

Reciprocal Relations in Evolutionary Processes

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I wish to propose “reciprocal relations” in evolutionary processes, considering a qualitative and phenomenological approach for evolutionary processes. In this article, the theory is descriptive, where no much calculations nor proofs at this moment are presented, and I wish to emphasize much more philosophical parts in the problem.

§1. Introduction

In nature, our biological world consists of many species of biological contents such as DNA, RNA, and proteins, etc. We frequently ask a question: “Which is first, egg or chicken?” In the evolution of life, we also encounter a similar question: “Which is first, RNA, DNA, or protein?” or “How do they co-evolute?” In such biological systems, a theory of co-evolution of biopolymers is necessary. However, we have not yet been able to tame such a tough issue in the problem.

Recently, Aita et al.¹⁾ have proposed a thermodynamic theory-like interpretation of evolutionary processes such as evolutions of proteins and biopolymers.*¹⁾ They found appropriate definitions for the concepts such as *free fitness*, *evolutionary temperature*, *constant*, *entropy*, *force*, and *flux*, etc. Using such quantities in evolutionary processes, they found a linear relationship between the evolutionary force and flux such as the linear response theory in thermodynamics. Their theory suggests that there may exist “a theory of irreversible processes” in evolution of a “single species” in biology. It can be thought of as a generalization of Onsager’s theory^{2),3)} of irreversible processes to that of evolutionary processes.

So, as a first step toward such a direction, I would like to postulate a generalization of Onsager’s theory of irreversible processes-like approach¹⁾ to the theory of evolutionary/co-evolutionary processes. In this paper, if there is no confusion, I would like to mean “co-evolutionary” (or “co-evolution”) simply by “evolutionary” (or “evolution”). Finally, I would like to give some comments on the relationship between Aita-Husimi’s interpretation,¹⁾ Kauffman’s point of view of generalized thermodynamics⁴⁾ and Fuller’s synergetics philosophy.^{5),6)} They are essentially all the same.

*¹⁾ The term “thermodynamic interpretation” in their papers is quite misleading. It usually means that when we consider a physical problem from the point of view of thermodynamics, we may put such terminology. However, in their theory, it means that we can regard an evolutionary process in biology as an irreversible process in physics, using a metaphor or an analogy of thermodynamics. Therefore, I prefer to use “thermodynamic theory-like” (or “thermodynamics-like”) interpretation rather than to use “thermodynamic” interpretation.

§2. Formalism

2.1. NK-Kauffman model for rugged fitness landscape

Let us introduce the famous NK-Kauffman model, introduced by Kauffman a long time ago.⁴⁾ Since then, it has been studied in many areas for about 4 decades. This model is described as follows. Suppose that a certain network of N nodes is given, where the j -th node may receive k_j inputs from surrounding other nodes; it represents that the in-degree of the node is k_j . The distribution of k_j is characterized by the network topology. In the original Kauffman model for the random network, $k_j = K = \text{constant}$ is assumed.

Let us next define the sequence space. To do so, let us define an alphabet \mathcal{A}_ν of ν letters. For example, on-off switching of genes can be represented by the alphabet \mathcal{A}_2 of 2 letters $\{0, 1\}$, DNAs by the alphabet \mathcal{A}_4 of 4 letters $\{A, G, C, T\}$, and proteins by the alphabet \mathcal{A}_{20} of 20 letters of amino acids, respectively. Define a sequence(or code) by “ $A_1 A_2 \cdots A_N$ ”, where each symbol A_j belongs to the alphabet \mathcal{A}_ν of ν letters such that $A_j \in \mathcal{A}_\nu$. This represents a state of the system. Hence, the set of all sequences of the N nodes construct a sequence space $(\mathcal{A}_\nu)^N$. This is the ν -valued N -dimensional sequence space of all possible sequences of the biopolymers whose length is N .

Let us define the fitness of a sequence. The fitness W for the sequence $P \equiv “A_1 A_2 \cdots A_N”$ is given by $W = \sum_{j=1}^N w_j(A_j | A_{j_1}, A_{j_2}, \cdots, A_{j_{k_j}})$, where $w_j(A_j | A_{j_1}, A_{j_2}, \cdots, A_{j_{k_j}})$ represents the local fitness on the j -th node affected by inputs from the surrounding k_j nodes (Fig. 1).

2.2. Aita-Husimi model (NK-Kauffman model with $K = 0$)

Let us now introduce the Aita-Husimi model,¹⁾ which deals with an *ideal network* model without connectivity so that all nodes behave independently. Therefore, it can be regarded as NK-Kauffman model with $K = 0$. Since $w_j(A_j | A_{j_1}, A_{j_2}, \cdots, A_{j_{k_j}}) = w_j(A_j)$, I can write as $W = \sum_{j=1}^N w_j(A_j)$. If I denote the sequence as $P \equiv “A_1 \cdots A_N”$ then $W \equiv W(P)$. Fortunately, this model provides the Mt. Fuji-type fitness landscape, which has been thought of as the analog of an *ideal gas* in statistical mechanics. I would like to denote by \mathcal{V} the variance of fluctuations of fitness landscape such that $\mathcal{V} = N\sigma^2$, where σ is the variance of local fitness for each node.

Following their theory,¹⁾ let us define an evolution by *mutation* from M parent sequences to M' children sequences, where I assume that $M' \gg M$ and the Hamming

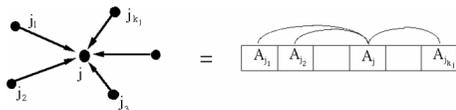


Fig. 1. Definition of local fitness. The local fitness at the j -th node is determined by itself and the surrounding k_j nodes. This provides a network structure.

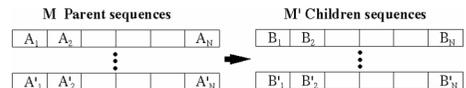


Fig. 2. Evolutionary process. M parent sequences yield M' children sequences. The Hamming distance d_H between parents and children is kept a constant.

distance d_H between the parent sequences and children sequences is kept constant (Fig. 2). This means that there are M parent sequences of N letters, P_1, \dots, P_M , providing the fitnesses $W(P_1), \dots, W(P_M)$. Each parent sequence P_j produces ν_j children sequences P'_1, \dots, P'_{ν_j} , producing fitnesses $W(P'_1), \dots, W(P'_{\nu_j})$ with having the relation $M' = \sum_{j=1}^M \nu_j$, where the numbers ν_j are randomly generated. Then the fittest children sequence becomes the parent sequence for the next generation.

Denote by \mathcal{W} the average fitness among the M parent sequences of P_j , namely, $\mathcal{W} = (1/M) \sum_{j=1}^M W(P_j)$. Denote by $\Delta\mathcal{W}$ the difference between the best fit M mutant sequences and the M parent sequences such that $\Delta\mathcal{W} = \mathcal{W}$ (best M mutants) $- \mathcal{W}$ (M parents), which then represents the *climbing rate* of the M walkers in the sequence space. Now Aita-Husimi¹⁾ derive the expectation $E[\Delta\mathcal{W}|\mathcal{W}]$ of $\Delta\mathcal{W}$ with given \mathcal{W} and the standard deviation $V[\Delta\mathcal{W}|\mathcal{W}]$ as $E[\Delta\mathcal{W}|\mathcal{W}] = -\frac{d_H}{N}(\mathcal{W} - \mathcal{W}_0) + \zeta \sqrt{\frac{2\nu d_H}{N}}$ and $V[\Delta\mathcal{W}|\mathcal{W}] \approx \frac{\sqrt{\frac{2\nu d_H}{N}}}{\zeta(1+\sqrt{M})}$, respectively, where $\zeta = \sqrt{2 \ln(M'/M)}$ and \mathcal{W}_0 is the fitness value at the foot of the fitness landscape. The first term in $E[\Delta\mathcal{W}|\mathcal{W}]$ comes from the ensemble of parent sequences while the second term comes from the variation in the ensemble of fitnesses for children sequences.

2.3. Evolutionary equilibrium

In evolutionary equilibrium, the natural selection pressure and the mutation drift for walkers can balance to each other so that the climbing rate becomes zero. Therefore, I can impose that the condition $E[\Delta\mathcal{W}|\mathcal{W}] = 0$ in the evolutionary equilibrium. This provides the fitness in evolutionary equilibrium \mathcal{W}^* as $\mathcal{W}^* = \mathcal{W}_0 + \frac{\sqrt{\nu N}}{\tau} = \mathcal{W}_0 + \frac{N\sigma}{\tau}$ and $\tau = \sqrt{\frac{d_H}{4 \ln(M'/M)}}$. Using this for the former equation, I obtain $E[\Delta\mathcal{W}|\mathcal{W}] \equiv J = -\frac{d_H}{N}(\mathcal{W} - \mathcal{W}^*)$ and $V[\Delta\mathcal{W}|\mathcal{W}] \equiv \Sigma = \frac{4\sigma\tau}{1+\sqrt{M}}$. Here $\tau \equiv \mathcal{T}$ means the *evolutionary temperature*, J the *evolutionary flux*, and Σ the *uncertainty* of the fitness landscape, respectively. This means that the evolutionary rate can be given as a linear deviation from the evolutionary equilibrium.

From the expression of τ , I find the following: If $M' = M$ then $\tau = \infty$, and if $M' = \infty$ then $\tau = 0$, and if $M' \gg M$ then $\tau = \text{finite}$. Therefore, the ability of producing children depends on the evolutionary temperature.

§3. Thermodynamics analogy

3.1. Thermodynamics theory-like quantities

As was first recognized by Aita-Husimi,¹⁾ I can reformulate the above procedure for the evolution of sequences over fitness landscape in terms of the language that is quite similar to thermodynamics theory in physics. Define the fitness \mathcal{W} . The probability distribution $\Omega(\mathcal{W})$ of \mathcal{W} can be represented by $\Omega(\mathcal{W}) = \sqrt{\frac{(\Lambda_\nu)^N}{2\pi\nu}} e^{-\frac{(\mathcal{W}-\mathcal{W}_0)^2}{2\nu}}$, where $\Lambda_{20} = 20$ for protein and $\Lambda_4 = 4$ for DNA and RNA. From this, I am able to define the *evolutionary entropy* $\mathcal{S}(\mathcal{W})$ by $\mathcal{S}(\mathcal{W}) = \mathcal{K} \ln \Omega(\mathcal{W})$, where \mathcal{K} is the evolutionary constant defined as $\mathcal{K} \equiv \sigma$. *Evolutionary potential* $\mu(\mathcal{W})$ and *free fitness* $\mathcal{G}(\mathcal{W})$ are defined as $\mu(\mathcal{W}) = \mathcal{W} + \mathcal{T}\mathcal{S}(\mathcal{W})$ and $\mathcal{G}(\mathcal{W}) = M\mu(\mathcal{W})$, respec-

tively. + sign in the μ stands for the direction of the movement of walkers on the fitness landscape; the system prefers to go up to the top of the fitness landscape as in thermodynamics the system prefers to go down to the lowest free energy where the free energy is given by $F = E - TS(E)$. Similarly, the *evolutionary force* $X(\mathcal{W})$ is define by $X \equiv \frac{\partial(\mu(\mathcal{W})/T)}{\partial\mathcal{W}} = -\frac{\mathcal{K}}{\mathcal{V}}(\mathcal{W} - \mathcal{W}^*)$. The last expression is obtained from the definition.

3.2. Onsager's theory analogy

Eliminating $\mathcal{W} - \mathcal{W}^*$ from both expressions of J and X , I find a simple linear relation: $J = \mathcal{L}X$ and $\mathcal{L} = \frac{M\mathcal{D}}{\mathcal{K}}$, where $\mathcal{D} = d_H\sigma^2/M$ means the *evolutionary diffusion constant* mediated by mutations, M the number of walkers and d_H the Hamming distance in the generation step. The equation is regarded as an analog of Onsager's theory for the irreversible processes in thermodynamics,²⁾ while the expression for \mathcal{L} is regarded as an analog of *Einstein relation* for diffusion in thermodynamics.³⁾

Considering the evolutionary temperature τ defined in the previous section, I find the following: If $\tau = \infty$ (i.e., $M' = M$) then $\mathcal{W}^* = \mathcal{W}_0$ and $X = -\frac{\mathcal{K}}{\mathcal{V}}(\mathcal{W} - \mathcal{W}_0) < 0$ since $\mathcal{W} - \mathcal{W}_0 > 0$. If $\tau = 0$ (i.e., $M' = \infty$) then $\mathcal{W}^* = \infty$ and $X > 0$. And if $\tau =$ finite (i.e., $M' \gg M$) then $\mathcal{W}^* = \mathcal{W}_0 + \frac{\sqrt{\mathcal{V}N}}{\tau}$ and the sign of X depends on whether \mathcal{W} exceeds \mathcal{W}^* or not. Obviously, the sign of X coincides with that of J , since they are proportional to each other. This is the importance of the Einstein-like relation between X and J .

3.3. Evolutionary information entropies

Let us define three types of information entropy. Denote the fitness information entropy by I_{fit} , the Shannon information entropy by I_{Shan} , the biological information entropy by I_{bio} , respectively. Then I have $I_{fit} = \frac{\mathcal{W}}{T} - \frac{\mathcal{W}_0}{T}$, $I_{Shan} = \mathcal{S}(\mathcal{W}_0) - \mathcal{S}(\mathcal{W})$, $I_{bio} = I_{fit} - I_{Shan}$, respectively, where \mathcal{W}_0 is the fitness value at foot of the fitness landscape. Using these, the changes of the information entropies are obtained as $\Delta I_{fit} = \frac{\Delta\mathcal{W}}{T}$ and $\Delta I_{Shan} = -\Delta\mathcal{S}(\mathcal{W})$ and $\Delta I_{bio} = -\frac{\Delta\mathcal{G}(\mathcal{W})}{T} = \Delta I_{fit} - \Delta I_{Shan}$, where $\Delta\mathcal{G}(\mathcal{W}) \equiv \mathcal{G}(\mathcal{W}) - \mathcal{G}(\mathcal{W}_0)$. The evolutionary entropy production \mathcal{P} is given by $\mathcal{P} \equiv E[\Delta I_{bio}] = JX = \mathcal{L}X^2 \geq 0$.

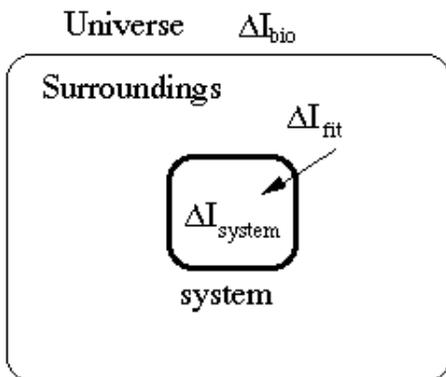


Fig. 3. Evolution.

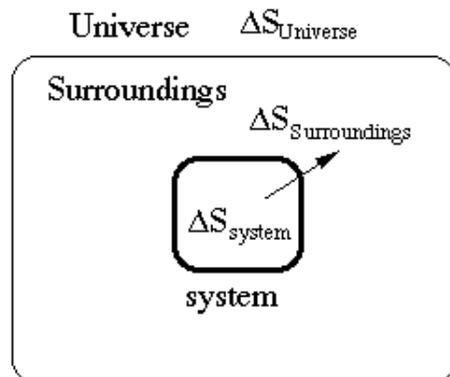


Fig. 4. Thermodynamics.

The meaning of the fitness entropy ΔI_{fit} is as follows: Since using the expression of Σ we have $\Delta I_{fit}/\mathcal{K} = \Delta\mathcal{W}/\mathcal{K}\mathcal{T} = \frac{\Delta\mathcal{W}}{\Sigma} \frac{4}{\sqrt{M+1}}$, ΔI_{fit} is interpreted as a quantity that is evolutionary rate $\Delta\mathcal{W}$ divided by uncertainty Σ . This is quite similar to that entropy change ΔS is given as heat ΔQ divided by thermal fluctuation energy of $k_B T$ in thermodynamics. Hence, by analogy to thermodynamics, $\Delta I_{fit} = \Delta\mathcal{W}/\mathcal{T}$ can be interpreted as *negative entropy* that evolutionary system absorbs from external environment, which is quite analogous to *negentropy* of Schrödinger⁷⁾ who suggested that a biological object eats negentropy from its environment. The correspondence between the evolutionary system (Fig. 3) and the thermodynamic system (Fig. 4) is given. This is the discovery of Aita-Husimi.¹⁾

§4. Generalization to evolutionary processes with multi-species

4.1. Two species case

Let us now generalize the above theory to evolutionary processes with multi-species. Let us first consider an evolutionary process of two species. Suppose that there exists an evolutionary system of multi-species such as protein (say species 1) and DNA (say species 2). Each evolves independently as an evolutionary system under the circumstance of other species evolution. The evolutionary entropy production \mathcal{P} for two species can be represented as $\mathcal{P} \equiv \mathcal{T} \frac{dS(t)}{dt} = J_1 X_1 + J_2 X_2$, where \mathcal{T} is the evolutionary temperature, J_k the evolutionary fluxes and X_k the evolutionary forces. We now have $J_1 = \mathcal{L}_{11} X_1 + \mathcal{L}_{12} X_2$ and $J_2 = \mathcal{L}_{21} X_1 + \mathcal{L}_{22} X_2$, respectively. Here, \mathcal{L}_{11} (\mathcal{L}_{22}) means the self-evolution of species 1 (2), which is given by $\mathcal{L}_{11} = M_1 \mathcal{D}_1 / \mathcal{K}_1$, while \mathcal{L}_{12} (\mathcal{L}_{21}) means co-evolution (mutual evolution) of species 1 (2) induced by evolution of species 2 (1), respectively.

Generally speaking, since I do not yet perform the explicit calculations of the NK -Kauffman models for the two-species systems, it is difficult to determine the explicit expression for \mathcal{L}_{12} such as $\mathcal{L}_{12} = M_1 \mathcal{D}_{12} / \mathcal{K}_1$, so far. However, I expect that Onsager's reciprocal relation: $\mathcal{L}_{12} = \mathcal{L}_{21}$, holds true for evolutionary processes as well. It ensures that the reciprocity in the evolutionary processes. This means that evolution of species 1 preceding evolution of species 2 is the same as evolution of species 2 preceding the evolution of species 1. Therefore, it may suggest us a way to solve the "egg or chicken" problem.

4.2. Multi-species case

This type of theory can be generalized to the evolutionary processes of multi-species as well. Borrowing Onsager's theoretical framework for chemical reactions, the evolutionary rate $J_i = d\mathcal{W}_i/dt$ for species i ($i = 1, \dots, s$) and the evolutionary entropy production $\mathcal{P} = \mathcal{T} dS/dt$ are formally given as $J_i = \sum_{j=1}^s \mathcal{L}_{ij} X_j = -\sum_{j=1}^s \mathcal{M}_{ij} \alpha_j$ and $\mathcal{P} = \sum_{i=1}^s J_i X_i$, respectively. Here I have defined as $X_i = -\sum_{j=1}^s g_{ij} \alpha_j$, $\mathcal{L}_{ij} = -\sum_{k=1}^s \mathcal{M}_{ik} g_{jk}^{-1}$, $g_{ij} \equiv -\frac{\partial^2 \mathcal{S}}{\partial \alpha_i \partial \alpha_j}$, and $\alpha_i \equiv \mathcal{W}_i - \mathcal{W}_i^*$. Then, in evolutionary equilibrium, we have $\mathcal{L}_{ij} = \mathcal{L}_{ji}$ for $i \neq j$.

I would like to point out that the broken reciprocity of $\mathcal{L}_{ij} \neq \mathcal{L}_{ji}$ may be also possible. In this case, our argument in evolutionary processes should be an analog

of the *broken reciprocity* of Onsager's relation in the line of Tomita⁸⁾ in thermodynamics, where a circular relation would hold valid. In this way, I believe that this kind of theory will be very interesting for further research.

§5. Discussion

5.1. *What is fitness?*

Let us now consider the *biological* meaning of "fitness", which is somehow a *metaphysical* concept. A long time ago, Richard Buckminster Fuller⁵⁾ once wrote the following short poem:

*Environment is everything that excludes "self".
The universe is everything that includes "self", on the other hand.
Only the boundary between the universe and the environment is "self".
It is an experiencing thinker.*

What he meant by the above poem is quite suggestive. Since "self" is the boundary between the universe and outside the "self", "self" is defined from outside to inside of the "system" (or "body") in the universe. The interactions between "self"s include not only the interactions among themselves but also the environment simultaneously. On the other hand, in thermodynamics, "self" is usually defined from inside to outside of the "system" in the universe, such that the "system" itself becomes "self". One must add the interactions between "self"s besides the existence of "self"s, while the environment is its surroundings and nothing but the external matter that is outside of the "system" such as heat bath which is not shared by "self"s. Thus, Fuller's definition of "self" is *complementary* to the traditional one.

Fuller's idea seems to be consistent with Aita-Husimi's idea. Synergy of Fuller and fitness in evolutionary processes are something like energy in the physical or the irreversible processes. As the system prefers to the lowest energy in thermodynamics, evolution occurs in order to get higher and higher the fitness such that the walkers climb up higher and higher the mountain of fitness landscape. As proposed by Aita-Husimi,¹⁾ an evolutionary system acquires information from its surroundings (i.e., environment). A biological system is nothing but "self" in the universe. This point of view is very different from that of an "isolated system" in thermodynamics. Hence, fitness concept as well as synergy concept seems to be a much better concept to describe a biological system than energy concept to describe a physical system. Thus, to think "What is fitness?" or "What does fitness really mean?" seems to be a very important question for us to think about "What is life?".

5.2. *Is there the 4th law of thermodynamics?*

About a decade ago, on the other hand, Kauffman⁴⁾ presented the following questions in his book, "Investigations":

Is there the 4th law of thermodynamics for an open thermodynamic system, besides

known thermodynamics laws? Equivalently, is there a law that governs the biological world in the universe or the universe itself? Does life control the world itself?

In some sense, Aita-Husimi's interpretation¹⁾ suggestively answers Kauffman's questions.⁴⁾ The answer is affirmative. But the 4th law of thermodynamics exists not in *physical space* but in *sequence space* (i.e., *shape space* in Kauffman's terminology and *design space* in Fuller's terminology). "Fitness" and "fitness landscape" etc. in sequence space are like-energy and like-potential etc. in physical space, respectively.

5.3. Relationship between concepts of Fuller's and Kauffman's

As discussed in the above, I have recently recognized that Kauffman's ideas⁴⁾ in *biology* after 1990's and Fuller's ideas⁵⁾ in *architecture* until 1980's are almost equivalent. The concept of "synergy" has been used in many sciences as a concept of representing a kind of nonlinear effect in the system. Therefore, "synergetics" means sometimes the study of nonlinear phenomena such as cooperative phenomena in physics. However, as you read the books of synergetics of Fuller,⁵⁾ it means more than that. As the synergy effect is phrased as *maximum effect by minimum parts*, he meant by synergy the "integrity" of the whole system. Hence, this concept led to the famous Fuller dome. As the consequence of synergetics, some kind of cooperative evolutions of designs emerge in technology developments such as in architecture etc. In such a development, the system may evolve so as to receive great "syntropy" where the getting varieties is called "ephemeralization" and its expanding speed "acceleration". Thus, we meet the equivalence between Fuller's and Kauffman's ideas, but somehow complementary to each other.⁶⁾ I would like to summarize the relationship between Fuller's ideas and Kauffman's ideas in Table I.

Table I. Relationship between Fuller's concepts in architecture and Kauffman's concepts in biology.

Fuller(Architect)	Kauffman(Biologist)
Synergetics	The origins of Order
Critical path	Investigations
Synergy	Fitness
Synergetics	Co-evolution
Integrity	Co-construction
Syntropy	Entropy
know-what	know-that
know-how	know-how
Self	Autonomous system
Scenario universe	Constructive universe
Reproductive	Self-replicative
Ephemeralization	Getting varieties
Acceleration	Expansion of varieties

§6. Conclusion

In conclusion, I have shown that there might exist the reciprocal relations in evolutionary systems as a kind of generalization of Onsager's theory of irreversible processes. This suggests that if protein evolves interacting with DNA, then DNA can evolve stimulated by the evolution of protein, vice versa. Hence, the reciprocal relation may have a possibility to solve "egg-chicken problem". At this moment, since our theory is based on the landscape of free fitness calculated from Aita-Husimi's *NK*-Kauffman model with $K = 0$, it is very interesting to consider whether or not

the concepts work for the more general NK -Kauffman models such as scale-free NK -Kauffman models.⁹⁾ I speculate that the concepts work and the essential features are preserved as well. Finally, I have also discussed that the philosophical concepts of Aita-Husimi,¹⁾ Kauffman⁴⁾ and Fuller⁵⁾ are essentially all the equivalent to each other. I suggest that there might exist a kind of thermodynamics-like theory in the spaces of *configuration*, *shape* and *design*, where energy-correspondent is *fitness* or *synergy* and entropy-correspondent the *evolutionary entropy* or *syntropy*, respectively.

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