Ecosystems as Chimeras: A Thought Experiment in Rosennean Complexity

By

Patricia A. Lane
Department of Biology
Dalhousie University, 1459 Oxford Street
Halifax, Nova Scotia, Canada, B3H 4R2
*Correspond to Patricia.Lane@Dal.Ca

Highlights:

Robert Rosen said that ecosystems are chimeras with their own genotype and phenotype.

Chimera members provide functions to each other that they cannot do for themselves.

Loop analysis of a marine plankton community illustrates how chimeras could work.

A thought experiment is used to explore ecosystem chimeran problems and solutions.

Evolution: The Complexity Synthesis should replace Evolution: The Modern/Extended Synthesis

Conflicts of Interest: None

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.

1.0 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, 2017a, c, 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 1950s, he had identified key 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 as Section 9.1 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 on the Arctic Circle 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).
    (1) Ecosystems are Rosennean Complex (RC) chimeras.
    (2) 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.
    (3) 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.

2.0 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 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 monsters Typhon and Echidna produced a two-headed offspring with the head of a goat, the head of a lion, and the tail of a serpent. Egyptian gods were chimeric. In 1818, Mary Shelley published her novel 'Frankenstein: or, The Modern Prometheus' about the good doctor sewing assorted cadaver parts together, and animating the dead tissues with electricity, to create a new living individual: the monster. This plot was not all imagination but reflected questionable medical experiments in the early 19th century. Thus, Dr. Frankenstein's creature was a chimera. Laypeople often consider a chimera to be an imaginary creature, but in nature, they exist profusely.

There are many different types of chimeras at the organismal level.   Aanen and Eggleton (2017) discussed how lichens, chimeras of fungi and algae or cyanobacteria, were important in land-colonization, and how symbiogenesis was important in the eusociability of termites. These animals have chimeric relationships with flagellated gut protists that aid in the

breakdown of cellulose. Most tree species are chimeric with fungi. Other animal chimeras can be produced by the merger of multiple fertilized eggs, each with their own DNA. Marmosets, usually born as twins, are often hematopoietic or blood-based chimeras. The male and female anglerfish fuse their bodies into chimeras during reproduction and the male gives up his independence to become a sack of enlarged testes for the new hermaphrodite form. Bats, representing about 25% of all mammals, are considered chimeras with their fox-like faces, mouse bodies, and pterosaur wings (Jacobs, 2016).

Many types of human chimeras have also been identified, ranging from the cellular to ecosystem level. Approximately 8% of non-identical twins are chimeras especially in regard to blood type, which has frequently resulted in misinterpreted DNA tests. Human mothers have been shown to contain fetal-derived cells of their children in many organs including the brain via fetal cell migration across the leaky placental blood barrier; these cells can remain in the mother over her lifetime making her a chimera.   Gut and skin flora communities, consisting of hundreds of species, are considered chimeras in partnership with their human hosts.   The skin has an important role in the body's immune system and many microbes (bacteria, fungi, and viruses) act as mutualists with their host (Sanford and Gallo, 2013).   Chimeras can also be produced and manipulated artificially.   Many traditional plant breeding and animal husbandry technologies in agriculture and forestry like grafting have produced chimeras as well as more recent biotechnologies that create human stem cell-pig combinations for tissue and organ transplants for humans. Boklage (2010) concluded that "chimerization itself is not a developmental abnormality and does not imply the presence of any abnormality", but it is probable that the long-term ramifications of chimerization are not well-understood.

A noted chimera champion was microbiologist Lynn Margulis (1938-2011), who was convinced of the universality of chimeras and their key role in evolution. Margulis et al. (1997) concluded that: "We are all of us walking communities of bacteria. The world shimmers, a pointillist landscape made of tiny living beings". She advocated symbiogenesis in the evolution of eukaryotes and was also a co-founder of the GAIA hypothesis with James Lovelock (Barlowe, 1992; Fet, 2011).   Margulis et al. (2011) concluded that a "swimming, sulfur-metabolizing chimera was an ancestor to all nucleated lifeforms alive today" and this ancient organism arose in the mid-Proterozoic Eon about 1,200 million years ago from the fusion of two kinds of bacteria. Hall and Margulis (2011) concluded that: "all organisms visible to the unaided eye are chimeras", that is, "all cells, protests, fungi, plants, and animals have multiple ancestry".

It is not a large chasm to cross from Margulis' ideas on symbiogenesis to marine plankton communities that are populated by bacteria, single and multi-cellular algae, and single and multicellular animals.   Endosymbiosis occurs at the organism level in plankton communities. Decelle (2013) summarized photo-symbiosis in plankton using Acantharia spp., a heterotrophic protist, which contains endosymbiotic microalgae. He found over 100 discrete host-symbiont pairs in the Foraminifera and Radiolaria. They are integral members of plankton communities and appear to provide important functional capabilities to the community. The planktonic mode of existence is an ancient one, approximately 2.7 billion years old, and it is resplendent in chimeras.

Many types of chimeras exist in other marine ecosystems (Keeling and McCutcheon, 2017). For example, some cnidarians (hydroids, jellyfish, anemones, and corals) contain a dinoflagellate (<u>Symbionium</u> sp.), which photosynthesizes and produces oxygen inside its animal partner (Furla et al., 2005). These authors reported that symbiosis and endosymbiosis of anthozoans and single-celled organisms, mostly bacteria and algae with photosynthetic capacity, have existed since the Triassic, 225 million years ago. This important chimeran relationship is a key component of the creation and maintenance of coral reefs and their biodiversity. The dinoflagellate provides oxygen and organic carbon compounds for the animal, which in turn provides the protist with inorganic nutrients for photosynthesis. Thus, the relationship is largely based on nutritional benefits in both directions. Through this symbiotrophy, the animal partner gains several new metabolic capacities not present in its non-chimeran relatives. Photosynthetic endosymbionts have also occurred with other animal groups such as sponges, annelids, and mollusks (Furla et al., 2005).

Generally, the chimeran lifestyle is considered to be a cooperative one, that is, mutualistic, in which all participants benefit. The degree and type of benefit, however, can change over an organism's life history or a food web's coevolution. Benefits can be asymmetrical and can vary in different environments with different species combinations, food web configurations, and selection pressures. Benefits can also necessitate additional adaptations with associated costs for the chimera ensuring many biological process descriptions are complicated or inadequate. Furla et al. (2005) reported that cnidarians have many adaptations that are not generally present in other animals, which appear to have arisen to counter the negative aspects of its chimeran lifestyle. These animals have developed: (1) specialized amino acids for UV protection in the upper euphotic zone where their dinoflagellate symbiont needs light for photosynthesis, (2) exogenous inorganic carbon transfer to aid dinoflagellate photosynthesis, (3) anti-oxidative metabolic measures to protect against the hyper-oxygenation caused by the internal dinoflagellate's photosynthesis, as well as (4) several mechanisms for nitrogen uptake and conservation to ensure an adequate nutritional supply for the dinoflagellate. There seems to be a delicate balance of adaptations between these chimeran partners as their life histories coevolve. In addition, many cnidarian chimeras have close relatives that are non-chimeric, especially at the organism level. This indicates a broader range of potential adaptive possibilities for a group.

In summary, chimeras occur throughout the bacteria, plant, and animal kingdoms in both unicellular and multicellular organisms; they can include very complicated co-adaptations. The chimeran lifestyle is clearly ubiquitous. It would appear that chimerization has multiple adaptive values and has occurred throughout the evolutionary record. The array of potential chimera types and examples constitutes an extensive smorgasbord with a very pungent biological flavor. Modern definitions of a chimera have become more complicated with developments in genetics, evo-devo, and biotechnology, as well as their expansion throughout the biological hierarchy to ecological levels with less obvious genetic integration (see below). While it is often difficult to give an unequivocal biological description for a two-species interaction; it is certainly impossible to identify a single biological process description for all types of chimeras across the whole biological hierarchy. To interrelate the three terms defined above, mutualists and chimeras are both symbionts, chimeras are often mutualistic associations at least in their origin, but there are many other types of non-mutualistic symbionts.

3.0 Rosen's Concept of Chimera

Rosen's (2000) essay (Cooperation and Chimeras) exposes some major gaps in evolutionary theory that have largely gone unrecognized and unappreciated especially at the ecological level. This section includes only the main points of the argument he makes for how and why chimeras arise. For the full argument and mathematical detail, the Reader is referred to his original paper. I paraphrase Rosen fairly heavily in this section to allow the Reader to hear his voice and appreciate the originality of his ideas, but also because it is difficult to summarize his thought more clearly than he did himself. All quotations in this section are taken from Rosen (2000, Chapter 21). I use square brackets in these quotations to insert some additional explanation.

Rosen (2000) defined chimeras quite broadly. His definition expanded the concept from the individual to the ecosystem level and beyond. His favorite example of a chimera at the organism level was the soft-bodied hermit crab (crustacean), which inserts itself into a discarded snail shell (mollusk: gastropod) and selectively collects anemones (echinoderm) to grow on the shell.[1] Thus, this chimera contains components from three different phyla. The shell provides protection for the crab's soft underbelly and the anemones act as bodyguards for the crab using their stinging tentacles especially against octopus and fish predators. After the crab captures and consumes its dinner, the anemones eat the 'crumbs' from the crab, who is an untidy eater. They also benefit by riding free through a larger foraging space than they can achieve existing only in a sessile condition. As the crab grows, it trades upward for larger shells and transfers its anemone protectors to its next gastropod shell. It even arranges them on the new shell so that they are well-balanced for transport (Brooks, 1989). The crab alone can easily detach the anemones whereas most predators cannot. Thus, the crab and anemones are mutualistic symbionts that form a chimera with themselves and the shell.

Rosen (2000) considered chimeric interactions are largely cooperative since each participant could provide functional capabilities absent in their partners. As Rosen (2000) observed, "…the hermit crab, the chimera, is the exemplar of technology. It exploits other genomes to realize functions that its own cannot…But behaviors that generate such chimeras, which augment functional capabilities and thereby create new life, are not themselves programmed in any sense." Rosen used the term 'technology' broadly here as a solution to a problem a living organism has to solve to survive and persist. To Rosen (2000), "phenotypes are where the functions are, where the technology resides". His chimera concept also informs the growing area of biotechnology. Marinakis et al. (2018, this issue) conducted a Participatory Technology Assessment of a terrestrial cyborg ecosystem that was Rosennean complex.

In this section, first, we will consider several dualities that Rosen said were generally applicable to all systems including chimeras; and consider how these dualities arise and operate in chimera formation; second, elaborate upon another duality: structure versus function, and the relevance of function to chimeras as cooperative systems, and third, conclude with some comments on still another duality: Rosen's notions of ontology and epistemology.

First, the initial dualities to consider are: identity-behavior, genotype-phenotype (the set of all behaviors and properties), system-environment, admissible-nonadmissible environments,

---

[1] This interesting behavior can be viewed on You Tube: https://www.youtube.com/watch?v=dYFALyP2e7U.

and autonomous versus non-autonomous forced behaviors. Rosen (2000) began by asking: "in what sense is a chimera, a cooperative thing, an adaptive response in an evolutionary context and how could such a thing arise, let alone prosper, in a situation presumably driven by competition? Our point of departure will be the statement that to qualify as adaptive, a behavior must enhance the survival of the individual manifesting it." Rosen's chapter is essentially an elegant comparison of physical systems and living systems, emphasizing how we use the conceptual framework of a physical system to understand the living one, it creates considerable confusion and error.

Rosen (2000) pointed out that natural selection in Standard Evolutionary Theory (SET) regarded environment in different ways: "the organism struggles for the prerequisites for survival in the environment, but they also struggle against aspects of the environment that threaten survival. Fitness has always been a vague measure of success integrating both reproductive output and survival, and presumably, more fit individuals are better adapted to their environments." Rosen criticized the Darwinian view of evolution and its emphasis upon changes in [gene frequency] because this approach is based upon a mechanistic understanding of a simple world, rather than a complex one. In simplification, many concepts become mangled. For example, survival is a term that is used pervasively in evolutionary studies, but it has no counterpart in mechanics although many Darwinians have had an overt penchant for mechanisms and the machine metaphor. Rosen also concluded that reproductive fitness and survival fitness do not involve the same behaviors, and they do not have to have the same outcomes since they are very different measures of fitness.

Environments can be separated into two types: admissible and non-admissible. The former does not change the identity of the system similar to when a mechanical system is isolated, whereas the latter can. For living systems, system identity becomes context-dependent as a function of a larger environmental system in non-admissible environments. For example, plankton living in an ocean are coexisting in a non-admissible environment. As Rosen (2000) pointed out: "Only admissible environments, which keep identity context-independent, allow us to do traditional mechanics at all." Rosen was not, however, interested in 'doing mechanics'; his focus was on non-admissible environments and how they relate to the overall concept of survival in evolutionary theory, and under what conditions they change the identity of a living system.

He then likened identity to genome and behavior to phenotype by stating: "Genome in any kind of system, biological or not, is what conveys identity, or determines species, independent of all system behaviors. In biology, however, more is true: genome is what forces phenotype… Forced behavior occurs when there is a difference in behavior between the isolated system [in an admissible environment] and one [living system] in a non-admissible environment (Rosen, 2000)." In a mechanical system, identity is related to how forces are perceived *per se* and not the behaviors that emanate from the system itself as in RC living systems. Rosen discussed how mechanics defines an isolated system as not being able to change its identity, although it can have behaviors. In contrast, living systems are *a priori* open to their environments and never isolated. Thus, "a system that is open in any sense is one whose behaviors depend on something outside the system itself, where in a closed system, there is no outside (Rosen, 2000)."

Rosen (2000) emphasized that "survival must pertain to the identity of the system, which we have tied to the formal causes [purpose, goal] of its behaviors. That is, survival is tied to…what we have called its genome; …Survival must inherently involve non-admissible environments – environments that can change system identity… This fact alone, as we have seen, is sufficient to remove survival from the realm of mechanism, in which only admissible forces are allowed." He then continued to show how behavior has always been seen as being able to change environments…the capacity of a system to change environment is the crux of our characterization of behavior as adaptive, and adaptivity as favoring survival."

Rosen (2000) also distinguished forced behavior as being either autonomous or non-autonomous, that is, in the first case, "an autonomous dynamical system is one for which the time variable does not enter explicitly into the dynamical equations. For this reason, such systems are often called state determined". In the latter case, "a system which is both open and autonomous…must have the property that the flows from the environment to system, and from system to environment, are determined by what is inside the system". "Non-autonomous admissible forcings are often called inputs, and the resultant system behavior, outputs…a material system would not be called an organism, would not be recognized as "alive", unless those senses of genome coincided, unless what conveyed identity also forced its phenotypes, and hence determined their functions."   "It should be clear that this concept of system identity, or species, represents a natural generalization of the biological concept of genome; and accordingly, that the genotype-phenotype dualism, which arose originally out of biological considerations, is in fact of universal currency – a corollary of the system-environment dualism."

Rosen used a mathematical analysis from a previous paper on activation and inhibition (Rosen, 1979) to illustrate two systems and their joint effects on a common environment. He believed this situation could be adaptive and preliminary to chimera formation. He defined a behavior as adaptive as follows: "a behavior is adaptive if its impact on the environment lowers the impact of the environment on the genome [i.e. identity]…We may say that X is adaptive to the extent it is an inhibitor of genome change in a non-admissible environment, and that adaptivity requires more causal entailment than purely mechanical approaches allow. This extra entailment can, perfectly rigorously, be regarded as the final causation [purpose] that seems inherent in adaptation." Here he is talking about Aristotle's final cause that most of science rejects as teleology (answering the why question), but to Rosen, 'purpose' is a completely useful concept for complex biological systems, and has nothing to do with vitalism or metaphysics (See also Poli (2018, this issue). Mossio and Bich (2017) have elaborated on Rosen's concept of purpose using the notion of self-determination. Allen et al. (1998) have reviewed the definition and use of 'purpose' in the biological literature.

Rosen explained, "Adaptation is a meaningless concept unless it is tied to an individual who survival is enhanced by it… We have tied our identification of an individual to its genome, and hence with the formal causes of its behaviors. A behavior itself could be adaptive or not, in this context, depending on its effect on genome preservation. In this context, then, the fittest behaviors are those that minimize change of genome (identity) in the face of environments that can change it [that is, non-admissible environments]".

Rosen (2000) thought that "too much adaptation was a bad thing" and that it could pull apart cooperative structures; he suggested that it had to be apportioned carefully within a system. He also recognized that a subsystem could be adapted for itself and maladapted for the whole. The individual that we are concerned with here is the ecosystem chimera and not the individual species. Thus, the advantages of chimerism are inherently adaptive and functional as discussed above for the hermit crab and endosymbiosis in the cnidarians. Rosen related these ideas to ecosystems as follows, "In fact, we live in a highly chimeric world. Any ecosystem, for instance, is a chimera in the strictest biological sense; the functional distinction between, for example, predator and prey in such a system has nothing to do with differentiation or development as normally understood." Thus, ecosystems are chimeran individuals that adapt and have functions; they also have a purpose.

Rosen then considered two systems interacting with one non-admissible environment. "Each system is now part of the environment of the other. In general, as always, we will allow environments to be non-admissible…we say that the systems compete when the behaviors of each of them lower the fitness or survivability of the other and they cooperate when they increase the survival or fitness of the other…It, thus, indirectly increases its own fitness by favoring something that inhibits the impact of the total environment on its genome." "This type of cooperative strategy constitutes, in the broadest sense, a symbiosis of our two systems. It is not yet a chimera in our sense, in that it does not yet have a real identity and behaviors of its own; it is as yet only a kind of a direct product of the individual systems that comprise it." Eventually, "the two effects of each system on the environment become correlated", although "the behaviors are causally independent". "This indirect interaction results in our correlation of causally independent behaviors of the two systems separately."

In explaining how chimeras form, Rosen (2000) showed how indirectly-linked species could share functionalities as follows: "Note, we have supposed no direct interaction between our two systems [species], only indirect interaction through activations and inhibitions of environmental effects…This indirect interaction results in our correlation of causally independent behaviors of the two systems separately. But, if the systems do interact directly, their joint behaviors are no longer causally independent; we can no longer answer why questions about the one without invoking the other. A pair of such systems in direct interaction constitutes a new system, with its own behavior $\dot{z}$, its own states z, its own identity γ and its own environment H. In terms of the original system, the interactions themselves take the form of constraints, identical relations between behaviors, states, and genomes of which, $\dot{z}$, z, and γ are built…It is easy to write down in these terms the conditions under which a pair of interacting systems, in which behaviors are constrained rather than correlated survives better, preserves more of its genome in a non-admissible environment than either system can by itself… From groups to individuals, shared functionality is more important than shared genetic history".

"When is chimera formation adaptive?…we shall identify a second system in the environment of the first, and instead of looking at the interplay between our initial system and its undifferentiated environment, divide it into the interplay between the two systems and their environment… In this case, the behavior of each system increases the survival or fitness of the other. It, thus, indirectly increases fitness by favoring something that inhibits the impact of the

total environment on its genome…We've identified survival with persistence of genome and measured fitness of a behavior in terms of inhibition of rate of change of genome" and "I have given some very general conditions for the fitness of chimera formation (e. g. cooperation) in this situation" (Rosen, 2000). Thus, non-admissible environments provide a rich source of new genomes and their behaviors.

Second, the notion of function is critical in chimera formation. In traditional biology structure determines function, but Rosen considered this a backward idea. He believed function determines structure. In integrating components (genes, organisms, populations, or groups of species), chimeras become systems in their own right with their own identity (genotype), and their own behavior (phenotype), within their own environment. Rosen went further in distinguishing chimeras from other systems: "But in a chimeric system, we have further information. We know in advance that a chimera is a composite whose elements were themselves originally systems, or parts of other systems. Hence at some earlier time, these parts had their own identities, their own genomes, their own behaviors (phenotypes), and their own laws… Thus, we presume a privileged set of parts, into which the behaviors (phenotypes) of the chimera as a whole can be analyzed, and out of which they can be synthesized, and likewise for the chimeric identity (or genome) that forces them." "The mysterious interplay between genotype and phenotype is deeply probed by chimera. And the notion of function is central… it is an inherently cooperative notion, not a competitive one… One of the deepest lessons of biology is that such cooperation is selected for; indeed, that life would be impossible without it; and hence that complex organizational problems can be solved via cooperation and not by power and competition" (Rosen, 2000)."

Understanding how he conceptualized the hermit crab-anemone-shell provides insights into how chimeras could develop and operate at the community-ecosystem level. In explaining this chimera, Rosen (2000) said: "it is an extremely composite, heterogeneous structure… Yet, the entire assemblage, considered as a unity, has its own form or phenotype coded for by a corresponding genotype." He then asked, "What do conventional categories of genotype and phenotype mean when we are dealing with a chimerical creature like the hermit crab? … unity out of plurality". This is a decided contrast to the traditional focus in biology on differentiation or "diversity out of unity", which appears so arduous and tenuous one mutation at a time. He concluded, "The idea that everything is differentiation has led biology to reject the concept of function, which is a perfectly rigorous notion, and replace it with the mystical concept of program. This replacement is, ironically, supposed to mechanize biology; to make it truly scientific thinking." Thus, Rosen (2000) believed that individual entities associate as chimeras so that each partner can garner one or more functionalities from the others, which a single partner cannot provide for itself.

Cooperating functionally is clear in the hermit crab chimera with benefits for members as well as with the earlier cnidarian example with endosymbiosis. This is important in considering a plankton food web chimera since it permits us to consider a plethora of functions that this chimera might be able to perform in an overarching collaborative framework of hundreds of species. Clearly in a hierarchy like the biological hierarchy, 'individuals' populate different levels; a chimeran food web is such an individual. As Manfred Eigen (2013), the Nobel Laureate in Chemistry, observed, "life is governed by its function not its structure… There is no particular physical structure that is equivalent to life"…"The idea of function is resisted in

orthodox biology because it seems to carry with it a notion of design, and it seems necessary to expunge this at any cost. This is because design seems to presuppose a category of final causation, which in turn is [mistaken for] teleology" (Rosen, 2000). "And, as it turns out, the concept of function constitutes a common currency for expressing this commonality...." among different systems.

Third, the duality of ontology versus epistemology. Rosen explained the difference as follows: "In the former, we are interested in the identity and states of the system, whereas, in the latter, we are interested in the underlying causal organization of 'why a system changes state the way it does.' Thus, asking how a chimera is created and defined, is different from asking how it behaves. In the simple mechanical world, ontological and epistemological questions are often co-mingled, but this is not possible in the complex world we inhabit". He pointed out that to answer ontological questions we need to refer to the larger environmental system using a synthetic approach in contrast to answering epistemological questions that can be answered analytically. He concluded: "… We must view synthesis as highly context-dependent, quite in contrast to the completely context-independent analytical units that reductionism seeks." "If we are given a system, we can talk about its behaviors, its phenotypic types, and the genotypes that force them in given environments. Each of these gives rise to a model of that given system, all this is utterly independent of the system's ontology – i.e. where the system came from; it concerns only its epistemology as it exists. In a simple world, it turns out the two can coincide. In a complex world, on the other hand, they need not; we can know all about the one without knowing anything at all about the other". This is why Rosen felt he did not need evolution to understand what life is. "Thus, when we describe chimera as a new individual, with its own new identity, and its own behaviors (i.e., a system in its own right), we are asking inherently ontological questions. In particular, we are focusing on the chimera as an adaptive response of other systems, other individuals, with their own behaviors and epistemologies…Roughly, the argument is that the "creation" of the new individual is simply another way of talking about the behavior of some larger system…Any question relating to ontology of something finds its answers in how that bigger system is behaving – that is, how the bigger system is merely changing state." "If nothing else, it requires us to give up the view that analysis (as a tool for understanding a given system's behavior in terms of some of its subsystems) and synthesis (the assembly or reassembly of such analytical parts, to re-create the system itself) are generally inverse processes (Rosen, 1988). Indeed, we must view synthesis as highly context-dependent, quite in contrast to the completely context-independent (or objective) analytical use units that reductionism seeks."

In summary, Rosen concluded, "Chimera formation culminates in the generation of new kinds of individuals; it causes new identities, new genomes and new behaviors to emerge, which could never be generated in any other way, and certainly not by processes of differentiation alone. I have tried to give conditions under which chimera formation is adaptive, in the sense it favors the survival of its constituents more than the survival they could achieve otherwise. But I certainly cannot say that, if fitness is measured in terms of … [gene frequencies], as it is when we speak of Darwinian evolution, such considerations have any significance at all. The two issues are clearly not the same. Indeed, in the establishment of relations between these two distinct playgrounds for adaptiveness, the evolutionary and the physiological, would in itself be an instance of chimera formation."

4.0   Using Loop Analysis to Understand Chimeran Food Webs

In this section, a plankton food web for Narragansett Bay analyzed by loop analysis (LA) is discussed and some results for marine plankton communities are examined in a 'chimeran' context. The methodology and applications of LA are provided in Appendix 2, Section 9.2.

Figure 1 depicts a plankton food web in Narragansett Bay as discussed in Lane (2017b). This 'food web' contains abiotic variables and some non-trophic links, and could also be termed an ecological network. It is a composite model or 'ecological skeleton' (ES) of nine individual loop models constructed around an annual cycle. Narragansett Bay is a shallow productive environment in which there is more pelagic-benthic coupling, with more benthic larvae species found in the plankton, than would be expected in the open ocean. Table 1 contains a taxonomic explanation of the variables. There are 3 nutrients, 6 algal groups with A_2, dinoflagellates, as protists with both photosynthetic and phagotrophic capabilities, and 11 animal variables for a total of 20 variables. The mathematically possible number of networks for 20 variables with three types of links is 400^3 or 7.06E190-much larger than a google. The variables have essentially been selected for their functional capacities and relationships in the overall food web. Some variables contain dozens of species like some of the algal variables while others contain only one stage of the life history of one or more closely-related animal species.

All of the biotic variables are symbionts in that they coexist closely together within a single food web; each variable has formed part of the environment of all the others. In addition, each variable can affect all of the others through various pathways with evolutionary outcomes (++, --, +-, etc.) that can be very different from their biological process descriptions. Thus, biological interactions occur not only as two-way links but indirectly by way of intervening variables on pathways of effect. There is no rule that direct effects are stronger than indirect ones (Lane, 2017b). These food web components are also all chimeras by virtue of being eukaryotes, fused from two ancient prokaryotes, and also having mitochondrial endosymbionts. The photosynthesizing algal variables also have plastid endosymbionts. Many of the dinoflagellates (A_2) possess both plant and animal traits that suggest extensive chimerization in their ancestry. In this long-evolving ecosystem, the universal presence of chimeras is no surprise. Although it is clear there are multiple chimeras at the cell and organism levels, the question here is whether the total network is, in essence, an ecosystem-level chimera?

The overall food web structure appears to be a single module as a three food chain lattice with particular subsystems and substructures. The plankton community depicted here encompasses a particular size range; in the ocean, there are many other smaller organisms such as pico- and femtoplankton, as well as much larger ones (largest invertebrates, fish, reptiles, amphibians, and mammals) not represented in this ES. To date, it has not been possible to assemble field data sets that could be used to model these other size groups using LA. Each size range requires different sampling methods, spatial and temporal scales, etc. None of these very small and very large organisms are adequately sampled by standard plankton collection methods. Some animals such as fish larvae of various life history stages, successfully avoid most collection
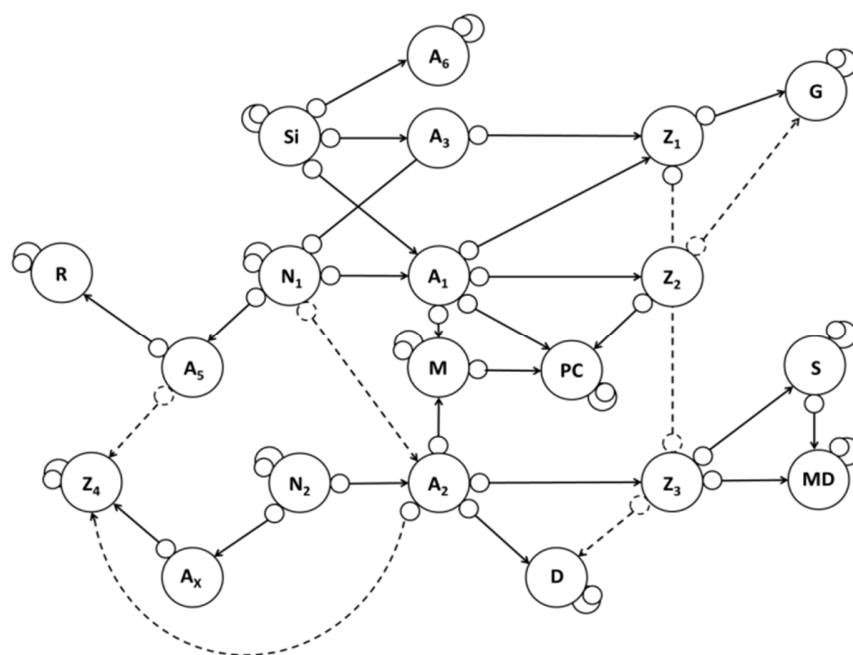
Figure 1. Ecological Skeleton of Nine Loop Models of the Plankton Community in Narragansett Bay (Reprinted from Lane, 2017b). (Key is in Table 1, which contains a taxonomic listing of the 20 variables.)

apparatus often making it necessary to extrapolate abundances for some age classes needed for fishery management models. Thus, in terms of the overall oceanic food web, it is unclear whether it is constructed as modules, perhaps with other lattice templates, or whether these other groups of organisms have totally different food web structures. It is also possible that there are other interior structures within particular multi-species variables such as the algal groups that loop analysis is unable to discern. What does seem clear, however, is that most (90-95%) of the observed dynamics of the included loop variables are adequately captured by the food web in Figure 1 without requiring reference to the smaller or larger organisms, or other abiotic variables.

The smallest forms (A_5, A_X, R, and Z_4) that were sampled appear to form their own food web or at least some branches attached to the two main nutrient variables (N1 and N2) on the left-hand side of the main food web, as well as a smaller subsystem of the silica variable (Si) and A_6, a group of algal silica flagellates. It appears these are only fragmentary portions of what could be a much more detailed small plankton food web, given the sampling resolution used here for the largely meso- and small macro-plankton. For example, it could be possible that these undeveloped branches are actually a three-tier lattice structure similar to the food web on the right-hand side. The smallest organisms to the left are notoriously difficult to sample because some species rapidly disintegrate upon collection. There are also enumeration and taxonomic difficulties. Some species need to be cultured, which often only provides a set of presence/absence data especially for bacterial species with little or no data on relative abundances.

Several other food web features of ecological interest related to Figure 1 are listed and explained in Table 2. First, in constructing approximately a thousand models for field and

laboratory plankton food webs, using different data sets, models come out remarkably similar. Plankton communities from Delaware Bay in the United States to Halifax Harbor in Canada have similar structures repeating redundantly across this broad geographic area. There has also been good correspondence between two sets of field-laboratory datasets (Narragansett Bay and the MERL mesocosms, and Halifax Inlet/Bedford Basin and the Dalhousie Tower Tank). These communities exist throughout the ocean without any imposed external instructions for a set of taxonomically and size-diverse organisms that have no brains (phytoplankton) or only primitive neural systems (zooplankton). They appear to form resilient ecological structures that have the capacity to persist.

Whereas the total feedback (F_N) of an individual loop model is negative because of the predominance of short negative loops, the total feedback of an ecological skeleton is positive because it contains many longer positive loops that the individual model does not. At the level of the direct interactions between most pairs of variables, feedback is also negative. It appears that these longer positive loops come in and out of focus around the annual cycle indicating mutualistic loops and overall system cooperation. Because of all of the positive feedback, the ES is unstable. Two initial hypotheses can be suggested, perhaps there are more: (1) while the ES contains variables and links that occur in biologically-reasonable networks, they may not occur altogether at one time in nature. Like a solution of chemical isomers, the community may fluctuate among many network states over the annual cycle, and (2) the ES may represent real positive feedbacks that provide the basis of functional cooperation among the disparate components of the food web chimera, and we do not understand exactly how this works, or our notion of stability may be incorrect especially when it is considered at the higher levels of the biological hierarchy. Bahar (2018) said, "There is an essential tension – a balance between cooperation and competition" in living systems and their evolution. LA confirms this.

Loop Variable		Description of Variables and Taxonomy of Dominant Species and Higher Taxa
Symbol	Name	
Si	Silica	Silica
N_1	N/P ratio	(NO_3 + NO_2 + Ammonia) divided by ortho-phosphate (PO_4)
N_2	Organic nitrogen	Not measured
A_1	Diatoms	*Cyclotella striata, Chaetoceros affinis, C. didymus, Chaetoceros sp., C. compressus, C. lacinosus, Leptocylinduleus danicus,, Nitzschia closterium, N. longissima, N. seriata, N. sp., N. paradoxa, Gyrosigma sp., Guinaroia flaccida, Pleurosigma spp., Rhizosolenia fragilaria, R. setigera, R. alata, Asterionella bleakeleyi, Certulina begonii, Thalassiossira sp., Tropidoneis sp., Amphidunium spp., Litodesmium undulatium*
A_2	Dinoflagellates	Protists: *Dinophysis acuminata, D. ellipspodes, Gymnodinium sp., Hetercapsa tiquitra, Dissodium lenticulum, Peridinium sp., Scrippsiella sp., Prorocentrium gracile,* UID Flagellate-I, *Scrippsiella trochoideam*
A_3	Luxury consuming diatoms	*Asterionella japonica, Coscinodiscus sp.,, Melosira sulcata, Navicula sp-II, Skeletonema costatum, Thallassionema nitzschiodes, T. rotula,* T.-II, *Grammatophora spp., Leptocylind minimus, Ditylum brightwellii,*
A_5	Microflagellates and monads	Microflagellates and monads
A_6	Silica flagellates	Silica flagellates and monads, *Distephanus speculum*
A_x	Unknown algal gr.	Unknown algal group
Z_1	Adult copepods-I	*Acartia tonsa, Microcalanus pusillus, Pseudodiaptomus cornatus, Oithona colcarva, O. similis, O.sp.*
Z_2	Immature copepods	All copepodites and nauplii
Z_3	Adult copepods-II	*Acartia hudsonica, Pseudocalanus spp., Eurytemora hermanii, Temora longicornis, Centropages hematus, C. typicus*
Z_4	Cladocerans	*Evadne spp. and Podon spp.*
M	Mollusc larvae	Pelecypoda and Gastropoda larvae
PC	Polychaete/Cirriped	Combined group of Annelida and Barnacle larvae and nauplii
S	Sagitta spp. larvae	Chaetognaths
MD	Medusae	Coelenterate
D	Decapods	Crustacea
G	Gammarids	Crustacea
R	Rotifers	Rotifers

Table 1. Listing of Loop Variables, Major Species, and other Taxonomic Groups. (Modified from Lane 2017a).

No.	Feature	Comments
2a.	Overall Structure	This ecological skeleton (ES) is a composite diagram for ten field cruises representing nine loop models that were summarized by determining their most frequent variables and links over the annual cycle. It has three tiers with some cross-links in an overall lattice pattern. The food web may have arisen originally as three separate food chains that later congealed (one of normal autotrophic diatoms, A_1; one of Si storage-capable diatoms that could anticipate and survive nutrient poor periods, A_3; and one that could both photosynthesize and consume larger, organic particles by ingestion A_2). The ES is the most parsimonious description of the dynamics that are observed in the food web over an annual cycle.
2b.	Variables	20 variables including three abiotic nutrients and 17 biotic components. Each variable exhibits a unique set of in and out links that characterize its functionality; redundant variables collapse into each other. This diagram represents approximately 500 species that were taxonomically distinguishable.
2c.	Links and Loops	There are 72 links and nine possible qualitative link types. The predominant links in this model are self-damping terms (negative loops of length one) and bivariate predator-prey relationships that are negative loops of length two.
2d.	Feedbacks	Because loop models are constructed as sets of feedback loops, they capture a considerable amount of causal entailment. There are 63 feedback loops in total.
2e.	Parameter Inputs	85% Rule-for all loop models constructed to date, based upon matching model predictions to field and laboratory observations, 85% of all parameter inputs enter the networks at the nutrient and algal levels, despite the large number of environmental perturbations that affect marine plankton communities. This indicates that perhaps the structure, as an open material system, is most sensitive to inputs of matter and energy. The pathways that begin at or near the bottom of food web are termed trophic escalades (Lane, 2017a) This result agrees with many decades of marine observation, however, is contrary to recent trophic cascade papers that claim the food web is 'controlled' from the top (Lane, 2017a,b). There is a range of 5-20% for the transfer of energy between trophic levels, although the 10% rule is most frequently cited. This is close to the 85% rule in LA. whether this is a coincidence or something more meaningful about ecosystem function is unknown.
2f.	Connectivity/ Connectance	Connectivity is 3.55 if self-damping is included and 2.95, if it is not. Connectance is 18% if self-damping is included and 16%, if it is not.
2g.	Paths	There are approximately 4400 paths.
2h.	Network Similarity	Another 85% Rule-when considering the variables and links of the individual loop models that were summarized to construct this ES, there is on average an 85% similarity among the models. This suggests that about 85% of the overall structure constitutes the core identity of the system, with about 15% of the structure appearing to change randomly. This latter percentage may be necessary for overall system flexibility/adaptability in changing environmental conditions.
2i.	Micro-universe	The micro-universe for plankton communities has been estimated to be between 10^9 and 10^{13} possible networks. This range is calculated by

		multiplying all pair-wise link types observed in the nine individual models.
2j.	Variable N_1	This abiotic variable is a combination of inorganic nitrogen and phosphorus as a ratio (Redfield Ratio of N: P = 16:1). It essentially serves as a connective hub between the subsystem of the smallest organisms at the left and the rest of the food web on the right. Any attempt to treat these two nutrients as separate variables met with failure. When this ratio is greater than 16, nitrogen fixers are outcompeted. Changes in this ratio may serve to favor the movement of matter and energy up the various tiers in the food web.
2k.	Variable Z_2	This variable is a combination of the 11 immature copepod stages for all species of copepods in the food web. Its links to the two adult copepod variables: Z_1 and Z_3, are termed 'volatile' because they change sign frequently as well as mostly being one way with occasional two-way interactions. This is the source of considerable nonlinearity in the loop models, and may indicate that Z_2 acts as a kind of reversing pump for moving matter and energy up through the middle tier to the top and bottom tiers and eventually to larger invertebrate predators and their vertebrate predators. This variable may also serve as a timekeeper or time coordinator by reversing flows as necessary between the juveniles and the adults. In addition, the fact that all of the immatures of all species including 11 life history stages are grouped together into a single variable may also say something about chimerization and considerations of what functions are traded among these species with the other members of the food web. Around an annual cycle, the collective timing of all of these life history stages could enhance the predictability of temporal sequencing of various-sized food particles for consumers including some of the copepod species and stages themselves.
2l.	Variables A_1, A_3	Both of these variables are diatoms. The second (A_3) consists of luxury consumers that can store nutrients in their central vacuole. This may be an important mechanism to survive nutrient-poor conditions by essentially cheating time and waiting for more advantageous levels of nutrient availability.
2m.	Variables P, C, M, MD	Benthic larval variables appear to be wedged into the interstitial spaces between the two lower tiers-perhaps as a way to obtain some of the leftovers from the adjacent variables reminiscent of the anenomes that consume the crumbs of the hermit crab discussed earlier.

Table 2. A Summary of Some Features of the Ecological Skeleton of the Narragansett Bay (Figure 1) and other Field Loop Models.

Life is a process in which an array of functions needs to be operational and temporally congruent at all times. One loop model, therefore, captures a considerable amount of relational and causal information, and this is also true for ecological skeletons (ESs) that facilitate the calculation of micro-universes, which generally contain 10^9 to 10^{13} possible alternative descriptions of plankton food webs for one location. Although the number of alternative descriptions is large, this is probably a more realistic number given the number of components and links within a single, biologically reasonable, food web. The micro-universe helps to prune away food webs that are not useful, thus, identifying the underlying most important relationships. Thus, in a fundamental way, LA captures functional relationships and dynamics better than it does structural ones, although standard structural measures like connectivity and connectance can be calculated. Throughout evolutionary history, old structures have been repurposed over and over again, essentially re-gifted, as new functions have been needed by living systems.

In summary, ecosystems like the Narragansett Bay plankton community are chimeras in which their components bring memories of other systems they once participated in. This information can be used to solve new problems. In life itself, chimeras have likely always been there at least since the time of lateral gene flow, eukaryotes, sexual reproduction, but also in other existing life forms. Chimerization can be expected to continue as long as life exists, and may even be accelerated with global change such as planetary warming and biodiversity loss as species around the world have new problems to solve that require new functionalities.

5.0 A Thought Experiment on Food Web Chimeras

Thought experiments (TEs) have been undertaken since imagination became available as a human capability, and long before there were laboratories. The Stanford Encyclopedia of Philosophy (1996, Rev. 2014) defines TEs as "devices of the imagination used to investigate the nature of things". Einstein frequently created TEs and asked 'what if' questions. He was a great believer in the value of imagination; he said, "Logic will get you from A to B. Imagination will take you everywhere".[2] Many other physicists have also used TEs: Schrödinger had his imaginary cat and Maxwell his imaginary demon. In biology, TEs have been most often utilized for evolutionary questions (Buzzoni, 2015). For example, Darwin (1859) frequently exercised his imagination in the Origin of Species. The Daisy World of James Lovelock can be considered a TE in which he established a world with two types of daisies: one light and one dark, and then imagined the interplay between the daisies and planetary temperature. In this section, a TE entitled: "The Fundamental Processes in Ecology: A Thought Experiment on Extraterrestrial Biospheres" by Wilkinson (2003) is summarized to illustrate his minimal requirements for planetary life and biosphere formation. His results are then related to the example of Narragansett Bay (Section 4) food web since we would expect a RC ecosystem chimera to develop over eons of time from these minimum requirements (Table 3). Then a new TE is described that illustrates various aspects of considering the Narragansett Bay plankton food web as a RC chimera. For example, how do participants benefit within a cooperative chimeran framework?

---

[2] https://www.brainyquote.com/quotes/albert_einstein_121643

Wilkenson (2003) asked, "For any planet with carbon-based life, which persists over geological time scales, what is the minimum set of ecological processes that must be present… And what effect would they have on the lifespan of any biosphere?" Wilkenson listed seven processes that he believed were more important than structural arrangements like the biological hierarchy for life on Earth (Table 3). At the end of his paper, however, he admits that these processes relate more to life itself than ecology, but he was correct in assuming all life, both cellular and multicellular, has an environment and therefore ecological relationships. Table 3 defines these processes according to Wilkenson (2003) and indicates their relevance for the Narragansett Bay (NB) plankton community and its loop analysis results.

Wilkenson (2003) concluded that it is difficult to see how a single type of organism could live totally isolated from any other and provide all of its own requisites for survival.   In addition, he viewed nutrient cycling as emerging from all of the above processes, since it becomes increasingly necessary as more diverse biota, with their more diverse waste products, require secure nutrient sources. Referring to a model of Downing and Zvirinsky (1999), Wilkenson observed that: "Many biochemical guilds will emerge, with one guild's waste products becoming another's resources. These transfers eventually feedback into one another to form recycling loops, thus enabling the biota to achieve a total biomass well beyond that which the external flux would alone support." This is another case of eating leftovers like Rosen's hermit crab-anemone chimera, and Brinkhurst's mutualistic tube worms mentioned earlier.

Although Wilkenson (2003) focused upon imagining the minimum conditions for a planetary biosphere to be functional, his TE provides a foundation for considering ecological RC in extant ecosystems after the original conditions for life were established on the planet. Of interest here is how contemporaneous ecosystems exist in full operating mode in ecological time rather than the origin of life, the ontogeny of the biosphere, or evolutionary persistence per se. Ecological time is defined here as approximately 10 times the mean lifespan of the individual species within the community. The Narragansett Bay plankton community satisfies all of his minimal requirements (Table 3), however, the food web has developed far beyond the minimal set.   Likewise, while some of Wilkenson's processes overlap with Rosen's chimera functions, the latter includes a much more extensive set of biological phenomena and conditions.

There is no way to provide real-world observations or a definitive experiment to prove Rosen's premise true that ecosystems are chimeras, but if true, there are some potentially-important conclusions to consider. Whether these conclusions are also true and the whole argument sound is left to the Reader to decide. The goal of the TE is to imagine some possibilities consistent with what we know.

Process	Relevance
Energy Flow	Energy is necessary for life and all metabolizing organisms must have an energy source and a way to excrete wastes. NB–all of the organisms in the plankton food web have various energy sources and all excrete wastes.
Multiple Guilds	Since wastes contain matter and energy that could be harmful if accumulating in large amounts, yet, beneficial if used by others, it would be necessary to have at least two guilds: autotrophs and decomposers. Wilkenson hypothesized that predation is not a basic process and would not have arisen until phagocytosis was possible with the arrival of the eukaryotes, although parasitism could have been operating much earlier. NB–the plankton food web contains multiple guilds and other variables including autotrophs, heterotrophs, protists, micro- to macro-predators using diverse food capture methods, and abiotic nutrients.
Tradeoffs	He further hypothesized that specialists would do better than generalists in any given situation so that increasing biodiversity within a guild would be selected for "in all persistent biospheres". NB–Several algal and zooplankton variables are composed of multiple species that can be considered guilds. There appears to be functional specialization within some loop variables, which requires more study.
Ecological Hypercycles	He defines a hypercycle as "the rate of replication of one group as a function of the abundance of the group upon which it feeds with all the groups forming a closed loop… Once such cycles develop they become effectively auto-catalytic and could very quickly lead to life covering a planet". NB–Several hypercycles appear to be operating in the loop diagrams.
Integrated Physiology (Organism-Ecology)	If life does cover a planet, biomass levels are expected to become large and contribute to global biogeochemical cycling with Gaian-like feedbacks. NB–Plankton communities have a large influence on planetary biogeochemical cycles and also climate change. They are important on a planetary level as a reservoir of biodiversity that produces 70 to 80% of atmospheric oxygen (~330 x 10^9 tons), 50% plant productivity, and 50% CO_2 assimilation needed to moderate climate change. Marine photosynthesis creates 45% of the global net primary production while employing less than 1% of the global plant biomass.
Carbon Sequestration	This would occur because carbon cycling is never 100% efficient and carbon is lost to the sediments in a marine ecosystem. NB–All marine ecosystems exhibit carbon sequestration in their sediments. Falkowski et al. (2004) calculated that phytoplankton utilize 45 billion tons of organic carbon per year while losing 16 billion tons or 26% to the sediments.
Photosynthesis (possibly)	Wilkenson concluded that although "photosynthesis is not required for the support of food chains"… "It may have such importance as a long-term source of energy to a planet's ecosystem that it could evolve on most planets with persistent ecologies." Photosynthesis would also have facilitated longer food chains than alternative energy sources. Adaptations to tolerate oxygen would have also been necessary. NB–This food web has developed long enough to have many photosynthesizing organisms and oxygen tolerance adaptations.

Table 3. Minimum Set of Ecological Processes that Wilkenson (2003) Suggested as Necessary to Establish an Extraterrestrial Biosphere with Comparisons to Narragansett Bay Food Web.

5.1 Mother Nature's Problems to Solve

Imagine Mother Nature is standing on the shore of Narragansett Bay in Rhode Island, checking on how the plankton community she has created will persist over eons of time. Imagine you can read her mind and understand how she analyses her creation while planning for its success. She first thinks back to how she started this ecosystem with the minimum conditions laid out by Wilkenson (2003), but she knows she can do better than the minimum. She carries a clipboard with a thin sheet of paper labeled 'problems'. Over her shoulder, is slung a worn leather satchel labeled 'top-secret solutions', it is open to the salt air. Neatly organized inside the satchel are plain manila folders each with a different sticky tag: chimeras, self-reference, self-organization, self-damping, cooperation, feedforward, anticipation, closed loops, entailment, final cause, CLEF, , hypercycles, models, complexity, emergence, and a few more. The very back, barely visible, is a single green folder, labeled 'LIFE ITSELF'. These folders contain her best solutions or entries from what Rosen has termed the vast encyclopedia she wrote entitled "Biological Evolution" (Rosen, 2000). She remembers how that interfering Rosen man was always snooping around my satchel, trying to open it and read my secrets, especially those in the special green folder. He became too familiar, much too familiar, especially when he overstepped in criticizing me for being "profligate, wasteful and cruel", although to be fair, he also praised me for creating solutions of the "greatest elegance and beauty, utterly opposite to the discordances and mortal conflicts that created them" (Rosen, 2000). She sighs, and thinks to herself, yes, the 'trial and error' approach can be a little inconvenient for those on the error side; and yes, with 99% of all species that ever lived now extinct, perhaps "profligate" and "wasteful" are somewhat fair modifiers.

She finds a rock to perch on, and with a small quiver of her shoulders as if to shake the memory of the Rosen man away, she lowers her satchel onto the sand. With an experienced focus, she starts listing problems on her clipboard that must be overcome for the plankton community to survive over ecological time—a clear prerequisite to evolutionary persistence. Of course, Mother Nature's role is not to impose specific solutions, but to make opportunities available once she initiates a living system. She lists: (1) to secure nutrients and energy, (2) to maintain integrity as a chimeran individual, and (3) to manipulate time effectively. Although Mother Nature lists the three problems individually, their solutions are intertwined. A complex system does not have the largest model, and it is impossible to disentangle structures and functions into component parts. Rosen (2000) used the example of how the bird's wing helps understand how the bird flies, but no one would accept that a dissected wing encompasses flight per se. It is the whole system of the bird that makes flight possible, as compared to an airplane which can be disassembled into its parts and their functions. Rosen (2000) claimed that "function is always localized in structure" in a machine, but not in organisms.

Life always has problems to solve: large ones and small ones, and since the environment is always changing, yesterday's solutions may not work tomorrow. We know this absolutely from the extinction record. This is why Mother Nature must be constantly vigilant in ensuring feasible solutions are continually available. Each habitat on Earth provides both opportunities and challenges for living organisms. In terms of the marine plankton, the contrast between the smallness of the organisms, and their limited mobility, and the vastness of the ocean in all three dimensions is striking. Here these three problems serve as a backdrop to the TE for how contemporary marine ecosystems may operate. The problems are real and the community

must solve them for both its short-term ecological survival and long-term evolutionary persistence. It does this by developing a successful mosaic of carefully-synchronized and cooperatively-shared functionalities.

The first problem is how can plankton secure the appropriate amounts and types of nutrients and energy at the times and places they are required? Living material systems are open and dependent upon inputs of matter and energy and outputs of wastes on a more or less continual basis. Largely because of the uniqueness of water, the ocean is a fairly stable environment in many ways, but one key uncertain feature is how to retain matter and energy in the photic zone. Even after billions of years of evolution about 1/4 of all matter is lost to the sediments. The world ocean has large nutrient-poor areas and a small plankter does not have the possibility of relocating to a more productive area like an upwelling zone. In the upper water column, cyanobacteria fix atmospheric nitrogen, however, dinitrogen, is not available to many phytoplankton species unless it undergoes further chemical transformations into NO_3 and NH_4 (Zehr and Ward, 2002).   Terrestrial ecosystems abutting oceans can be a considerable source of nutrients as can shallow environments in which sediments are periodically resuspended by wind and biological action. Atmospheric deposition provides much of the iron and phosphorus as aerosol particles from arid regions for the open ocean (Krishnamurthy et al., 2010), but the farther from land and the deeper the water column, maintaining adequate nutrient supplies is an increasing challenge. Dozens of macro- and micro-nutrients, vitamins and cofactors can be required by a diverse plankton community especially in the upper waters, the only place where there is adequate light for photosynthesis. Phytoplankton turnover approximately every 24 hours in an endless life-and-death cycle. Many nutrients are tied up in dead organisms and their waste products that form detritus and sink to the bottom sediments (carbon sequestration). In deeper waters, much of the associated matter and energy can be lost irreversibly. Thus, nutrient security is a critical problem for the whole food web, and while autotrophs can transform solar energy making their own food, but only if they can maintain themselves in the photic zone, heterotrophs require organic resources that can be irreversibly lost in settling detritus.

The second problem is for life forms to evolve the functionalities they require to secure the requisites for existence especially nutrients and energy (Cummings, 1998). Whereas individual plankton species exhibit a multitude of adaptations to capture nutrients and either produce or consume energy sources, to solve the system-wide nutrient/energy security problem appears to require a number of functional capabilities that an individual plankter does not possess. Chimerization of the food web provides an opportunity to harness a multitude of functional capabilities into a single identity (genotype) and a single set of behaviors (phenotype) with its own survival purpose. But how can this be accomplished with thousands of tiny plankton individuals in each m^3 of seawater? How can they create a collaborative multi-organism community chimera in the sense of a multicellular organism in which all cells and organs work together for the survival and persistence of the individual?

The third problem is how a community chimera can maintain its functional integrity over eons of time. Success in evolutionary terms has most often been analyzed as fitness measured as reproductive output with assorted measures such as numbers of individuals or gene frequencies. These are perhaps the most convenient measures, but not necessarily the most meaningful ones. Reproductive fitness has serious limitations as a success measure. Survival

measures seem to be better candidates. Each reproductive module has to survive to reproduce itself and survival can be a complicated and perilous process requiring a large number of functional capabilities. It inherently necessitates a time period of uncertainty, some minute fraction of the persistence period, in which many requisites and conditions for life can become scarce or even nonexistent. Most functional capacities involve rates of doing something like photosynthesizing or catching a prey or processing a meal. Time itself enters the quest for persistence in many ways, and it is not surprising that the community chimera coordinates time to ensure the critical functionalities can occur as synchronized processes with various rate functions. Everything cannot happen at once; life requires a certain temporal order. This often necessitates using time in different ways, which is discussed below. How organisms perceive and manage time may be one of the most neglected areas in ecology and evolution, but one cannot approach survival of an individual from one reproductive event to the next, or persistence of a community without reference to time and its management. At the ecosystem level, the chimera must synchronize a number of functions temporally that are operating in entangled cycles at varying speeds, if its functional integrity it is to persist, with nutrient-energy security. Time is always of the essence.

5.2 Mother Nature's Solutions

Although not always appreciated, Mother Nature does not work by having unique solutions for each level of the biological hierarchy, but rather providing a restricted set of solutions throughout all of nature with great redundancy.   Cottam (2018, this issue) also concluded that nature does a lot of scavenging and repurposing of solutions. Yanai and Lercher (2016) termed one bacteria's use of another's DNA as "intellectual theft". Mother Nature's plain manila folders are few in number considering the richness and diversity of what she has created. Jacobs (2001) remarked: "nature is prodigal with the details but parsimonious with principles". Mother Nature also knows that the problems of (1) nutrient-energy security, (2) integrity of functional cooperation, and (3) time management, have been solved many times. Food web pathways, while numerous and complicated, are less so than their counterparts at the levels of cellular metabolism and neural nets. Not only do brain networks require fuelling and waste disposal, but they also produce a rather amazing emergent property: consciousness. Actually, she does not even recognize the biological hierarchy created by humans, but she does understand chimeras – they are one of her favorite solutions and that folder is always first in her satchel.

Table 4 contains three aspects of Mother Nature's TE. She begins by listing three premises (1P-3P) and then three conclusions (1C-3C) that follow from their corresponding premises.   Neither the premises nor the conclusions can be definitively proven; this is necessarily an exercise in imagining 'what if?' If the premises are true and the conclusions correctly follow, however, this may be a useful way to understand marine plankton communities and could have important conceptual and applied ramifications for marine ecosystems. Each premise-conclusion is discussed below.

No.	Premises (What if?)	No.	Conclusions (Then, …)
1P.	Ecosystems are chimeras.	1C.	As chimeras, ecosystems have a genotype (identity), a phenotype (set of behaviors), and they are individuals that can function like any other individuals in the rest of the biological hierarchy.
2P.	Ecosystems are Rosennean complex.	2C.	Ecosystems possess all properties of Rosennean Complexity as defined in Appendix 1 including purpose and anticipation.
3P.	Ecosystems operate cooperatively, with their parts sharing and trading functions especially related to (a) nutrient cycling, (b) module integrity, and (c) managing time.	3C.	Various functional groups provide several services to other functional groups that they are not able to provide for themselves.

Table 4. How Mother Nature Thinks About Marine Plankton Chimeras.

Premise 1: Ecosystems are chimeras.

Conclusion 1: As chimeras, ecosystems have a genotype (identity), a phenotype (set of behaviors), and they are individuals that can function like any other individuals in the rest of the biological hierarchy.

Chimeras appear everywhere in nature throughout the biological hierarchy and many organisms participate in multiple chimeran interactions with a variety of organisms and multiple genetic lineages across that hierarchy especially when community-food web level chimeras are included. Entanglements abound and singular evolutionary outcomes seem unlikely. An individual chimera can constitute a multiplex of adaptations, benefits, and costs as illustrated by the cnidarian example above. All species evolve in chimeran communities that have environments, *a priori* since living systems are open, they require matter and energy from their environment as well as using it as a waste receptacle, and thus, being alive is always accomplished in an ecological context. The species are continually co-evolving. The chimera also entails a set of interrelationships that are entangled not only at the ecosystem level but throughout the biological hierarchy. Chimeran cooperation provides an enhanced functional capacity for the chimeran members that exceeds the sum of functionalities of the members considered individually, and more importantly, some members provide functions that are critical for the survival of other ones, which these latter members cannot provide for themselves. Thus, an ecosystem chimera is much more than a collection of coexisting symbionts.

The network of relationships among variables ensures the functional integrity of the food web is not random (Nunes-Neto et al. 2013; 2014). Thompson (1999, quoted in Decelle, 2013) said: "the more we learn about the diversity of life in the structure of genomes, the more it appears that much of the evolution of biodiversity is about the manipulation of other species –

to gain resources, and in turn, to avoid being manipulated". Rosen's (2000) concept of ecosystem as chimera goes farther than Thompson and Decelle (2013). It appears that an ecosystem chimera is more like a global trading agreement; everyone receives some benefits and everyone pays some costs. The benefits and costs are not necessarily equal for all members. Benefits are diverse, but largely in the form of decreased risks to succumbing to survival uncertainties. In addition, Rosen considers each chimera, regardless of its location in the biological hierarchy, to be an individual. Thus, the plankton community is also a unique individual, such as individuals of a population. Despite the pervasive redundancy of these food webs throughout the western Atlantic pelagic zone, no two networks have ever been found to be identical, not even for a single ecosystem using LA.

Chimerization involves the whole food web; a pair of its members cannot be isolated from the rest. In nature, all organisms exist in communities, that is, in networks of direct bivariate links and indirect pathways, where the latter can often dominate the direct links (Lane, 2017a). We extract pairwise species interactions to study because they are convenient, but this reduction is largely artificial, although much ecological and evolutionary theory is based upon this reduction. There has also been a marked bias towards competition and predation, and against mutualism and facilitation in evolution studies. Mittelbach (2012) explained the latter by saying, "mutualism has always been the 'bastard child' of community ecology".

It appears that mutualism and cooperation of all living forms were baked early into the ancient cake of life. Herre et al. (1999) concluded that: "from the algae that help power reef-building corals, to the diverse array of pollinators that mediate sexual reproduction in many plant species, to the myriad nutritional symbionts that fix nitrogen and aid digestion, and even down to the mitochondria found in eukaryotes, mutualisms are ubiquitous, often ecologically dominant, and profoundly influential at all levels of biological organization". Mittelbach (2012) defined facilitation as, "an interaction in which the presence of one species alters the environment in a way that enhances the growth, survival, or reproduction of a second, neighboring species…Facilitation by means of habitat modification plays an important role in most communities". It is also an important aspect of how Rosen viewed ecosystem chimera formation.

Kikvidze and Callaway (2009) concluded that "… Facilitation can increase the probability of survival of aggregated self-replicating entities more than competition can reduce their fitness…We argue that facilitation between individuals at different levels of biological organization can act as a cohesive force that generates a new level of organization with higher complexity, and thus, allows for major evolutionary transitions at all levels of the biological hierarchy." Many of the habitat modifications in plankton communities could come about by alterations in water chemistry and the composition of nutrients. For example, phytoplankton release many different kinds of extracellular metabolites into the water column and zooplankton release waste products. In addition, for a group of organisms that has had such a large effect on the global atmosphere and climate, it seems totally plausible that this group could also generate substantial chemical and biological modifications of its local habitat.

This is also true of bacteria such as *Prochlorococcus,* a photosynthesizing cyanobacterial genus. Sultan (2015) reported that "despite their small size, the collective habitat-constructing impact of these minute, free-living organisms is enormous… The primary productivity of

Prochlorococcus it is estimated to equal that of the earth's combined croplands… In addition, to providing a massive input of carbon and other nutrients to marine ecosystems and releasing substantial quantities of atmospheric oxygen." With climate change, distributions of this species like many others will "shift selection pressures in the entire ecosystem" (Biller et al., 2015, quoted in Sultan, 2015).

Premise 2: Ecosystems are Rosennean complex.

Conclusion 2: Ecosystems possess all properties of Rosennean Complexity as defined in Appendix 1 including purpose and anticipation.

In this subsection, the properties of RC listed in the Appendix 1 Section 9.1) are applied to plankton communities as chimeras.   The discussion is brief, although any point could be a whole paper by itself. See also Rosen (1991, 2000).

Genericity-plankton communities are generic; we do not find a plankton species living alone, but rather in a plankton community.   These communities are ubiquitous and generic throughout the planet. A plankton community cannot be viewed as a mechanism or a machine.

Impredicativity- Essentially, ecosystem chimeras arise by self-organizing and become self-maintaining, and self-reproducing, all properties of a complex system. They are autopoietic, as Margulis et al. (2011) defined the term: "Autopoiesis is the process of identity and self-maintenance of life, a behavior characteristic of the living." It is an entangled complex of feedforward and feedback loops that cannot be separated into simple isolated pathways. Wilkenson (2003) said, "Ecology is...a self-organizing phenomenon in that it originated without an external *a priori* blueprint. Therefore, as it develops, an ecological system produces its own conditions for dynamic stability." Thus, a cause of P entails P. Life is self-referential and has non-computable models that are entailed within its organization.   Cause and effect are everywhere apparent in the feedback and feedforward loops of food webs, which have been working for eons of time. What might have been an initial cause is no longer discernible. All the causes and effects are intermingled. RC also imposes additional aspects of impredicativity (see below).

Computability-it is not possible to construct a single model that can encompass all of the functional dynamics of an ecosystem chimera. LA can capture some aspects of these systems, in particular, their complication, but not their inherent complexity.

Fractionality-RC systems do not have a largest model. We too often view ecosystems as ensembles or collections of parts instead of as a single chimeran individual, with its own set of problems and its own functional capacities to solve those problems. Rosen believed that for living systems, "function is the currency of commonality among different systems".   The ecosystem chimera needs to survive in the near future (ecological time) as well as to persist for all eternity (evolutionary time) despite the evidence from the fossil record that illustrates that eternity too often comes with an expiration date in nature (extinction). The chimera, however, is organized to persist indefinitely despite the probability that such forever success will probably not be achieved.

Analysis versus Synthesis-LA can facilitate some types of analysis on plankton communities, but there are no comprehensive rules of construction that would produce and synthesize an understanding of total system complexity out of a set of individual species and abiotic components.

Ontogeny versus Epistemology-likewise, because these systems are complex, ontogeny and epistemology do not coincide in a single description. It is not possible to determine the ontogeny of a plankton community by describing its present state, even if that description was much improved over those that exist today including LA.

Anticipation-Rosen often used a sequence of enzymes and substrates on a pathway to describe how a cellular system can anticipate or read off of the future. An enzyme would appear before the substrate requiring that enzyme itself appeared. It is quite possible that the pathways in a plankton food web could work similarly in that when the system is perturbed by parameter input, it puts a particular pathway in motion with all of the variables on the pathway in place in an anticipatory manner.

Entailment-LA gives us some notion of how closed loops work in plankton communities and the playoff between positive and negative feedback at the total system level. In particular, the variables not on the pathway are present in complements of disjunct loops if that pathway is to operate. This indicates an entailment of all the variables in the system in either a pathway or complement role and both consist of causal relationships. Whereas loop analysis gives us an insight into this entailment at a particular time, it is at best representing local conditions and not the overall entailment of the system.

Efficient Cause-For a plankton chimera to be an individual in the sense of an organism with its own genotype and phenotype, it must be closed to efficient cause or CLEF. Poli (2018, this issue) gives an extensive classification system and set of definitions for CLEF for RC systems. Essentially, there is no builder or creator of the ecosystem like a carpenter might build a house. The complexity and organization of a plankton community are clearly originating within the community itself.

Final Cause-refers to the purpose or goal of the system. Rosen showed how all systems have goals. When we build a machine, we endow it with a purpose. It is constructed to do something like heat food (microwave) or illuminate a room (lamp). Rosen was able to show that living organisms also have a final cause, which I believe is to survive and to persist. The struggle to survive is apparent in all living things. Rosen stipulates final cause without referring to the old argument of mechanism versus vitalism. Thus, ecosystems are organized to achieve a goal and that goal is persistence – it is the singular goal of all life. The organization of the system itself brings life into existence and an autopoietic system forms itself for a purpose. Science has been very reluctant to admit final cause into the definition of science since to do so also lets in function as well as anticipation and feedforward (Anticipatory Paradigm) in violation of the very restricted linear, one-way cause-effect sequence (Reactive Paradigm) traditionally required by the Newtonian Paradigm. Rosen said, "science does not allow the future to affect the present". This is why physics cannot inform biology except in a very restricted mechanistic sense. All living systems are intensely anticipatory.

Premise 3: Ecosystems operate cooperatively.

Conclusion 3: Various functional groups provide several services to other functional groups that they are not able to provide them for themselves.

Functionalities are associated with a system's phenotype and its behaviors.   How functionalities arise in chimeras was explained earlier. Rosen defined function as follows: "I use the word function in the biological rather than the mathematical sense –e.g. the function of X is to do Y… We thus inch toward a legitimation of the Aristotelian category of final causation, bound up with what something entails rather than that with what entails it." Problems are solved by executing functions.   In this section, how ecosystem chimeras share and trade functions specifically related to (1) nutrient cycling, (2) module integrity, and (3) time management are discussed as per Mother Nature's list of problems to solve. This is not meant to be a complete list of all ecosystem functionalities, but only some important examples.

 (1) **Nutrient Cycling**
Living systems being open cannot stay functional and organized without adequate supplies of nutrients and energy. Food webs have become a dominant area of interest in ecology because of the critical role of nutrition in these open material systems. All of the components in the food web are dependent upon their environment for these resources. Trying to secure nutrients and energy in a nutrient-poor ocean, with a sediment sink always lying below the photic zone, is more problematic than nutrient recycling on land or in lakes that are mono- or dimictic. Solving this problem requires the appropriate functionalities at the appropriate times. Jane Jacobs (2001) suggested that nature does this by using sunlight as an initial energy source and then self-refueling, that is, the system uses a part of the energy that it obtains to capture more energy to achieve its maintenance and reproduction requirements. Matter and energy are cycled through ecosystems in as many cycles as possible so as to minimize waste. How these cycles are organized may vary in different parts of the ocean. There are some areas that are like virtual deserts as well as coastal areas with substantial benthic-pelagic coupling like Narragansett Bay. In other areas, various physical forces operate such as upwelling and gyres that influence productivity levels.

Each variable representing a functional group of one or more species in a food web has unique trophic relationships with the rest of the web. Thus, each variable is either making or metabolizing particular nutrient sources and releasing particular waste products. There are clear parallels between cellular metabolic pathways and food web pathways that capture and process matter and energy for self-maintenance, self-organization, and self-generation of all components. Food webs are essentially organized to push matter and energy from the bottom to the top in trophic escalades (Lane, 2017a). It is not enough for every predator to have its prey resource, but every prey must have its food resource, etc., essentially down to the photosynthesizing organisms, which require carbon, vitamins, and various cofactors. Every member of the food web requires security with the right types of resources appearing at the right times in the right places in the network. Just like cells have organized metabolic cycles to do this, the food web also has its own metabolic cycles working on feedback, feedforward, and anticipation.   Cooperative nutrient cycling at the chimera level dominates the negative feedback inherent in two-way competitive and predator-prey interactions that make up most of

the bivariate links.   The marine food web as a whole maintains the nutrient and energy cycling with a minimum of losses. It is not a perfect system since more than 25% is eventually lost to the sediments, but it is successful in fuelling all component species and in ensuring that pathways and cycles are continually in motion.

(2) **Module Integrity**

Modularity has become a popular topic among many scientists, scholars, and artists (Montoya et al., 2015).   In biology, the focus has been upon the organismal level of the biological hierarchy especially in disciplinary areas such as neuroscience, developmental biology, evolutionary biology, and Evo-Devo, an emergent discipline from the latter two.   To date, there has been no unanimous agreement on how to define a module.   In ecology, Stouffer and Bascompte (2011) defined modularity as "subsets of species that interact more frequently among themselves than with other species in the community". Thus, modularity relates to the link structure of the food web.

Since modularity and compartmentalization are network properties, they can be measured in food webs using the notion of subtracting the number of expected edges or links for a group of variables from the number of edges or links that actually connect these variables. There are several ways to calculate modularity. Garay-Narvaez, et al. (2014) and Takemoto and Kajihara (2015) have hypothesized that food web modularity helps combat perturbations that threaten ecological stability, which was a theoretical notion advanced earlier by Robert May (1972).   Stouffer and Bascompte (2011) claimed that "we unambiguously demonstrate that compartmentalization acts to increase the persistence of multi-trophic food webs".   Rasskin-Gutman (2005) suggested that "modularity is the nexus between morphological organization and functional integrity of an organic structure".   Here, it is considered as a quasi-autonomous structure embedded in a larger one, but acting more or less independently, somewhat akin to Kauffman's (2000) autonomous agent concept.   Repeating modules are also consistent with Jane Jacobs'(2001) notion of the importance of redundancy in nature.   In this section, some structural aspects of ecosystems will be discussed, and in the following section, community functionality in regard to time will be considered.

The search for evidence for modularity in marine plankton communities is intensifying, but not yet complete. Using LA, the plankton community appears to act as a more or less autonomous unit or module, in that its dynamics can be explained by the set of operating pathways that are summarized in its ecological skeleton. Thus, it is not necessary to refer to all the other larger or smaller species in the marine ecosystem to understand the plankton community's dynamics.   Potential linkages with either the smaller or larger species are constrained.   Evidence from marine trophic cascade studies involving vertebrate predators rarely shows definitive changes in the plankton community (Lane, 2017a, b).   Unfortunately, loop models are not available for these other groups and questions remain as to (1) how many overall modules might exist in a total marine ecosystem, (2) are they structurally similar, and (3) how are they connected to the plankton community?   With the plankton community of Narragansett Bay, it can be assumed that there are larger invertebrate predators consuming the adult copepods (Z_1 and Z_3) as well as some of the fish species. When predators are omitted in a loop diagram, their negative effects are represented by self-damping loops on their potential prey variables.

Besides (1) higher connectivity amongst species in the plankton community than connections to species outside the community, and (2) the average level of network connectivity, there are other structural features in place that help develop and maintain modular integrity. Self-pruning is one way that networks ensure operable parsimony in their structures. The plankton module exhibits limited interactions between many pairs of variables. Of the nine qualitative bivariate link types possible, most pair-wise interactions are represented by only one or two types whereas the most volatile links are related to the immature copepods Z_2 with 4 to 5 types. This, in turn, decreases the number of possible pathways and complements in the network to those that serve its overall purpose most effectively. Excessive connection is a problem in all networks if some simplification is not undertaken (see also Cottam et al. 2018, this issue). For example, in neuroscience research, one current hypothesis explaining autism is that it constitutes a failure of self-pruning during brain development so that neurons are over-connected and sensory inputs overwhelm too many neural pathways simultaneously.

The modular structure of the Narragansett Bay plankton communities appears to have a three-tiered structure of connected food chains beginning with three different nutrient components at the base of the food web. Although the number of possible food webs using the links identified in operating pathways around an annual cycle (micro-universe) is large in terms of the human mind attempting to imagine all of those combinations simultaneously (10^9 and 10^{13}), the percent of potential biologically reasonable food webs is a very small percentage of those that are mathematically possible. Miranda and La Guardia (2017) concluded that function implies structure (as did Rosen) and not the other way around and that "plasticity in food webs is the capability of changing the directed graph structure, ergo its transition matrix". The set of plankton food webs for a single ecosystem are approximately 85% similar, that is, they have the same variables and links in common, and in about a thousand loop models constructed to date, no two models have been identical. The 15% non-similarity value remains unexplained; it may be attributed to randomness or current lack of understanding of food webs, but more likely it is adaptive and facilitates ecological and evolutionary flexibility in changing environments.

Locations of the dominant parameter inputs that put particular pathways in motion, as well as the sequencing of changing parameter inputs around the annual cycle, seem arbitrary. At least, there is no theory to explain them at the present time. If we consider the operating pathways to be like threads in the fabric of the whole cloth, they seem to have the elasticity or the resilience of Spandex as the system moves from one set of directed changes to the next, stretching and bouncing back continuously. Volatile links also enhance elasticity. Whether these phenomena are similar to topological deformations is unclear. Whereas variables not on an operating pathway must be in a valid complement, these non-path variables could not stay in these closed complement feedback loops for long since their variables would be blocked from sources of matter and energy. This supports the notion that pathways of effect would be in constant flux in an ecological network. Perhaps this is how Mother Nature carries out her preferred trial and error approach to facilitate persistence.

The plankton food web module can be considered to be analogous to a bounded chaos or anarchy of the whole. Thus, life in a food web chimera is essentially a bundle of transitory networks composing, decomposing, coming into being and then nonbeing, endlessly vibrating, never still, and always dangerously close to the precipice of chaos. Stuart Kauffmann (2000)

described autonomous agents existing at the "edge of chaos" in cells where there is "a phase transition between an ordered regime and a chaotic one". Ulanowicz (1997) expressed a similar idea when he suggested: "living systems are continually making compromises between order and disorder".

Complex systems are not controllable by command-control structures. The modular lattice allows for a dissipated control of fluctuating constraints and a more flexible set of 'guided' bivariate interactions without a central controller or rigidity that could not accommodate extreme environmental perturbations and monopolizing species. This elastic structure also allows for the destabilizing effects of positive feedback found in cooperative systems to be balanced against negative feedbacks among the parts. Slobodkin (1961) once claimed that interspecific competition is the great homeostatic mechanism of the world. It exists in the Narragansett Bay plankton community, and it appears to plays a role in system stability.

Certainly, an external observer viewing only plankton abundances from t_1 to t_2 sees dynamics that appear difficult to understand. Miranda and La Guardia (2017) pointed out that "change is an omnipresent aspect of biological phenomenon, and this aspect is almost a synonym of dynamics…roughly speaking, biological dynamics is cornered between its plasticity and its environmental constraints." The set of abundance changes usually defies explanation in marine plankton communities. Other than a recognizable pattern of some diatom species succession in the spring and its reverse in the fall, plus the appearance and disappearance of a few plankton species at particular times of the year, there is little that can be explained or predicted. This has been true for more than 100 years of investigators failing to explain plankton abundance records. The ecological skeleton itself is dominated by positive feedback indicating a mutualistic, cooperative whole, however, negative feedback is operating at most of the loops of length two and one (self-damping). Thus, it is possible that there is a continual push and pull among the variables (functional groups) that is bounded by the lattice structure, while pathways appear to operate chaotically along the course of least resistance pushing and pulling matter and energy through the network toward the top levels.

In summary, cooperation and constraint endlessly dance the dance of survival repetitively cycling around the core structure or ecological skeleton of the Narragansett Bay plankton community while keeping chaos constrained. The ever-present proximity of chaos should not be under-appreciated. It provides, on a continual basis, a richness of opportunity for evolving systems. Chaos is at least as constructive as it is destructive if associated with bounded conditions such as the modular lattice structure. Thus, the Narragansett Bay food web is a bundle of transitory networks representing operational pathways, coming in and out of focus within the boundary conditions the lattice provides.

(3) Time Management

To survive over endless sequences of ecological time and to persist over evolutionary time, ecosystem chimeras must manage time successfully minute to minute through the eons. It is not enough to have a diverse set of functionalities actively available or an overall structure to bound the various providers of the functions so that chaos is kept within operational limits. Community chimera fitness, based upon survival and persistence, are both directly related to time and its management, and not the more limiting notion of changes in gene frequency

related to the reproductive output of individual species, which has long served as a brake on imagination and progress in evolutionary studies.   Reproduction can often be delayed even to the benefit of the parents, especially mothers, but day-to-day survival cannot.   Rosen also pointed out that the fitness of a biological system at one level of the biological hierarchy (e.g. organism) might have little relation with fitness at a higher level in the hierarchy (e.g. ecosystem) because these two levels constitute different individuals.   Here we discuss time management and perception in biological systems generally and ecological chimeras specifically.

Time is not an easy concept.   Rosen thought deeply about time and called it: "central to any notion of change" and "difficult and complex".   Rosen (2012) began by contrasting two ways that time is perceived: (1) events occur at the same time or simultaneity, or (2) one event follows another so that there is both a past and a future, that is, a succession in time.   He then surveyed all the ways time is used in mathematical formalisms, both continuous and discontinuous.   He wrote a paper on time in ecosystems where he illustrated that dynamic trajectories are not necessarily connected to clock time.[3]   He also wrote about the symmetry and asymmetry of time. For example, conservative mechanical systems exhibit temporal symmetry since time is reversible, whereas in thermodynamics time has an asymmetrical arrow. Humans perceive the asymmetry of time in the sense that we can distinguish a past, a present, and a future.   Albert Einstein, who developed relativity theory in the space-time continuum, believed that time is a direction in space as a system trajectory goes from one state to another in its phase space.   He pointed out that "the distinction between the past, present, and future is only a stubbornly persistent illusion". This trajectory transverses a succession of 'slices of time', and if the system is an individual at whatever level (cell, organism, ecosystem), it demonstrates fitness in its traversing because it must survive from one slice of time to the next.   Poli (2017) also discussed and contrasted other types of ways that time is perceived and used, especially in regard to anticipation.

Time management is a necessary feature of life.   Since life is a process involving a material system, it cannot be separated from time. For a system like an ecological chimera to be operational, critical functions need to follow a particular order.   Clearly, 'everything' cannot occur simultaneously.   Einstein concluded that: "The only reason for time is so that everything doesn't happen at once".   For example, all four-way traffic approaching a stop light cannot all transverse the intersection simultaneously without crashing; some vehicles must stop and wait while others move through.   An organism is not born, and does not mature, reproduce, and die in an instant; complicated time lags are continuously present and intricately embedded in the networks that make up living systems.   Neither does only one thing happen at a given time. Living systems can multi-task; survival requires it.   Biological functions or processes have time in their denominator, that is, in their rate of change.   Thus, biological functions take time and each link in a biological network like a food web also has a temporal aspect.   In addition, life exhibits order, some things must precede or follow other events in an ordered sequence. This is well-documented in the organization of metabolic pathways or in lifecycles of organisms or forest succession.   The origin of life must have been overwhelmed with enormous scheduling problems to ensure that matter and energy were in the right places at the right times.   In

---

[3] "On the Role of Time and Interaction in Ecosystem Modelling" by Robert Rosen. 12 pp. Date is unknown, but is probably after 1977. I only have a preprint of this paper and was unable to find any record of its publication.

addition, the nascent living system was immediately open to its environment, in fact, environment proceeded life, and wherever there is life, there is the environment. It has always been so.

Biological systems, being complex, are anticipatory, which involves making predictive internal models of the future that can influence the present, using feedforward loops. These models inherently work on temporal relationships that may or may not be associated with clock time. Of course, feedforward can be built into a machine and frequently is, but organisms come with feedforward and anticipatory capacities in their 'basic package'; they are not add-ons. Rosen defined an "anticipatory system as a system containing a predictive model of itself and/or its environment, which allows the system to change state at one instance in accord with the model's predictions pertaining to a later instant". He used to say that organisms can read off of the future, and these future predictions can change present behavior. I remember asking him if feedforward and anticipation could occur in systems without a memory since *a priori* a memory encodes many 'pasts' that subsequently passed into 'futures', that then became recorded as 'pasts'. His answer was somewhat ambiguous: "I am not sure, probably not."

Poli (2017) gave an excellent overview of anticipation as ubiquitous in biological, psychological, and social systems – all impredicative ones. He defined anticipatory behavior as "a behavior that uses the future in its actual decision process". Life itself would not be possible without anticipation. Poli (2017) concluded that for living systems, "behavior is primarily anticipatory not reactive". He used the example of a person listening to a weather forecast that predicted rain later in the day. The forecast itself while predictive is not anticipatory behavior, but if the listener then takes an umbrella when leaving the house that is considered anticipatory behavior. Poli (2018, this issue) also provided a detailed categorization of impredicative systems. (See also Appendix 1, Section 9.1 for more definition).

Time management in many biological networks involves both feedback and feedforward loops. Feedback is the effect of a variable on itself by way of intervening variables. It cannot affect the future until it returns to the initial variable. In contrast, feed forward can use a model of the future to influence present behavior in a more immediate way. It does not have to 'wait' for the present to become the future to validate the model, and thus, it is an efficient way to save time. Time is always finite and limiting for a biological system since it must undergo continual cycling of successful survival and reproduction if it is to survive in the short term and then persist indefinitely. The individual, whether a single organism, or population, or ecological chimera, must survive while waiting for things to happen such as a nutrient to become available, or a predator to swim away or for a prey to emerge from hiding. Bad timing has caused a lot of death and extinction. There is even a cliché for this: "being in the wrong place at the wrong time".

Adaptations involving time are numerous throughout the biological hierarchy. To manage time, one needs to perceive it. This is true of all organisms and many biological adaptations have arisen in regard to time perception and regulation. For example, organisms exhibit biorhythms, internal clocks of various kinds, and many are photoperiodic. Light sensitivity has arisen in most groups and daylight is an important way to sense time. The eye, a very complicated structure, has evolved separately in many lineages. Cells exhibit the Hayflick limit,

which is measured as the maximum number of times cells can double over their lifespan before losing their ability to divide. Resting stages, hibernation, luxury consumption, and diapause are ways to ensure surviving through poor times (time avoidance) with minimal resource requirements, for example, in marine ecosystems.

Time perception can also be relative. For example, organisms sometimes perceive time relative to their lifespan and not clock time. Richard Lewontin (1966) asked: Is Nature Probable or Capricious? In the North Temperate Zone, there is an annual periodic temperature cycle of warm summers and cold winters. If there are three species with generation times of 20 minutes (bacteria), six months (insect), and 80 years (human), then both the bacterial species and the human will perceive the world as orderly and probable, that is, the human will understand the regular periodic cycles of temperature because s/he experiences so many of these cycles over her or his lifespan, while the bacterial species will experience little change in temperature relative to its short lifespan. The insect that is born in the spring and dies in the fall, however, will only experience warm weather, whereas its offspring, born in the fall and dying in the spring, will always experience cold weather. This species will perceive the environment as capricious because as the parent lives only in the warm season and develops adaptations to higher temperatures, its offspring will be poorly adapted to the cold, and vice versa as the six-month reproductive periods continue. Thus, organisms with different life histories can perceive the temporal dynamics of even a single stable environmental factor very differently. Time perception can also change over an individual's life span: a summer holiday is an eternity for a six-year-old and only a brief respite for an older person.

At the cellular level, many types of enzymes play a large role in altering and synchronizing temporal relationships especially in metabolic pathways usually in a highly specific fashion. Enzymes catalyze chemical reactions of substrates to products, at much faster rates, even millions of times faster than they would occur in an abiotic world. Several thousand enzyme-substrate reactions are known to be operating in metabolic feedback and feed forward cycles. The enzymes are neither altered nor consumed in the process nor do they alter the reaction by decreasing the energy of activation. They also have a large role in regulating metabolic reactions by selecting which pathways will operate at a particular time. Without enzymes, life would be impossible, because of the discordant time relationships within the cell. Metabolic pathways also have a particular ordering of substrates and enzymes. Rosen has frequently used an enzyme-substrate model to explain feed forward of how a cell or organism could read off of the future, essentially the cell's internal model unfolds faster than real time. Catalysts seem to be only limited by diffusion rates of the chemical species.

Levins (unpubl.ms-year unknown) wrote a paper entitled, Dust to Dust[4], in which he suggested that life arises out of a glacially-slow abiotic world via a carefully constructed set of temporal relationships, mediated by enzymes, and then in death, the organism becomes dust as the glacially-slow interactions return. Enzymes bring life's required reactions into focus by pulling them into synchronicity out of the amorphous dust, with appropriate sequencing, and by keeping them isolated or compartmentalized from the multitude of interactions in the dust. The role of enzymes and metabolic pathways is an example of how network pathways function

---

[4] "Dust to Dust" by Richard Levins. 4 pp. Date is unknown, but probably after 1980. I only have a preprint of this paper and was unable to find any record of its publication.

in time management and have been well-documented at the cellular level. But since we surmise nature has a limited set of ways of solving problems, it is not surprising that the enzymatic function could appear at several levels of the biological hierarchy. For example, Wilkenson (2003) mentioned how life can affect geo-chemical cycles such as weathering of silicate minerals by "altering the rate of this reaction and so can loosely be thought of as a catalyst of the above reaction". Levins went further in suggesting that enzymes also have a qualitative role in achieving simplification out of primordial complexity.

Ecosystem chimeras are also composed of complicated pathways of largely trophic interactions. Matter and energy move through these pathways continually cycling somewhat analogous to cellular metabolic pathways, but also analogous to many other cyclic phenomena. Life cannot stand still, but then nothing in the universe is stationary not even the electron that finds itself alone in a great deal of empty space, cycling around its nucleus. Much of the universe appears to be cycling from the electrons of atoms, which comprise all matter, to metabolic pathways in cells like the citric acid cycle, to neural nets in brains, to various physiological cycles like blood circulation in organisms, to biogeochemical cycles like those of water, carbon and nitrogen in the biosphere, to planetary cycles in the solar system, and finally, to the movement of galaxies. Cycling is ubiquitous and there is always an associated amount of time necessary to transit one cycle. Again, this need not be clock time as Rosen (2012) pointed out.

When ecological chimeras form, they become new individuals with new time management problems. We know from the paleological records, especially of planktonic fossils, that plankton communities can persist over very long periods of time such as thousands of years with a similar list of species. It also seems likely that ensuring temporal certainty, especially with matter and energy flows, cannot be managed by a single individual or population. Likewise, there is no central ecosystem controller, but biological networks can exhibit distributed control and regulation capabilities. Ehresmann and Vanbremeersch (2007) discuss how this could work in their book entitled: Memory Evolutive Systems. To the degree that ecosystem chimeras have 'memory' based upon their individual capacities, and overall network configuration and feedforward loops, the whole network can be an anticipatory system that employs its integrated genotype to use the future to guide the present. Individual components that are directly connected receive and send time information via their interactions. For example, prey species can act as time-givers and predators as time-robbers within their food webs. Those components that are indirectly connected, however, are also sending and receiving temporal information via the environment, which reinforces why the frequently-used dichotomy between direct and indirect species interactions is not very useful (Lane, 2017b).

Each ecological chimera has a certain amount of space and time to exploit especially in keeping matter and energy entering the network and recycling as frequently as possible so as to gain maximum benefit from these resources. As Wilkenson (2003) described above, diversity is selected for and increasing numbers of components become specialized on particular chunks of the space-time continuum. This creates a mosaic of individuals in populations each providing their unique functional capabilities to carry out all of the processes related to self-organization and self-regulation. In the Narragansett Bay plankton community, it appears that the shortest-lived organisms (phytoplankton) require more species per functional group than the longer-

lived organisms (copepods), which in turn have more diversity than the longest lived organisms (invertebrate predators). Essentially, generation times may play a role in biodiversity generation to ensure the integrity of particular functional components is secured in a timely fashion. Because the small organisms turnover so quickly, it is necessary to have more redundancy in species to cover the temporal spans of ecological time and improve time management. This species sequence is inverted for abundances, however, this can be explained based upon ecological efficiencies of energy transfer from one trophic level to another. As chimeran partners trade functions, many of those functions come with process rates with time in the denominator, and all of these time relationships have to be successfully integrated if the ecological chimera is to work as a new individual. Ecological chimeras are essentially time managers and manipulators. G.E. Hutchinson (1961) once posed the "Paradox of the Plankton" in which he asked how can so many similar phytoplankton species coexist in a relatively homogeneous environment. A large number of hypotheses have been suggested to answer his question, but time management in an ecosystem chimera may be a possible answer.

Time that is perceived, manipulated, and managed at the food web level is at also partially related to pre-existing adaptations at the lower levels of the biological hierarchy. Only two plankton examples are given here (life history and vertical migration), however, many more operate, and probably even more are not yet discovered. First, many planktonic species have apparently complicated life histories including chimeric ones. The main zooplankton component, copepods, exhibit 12 life stages. No one, to my knowledge, has been able to explain why 12 are necessary and why not five or 25? A particular plankton community contains approximately 15-25 copepod species, so that totals 180-300 discrete life stages, each with many individualized phenotypic behaviors and feeding preferences. Each life stage has a particular duration associated with it, and many have a known seasonality. For example, given a copepod egg hatches into a first stage nauplius and then passes through 10 more stages, it is predictable when it will become an adult and produce its first egg, subject to some environmental factors like temperature. Perhaps, the complicated sequencing of these life stages enables copepods to exploit their space-time environment more completely and systematically by essentially marking time around the annual cycle to gain temporal security while achieving a beneficial balance between maximizing resources needed by each life stage, and minimizing predation.

At any one time, the food web configuration has various pathways of sequential resources/prey and their predators undergoing consumption somewhat analogous to a pathway of substrates undergoing chemical transformation. Just like metabolic pathways come in and out of focus, so do food web pathways. Both can be quite transitory from one time to the next, but the timing is very important in both situations. Life cannot operate with monopolies of cellular substrates or food web components. To maintain the appropriate balance or modular integrity, all components in a given biological network require correct sequencing especially in relation to their nearest neighbors. Proper sequencing also requires anticipation.

Although there are no directly analogous components like enzymes at the food web level, some of the functionality of enzymes could be possible. First, the presence or absence of particular components, regardless of being a life stage or a population, often directs matter and energy flow through food web links in various directions like regulatory enzymes do in

metabolic pathways. Second, each pathway in a food web has a unique temporal duration or time span. By making some pathways more probable than others, this will make the overall food web dynamics faster or slower similar to how enzymes change rates of chemical interactions. Third, while it is agreed that enzymes lower the activation energy of the chemical interactions that they catalyze, without the enzymes being chemically altered themselves and leaving the chemical equilibrium unchanged, the exact way enzymes do this is not known. One concept has the enzyme stretching the configuration of the substrate and possibly of itself during catalysis. The immature zooplankton variable, $Z2$, shown in Figure 1, enters into numerous link types with the adult copepods ($Z1$ and $Z3$), which appears analogous to stretching and transforming the right hand side of the food web into many alternative configurations.

Second, many marine species, representing a large number of phyla, undergo diel vertical migrations, with species generally exhibiting an upward position in the water column in the middle of the night, and a lower position during daylight. These small animals can travel tens of meters up and down the water column in a 24-hour period. Most of the upward and downward movement occurs at dusk and dawn respectively at the times when light intensity is changing the most. Species have their own distinct migration patterns, which can change seasonally and are somewhat phase-shifted among the community members. Usually no two species have identical patterns or identical mean night and day depths. Some of the larger invertebrate predators also vertically migrate and follow their prey, whereas others appear to remain at a preferred depth with a sit and wait approach.

Light is believed to be the main proximal cue/cause for vertical migration behavior and this is well-documented in physiological and ecological studies. Light is one of the more reliable indicators of vertical depth in water since sunlight is always more intense above than below a given depth, and the animals can detect differences in light intensity. In addition, because water attenuates different wavelengths of light with depth, the ocean acts as a selective filter creating many different photic environments on the vertical axis. Animals often have separate eye pigments for different wavelengths of light and proportions of these pigments can be easily manipulated in the laboratory indicating adaptive plasticity. Light is also intimately tied to the photosynthesis that produces food for herbivores, and the algae also affects light attenuation at depth, not only where the maximum amount of primary production is occurring, but often in lower density layers where phytoplankton, bacteria, and detritus accumulate. Overall, vertical migration behavior can be considered highly plastic as is zooplankton community structure.

Whereas the proximal cause of vertical migration is well understood as well are many of the associated physiological adaptations, the ultimate cause or adaptive significance of vertical migration is not. Three major hypotheses include: (1) a habitat selection mechanism to avoid interspecific food competition by using a range of space-time micro-habitats, (2) predator avoidance in the well-lit upper waters in the daytime, and (3) the refrigerator hypothesis that proposes animals inhabiting the lower colder waters would achieve a metabolic advantage by conserving energy due to the Q10 effect. Of course, none of these hypotheses are mutually-exclusive and all could be operating simultaneously, with each providing some selective advantage. Vertical migration also has an energetic cost. For a 1-2 mm animal to swim a 20-100 meters round trip, calories must be expended.

It has been demonstrated in lakes that are subject to nutrient enrichment that vertical migration patterns that were once pronounced with the large amplitudes when the lake was oligotrophic become diffuse and almost unrecognizable as the lake became eutrophic (Lane, unpubl.) In addition, as these ecosystems undergo eutrophication, the zooplankton community changes from a predominance of larger zooplankton with longer survival times and slower turnover rates to higher relative abundance values for smaller zooplankton with shorter survivor times and faster turnover rates. It appears there are two alternative steady states for the zooplankton community, even though the species list is the same. These results have been more difficult to document in more nutrient-poor marine ecosystems that rarely undergo eutrophication.

Given the occurrence of vertical migration across so many taxa, the energy costs of the behavior, and the extensive morphological, physiological, and behavioral adaptations involved, it is one of the most striking behaviors of marine animals for promoting survival and persistence. In addition, because this diurnal behavior is so plastic, whatever its benefit, the community is able to quickly modify vertical migration patterns as necessary. The animals are not migrating robotically. If the freshwater results are applicable to marine ecosystems, it appears that vertical migration is most closely aligned with phytoplankton primary productivity patterns. This could be important to time management in the ecological chimera. In oligotrophic environments, which involves most of the open ocean, zooplankton will have more food available if they consume it in the night by avoiding the peak daytime photosynthetic periods leaving algae to make as much photosynthate as possible. There could be an added benefit of consuming settling detritus as the animals migrate to and from their day depth, essentially returning organic matter to the upper waters by releasing wastes for recycling that would also increase algal photosynthetic rates. This appears to be form of time management. Thus, vertical migration could be a complicated timing mechanism to ensure food security by promoting nutrient recycling and maximizing photosynthesis. Modular integrity would also be enhanced having two alternative community structures (day and night) with better exploitation of their three-dimensional habitat. Finally, time management would be fine-tuned by having different pathways operating night and day at different rates.   The Q10 factor would change several key metabolic processes between the upper warm and lower cold water community networks that would also affect temporal relationships. Essentially, zooplankton are spending their nights on a faster clock and their days on a slower one.

In summary, for life to persist, the supply of matter and energy must be reliable. This necessitates both a suitable combination of required functionalities working cooperatively at the ecosystem level supported by both a responsive community structure (modularity, link organization, subsystems structures, etc.) and effective time management of simultaneous and sequential activities (operating versus non-operating pathways).   Life history dynamics at the population/food web level and vertical migration in marine plankton may also supplement time management for planktonic ecological chimeras.

6.0 Discussion and Conclusions

There are three conclusions:

(1) Ecosystems are Rosennean Complex (RC) chimeras.

(2) RC chimeran construction theory needs development at the ecosystem level.

(3) Standard Evolutionary Theory (SET) should be replaced by a Complexity Synthesis based upon RC.

Each conclusion is discussed below in terms of its ramifications for ecological and evolutionary theory. These are my own conclusions based upon combining Rosen's notion of an ecosystem chimera with results from loop analysis, and in no way is meant to infer that these points would have been advocated by Rosen. In his lifetime, he was reluctant to discuss ecology and evolution, and no one can know his opinions with certainty 20 years after his death.

(1) Ecosystems are Rosennean Complex (RC) chimeras.

Environment predates life, predates genes, and has always been present since the earth's earliest formation. It was there when life first twitched into being. All life consists of open material systems whereby each system occupies a non-admissible environment, and *a priori* all life evolves in ecosystems, it could not be otherwise. As open systems, ecosystems constantly communicate with their environments and their behaviors (phenotypes) are modified by those environments. Rosen (2000) pointed out "what a shambles that the concept of the 'open system' has made of classical thermodynamics (where after 50 years or more there is still no real physics capable of properly coping with even the most elementary open systems dynamics) is nothing compared to the impact of complexity; and thermodynamics has long been regarded with complacency as the repository of the most universal truths of physics." Life maintains a non-equilibrium thermodynamic state and is Rosennean complex. Rosen liked to quote Einstein as saying, "one can best appreciate, from the study of living things, how primitive physics still is".

All life (cell, organism, population, and ecosystem) functions in an ecological network including itself and its biotic-abiotic environment. Each element of these networks is a functional entity that is involved in multiple causal pathways and relationships with its other network components and their shared environment. All life is also cooperative and chimeric, often at multiple levels and in multiple ways. Ecosystems are chimeran individuals whose components cooperate functionally with each other to gain matter and energy, maintain system integrity, and manage time in uniquely biological ways–all necessary to achieve the final cause or purpose: ecological survival and evolutionary persistence. Understanding RC provides new insights into all complex systems. The science of simple systems cannot fully inform life or ecology, except in limited instances, when something living contains a simple system or mechanism, or when we are studying a single aspect in a limited context. Every time we focus on a level lower than the ecosystem, we must recognize that while simpler systems are convenient for analysis, relationships and linkages are broken by that reduction and cannot be restored by synthesis. This can result in incomplete and even counterintuitive results.

Once we decide that ecosystems are RC, and function as chimeran individuals, we can better understand them as whole systems, and this has substantial ramifications for current ecological and evolutionary theory. Rosen left his life's work as a worthwhile base to build upon, but more will be needed to be done both in ecology and mathematics. Ecologists could

greatly benefit from studying Rosen's work as could mathematicians who perhaps would be inspired to continue to develop Category Theory and other mathematical areas that could potentially yield better models and insights into RC. Thus, the first task is to recognize the inadequacies of our toolkits and conceptualizations and to explore RC at the ecological level. Rosen (1985) once said, "like the early man, who could see the rotation of the earth every evening just by watching the sky, but could not understand what he was seeing, we have been unable to understand what every organism is telling us." And I would add, what every ecosystem is telling us as a RC chimeran individual. Chimerization plays a large role on every level of the biological hierarchy throughout all of nature, but it is perhaps most important and least appreciated at the ecological level.

(2) RC chimeran construction theory needs development at the ecosystem level.

The area closest to Rosen's concept of an ecosystem chimera in current ecological theory is that of niche construction (NC). The term was coined by Odling-Smee (1988); it is an old idea dating back to Darwin and possibly earlier (Odling-Smee, et al. 1996; Turner, 2016). Erwin Schrödinger (1944), an important influence on Rosen, also suggested a notion similar to NC in his "What Is Life?" book (Gumbrecht, et al., 2011). NC is a fertile research area with currently over 1.4 million Internet references. In 2003, John Odling-Smee, Kevin Laland, and Marcus Feldman published a landmark volume entitled, "Niche Construction – the Neglected Process in Evolution". The authors defined NC as: "the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches. NC may result in changes in one or more natural selection processes in the external environment of populations. Niche-constructing organisms may alter the natural selection pressures of their own population, of other populations, or of both". NC is sometimes termed 'triple-inheritance theory' (Semiotics Encyclopedia Online[5]). This refers to Lewontin's paper (1983) and book (2000), entitled, "The Triple Helix: Gene, Organism, And Environment".

Odling-Smee, et al (2003) provided detailed empirical evidence for NC and also a thermodynamic argument using Maxwell's demon since life is so far from equilibrium. They concluded: "only when the two selected processes of natural selection and NC are combined do they provide organisms with all the Maxwell's-demon-type properties needed to support life (Schrödinger, 1944). NC is an ontogenetic process that allows individual organisms the opportunity to gain sufficient energy and material resources from their environment to survive and reproduce. It therefore both contributes to the building of the next generation of a population of organisms in the conventional manner and causes changes in the niche-construction organisms' own selective environments, as well as in the environments of others." They also quote Schrödinger (1944) as saying: "an organism must…feed upon negative entropy…continually sucking orderliness from its environment". "In this sense, organisms can stay alive only at their environment's expense" (Odling-Smee, et al., 2003).

Like all other areas in ecology and evolution, there has been a range of approaches to NC (Matthews, et al., 2014; Odling-Smee et al., 2013). Scott-Phillips et al. (2014) has provided a systematic review of the NC concept. Some have focused on 'ecological engineering' and how animals make physical alterations to their environments, like beavers building a dam, or ants

---

[5] https://semioticon.com/seo/n/niche.html, accessed January 17, 2018.

constructing a nest. Many NC investigators, however, believe ecological engineering is something separate from NC since it consists of relatively simple habitat modifications (Laland, Matthews, and Feldman, 2016). These latter authors also believe that NC is separate from the extended phenotype concept of Richard Dawkins (Laland, Matthews, and Feldman, 2016).

NC theory presently suffers from conceptual baggage that is not easy to dissociate because of the term 'niche', which is a population-level concept based upon an original physiological foundation, and not an ecological-functional one. In 1935, Gause, a Russian microbiologist, declared that "no two species can occupy the same niche", which focussed ecologists' attention on the population level. Subsequent developments in niche theory have stressed niche space, niche overlap, niche breath, and limiting similarity largely based upon competition. The niche concept works well for populations; it provides some very worthwhile examples of how species interact and adapt, but it is much less useful at the ecosystem level.

Many ecologists struggle to use population level niche concepts to describe ecosystem phenomenon and many of their arguments are convoluted, difficult to follow, and illogical. By starting at the population level, so many ecosystem level relationships have already been severed and the analysis versus synthesis problem in complex systems resurfaces (See Rosen, 1991, 2000; Appendix 1, Section 9.2). Much in NC does not translate well into the ecosystem level. There is a loss in ecosystem-level understanding when talking about two-species competition and predation, physiological tolerance curves, environmental factors, and niche space. Although many NC authors have given admirable, even valiant effort, to extrapolating the niche to the ecosystem, the truth is one cannot get to ecosystem chimeras from a lower-level except as a set of collective, not emergent properties. The organism, population, and ecosystem levels represent different individuals, with different ecological and evolutionary strategies.

In contrast to NC, with ecosystem chimeras the focus is upon function, purpose, cooperation, time management, survival, and persistence. For ecosystems, NC restrains imagination and gets in the way of understanding ecosystem phenomenon. I suggest that ecologists use the 'NC' concepts when working at the population level with one to a few species, and the 'ecosystem chimera construction' (ECC) concept with RC when working at the ecosystem level. NC itself also needs to be reviewed in terms of RC. Most of niche theory was developed under the shadow of the Newtonian Paradigm and does not provide the systematic and creative synthesis that Rosen provided based upon his notions of complex systems and chimeras. The Rosen view of the chimeran individual with its own genotype (identity), phenotype (behaviors), and environment, and its relationship to NC seems to be lacking in the related literature, which reinforces the purpose for this Special Issue.[6] In Rosen's concept, chimerization occurs as components interact with each other through modifications of non-admissible environments. Thus, by modifying the environment one component can change the phenotype of another since phenotype *a priori* is the interaction of the genotype with the environment. This process of chimerization works to create new cooperating individuals including functional ensembles of species as well as whole ecosystems.

---

[6] I could only find one web presentation (J. Kineman, 2004) that combines NC and Rosen's ideas, but without mentioning ecosystem chimeras and an undated manuscript at:
https://debategraph.org/Handler.ashx?path=ROOT/u15236/The+Atomic+Structure+of+Relationship.pdf
(Accessed February 2018). It discusses niche theory and Rosen's ideas, but not NC or chimeras.

(3) Standard Evolutionary Theory should be replaced by 'The Complexity Synthesis' based upon RC.

In 1942, Julian Huxley published his classic book entitled, "Evolution: The Modern Synthesis" that cemented the integration of Darwinian ideas and Mendelian genetics that had begun consolidating about 100 years ago at the close of World War I. Pigliucci and Müller (2010) summarized "Evolution: The Extended Synthesis" as an expansion of the Modern Synthesis, which started around 1970, and it will soon celebrate its 50th anniversary. Together, The Modern Synthesis and The Extended Synthesis constitute the Standard Evolutionary Theory or SET we use today. The latter authors provide a history and overview of SET based upon the idea that evolution is central to life itself – a view not held by Rosen (2000), although life is central to evolution. More recently, SET has become difficult to support with so many exposed omissions, unnecessary constraints, and strong criticisms coming from many different areas of current research such as developmental biology-EVO-DEVO, epigenetics and transgenerational epigenetic inheritance, phenotypic plasticity, molecular biology, microbiology, genomics and genetic networks, systems biology, bio-informatics, symbiogenesis, multi-level selection, ecosystem-level ecology and NC, etc., (Danchin, et al., 2011; Koonin, 2009a, b; Laland, et al., 2015; Laubichler and Renn, 2015 as well as others mentioned below).

SET appears to be exhibiting those telltale cracks and fissures that precede a paradigm shift (Kuhn, 1970; Lane 2018c, this issue). Darwin considered both reproduction and survival as important, but with the advent of Mendelian genetics and the many exciting genetic discoveries that followed throughout the 20th century to the present, survival has become a neglected topic and SET has always had a focus on the genetic aspects of evolution. O'Malley (2015) questioned how gene frequencies could explain many of the phenomena associated with endosymbiosis. As Margulis (2011) concluded, it has become much clearer that most of the innovation and major transitions in evolution could not have occurred only through mutations, genetic drift, migration, non-random mating, leading to changes in gene frequencies, etc. Genes have also become much less reliable than previously thought, not only in terms of lineages, but also as surrogates for fitness. Genetic networks are also complex and can yield counterintuitive results.

Many authors and academic societies are beginning to call for a major update to SET. The journal Nature published a debate entitled, Does Evolutionary Theory Need a Rethink? between Laland et.al (2014) and Wray et al. (2014). In 2016, a joint discussion meeting between the Royal Society and the British Academy entitled, New Trends In Evolutionary Biology: Biological, Philosophy Philosophical, and Social Science Perspectives discussed a potential update to SET (See Special Issue: Interface Focus 7(5): October 2017.) There are two main options: (1) to continue to update SET: The Modern Synthesis/The Extended Synthesis by making modifications to what exists, and (2) to undertake a more major paradigm shift (Rose and Oakley, 2007).

In support of Option 1, Pigliucci and Müller (2010, 2011) make the conservative case that The Modern Synthesis only needs to be extended to encompass the recent concerns and new developments in evolution, that is, they support Option 1. They conclude that there are only three problematic restrictions: gradualism, externalism, and gene centrism, but those they can be addressed within the existing paradigm. Thus, in their opinion, there is no reason to

consider these changes as little more than an expansion of what already exists, and the phrase, 'Extended Synthesis', already captures their viewpoint. There is not even a need to change the name. These authors also seem to be fairly wedded to the machine metaphor and the Newtonian Paradigm. They use phrases such as: "causal mechanistic theory of evolution" and "theory of mechanistic conditions for the origin and innovation of traits" and discourage as much as possible any thought of Option 2. In contrast, Henning and Scarfe (2013) and Kauffman (2013) provide a rigorous rationale for abandoning the machine metaphor as does Rosen (1991, 2000). It seems unlikely that the machine metaphor/Newtonian Paradigm can persist much longer as the conceptual scaffolding for living systems and their evolution.

Others call for Option 2. Huneman and Walsh (2017) recently edited a compilation of papers entitled, Challenging The Modern Synthesis – Adaptation, Development, and Inheritance", which also contained discussions on NC. The Editors ask an interesting question in the Introduction: "if adaptation is not the gradual accumulation of minutely favorable random mutations, what is it?" Perhaps Rosen's chimeran ecosystems could provide a satisfactory answer. In 2013, Frédéric Bouchard and Philippe Huneman provided a volume of papers entitled, "From Groups to Individuals, Evolution and Emerging Individuality" that also challenges SET. It contains multiple, but broad definitions of what an individual is. In Chapter 2, Goodnight (2013) discussed the example of an individual who is really a complex community of symbionts, which here is equated to a chimera. He concluded that the individual is the lowest level of possible selection response, but individuals can be multi-specific. In this paper ecosystems are also considered as multi-specific individuals, which can both modify and be modified by their environments. Thus, individuals are complex systems on all levels of the biological hierarchy. In the last paper, Bouchard (2013) concluded, "most current definitions of individuals are too restrictive… single-species collectives… as we have abandoned physical continuity, we may also have to abandon species homogeneity…one must understand fitness in a way that does not demand differential reproduction". Ecosystem chimeras also do this with a focus on survival.

While Option 1 would be the easiest approach in the short term, Option 2 is both necessary and preferable. SET requires replacement. Our view of what life itself is has changed fundamentally in the last hundred years, and there are now too many outdated assumptions like heavy extinct dodos hanging from the neck of the Modern Synthesis even in its extended form. To be clear, paradigm replacement is required not because evolution is an illusion, or a conceptual failure, but rather because it encompasses a much richer reality than the old theory permits, perhaps even richer than we can presently imagine. The Biological Complexity Revolution (BCR) is upon us (Lane, 2018c, this issue*),* and it will provide a new conceptual base and way of thinking. It is inevitable that the BCR will have profound effects on evolutionary theory – either sooner or later, but sooner would be better.

Once notions of RC, impredicativity, anticipation, emergence, self-organization, function, survival-persistence, closed to efficient cause (CLEF), purpose-final cause, etc. have become fully established in the collective scientific brain, it seems impossible to view evolution as a factory called Nature Inc. that manufactures biotic machines like so many robots receiving one rivet (mutation) at a time on an assembly line. As Rosen said, "life is not an algorithm" (Rosen, 2012) and we will not be able to comprehend its essence by using algorithms. Evolutionary theory requires a complete reconceptualization in terms of RC. A better understanding of what

biological complexity is and what it means to be alive will undoubtedly produce a better understanding of evolution.

Thus, I am only one more voice adding to an already loud chorus suggesting paradigm shift in evolution (Kuhn, 1970), but for somewhat different reasons. Chimeras are ubiquitous. They are ancient and modern, primordial and contemporary. The ecosystem/food web chimera subsumes the many lower-level chimeras at the cellular, organism, and population levels, but it is this ecological chimera, that provides some significant evolutionary opportunities. Throughout evolutionary history, each chimera is refashioned and repurposed out of old parts and old identities – a kind of shabby chic for ecosystems. Since time immemorial, organisms at every level of the biological hierarchy have scavenged, appropriated, manipulated, and even stolen whatever they can to enhance their functionality and survival. Chimera formation involves a major source of innovation in evolution and perhaps much more (Margulis, et al., 2011). Any meaningful evolutionary theory needs to include ecosystem chimera construction (ECC) with a Rosennean flavor.

In summary, Rosen possessed a remarkable evolutionary insight that many lifelong evolutionists might envy, especially considering he was someone who was not very interested in evolution and ontology, and who vociferously resisted the attempts of his peers to recast biology as evolution, which he considered to be an equivocation. Although the evolutionary ramifications of ecosystem chimeras are extensive and even exciting, it is not possible to explore them systematically here. It appears, however, evolutionary biologists may have missed some critical ecological-level phenomenon in their emphasis on the role of gene frequency as a surrogate for fitness at the organism level. All organisms evolve in ecosystems. If all of these environments are non-admissible and can alter identity and hence genome, opportunities for evolutionary problem-solving are limitless as well as adaptation being faster and more efficient than previously realized. Furthermore, the ramifications of life as a cooperative rather than a competitive undertaking are poorly appreciated. As part of the Biological Complexity Revolution (BCR) (submitted Lane, 2018c, this issue), we should consider creating a more realistic and chimeran theory of evolution for complex systems. Although my reasons are not identical to others calling for Option 2, evolutionary theory requires a wholescale paradigm shift. It could be called "Evolution: The Complexity Synthesis".

7.0 Acknowledgements

8.0 Bibliography

Aanen, D. K., Eggleton, P. (2017). Symbiogenesis: beyond the endosymbiosis theory? *Journal of Theoretical Biology, 434:99-103*. http://dx.doi.org/10.1016/j.jtbi.2017.08.001

Allen, C., Bekoff, M., Lauder, G. (Eds.). (1998). *Nature's Purposes: Analysis of Function and Design in Biology*. Cambridge, MA: The MIT Press.

Aristotle on Causality. (11 March 2015). In *Stanford Encyclopedia of Philosophy*. https://plato.stanford.edu/entries/aristotle-causality/   Accessed January 14, 2018.

Bahar, S. (2018). *The Essential Tension: Competition, Cooperation and Multilevel Selection in Evolution*. Dordrecht, Netherlands: Springer.

Barlowe, C. (1992). *From Gaia to Selfish Genes: Selected Writings in the Life of Sciences*. Cambridge, MA: MIT Press.

Biller, S. J., Berube, P. M., Lindell, D., Chisholm, S. W. (2015). Prochlorococcus: The structure and function of collective diversity. *Nature Reviews Microbiology 13:13-27*.

Boklage, C. E. (2010). *How New Humans are Made*. Toh Tuck Link, Singapore: World Scientific Publishing Co.

Bouchard, F. (2008). Casual processes, fitness, and the differential persistence of lineages. *Philosophy of Science 75(5):240-246*.

Bouchard, F. (2013). What is a symbiotic superindividual and how so you measure its fitness? Pp. 243-264. In Huneman, P., Bouchard, F. (Eds.), *From Groups to Individuals. Evolution and Emerging Individuality*. Cambridge, MA: MIT Press.

Bouchard, F., Huneman, P. (Eds.). (2013). *From Groups to Individuals: Evolution and Emerging Individuality*. Cambridge, MA: The MIT Press.

Brinkhurst, R. O. (1970). Distribution and abundance of tubificid (Oligochaeta) species in Toronto Harbour, Lake Ontario. *J. Fishery Research Board Canada 27:1961-1969.*

Brinkhurst, R. O., Chua, K.E., Kaushik, N.K. (1972). Interspecific interactions and selective feeding by tubificid oligochaetes. *Limnology and Oceanography 17:122-133.*

Brooks, W. R. (1989). Hermit crabs alter sea anemone placement patterns for shell balance and reduced predation. *Journal of Experimental Marine Biology and Ecology 132(2):109-121*. https://doi.org/10.1016/00220981(89)90218-9

Buzzoni, M. (2015). Causality, Teleology, and Thought Experiments in Biology. *Journal for General Philosophy of Sci. 46(2):279-299*. https://doi.org/10.1007/s10838-015-9293-9

Callebaut, W., Rasskin-Gutman, D. (Eds.). (2005). *Modularity: Understanding the Development and Evolution of Natural Complex Systems*. Cambridge, MA: The MIT Press.

Casti, J.L., Karlqvist, A. (1995). Cooperation and Conflict in General Evolutionary Processes. New York, NY: John Wiley and Sons, Inc.

Cottam, R., W. Ranson and R. Vounckx. (2018, this issue). Scaled Ecosystemic Rosennean Complexity. *Ecological Complexity.*

Cummings, R. (1998). Functional Analysis. Pp. 169-196 In Allen, C., Bekoff, M., Lauder, G. (Eds.), *Nature's Purposes: Analysis of Function and Design in Biology.* Cambridge, MA: The MIT Press.

Danchin, E., Charmanteir, A., Champagne, F. A., Mesoudi, A., Pujol, B., Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution [Abstract]. *Nature Reviews Genetics 12(7):475-486*. doi: 10.1038/nrg3028

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection*. London, UK: John Murray.

Decelle, J. (2013). New perspectives on the functioning and evolution of photosymbiosis in plankton. *Communicative and Integrative Biology 6(4)*. http://doi.org/10.4161/cib.24560

Downing, K., Zvirinsky, P. (1999). The simulated evolution of biochemical guilds: reconciling Gaia theory and natural selection. *Artificial Life 5:291-318.*

Eigen, M. (2013). *From Strange Simplicity to Complex Familiarity: A Treatise on Matter, Information, Life and Thought*. Oxford, UK: Oxford University Press.

Ehresmann, A.C., Vanbremeersch, J.P. (2007). *Memory Evolutive Systems, Hierarchy, Emergence, Cognition.* Oxford, UK: Elsevier.

Falkowski, P. G., Katz, M. E., Knoll, A. H., Quigg, A., Raven, J. A., Schofield, O., Taylor, J. R. (2004). The Evolution of Modern Eukaryotic Phytoplankton. *Science 305(5682):354-360*. doi: 10.1126/science.1095964

Fet, V. (2011). Symbiogenesis in Russia. Pp. 153-158. In Margulis, L., Asikainen, C. A., Krumbein, W. E. (Eds.), *Chimeras and Consciousness: Evolution of the Sensory Self*. Cambridge, MA: The MIT Press.

Furla, P., Allemand, D., Shick, J. M., Ferrier-Pages, C., Richier, S., Plantivaux, A., …,Tambutte, S. (2005). The symbiotic anthozoan: a physiological chimera between alga and animal. *Integrative and Comparative Biology 45(4):595-604.*http://www.jstor.org/stable/4485835 Accessed January 26, 2018.

Garay-Narvaez, L., Flores, J. D., Arim, M., Ramos-Jiliberto, R. (2014). Food web modularity and biodiversity promote species persistence in polluted environments. *Oikos 123(5):583-588*. doi: 10.1111/j.1600-0706.2013.00764.x

Goodnight, C. J. (2013). Defining the Individual. Pp. 37-53. In Bouchard, F., Huneman, P. (Eds.), *From Groups to Individuals: Evolution and Emerging Individuality*. Cambridge, MA: The MIT Press.

Gumbrecht, H. U., Harrison, R. P., Hendrickson, M. B., Laughlin, R. B. (2011). *What is Life? The intellectual pertinence of Erwin Schrodinger*. Stanford, CA: Stanford University Press.

Hall, J. I., Margulis, L. (2011). From movement to sensation. Pp. 159-166 in Margulis, L., Asikainen, C. A., Krumbein, W. E. (Eds.). (2011). *Chimeras and Consciousness: Evolution of the Sensory Self*. Cambridge, MA: The MIT Press.

Henning, B., Scarfe, A. C. (Eds.). (2013). *Beyond Mechanism: Putting Life Back Into Biology*. Plymouth, UK: Lexington Books.

Herre, E. A., Knowlton, N., Mueller, U. G., Rehner, S. A. (1999). The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecology and Evolution 14:49-53.*

Huneman, P., Walsh, D. M. (Eds.). (2017). *Challenging the Modern Synthesis: Adaptation Development, and Inheritance*. Oxford, UK: Oxford University Press.

Hutchinson, G. E. (1961). The paradox of the plankton. *The American Naturalist 95(882):137-145.*

Huxley, J. 1942. *Evolution: The Modern Synthesis*. Allen and Unwin. London.

Jacobs, D. (2016). *Evolution's Chimera: Bats and the Marvel of Evolutionary Adaptation*. Cape Town, South Africa: University of Cape Town Press.

Jacobs, J. (2001). *The Nature of Economies*. Toronto, ON: Vintage Canada.

Karlqvist, A., Casti, J. L. (Eds.). (1995). *Cooperation and Conflict In General Evolutionary Processes*. New York, NY: Wiley.

Kauffman, S. (2000). *Investigations*. Oxford, UK: Oxford University Press.

Kauffman (2013). Foreword: evolution beyond Newton, Darwin, and entailing law. Pp. 1-24. In Henning, B., Scarfe, A. C. (Eds.). *Beyond Mechanism: Putting Life Back Into Biology*. Plymouth, UK: Lexington Books.

Keeling, P. J., McCutcheon, J. P. (2017). Endosymbiosis: The feeling is not mutual. *Journal of Theoretical Biology 434:75-79*. http://dx.doi.org/10.1016/j.jtbi.2017.06.008

Kikvidze, Z., Callaway, R. M. (2009). Ecological facilitation may drive major evolutionary transitions. *BioScience 59 (5):399-404*. https://doi.org/101525/bio.2009.59.5.7

Kim, H. J., Kim, H., Kim, J.J. …2018. Fragile skin micro-biomes in megacities are assembled by a predominantly niche-based process. *Science Advances* 4(3):e1701581.

Koonin, E. V. (2009a). The origin at 150: is a new evolutionary synthesis in sight? *Trends Genetics 25(11):473-475*. doi: 10.1016/j.tig.2009.09.007

Koonin, E. V. (2009b). Towards a postmodern synthesis of evolutionary biology. *Cell Cycle 8(6):799-800*. doi: 10.4161/cc.8.6.8187

Krishnamurthy, A., Moore, J.K., Mahowald, N., Luo, C., Zender, C.S. 2010. Impacts of atmospheric nutrient inputs on marine biogeochemistry. *Journal of Geophysical Research:* doi 10.1029/2009JG001115.

Kuhn, T.S. (1970). *Structure of Scientific Revolutions*. Chicago, IL: University of Chicago Press.

Laland, K., Uller, T., Feldman, M., Sterelny, K., Muller, G. B., Moczek, A., …, Odling-Smee, J. (2014). Does evolutionary theory need a rethink? Yes, urgently. *Nature 514:161-164*.

Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Muller, G. B., Moczek, A., …, Odling-Smee, J. (2015). The extended evolutionary synthesis: its structure, assumptions, and predictions. *Proceedings of the Royal Society B 282(1813)*. doi: 10.1098/rspb.2015.1019

Laland, K., Matthews, B., Feldman, M. W. (2016). An introduction to niche construction theory. *Evolutionary Ecology 30:191-202*. doi: 10.1007/s10682-016-9821-z

Lane, P. A. (1986a). Symmetry, change, perturbation and observing mode in natural communities. *Ecology 67:223-239*.

Lane, P. A. (1986b). Preparing marine plankton data sets for loop analysis. *Ecology 67: Supplementary Publication Source Document No. 8525A*

Lane, P. A. (2016). A Cautionary Tale: The Goldilocks' Effect in Measuring Ecological Complication in Food Webs. *Food Webs 8:1-11.*

Lane, P. A. (2017a). A review of the trophic cascade concept using the lens of loop analysis: "The truth is the whole". *Food Webs, 13, 1-11.* https://doi.org/10.1016/j.fooweb.2017.10.002

Lane, P. A. (2017b). Assumptions about trophic cascades: the inevitable collision between reductionist simplicity and ecological complexity. *Food Webs 13:12-26.* https://doi.org/10.1016/j.fooweb.2017.10.001

Lane, P. A. (2018a, this issue). The Road Before Us: Have We Come to a "Fork In The Road" in Defining Complexity? *Ecological Complexity*.

Lane, P. A. (2018c, this issue). The Road Ahead for Rosennean Complexity. *Ecological Complexity*.

Laubichler, M., Renn, J. (2015). *Extended Evolution.* Berlin: Max Planck Institute for Wissenschafftsgeschichte.

Levins, R. (1973). The qualitative analysis of partially specified systems. *Annals New York Academy Science 231:123-138*.

Levins, R. (1975). Evolution in communities near equilibrium. Pp. 16-50. In: Cody, M. L., Diamond, J. M. (Eds.). (1975). *Ecology and Evolution of Communities.* Cambridge, MA: Belknap Press of Harvard University Press.

Lewontin, R. C. (1966). Is Nature Probable or Capricious? *BioScience, Logic in Biological Investigation 16(1):25-27*. http://links.jstor.org/sici=0006-3568%28196601%2916%3A1%3C25%3AINPOC%3E2.0.CO%3B2-8

Lewontin, R. C. (1983). Gene, Organism and Environment. Pp. 273-285. In Bendall, D. S. (Ed.), *In Evolution from Molecules to Men.* Cambridge, UK: Cambridge University Press.

Lewontin, R. C. (2000). *The Triple Helix: Gene, Organism and Environment*. Cambridge, MA: Harvard University Press.

Louie, A. H. (2009). *More Than Life Itself: A Synthetic Continuation in Relational Biology*. Poli, R. (Ed.). Piscataway, NJ: Transaction Books.

Louie, A. H. (2013). *The Reflection of Life: Functional Entailment and Imminence in Relational Biology*. New York, NY: Springer.

Louie, A. H. (2017). *Intangible Life: Functorial Connections in Relational Biology*. Switzerland: Springer.

Margulis, L., Sagan, D., Thomas, L. (1997). *Microcosmos: Four Billion Years of Microbial Evolution*. Oakland, CA: University of California Press.

Margulis, L., Asikainen, C. A., Krumbein, W. E. (Eds.). (2011). *Chimeras and Consciousness: Evolution of the Sensory Self*. Cambridge, MA: The MIT Press.

Marinakis, Y. D. (2008). Ecosystem as a topos of complexification. *Ecological Complexity 5:303-312*.

Marinakis, Y. D., Harms, R., Milne, B. T., Walsh, S. T. (2018, this issue). Cyborged ecosystems: Scenario planning and participatory technology assessment of a potentially Rosennean-complex technology. *Ecological Complexity*.

Matthews, B., Meester, L. D., Jones, O. G., Ibelings, B. W., Bouma, T. J., Nuutinen, V., …, Odling-Smee, J. (2014). Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs 84(2):245-263*. doi: 10.1890/13-0953.1

May, R. M. (1972). Will a Large Complex System be Stable? *Nature 238:413-414*. doi: 10.1038/238413a0

Miranda, P. J., La Guardia, G. G. (2017). On a relational theory of biological systems: a natural model for complex biological behavior. https://arxiv.org/paf/1705.10394 Accessed January 15, 2008.

Mittelbach, G. G. (2012). *Community Ecology*. Sunderland, MA: Sinauer Associates Inc.

Montoya, D., Yallop, M. L., Memmott, J. (2015). Functional group diversity increases with modularity in complex food webs. *Nature Communications 6:7379*. doi: 10.1038/ncomms8379

Mossio, M., Bich, L. (2017). What makes biological organisation teleological? *Synthese 194:1089-1114*. doi: 10.1007/s11229-014-0594-z

Nadin, M. (2012). Prolegomena: what speaks in favour of an inquiry into anticipatory processes? Pp. xv-lx. In: Rosen, R. (2012). *Anticipatory Systems*. New York, NY: Springer.

Nadin, M. (Ed.). (2016). *Anticipation Across Disciplines*. Switzerland: Springer.

Nunes-Neto, N., Do Carmo, R. S., El-Hani, C. N. (2013). An epistemological analysis of the functional discourse in the Biodiversity and Ecosystem Research Program. Pp. 15-39. In

Nunes-Neto, N., El-Hani, C. N., Moreno, A. (Eds.). *The Functional Discourse in Contemporary Ecology*. Salvador: Doctoral Dissertation, Universidade Federal da Bahia.

Nunes-Neto, N., Moreno, A., El-Hani, C. H. (2014). Function in ecology: an organizational approach. *Biology and Philosophy 29(1):123-141*.

O'Malley, M. A. (2015). Endosymbiosis and its implications for evolutionary theory. *PNAS 122(33):10270-10277*. https://www.pnas.org/cgi/doi/10.1073/pnas.1421389112

Odling-Smee, F. J. (1988). Niche construction phenotypes. Pp. 73-132. In (Ed.) H.C. Plotkin. *The Role of Behaviour and Evolution.* Cambridge, MA: MIT press.

Odling-Smee, F. J., Laland, K. N., Feldman, M. W. (1996). Niche Construction. *The American Naturalist 147(4):641-648*.

Odling-Smee, F. J., Laland, K. N., Feldman, M. W. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton University Press.

Odling-Smee, F. J., Erwin, D. H., Palkovacs, E. P., Feldman, M. W., Laland, K. N. (2013). Niche construction theory: a practical guide for ecologists*. Quarterly Review Biology 88(1):4-28)*. https://www.ncbi.nlm.nih.gov/pubmed/23653966

Pigliucci, M., Müller, G. B. (Eds.). (2010). *Evolution-the Extended Synthesis*. Cambridge, MA: The MIT Press.

Pigliucci, M., Müller, G. B. (2011). Evolution-the extended synthesis. *BioScience 61(5):407-408*. http://doi.org/10.1525/bio.2011.61.5.10

Poli, R. (2013). A note on the difference between complicated and complex social systems. *Cadmus 2(1). Part 1.* http://www.cadmusjournal.org/node/362. Accessed April 7, 2014.

Poli, R. (2017). *Introduction to Anticipation Studies*. New York, NY: Springer.

Poli, R. (2018, this issue). Something about science: mulling over impredicative systems. *Ecological Complexity* (in Press).

Rashevsky, N., Kugelmass, I. N. (1961). *Mathematical Principles in Biology and their Applications*. Springfield, IL: Bannerstone House.

Rashevsky, N., Furness, F. N. (Eds.). (1962). Mathematical theories of biological phenomena. *Annals of the New York Academy of Sciences 96:895-1116*.

Rashevsky, N. (1969). Outline of a unified approach to physics, biology, and sociology. *Bull. Mathematical Biophysics 31:159-198*.

Rasskin-Gutman, D. (2005). Modularity: Jumping Forms within Morphospace. Pp. 207-220. In Callebaut, W., Rasskin-Gutman, D. (Eds.), *Modularity: Understanding the Development and Evolution of Natural Complex Systems*. Cambridge, MA: The MIT Press.

Rose, M. R., Oakley, T. H. (2007). The new biology: beyond the Modern Synthesis. *Biology Direct: 2:30*. doi: 10.1186/1745-6150-2-30.

Rosen, J. (2012). Introduction: the contribution of Robert Rosen to science. In Simeonov, P. L., Smith, L. S., Ehresmann, A. C. (Eds), *Integral Biomathics: Tracing the Road to Reality* (XIII-XIX). New York, NY: Springer.

Rosen, R. (1958a). The relational theory of biological systems. *Bulletin Mathematical Biophysics 20:245-260.*

Rosen, R. (1958b). The representation of biological systems from the standpoint of the theory of categories. *Bulletin Mathematical Biophysics 20:317-341*.

Rosen, R. (1959). Ontological paradox implicit in the notion of a self-reproducing automata. *Bulletin of Mathematical Biophysics 21:387-394*.

Rosen, R. (1963). Some results in graph theory and their application to abstract relational biology. *Bulletin of Mathematical Biophysics 25: 231-241.*

Rosen, R. (1977). Complexity as a system property. *International Journal of Genetic Systems 3: 227-232*.

Rosen, R. (1979). Some comments on activation and inhibition. *Bulletin of Mathematical Biophysics 41:427-445.*

Rosen, R. (Ed.). (1985). *Theoretical Biology and Complexity*. Orlando, FL: Academic Press Inc.

Rosen, R. (1987). On complex systems. *European Journal of Operational Research, 30(2):1-23*.

Rosen, R. (1988). How universal is universal unfolding? *Applied Mathematics Letters 1(2):105-7.*

Rosen, R. (1991). *Life Itself. A Comprehensive Inquiry into the Nature, Origin, and Fabrication of Life*. New York, NY: Columbia University Press.

Rosen, R. (1995). Cooperation and chimera. Pp. 343-358. In Casti, J.L., Karlqvist, A. 1995. *Cooperation and Conflict in General Evolutionary Processes*. New York, NY: John Wiley and Sons, Inc.

Rosen, R. (2000). *Essays on Life Itself*. New York, NY: Columbia University Press.

Rosen, R. (2012). *Anticipatory Systems*. New York, NY: Springer.

Rosen, R. (date unknown). On the role of time and interaction in ecosystem modelling. Unpubl. MS.

Sanford, J.A., Gallo, R.L. 2013. Functions of the skin microbiota in health and disease. *Semin. Immunology* 25(5):370-377.

Schrödinger, E. (1944, 18th reprint, 2006). *What is Life?* Cambridge University Press. Cambridge, U.K.

Scott-Phillips, T. C., Laland, K. N., Shuker, D. M., Dickens, T. E., West, S. A. (2014). The niche construction perspective: a critical appraisal. *Evolution 68(5):1231-1243*. doi: 10.1111/evo.12332

Simeonov, P.L., Smith, L.S., Ehresmann, A.C. Eds. 2012. *Integral Biomathics Tracing the Road to Reality.* New York, NY: Springer.

Slobodkin, L. B. (1961). *Growth and Regulation of Animal Populations*. New York, NY: Holt, Rineheart and Winston.

Stouffer, D. B., Bascompte, J. (2011). Compartmentalization increases food-web persistence. *PNAS 108(9):3648-3652*. doi: 10.1073/pnas.1014353108

Sultan, S. E. (2015). *Organism and Environment: Ecological Development, Niche Construction, and Adaptation*. Oxford, UK: Oxford University Press.

Stanford Encyclopedia of Philosophy. (1996, 12 August 2014). Thought Experiment. https://plato.stanford.edu/entries/thought-experiment/ Accessed January 24, 2018.

Takemoto, K., Kajihara, K. (2015). Human impacts and climate change influence nestedness and modularity in food-web and mutualistic networks. *PLOS ONE, 11(6). e0157929*. https://doi.org/10.1371/journal.pone.0157929

Thompson, J.N. 1999. The evolution of species interactions. *Science 284: 2116-2118.*

Turner, J. S. (2016). Homeostasis and the physiological dimension of niche construction theory in ecology and evolution. *Evolutionary Ecology 30:203-219*. doi: 10.1007/s10682-015-9795-2

Ulanowicz, R.E. 1997. *Ecology, the Ascendant Perspective*. New York, NY: Columbia University Press.

Wells, J. (2018, this issue). The Complexity Revolution: Pluralism, Polyvalence, and Paradox. *Ecological Complexity*.

Wilkinson, D. M. (2003). The fundamental process in ecology: a thought experiment on extraterrestrial biospheres. *Biological Review 78:171-179*. doi: 10.1017/S1464793102006048

Wray, G. A., Hoekstra, H. E., Futuyma, D. J., Lenski, R. E., Mackay, T. F. C., Schluter, D., and Strassmann, J. E. (2014). Does evolutionary theory need a rethink? No, all is well. *Nature 514:161-164*.

Wright, J. A., Lane, P. A. (1986). The theory of loop analysis. *Ecology 67. Supplementary Publication Source Document No. 8525b*.

Yanai, I., Lercher, M. 2016. *The Society if Genes.* Cambridge, MA: Harvard University Press.

Zehr, J.P., Ward, B.B. (2002). Nitrogen cycling in the ocean: new perspectives on processes and paradigms. *Applied Environmental Microbiology 68(3): 1015-1024.*

9.0 Appendices

9.1 Appendix 1: Terms in Rosennean Complexity

To Rosen, there are two types of systems: simple and complex. He explained this dichotomy as follows: "A complex system is one in which there must exist closed loops of entailment. Such loops cannot exist in a machine or simple system… In mathematics, loops of this kind are manifested by impredicativities or self-references – indeed by the inability to internalize every referent. In science, where entailment means causality, closed causal loops… allows us to talk rigorously about categories of final causation… This kind of finality, in turn, is what allows us to talk about function and anticipation, in terms of what an effect entails in a complex system, rather than exclusively in terms of what entails the effect." See also Rosen (1977, 1987).

Rosen (2000) conceptualized chimeras as complex systems. He explained how chimeras do not belong to the world of simple systems as follows: "Conceptually, there is such a world, the reductionist paradise, in which everything can be synthesized from fixed elements by following determinate rules (algorithms) expressed in a single coherent time frame from early to later… This is the world of machine or mechanism – what I call the world of simple systems in *Life Itself* (Rosen, 1991)…This kind of world is extremely feeble… In such a world, a chimera cannot exist as a thing in itself; there are only more- or less- differentiated mixtures synthesized from, and analyzed into, elements of fixed and unchangeable identity, whose own identities are therefore fixed and unchangeable. Accordingly, the concept of function has no meaning. The totality of all behaviors of the system, its entire phenotype, is wrapped up in the totality of all models that can be made of it; this constitutes its epistemology. If, and only if, a system is simple, which means that all of its models are computable or simulable, then this set of models becomes the reductionist paradise – otherwise, not…If a material system has a non-computable model (i.e., it is complex), then it's behaviors or phenotypes cannot all arise from algorithmic differentiation of a fixed finite set of elements, according to fixed identity-preserving rules or algorithms." Thus, chimeras *a priori* have at least one non-computable model and are complex systems *in sensu* Rosennean Complexity.

Tim Gwine, who provided a useful website entitled 'Panmere' to explain Rosen's ideas and contributions, concluded the following: "It is not unusual for people to imagine complex systems as being, in some sense, more rare or non-generic, than simple systems. Often this notion is tied up with the erroneous idea that it is somehow takes lots of simple pieces put together to make a complex system. However, if we view simple versus complex systems in other terms, we will see that, in fact, it is simple systems that are non-generic," and "Simple systems are very restricted subset of systems and they are exceedingly constrained in comparison to complex systems, as such, simple systems requiring an inordinately rare (and rarefied) set of circumstances to exist. It is, thus, quite evident that it is specious to presume that we can envision the world as composed of simple systems, or that we can understand the world via simple models alone."

Table A-1 compares the complex and simple systems as described by Rosen to provide the Reader with a list of definitions and explanations. Many authors in the SI elaborate on these terms and their relevance to ecological complexity.

Characteristic	Complex System
Genericity	"Complex systems are far more generic than simple context- independent ones". In contrast, simple systems are rare. "The world of systems that are simple in my sense is the world of mechanisms… It is a very nice, tidy, orderly world, this world of mechanisms. And it is a closed world, in the sense that once we are inside it, we cannot get out…"(Rosen, 2000).
Impredica-tivity	"I would rather, then, call a system complex if it has inherent impredicative loops in it... A system is thus complex if it has models which are themselves complex." "… Something is impredicative if it could be defined only in terms of a totality to which it itself had to belong… There is no algorithm for building something that is impredicative." In contrast, "in a formalization, computation and construction are the same; epistemology equals ontology, but construction (symbol manipulation) in this context involves the application of rote syntactic operations (production rules) in a given sequence… This is, in fact what an algorithm is. Whatever can be constructed in this way is sometimes called predicative. The whole point of formalization was to say that everything is predicative." Note: complex systems can also contain predicative loops and simple models. Rosen also termed impredicativities as self-references or vicious circles. (Rosen, 2000).
Computa-bility	"A system is complex if it has non-computable [non-simulable] models. This characterization has nothing to do with mere complication, or with counting of parts or interactions; such notions, being themselves predicative, are beside the point." (Rosen, 2000).
Fractiona-lity	".. We can partition, or fractionate, any material system x into independent pieces x_j. we mean … that these pieces can be separated from the larger system x, and from each other in such a way that their individual properties … are entirely independent of any fractionation process …" (Rosen, 2000). [Complex systems cannot be fractionated and they do not have a largest model.]
Analysis versus Synthesis	The expressions of a particular system in terms of its attributes are models which comprises a mode of analysis of that system… But in the world of complex systems, we cannot generally invert these modes of analysis to obtain corresponding modes of synthesis…" (Rosen, 2000).
Ontogeny versus Epistemo-logy	"Because analysis and synthesis are not inverse operations in this world [of complex systems] we cannot automatically entail a realization (i.e., an existence) from an essence, or produce an ontology from an epistemology." In contrast, "in a simple world, it turns out that the two coincide. In a complex world, on the other hand they need not; we can know all about the one without knowing anything at all about the other" (Rosen, 2000).
Anticipation	"…an anticipatory behavior is one in which a change of state in the present occurs as a function of some predicted future state, and the agency through that prediction is made must be, in the broadest sense, a model. I have also indicated that obvious examples of anticipatory behavior abound in the biosphere at all levels of organization, and that much (if not most) conscious human behavior is also of this character" (Rosen, 2012). [An anticipatory system is] "a system containing a predicative model of itself and/or of its environment, which allows it to change state in an instance in accord with the model's predictions pertaining to a later instant" (Rosen, 2012). "The behavior of such anticipatory systems is generally quite invulnerable to simple-minded reductionist fractionations" (Rosen, 2000). Nadin (2012) provided a useful introduction (Prolegomena) to Rosen's Anticipatory Systems (2nd edition) by integrating his own work on anticipation with Rosen's. (See also Nadin, 2016.)
Entailment	"A complex system is one in which there must exist closed loops of entailment." In contrast, "such loops cannot exist in a machine or simple system; this is indeed precisely why machines are so feeble" (i. e., There is not enough entailment in a simple system to close such a loop)" (Rosen, 2000).
Efficient Cause	"A material system is an organism if, and only if, it is closed to efficient causation [CLEF]" (Rosen, 2000). [Aristotle defined four causes: (1) material cause is the substance or matter that something is made of; (2) formal cause is the design, form or shape of something; (3) efficient cause is what brought the something into existence; and (4) final cause is the purpose or reason for something to exist.] See Poli (SI:2018) for an extensive discussion on CLEF and categorization of CLEF systems.
Final Cause	"In science, where entailment means causality, closed causal loops… Allow us to talk rigorously about categories of final causation, divorced… from every shred of telos. This kind of finality, in turn, is what allows us to talk about function and anticipation in terms of what an effect entails in a complex system, rather than exclusively in terms of what entails the effect." (Rosen, 2000). [Hoffmeyer (2013) has explained how Rosen substituted 'functional entailment' in the place of final cause.]

Table A-1. Rosen's Characteristics of Complex Systems with Some Contrasts to Simple Systems.

9.2 Appendix 2: Loop Analysis: Methods and Applications

9.2.1. Loop Analysis: What Is It?

Loop analysis is a qualitative network technique for analysing systems of interacting variables; it was created by Richard Levins (1973, 1975). It employs signed digraphs so that the two-way links (edges) between variables (nodes) can be +, -, or 0. A positive effect of X on Y is illustrated with a link from X with an arrowhead touching Y, and a negative effect of X on Y, is shown with a link from X with a circlehead touching Y. There are nine possible link types between every pair of variables including the null link. A path begins at one variable and ends at another by way of intervening variables, in which the path does not enter or leave any variable more than one time.   A loop is a closed path that comes back to the first variable, entering and leaving each variable only one time. Each loop represents a feedback relationship. Paths and loops are calculated by multiplying their algebraic signs. In addition, a path of length zero, $P_0 = +1$`and feedback of level 0, $F_0 = -1$.

"The calculation equation is:

$$E_{ij} = \in P_{ij}^{(k)} \cdot F_{n-k} \{ \text{compl } P_{ij}^{(k)} \}/ F_n,$$

where E_{ij} is the community effect of a parameter change to variable j on variable i; $P_{ij}^{(k)}$ is the algebraic product of links along a simple, open path k from variable j to variable i. k is the length of the path equal to the number of variables included on the path. $F_{n-k} \{\text{compl } P_{ij}^{(k)}\}$ is the feedback of order n-k variables that is essentially the determinant of the submatrix of the remaining variables not on the path. The sign of the complement is the sign of the determinant of this submatrix. F_n is the feedback for the total system, which is the determinant of the community matrix (level N). The feedback of any level k of the community matrix and its submatrices is calculated as:

$$F_k = (-1)^{m+1} \text{Loops}(m,k),$$

where m is the number of disjunct loops that total k variables. Disjunct loops do not have variables in common, while conjunct loops share at least one variable. The latter are not used in the expansion of determinants or in loop analysis" (Lane, 2016).

The calculation equation above is used to compute the changes in standing crops with a parameter input that is depicted as either positive or negative on the variable it touches, which in turn affects the whole network producing community effects as directed changes. The equation essentially multiplies the signs of: the parameter input (PI) x ∑ paths and their complements all divided by the feedback of the total system (F_N). Embedded in this equation are two determinants, one in the numerator or the complement, and one in the denominator F_N, which is the sign of the determinant of the total community matrix of N variables. The complement is a sign of the determinant of the matrix containing all variables not on the path. If the complement is zero, then that particular pathway has no effect. If the numerator contains both positive and negative combinations of paths times complements, then the prediction is ambiguous and a '?' is entered into the community effects matrix.   Thus, the qualitative structure of the overall network affects which pathways operate and which do not. In using a descriptive food web technique that does not have any calculation capacity, the

investigator usually assumes that any pathway that can be drawn out in the network is operating; yet many are not in nature.

The network structure can also be portrayed in a traditional square community matrix format in which every element (alpha value or interaction coefficient) could appear, that is, all elements (N^2) are possible including self-damping terms (-1) down the main diagonal. The analysis can be used for any set of interacting variables on any level of the biological hierarchy. Levins has employed his methodology in agricultural pest control and public health applications. Because it is a qualitative methodology and has only a loose relationship to measurement, it could also help bridge the cultural gap mentioned by Jennifer Wells (2018, this issue). In this paper, the focus is on the ecological relationships in a marine plankton food web.

Loop analysis as a graph is related to matrices through their determinants, since each sub-product of the expansion of the determinant is a set of one or more disjunct loops, which do not have any variables in common. In the following example of calculating a determinant for a 3 x 3 matrix, the first expansion steps are illustrated:

$$\det(A) = |A| = \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} = a_{11}\begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} - a_{12}\begin{vmatrix} a_{21} & a_{23} \\ a_{31} & a_{33} \end{vmatrix} + a_{13}\begin{vmatrix} a_{21} & a_{22} \\ a_{31} & a_{32} \end{vmatrix}$$

or more of the sub-products as a non-zero value. If all subproducts of the For example, for a determinant of the matrix given above, there are three factorial(3!) or 6 possible signed subproducts: $\alpha_{11}\alpha_{22}\alpha_{33} - \alpha_{11}\alpha_{23}\alpha_{32} + \alpha_{12}\alpha_{21}\alpha_{33} - \alpha_{12}\alpha_{23}\alpha_{31} + \alpha_{13}\alpha_{21}\alpha_{32} - \alpha_{13}\alpha_{22}\alpha_{31}$. These subproducts are essentially combinations of feedback loops in their order: 1) 3 loops of length one, 2) 1 loop of length one and 1 loop of length two, 3) 1 loop of length one and 1 loop of length two, 4) 1 one loop of length three, 5) 1 loop of length three, and 6) 1 loop of length one and 1 loop of length two, respectively. For a complement to be valid, it must have one determinant of the complement are zero, then the numerator of the calculation equation is also zero and the pathway is non-operative. A zero is entered in the prediction table.

For a pathway to operate and to pass effects from a parameter input that impacts the first variable to the end variable on the pathway, the rest of the variables in the total network must be in one or more disjunct loops. They have to be in motion; they cannot be 'dangling' alone as static entities; essentially all variables must be causally entailed. When we examine all kinds of systems in our solar system, from the movement of planets down to the movement of electrons, we observe many loops in motion and very little standing still. Whether or not the complement represents some deeper aspect of reality remains to be determined.

9.2.2 Loop Analysis: What Can It Do?

Loop analysis has several capabilities that more descriptive food web models do not. First, besides not requiring quantification and mathematical formalism like differential or difference equations, loop variables do not need to be in the same units so that different types of entities can be modelled together in the same network. For example, Levins has included a fish, fisherman, regulator, and regulation in one loop model. Variables can be both biotic and

abiotic. Loop analysis focuses upon the causality of the network and its organization, rather than the type of 'matter', which forms it.

Second, LA allows for predictions in standing crops as well as turnover rates for systems subject to parameter inputs (PI) coming from the environment outside the system, which are considered similar to driving forces or perturbations in quantitative systems ecology. Standing crop predictions are entered into the square prediction matrix termed the: Community Effects Matrix with PIs on the rows and variables in the columns, and read across a row. Turnover rates are inferred by observing changes in adjacent variables. By noting pairwise predictions across the PI row of interest provides how interactions of two species are correlated in a community context. For example, a predator prey pair might be both increasing (+,+) as if they were mutualists or both decreasing (-,-) as if they were resource competitors for a given PI. These predictions also help identify where PIs are entering and whether they are positive or negative. Lane (1986a, b) detailed the methodology for constructing loop models from prediction effects compared against observed abundance changes in a field or laboratory data set. Wright and Lane (1986) discussed the methodology.

Third, LA permits all of the usual structural network measures (i.e. connectivity, connectance, etc.) as well as the identification of the signs of the feedback loops at each level (0-N). In addition, it has measures for stability based on the Routh Hurwitz criteria, which are not employed in many more descriptive food web methodologies. Both positive (destabilizing) and negative (stabilizing) feedback loops occur in loop models. For stability, negative feedback needs to outweigh positive feedback; short negative loops are most stabilizing, and the overall feedback of the total network (F_N) should be negative. Generally, longer loops are considered to take a longer time to make one revolution then short loops since each link in the loop takes a finite amount of time.

Fourth, LA is excellent for calculating ecosystem complication. It facilitates the enumeration of many different measures including ecological skeletons (ESs), which are composite representations of several loop models over time for a given system. They constitute the parsimonious or 'bare-bones' of the most frequently-observed variables and links of a set of food webs. Once the ES is determined, a set of loop diagrams called the micro-universe (all combinations of observed variables and links in a set of loop diagrams for a particular ecosystem) and macro-universe (all mathematically-possible for a given number of variables, N) can be calculated. In addition, the methodology provides a way forward to compute the meso-universe (a set of all biologically-reasonable networks for one ecosystem), which may lie between the micro-universe and macro-universe. 'Biologically-reasonable' is defined as an ecological network that could occur in nature. The size of the meso-universe has not yet been calculated, but knowing this value could help to devise rules of construction for ecosystems.

Fifth, LA can also facilitate the development of experimental and field sampling designs – essentially as a guide to measurement. Too often ecologists come up against the brick wall of needing to measure everything. Having a tool that distinguishes what needs to be quantified from what does not can be very useful. All of the above five capabilities and uses of LA can be considered helpful to delineating ecological complication (Lane, 2016). For a good discussion on the differences between complication and complexity see Poli (2013). To what degree LA also provides insight into ecological complexity is discussed further in Section 4.0.

9.2.3 How Can Loop Analysis Be Used: Hypothetical or Real-World Models?

For plankton communities, LA has been used in two ways: (1) construction of hypothetical models, and (2) matching standing crop predictions against qualitative changes in real-world observables. Most investigators who model an ecosystem, regardless of their preferred methodology, use the first approach. Even in systems ecology, where there is a lot of attention on finely-tuned parameter fitting and employing solvable mathematical formalisms, there is less consideration of overall system organization. If the model gives good correspondence to nature quantitatively, then it is considered verified. Individual links are often assumed as given only by someone's intuition or an anecdotal feeding observation. Often, intuition is not enough. Because of the enormous number of ways that food webs can be and are routinely portrayed, there is not much basis for confidence that such food web depictions are accurately representative of biologically-reasonable food webs in nature where variables and links can change both in a predictable manner through well-established seasonal species successions or apparently more randomly in ways that seem to defy explanation. Given the disparate array of food web models in the current literature, it is clear that they cannot all be correct (choices of lumping vs. splitting variables, rigid vs. flexible links, restricted vs. unrestricted link types, signed vs. non-signed links, etc.) and some appear fairly arbitrary. There are also many difficulties experienced by all investigators in providing evidence that a particular representation is valid and biologically-reasonable. This has led many to be overly tolerant and uncritical of all food web models, lest their own are questioned (Lane, 2016, 2017a, b).

In the second LA approach, field or laboratory data are sorted by functional loop variable over a set of sampling dates and for each variable, whether it increases, decreases, or stays the same, is indicated by a qualitative sign (+, -, or 0, respectively). The loop predictions and the qualitative empirical data are compared, until the model structure is altered as necessary to try to achieve a 90-100% agreement. This is an in-depth iterative process, and the best predictive pathway is selected. This is a very different process from parameter fitting in systems analysis (Lane, 2016). Getting all of the feedback loops and complements to agree between the model and the real world results is a difficult undertaking involving the total network. Often, previously unknown biological variables and relationships are identified and need to be incorporated into the loop models. After constructing about 8-12 marine plankton models, for a particular ecosystem, from one date to another over a sequence of sampling dates, it is difficult to alter the overall model substantially, although single links change frequently and all variables are not present in all models. It is impossible, however, given the multitude of potential models for a given ecosystem, to claim that there is only one possible model that yields this high level of agreement. There are probably many such models. This is termed 'the uniqueness problem' (Lane, 1986a, 2017a). This is not just a consideration in LA, but applies to all types of food web models. I also cannot claim that any ES is complete, in fact, I am sure most are not. No one has determined how many sampling dates or 'slices of time' are necessary to ensure that all of the ecosystem 'bones' are identified and in their correct positions: 10 per year or 100 or 365?

As we gain more understanding of ecological complexity it seems inevitable that the the Biological Complexity Revolution (BCR) will include a sub-revolution in ecological approaches and concepts at the ecosystem level. Although there is not space to develop this observation

here, there are areas of ecology that are reductionist in the extreme and overdue for a paradigm shift; food webs in *rigor mortis* are only one example (Lane, 2017b).

9. 2. 4 How Does Loop Analysis Correspond to Relational Biology?

Loop analysis (LA) is a signed digraph methodology, which includes several similar notions under the field of Relational Biology in terms of emphasis upon: (1) the qualitative, (2) the relational (especially temporal relations), and (3) the functional (roles of variables, pathways, feedbacks, and subsystems). Because nodes in loop models can be considered as functions and edges or links can be considered relationships with temporal dimensions, LA can be considered related to Relational Biology methodologies as Rashevsky himself used graph theory. LA can also be used to model real-world datasets and bring some of the key notions of Relational Biology into concrete examples. I am confident LA yields more understanding than many current food web techniques, and provides insight into Relational Biology at the ecosystem level, but I am hesitant to claim more. Rosen illustrated how some results from graph theory can be applied to Relational Biology (Rosen, 1963).

LA is not Category Theory (CT), and does not provide its capabilities, although Marinakis (2008), writing about "the ecosystem as a topos of complexification", concluded that "directed digraphs [specifically loop analysis] that satisfy identity composition and associativity can be translated into categories". He thought it was also possible to use Category Theory with food webs, making each food web a category, and then develop a trajectory of other categories with morphisms between them as the food web structure changes, e.g. over the annual cycle. This is a somewhat similar idea to how a set of loop diagrams represents food web changes over the annual cycle, which is summarized in ecological skeletons (Lane, 20126; 2017b).

A listing of nine similarities between LA and Relational Biology follows:

(1) LA is a qualitative technique focused upon functional organization of systems. It certainly "throws the matter away and keeps the organization" as Rashevsky urged biologists and systems thinkers to do. The methodology is so flexible that not only does the type of matter not need to be specified, it is treated as irrelevant, and units of measurement are also irrelevant. Thus, many different types of components can be easily included within a single loop model.

(2) Relationally, a single loop model includes all of the variables and links that are connected to each other in regard to the dynamics of the system in terms of their pairwise interactions, but also all variables and interactions are considered temporally congruent, that is, they happen at roughly the same time. There is a limit to how broad the discordant temporal dynamics (e.g. generation times) among variables can be to still be included in one network before the model loses integrity. LA also identifies how many ways each pair of variables can interact in a single model, and which pairs of variables never directly interact. Thus, LA provides a great deal of relational information to an investigator especially when used with real-world data.

(3) Variables are designated and constructed by function. If two variables have identical links to all other variables then they are collapse into one, which has a unique functional role in the food web.

(4) The links also entail more information on function than merely their relationships (links) to the other variables. Each link takes a period of time to transverse the interaction distance between two variables.

(5) There is more functional information revealed with parameter inputs and how they put pathways of effect in motion to cause changes in standing crops and turnover rates. LA can give insight into which pathways of effect are operating from one time to another, but little information on how a series of loop models prefigure each other and change structure and function over time.

(6) Pathways and feedback loops also take time from their start variable to their end variable. LA being qualitative does not provide the duration values of the links, but a general assumption is that short paths and loops are faster than long paths and loops. Thus, the loop structure embeds a considerable amount of sequential temporal information in the paths and loops.

(7) The disjunct loops in a complement (set of variables not on the path) are functioning simultaneously if their associated path is active.

(8) The presence of particular substructures reveals still more functional information such as satellite variables or self-damping loops.

(9) Other functional measures include stability and identification of operating trophic cascades and trophic escalades (Lane, 2017a).

Whereas, the most we can hope to get out of any model is usefulness, and LA has proven useful for understanding food webs and ecological phenomena, it does not model RC in the sense of documenting that a particular food web is closed to efficient causation (CLEF). As a tool, it is ineffective on deep causal entailment and self-referential loops. It does not reveal that a food web has an anticipatory model of itself. It will take another methodology, perhaps Category Theory or something beyond it, not yet devised to model RC fully. There is a major initiative underway termed Biomathics to develop new mathematical tools that are 'biologically-driven' (Simeonov et al., Eds., 2012).

Perhaps the most that can be claimed for loop analysis is that it is useful in providing insight into areas of interest for Relational Biology. The underlying real-world food webs, however, are complex systems. As Rosen (2000) concluded, "complex systems may be thought of… as manifesting more entailment than can be accommodated by a model." Whereas LA suggests many causal relationships, even a micro-universe of loop diagrams does not encompass RC, and we are only observing ecological complication through the glass darkly with LA. In the meantime, while we make models of complex systems like food webs and ecosystems, we should not fool ourselves that we have depicted complexity (Lane, 2016). As Rosen (2000) concluded, "it must be emphasized that we can still make dynamical models of complex systems, just as we can formalize fragments of number theory. We can approximate, but only locally and temporarily, to inexact differential forms with exact ones under certain conditions. But we will have to keep shifting from model to model, as the causal structure in the complex system outstrips what is coded into any particular dynamics. The situation is analogous to trying to use pieces of planner maps to navigate on the surface of a sphere.… A complex system can be regarded as a limit of simple ones." This is exactly what happens with a succession of loop models. LA allows us to "shift from model to model" quite easily.

List of Figures and Tables

Figure 1. Ecological Skeleton of Nine Loop Models of the Plankton Community in Narragansett Bay (Reprinted from Lane, 2017b).

Table 1. Listing of Loop Variables, Major Species, and other Taxonomic Groups. (Modified from Lane 2017a).

Table 2. A Summary of Some Features of the Ecological Skeleton of the Narragansett Bay (Figure 1) and other Field Loop Models.

Table 3. Minimum Set of Ecological Processes that Wilkenson (2003) Suggested as Necessary to Establish an Extraterrestrial Biosphere.

Table 4. How Mother Nature Thinks About Marine Plankton Chimeras.

Table A-1. Rosen's Characteristics of Complex Systems with Some Contrasts to Simple Systems.