Molecular Ecosystems
Abstract

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Molecular mechanisms and processes, such as gene expression, are often depicted as rigid, self-regulated, deterministic gears where every little piece has its precise and independent role that is unaffected by the cellular and environmental context in which it is embedded. This picture, however, is misleading. To paraphrase a humorous analogy from molecular biologist Susan Lindquist, we should imagine the interactions between molecules not as dancers individually performing in a spacious ballroom but rather as the famous 'stateroom' scene from the Marx Brothers movie *A Night at the Opera*, where virtually every action and reaction is heavily constrained by the surrounding environment. Developmental biologists often employ a suggestive metaphor to describe the complexities of molecular interactions within cells and embryos: individual molecules are said to be part of *ecosystems* that integrate them in a complex network of relations with many other entities. The practice of exploiting ecological concepts to describe molecular interactions has a long history that traces its steps all the way back to the early 20^{th} century. Early embryologists used to refer to groups of cells whose position and fates are specified with respect to the same sets of boundaries as 'morphogenetic fields' (Gurwitsch 1910), 'fields of organization' (Spemann 1921), and 'cellular ecosystems' (Weiss 1939). Some of these concepts have recently been revived in contemporary molecular developmental biology (Gilbert et al. 1996) and systems biology (Raes and Bork 2008). However, the extent and respect in which the molecular microcosmos resembles the ecological macrocosmos is a question that has seldom been addressed explicitly. The aim of this essay is to scrutinize the metaphor of the *molecular ecosystem*. I argue that the cellular environment is analogous to the biosphere in important and surprising respects.

In ecology, ecosystems are usually defined as biological environments consisting of all the organisms living in a particular area, together with the abiotic (nonliving) physical components of the environment with which the organisms interact, such as air, soil, water and sunlight. Despite the intuitive appeal of this general definition, which is frequently employed both in popular and technical literature, from a philosophical perspective, the ecosystem is one of the most elusive concepts and one of the hardest to analyze. Consequently, instead of attempting to provide a precise definition of ecosystems and then identifying a molecular correlate that mirrors the ecological concept, in the first

part of the essay, I focus on some of the criteria that ecologists employ to characterize ecological units, and emphasize some remarkable and, perhaps, surprising analogies with the cellular environment. The three criteria, which I will discuss in turn, are: the delimitation of the ecosystem boundaries, the identification and interaction of organisms, populations, and species, and the characterization of the molecular environment.

But the metaphor is not only accurate; it is fruitful as well. In support of this claim, in the second part of the essay, I suggest some applications of the concept of the molecular ecosystem to developmental biology and ecology. First, I argue that ecosystems provide an accurate framework in which to describe the ontogeny of organisms. Recent years have witnessed an increase in popularity of 'systemic'—as opposed to 'analytic'—approaches to biology. Systems biologists attempt to provide quantitative measurement technologies that explain and predict the behavior of complex systems without breaking them down to their component parts. The 'dialectical' approach to biology inspired by Lewontin and Levins (1985) and Developmental Systems Theory (Oyama et al. 2001) go as far as rejecting interactionism, the conventional view that phenotypes are determined by the interaction of genotype and environment, and focus instead on complex systems as basic developmental units. The concept of the cellular ecosystem provides a more flexible metaphor than the developmental system for modeling ontogeny. First, viewing molecules as inhabiting ecosystems does not commit us to the causal parity thesis. Second, it is less holistic, in that it allows for the various components of the system to maintain their individual properties. Third, it is less inclusive, allowing for a more local identification of the boundaries of basic developmental and evolutionary units.

Finally, I discuss how molecular ecosystems can shed some light on our understanding of the biosphere. The relation between organisms and their environment has undergone a major conceptual shift over the past few decades. While ecologists traditionally conceived environmental changes as independent of the evolution of individual organisms or entire species, Lewontin famously argued that biological and environmental changes are a function of each other: "the environment is a product of the organism, just as the organism is a product of the environment." (Lewontin and Levins 1985, p. 69) This insight has led to a number of new approaches to ecology, such as *niche construction* (Odling-Smee et al. 2003) and *ecosystem engineering* (Jones et al. 1994). I argue that the metaphor of the molecular ecosystem captures some of the ways in which organisms and their environments can be seen as causally interdependent. The analogy between cellular and ecological habitats provides a rich framework to model and understand the relation between organisms and their environments and indicates how some conceptual tension between ecology and evolution could be solved.

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