicators increases its complexity through evolution. Some of the commentaries mention the topics that are not covered in our review. For the reader's convenience, we list these topics as follows:

- Di Mauro [2] mentioned the energetic and geochemical studies on the origin of life [3,4]. These studies deal with a crucial aspect of life's origin, namely, the source of energy required to drive primordial biochemical reactions.
- Peliti [5] mentioned the dichotomy between the metabolism-first and replicator-first scenarios for the origin of life [6] or, as he reformulated it, the dichotomy between analog information and digital information (or attractor-based inheritance and storage-based inheritance [7]). This dichotomy continues to be a focus of intense debate [8–11].
- Manrubia [12] mentioned theoretical studies on the origin of RNA replicators in the RNA world [13–15].
- Lehman [16] mentioned the importance of recombination for the evolution of RNA replicators [17–19]. Although not described in our review, the effect of recombination has been investigated in the quasi-species theory (see Ref. [20], for a pioneering study; see Refs. [21,22], for recent studies) and in a model of protocells [23]. It was also investigated, albeit cursorily, in the model incorporating the genotype–phenotype–interaction map of replicators (see Ref. [24], Authors' response to Reviewer's report 2).

In what follows, we give a point-by-point response to the comments that are directly concerned with the studies reviewed in our paper. Our response is divided into sections corresponding to those of our review.

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* Corresponding author.

E-mail addresses: takeuchi@ncbi.nlm.nih.gov, takeuchi.nobuto@gmail.com (N. Takeuchi).

2. Replicators without interactions

2.1. Quasi-species theory for finite populations

Hu questioned whether the quasi-species theory remains valid if it assumes a finite population to incorporate stochasticity [25]. The answer is “yes” as described below.

First, the quasi-species theory says that evolution operates not on individual genotypes, but on genotype neighborhoods (see our review, Section 3.2 “Quasi-species theory”). A corollary of this statement is the possibility of neutral evolution of mutational robustness. Although we did not emphasize it, this possibility has been actually demonstrated by the model assuming a finite population (see, e.g., our review, Section 4.1 “RNA folding genotype–phenotype map”). Therefore, the neutral evolution of mutational robustness does not require an infinite population. It, however, does require that an evolving population contain sufficiently great genetic heterogeneity (see Ref. [26], for details).

Second, the amount of information that can be maintained by evolution in non-interacting replicators is limited by erroneous replication. This statement, too, remains valid even if the quasi-species theory incorporates stochasticity; in fact, stochasticity decreases the maintainable amount of information [27–29]. This result makes intuitive sense because the population size of the fittest genotype becomes vanishingly small as the mutation rate increases to the error threshold (see, e.g., Ref. [1, Fig. 2]).

Hu also asked whether population genetics and the quasi-species theory are compatible with each other [25]. This issue has been dealt with in the paper by Wilke [30] (Wilke’s paper, however, contains an erroneous conclusion based on a study of Wagner and Krall [31], which investigates the model described by Eq. (9) of our review; see Ref. [32], for more details).

2.2. Product inhibition

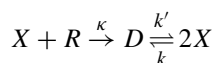
Schuster pointed out the problem of over-simplifying chemical reactions, which potentially leads to unrealistic conclusions (“paper chemistry” as he called it) [33]. As an example, he discussed the enzyme-free replication reaction of nucleic acid molecules. This reaction is commonly assumed to be a one-step process as in the quasi-species equation; namely, $X + R \rightarrow 2X$ where X denotes a replicator, and R denotes the resource for replication. Under this assumption, a replicator population undergoes exponential growth. However, in reality, he argued, such reaction entails the production of stable duplexes; consequently, a replicator population displays parabolic growth, and Darwinian selection does not occur, as opposed to what the quasi-species equation indicates.

Below, we briefly review how duplex formation can lead to the (partial) failure of Darwinian selection [34–41]. The following equation has been suggested as a model describing the population dynamics of replicators whose growth is parabolic (see Ref. [36] and the references therein)

$$\dot{x}_i = A_i x_i^p - \phi x_i \quad (1)$$

where $p = 1/2$ and $\phi = \sum_i A_i x_i^p$. In general, if $p < 1$, the growth of replicators is sub-exponential (if $p = 1$, the equation is identical to the quasi-species equation with mutations ignored). Eq. (1) assumes that the replication rate per individual of replicators approaches infinity as their concentration approaches zero; that is, $A_i x_i^p / x_i \rightarrow \infty$ as $x_i \rightarrow 0$. Under this assumption, no replicators can go extinct [36], hence the “survival of everybody” [37]. Thus, Eq. (1) indicates the absence of Darwinian selection, which, however, is due to the unrealistic assumption mentioned above.

Next, let us explicitly take account of duplex formation during replication (instead of directly assuming parabolic growth). To this end, we assume the following replication reaction [39]:



where X denotes a replicator; R , the resource for replication; and D , a duplex, which consists of two molecules of X . D is assumed to be unable to replicate. Thus, the above reaction involves a negative feedback loop, which can be referred to as product inhibition. The population dynamics of X and D can be described as follows (assuming a continuous population and well-mixed system) [39,40]:

$$\dot{X} = -\kappa R X - 2k X^2 + 2k' D - d_X X \quad (2)$$

$$\dot{D} = \kappa R X + k X^2 - k' D - d_D D \quad (3)$$

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