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Ecosystems as Chimeras: A thought experiment in Rosennean Complexity

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ABSTRACT

Robert Rosen wrote an interesting paper entitled, "Cooperation and Chimera" in which he explained how living systems or their parts often combine with those of others to create chimeran individuals with new genotypes, phenotypes, and environments. He concluded that these relationships are mainly cooperative in that the partners provide functional capabilities to each other that the recipients cannot provide for themselves. Rosen developed his concept of chimeras within the broader areas of Rosennean Complexity and Relational Biology, providing insights into notions of purpose, function, causality, survival, persistence, and complexity.

Chimeras are ubiquitous and occur throughout the biological hierarchy. At the ecosystem level, chimeras can be formed when the member populations are organized into functional groups such as the nodes of a food web, and they interact with each other through environmental modifications that feedback to change phenotypes and genotypes, and form a new individual with a purpose: ecological survival and evolutionary persistence. Thus, ecosystems are Rosennean Complex (RC) chimeras. This concept is applied to the Narragansett Bay plankton food web using loop analysis. Then a Thought Experiment involving Mother Nature is employed to illustrate how being a Rosennean Complex chimera helps the food web solve three critical problems: securing matter and energy, which is *a priori* necessary for all open systems; maintaining functional and modular integrity as a chimeran individual; and manipulating time especially using feedforward and anticipation – none of these functions could be accomplished by a single ecosystem member.

In ecology, Rosen's chimeras are closest to the concept of niche construction, however, since niche is a population-level concept, based largely on physiology and environmental factors, it is impossible to extrapolate niche construction to ecosystem chimera construction. The parts do not reveal the whole in complex systems. Rosennean Complex 'chimera construction' approaches should be used at the ecosystem level while retaining 'niche construction' at the population level. In evolution, the areas of symbiogenesis and coevolution align with chimeran concepts to provide adaptive advantages and opportunities not available with gene-centred individual and population-based fitness concepts. Evolutionary success for the ecosystem as a selection unit involves more than a collection of genes, and fitness is more than changes in gene frequencies. Ecological survival and persistence necessitate chimerization and the formation of new cooperative ecosystemic individuals. This study concludes that a paradigm shift is needed from Evolution: The Modern/Extended Synthesis to Evolution: The Complexity Synthesis.

1. Introduction

Robert Rosen (1934–1998) developed his concept of chimera within the context of Relational Biology with its emphasis on qualitative, relational, and functional properties of living systems. In doing this, he opposed the wholesale adoption of the Newtonian paradigm by biology and the characterization of living systems as machines. In this, he was a revolutionary trailblazer (Lane 2018a, b, this issue). Throughout his lifetime, biological research had been dominated by quantitative approaches; this is largely true two decades later. Rosen believed that biology is fundamentally a qualitative subject amenable to qualitative analysis. Ernst Mayr once said, "The physical world is a world of quantification (Newton's movements and forces) and of mass actions. By contrast, the world of life can be designated as a world of qualities. Individual differences, communication systems, stored information, properties of macro-molecules, interactions in ecosystems, and many other aspects of living organisms are prevailingly qualitative in nature. One can translate these qualitative aspects into quantitative ones, but one loses thereby the real significance of the respective biological phenomena…"

Rosen's academic mentor, Nicolas Rashevsky (1899–1972), originally trained as a theoretical physicist, became interested in biological systems and set out to establish mathematical biology as a new discipline (Rashevsky, 1961, 1969). By the 1950's, he had identified key

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differences between living and nonliving systems and had concluded: "life, while essentially closely related to complex structures, is basically a process" (Rashevsky, 1962). He also realized reduction of the whole into its parts is not the way to approach the study of life. His dictum was: "Throw away the matter and keep the underlying organization." He believed, "There is no successful mathematical theory, which would treat the integrated activities of the organism as a whole… The fundamental manifestation of life drops out from all our theories in mathematical biology". This led him to develop Relational Biology using many of the available tools of his time such as graph theory, set theory, and topology. For example, he used graphs with biological elements or functions as nodes and edges that were relations or mappings-essentially temporal relationships that were depicted as the interactions.

Relational Biology is built upon the assumption that function implies structure, whereas the reverse has been assumed in most traditional biological approaches (Miranda and LaGuardia, 2017). In the 1950′s, under the umbrella of Relational Biology, Rosen expanded Rashevsky's conceptual base using a more sophisticated and richer modeling formalism employing Category Theory developed by Samuel Eilenberg and Saunders MacLane. Rosen's first papers on relational metabolism/repair systems (M, R) (Rosen, 1958a, b; 1959) employed Category Theory. As Poli (2017) pointed out, Rosen "focused on functional aspects – what something is made for – rather than what it is made of". Rosen (1991) explained: "Organization, in its turn, inherently involves functions and their interrelations; the abandonment of fractionability, however, means that there is no one-to-one relationship between such relational, functional organizations and the structures which realize them. These are the basic differences between organisms and mechanisms or machines…Here I use the word function in the biological rather than the mathematical sense – e.g., the function of X is to do Y… Using this kind of language leads us in the direction of relational models, which have proved most appropriate for biological purposes (and, by implication, for any kind of human or social system)".

Although he was a highly accomplished mathematician, Rosen's first passion was always biology, and most of his emphasis was directed toward his main question or Imperative: "what is life?" Why is one piece of matter alive and another dead? In describing life, he concluded that complexity is a necessary, but not sufficient condition of being alive, and that complexity required careful definition. In this Special Issue, Rosennean Complexity (RC) has been discussed in detail by the authors; however, a brief summary of its features and definitions is included in Appendix 1 for the convenience of the Reader. See also Louie (2009, 2013, and 2017) for more information on Rosen's use of Relational Biology and Category Theory.

In 1992, Rosen attended a workshop entitled, Cooperation and Conflict in General Ecological Processes in Abisko, Sweden organized by Anders Karlqvist and John Casti, 1995; Rosen, 1995. He delivered a paper entitled "Cooperation and Chimera", which was later reprinted with the same title as Chapter 21 in Rosen (2000). Rosen stated that "chimeras are everywhere around us: ecosystems, social systems, man-machine interactions; even chemical reactions can be thus regarded". Chimeras exist as highly-organized entities, much more functionally integrated than mere symbionts. As RC individuals, chimeras have both a purpose and a set of functional capabilities to achieve that purpose. Rosen's paper was noteworthy in that he discussed both evolution and ecosystems, two subjects he rarely mentioned as neither was germane to answering his central question. To Rosen, evolution was about history and ontogeny. He stated, "to me, it is easy to conceive of life, and hence biology, without evolution, but not of evolution without life. Thus, evolution is a corollary of the living" (Rosen, 1991). Likewise, he thought that ecosystems involved unnecessary complications, too many species and too many interactions, which might obfuscate how he conceptualized the minimal essence of life. In this paper, the concept of an ecosystem chimera is explored to discover how it might be useful for ecologists. The objectives of this paper are:

(1) to introduce the concept of chimera at the cell and organismal levels (Section 2),
(2) to describe Rosen's concept of how chimeras form and function in a Rosennean-Complex theoretical framework (Section 3),
(3) to consider a real-world food web as an ecological chimera using loop analysis, a signed digraph technique (Section 4),
(4) to conduct a thought experiment on how a plankton ecosystem chimera might function in nature, (Section 5), and,
(5) to discuss three conclusions: (Section 6).

(a) Ecosystems are Rosennean Complex (RC) chimeras.
(b) RC chimeran construction theory needs development at the ecosystem level. A related concept, niche construction, is too population-centered to explain ecosystem chimerization, however, the two approaches could mutually-support each other.
(c) Standard Evolutionary Theory (SET) should be replaced by a Complexity Synthesis based upon RC.

Little, if anything has been written about ecosystems as chimeras other than Rosen's paper, yet, ramifications of this idea could affect both ecological and evolutionary theory. Some of these ramifications are considered here, not because they have been proven to be true, but if they are, their potential importance requires serious consideration.

2. Chimeras at the cell and organism levels

Before defining chimera, two other terms: symbiosis and mutualism require definition as to how they are used in this paper. All three of these terms have traditionally referred to organism-population levels of the biological hierarchy, which will later necessitate some extrapolation for the focus of this paper: the community/ecosystem level. Symbiosis occurs when organisms live in close proximity to each other regardless of the nature of their interaction(s). For example, a host and its parasites are symbionts as are two resource competitors consuming the same food. Thus, to be a symbiont does not reveal the nature of the interaction. Mutualism is usually defined as a pairwise population interaction that benefits both populations in which the interaction is based either upon a description of the biological process, which is frequently problematic (see below), or the evolutionary outcome (+ + for mutualism, + - for predation, and − − for competition). These symbols represent the signs of the first partial derivatives of the two population growth equations for a pair of species (i and j), and they also represent the qualitative values of the associated pair of alpha coefficients (α_{ij} and α_{ji}) in the Community Matrix. The coefficients are defined on the population level; for example, if i and j are interspecific competitors, then as each population increases it causes a decrease in the growth rate of the other (-, -).

Species have many things to do to ensure survival and reproduction. Although it is frequently assumed that each species pair exhibits a single type of interaction, there is no rule that this reductionist constraint is always or even usually valid. I suspect it is rarely valid. This makes concise biological descriptions of species interactions difficult. For example, Ralph Brinkhurst (1970) working with tube worms living in the sediments of Toronto Harbor assumed they were close interspecific competitors since they consumed the same food: refractory detritus that settled from the upper waters onto the benthic sediments. Field studies revealed the unexpected result that the two species lived very close together, and did not exhibit competitive exclusion in their distribution patterns, rather, they seemed attracted to each other. Brinkhurst, in subsequent laboratory experiments, discovered that the two species varied in their ability to metabolize detrital matter, and the feces of each species was a food source for the other, making them mutualists (Brinkhurst et al., 1972).

Long before anyone knew that cells exist; chimeras were defined as individuals that contain all or parts of two or more different organisms. An early concept of a chimera can be found in Greek mythology, when