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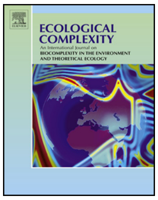

Original Research Article

Rosennean complexity and its relevance to ecology

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ABSTRACT

Complexity is not the same as complicatedness: a system is complicated if it has many components, but it is complex if it cannot be modelled as a machine and has emergent properties. The theoretical biologist Robert Rosen argued that living organisms are complex in this sense, and his (M, R) systems provide a description of a living organism in which the central point is that *organisms are closed to efficient causation*, which means that all the specific catalysts needed for the organism to maintain itself must be produced by the organism itself. This includes the catalysts needed to maintain the other catalysts. On the other hand an organism is not closed to material causation, because there must be a net overall irreversible process to provide the necessary thermodynamic driving force for metabolism. (M, R) systems are usually discussed in relation to individual organisms, but they can also be applied to interactions between different organisms, allowing analysis, for example, of how two or more species can exist in symbiotic relationships with one another, able to live together, but not separately. Application of Rosennean complexity to fields other than life is possible, as we discuss. Rosen's holistic vision of organisms, in which all components affect all others, has implications for the concepts of hierarchy and *downward causation* that are sometimes invoked in philosophical discussions, because it means that there is no hierarchy and no downward causation.

1. Introduction

Robert Rosen's book *Life Itself* (Rosen, 1991), a summary of more than three decades of research on the nature of life, starting with Rosen (1958), presented what he called (M, R) *systems* or *metabolism-repair*[1] *systems* as a way to understand life. It has now been cited about 550 times in the science literature—not a very large number for the major work of "biology's Newton" (Mikulecky, 2001).[2] Despite Rosen's interest in ecology, rather few of these citations have been in journals of ecology, just 12 in the past 10 years (Gabora et al., 2008; Kelso, 2008; Yates, 2008; Chemero and Turvey, 2008; Chemero, 2012; Turvey and Carello, 2012; Robinson, 2009; Van Orden et al., 2010; Browne et al., 2012; Cilliers et al., 2013; Keirstead, 2014). Here we shall discuss in particular how (M, R) systems can be applied to ecological interactions between organisms. However, we must first discuss the distinction that Rosen made in *Essays on Life Itself* between complexity and complicatedness (Rosen, 2000, p. 44):

> A system is complex if it has noncomputable models—this characterization has nothing to do with counting of parts or interactions; such notions, being themselves predicative, are beside the point.

In everyday language the adjectives "complex" and "complicated" are sometimes treated as synonymous, a tendency encouraged by dictionaries that give each as a definition of the other. However, Rosen (2000) insisted that they are different, as noted in the quotation above, and he regretted (Rosen, 2000, p. 43) that von Neumann had used the term "complexity" for what he regarded as "complication". Even if one takes care to distinguish between the two adjectives, a problem arises with the nouns, because "complicatedness" is such a cumbersome term that there is a temptation to use "complexity" as the noun for both. This temptation should be resisted.

Both *Life Itself* (Rosen, 1991) and *Essays on Life Itself* (Rosen, 2000) were published as part of a series entitled *Complexity in*

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[1] Rosen's *repair* has very little to do with ordinary uses of the word in biology. We prefer *replacement*, and use this term in this article. In general it is not a good idea to change an original author's terminology, but in Rosen's case it can hardly be avoided.

[2] This is probably due to the fact that his papers and books are difficult to read, because of the abstract mathematical language used. Readers are invited to consult a paper (Cornish-Bowden et al., 2007) that offers a non-mathematical explanation of Rosen's ideas for the general biological community.

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Ecological Systems, and although there is comparatively little in them that is particularly related to ecology, he definitely saw his ideas as being relevant to ecology, as he made clear when he recalled a year that he had spent as a Visiting Fellow at the Center for the Study of Democratic Institutions in Santa Barbara (Rosen, 1979):

> I thus almost in spite of myself found that I was fulfilling an exhortation of Rashevsky, who had told me years earlier that I would not be a true mathematical biologist until I had concerned myself (as he had) with problems of social organization. At the time, I had dismissed these remarks of Rashevsky with a shrug; but I later discovered (as did many others who tried to shrug Rashevsky off) that he had been right all along.

As with much of what Rosen wrote, his meaning in the first quotation does not immediately emerge at first reading: one needs to work at understanding him. The point is that a complicated system is one with many components, but with properties that can be regarded as the sum of the properties of the individual parts: in that sense a typical chart of metabolic pathways is complicated, but, as we shall see, it is not complex. Computer simulation of the entire metabolism of an organism has been attempted only by combining data from numerous sources (Karr et al., 2012), but some individual pathways have been simulated using kinetic parameters measured under uniform conditions, such as glycolysis in the bloodstream form of the parasite *Trypanosoma brucei* (Bakker et al., 1997; Eisenthal and Cornish-Bowden, 1998) and aspartate metabolism in *Arabidopsis thaliana* (Curien et al., 2009), a branched pathway with numerous isoenzymes, regulatory interactions, and multifunctional proteins, none of which can be taken into account by a stoichiometric model that does not incorporate kinetic equations. The results support the idea that the properties of the whole pathway are indeed the sum of the properties of the individual reactions (Van Eunen et al., 2012). However, simulations of this kind assume the classical view of metabolism, in which the enzymes are "given",[3] a view not shared by Rosen, who argued that an organism must be *closed to efficient causation* (Rosen, 1991), another somewhat obscure characterization, which can be understood to mean that all the specific catalysts (enzymes or ribozymes) needed by an organism must be products of the organism itself: organisms are therefore complex. Rosen's definitions are not exactly the same as those used by other writers interested in the essence of living systems, but they correspond approximately.

The examples of kinetic metabolic models cited above were *small* models, with fewer than 15 reactions, and even for a metabolism as simple as that of the bloodstream form of *T. brucei* this still falls far short of modelling the whole metabolism. Increased computer power and increased kinetic information about the reactions are bringing about large increases in the sizes of such models: for example, a recent kinetic model of liver metabolism (Berndt et al., 2017) is based on data for 221 reactions. Remember, however, that in the simulations of *T. brucei* metabolism the enzymes were taken as given, the question of where they come from being ignored (it is assumed that their concentrations do not change during the period of simulation). This is also true of all of the other simulations of real metabolism that we are aware of, and it restricts the period of validity to a time frame in which protein synthesis is negligible, 2 h for the model of aspartate metabolism in *A. thaliana* (Curien et al., 2009), but possibly much shorter in other systems. The trend to larger models will certainly continue, but, if we accept Rosen's view, they will never be models of a whole organism, no matter how large and "complete" they become.

In *Life Itself* Rosen (1991) argued that the essence of a living organism could be expressed as an (M, R) system in which the reactions are possible thanks to catalysts that are produced by the system itself. As mentioned earlier, we have changed the term *repair* by *replacement*, which is more exact: although DNA can be repaired to some degree, and inactivated proteins can sometimes be repaired by chaperones or other mechanisms, damaged enzymes are usually degraded and need to be resynthesized. This resynthesis is what Rosen meant by "repair". His idea that catalysts (enzymes, whether protein or RNA, and also including transporters) play a crucial role and that they are synthesized by the organism is correct, as they participate, not only in classical metabolism, but also in DNA duplication, transcription, translation, as well as in the degradation of different types of molecules. This, in essence, means that the catalysts needed for an organism to stay alive are products of the organism itself.

Although the concept of an (M, R) system applies to modern organisms, it acquires special significance in relation to the origin of life (Cornish-Bowden and Cárdenas, 2008), because in the transition from prebiotic to living organisms the intermediate entities must have been minimally simple.

We have analysed Rosen's view of an (M, R) system, established its range of validity (Letelier et al., 2006), explained it in simple terms, defined simple examples to illustrate it (Cornish-Bowden et al., 2007), and compared his ideas of life with those of others (Jaramillo et al., 2010; Letelier et al., 2011; Cornish-Bowden, 2015). In these we have always considered the systems at issue to be single organisms, but Rosen's ideas also apply in more ecological contexts, and that is what we shall be concerned with here, specifically in the context of consortia of different species of bacteria. In the laboratory bacteria have usually been studied in pure culture, and supplied with the nutrients that they need. That is not how they exist in the wild, however: on the contrary, natural colonies of bacteria exist in ecological systems that contain many species, and in environments that lack some of the nutrients that some of the species need. They are often found in a *biofilm*, which has been likened to a "city of microbes" (Watnick and Kolter, 2000). We are not yet at the stage where we can usefully study such mixtures in Rosennean terms, but a consortium of two species, *Clostridium acetobutylicum* and *Desulfovibrio vulgaris* Hildenborough (Benomar et al., 2015) provides a starting point for studying more natural mixtures. *D. vulgaris* cannot grow in pure culture on glucose or other sugars, but it can grow on a medium with glucose as the sole carbon source if *C. acetobutylicum* is present in the medium. This simple example will illustrate how Rosennean complexity might be applied to ecological systems. We may hope that in the future it may be possible to describe entire trophic chains in Rosennean terms, but for the present that would be too ambitious.

2. Metabolic closure and Aristotle's four causes

2.1. An organism is closed to efficient causation

For defining (M, R) systems Rosen adopted Aristotle's classification of the four αἰτία ("aitia"), or "causes", of which the only one that corresponds to the modern idea of a cause (derived from David Hume, 1748) is the *efficient cause*. Rosen understood this as the catalysts needed for life (f, Φ and β in Fig. 1), whether protein, RNA or others. In saying that organisms are closed to efficient causation, he meant that all of the specific catalysts needed to be provided by the organism itself, with none of them being harvested from the environment. That applies almost without exception to metabolic

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[3] That is to say synthesis and degradation of catalysts are not considered in the models.

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