FROM LAWS TO MODELS AND MECHANISMS:

ECOLOGY IN THE TWENTIETH CENTURY

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ABSTRACT:

Philosophers, and to a lesser degree historians, have paid much less attention to the discipline of ecology than to other areas of science (e.g. physics, chemistry, biology) as a focus for addressing issues in the philosophy of science. There are several reasons for this lack of attention. First, ecology comprises a wide variety of subfields, with different approaches to theorizing and experimentation. This variety can make it difficult to generalize in a way that is familiar to philosophers. Second, the relative youth of ecology as an identifiable scientific discipline, dating roughly from the end of the nineteenth century, means that many of the issues of concern to philosophers of science have long been understood in relation to the physical sciences and the more developed fields of biology. Third, ecologists themselves have been less engaged with the philosophy of science community than scientists in other disciplines.

In this paper, I hope to begin to address this imbalance. There is much to be learned from ecology about some of the current issues in the philosophy of science. Because ecology is a relatively young discipline, it is possible to trace significant changes in the relative importance of concepts such as laws, theories, models and mechanisms in historically short periods of time. To a large extent, the history of ecology serves as a microcosm of the larger history of science.

My focus is on the origins of population ecology in the 1920's and 30's (see Kingsland, 1985, for a good overview). This period was characterized by the influence of two non-ecologists (Alfred Lotka, Vito Volterra) who brought the perspectives of mathematics and the physical sciences to the study of biological populations. Combined with the work of experimental ecologists (especially Raymond Pearl; see Pearl, 1927), and promoted by them, ecology quickly established itself as a respectable scientific discipline. (It is worth noting that R.A. Fisher accomplished a similar feat in population genetics with the publication of The Genetical Theory of Natural Selection in 1929.) My thesis is that in this early period in the development of population ecology, for some ecologists (especially Pearl), the development of mathematics was integral to the search for laws in ecology. However, I will argue that while mathematical models continue to play a central role in ecology, the significance of generalizable ecological laws is much less prevalent today. In the early history of population ecology, emphasis was placed on the discovery of laws in the development of general theories. In contemporary ecological research, the emphasis is on modeling, with a corresponding search for underlying ecological mechanisms. Philosophers of science working in other areas have recognized a similar shift, from laws and theories to models and mechanisms. The context of ecology provides a new arena in which to examine this shift.

The early history of mathematical population biology begins with Alfred Lotka (1880-1949). Lotka, well known among ecologists for the Lotka-Volterra models of competition and predation (see Gotelli 1998), was strongly influential in incorporating into ecology the outlook and methods of the physical scientist. In 1925, Lotka published Elements of Physical Biology (later reprinted by Dover as Elements of Mathematical

Biology) in which he laid out a program for the study of the ecological properties within and among groups of organisms by analogy to the mathematical methods of physical chemistry.

In a chapter entitled "The Fundamental Equations of Kinetics of Evolving Systems," Lotka identified the simplest example of the application of these equations in the "Law of Population Growth," or what has come to be known as "logistic population growth" (see Lotka, p. 64ff.). The logistic equation expresses mathematically the basic idea that a population will initially grow at an exponential rate, but as resources become limited, its growth will slow down, peaking at a level compatible with the carrying capacity of the environment. While Lotka himself did not put a great deal of emphasis on the notion of a law (following Karl Pearson, he saw laws primarily as empirical regularities), the ecologist Raymond Pearl had a stronger notion in mind. Pearl argued that the aforementioned law not only captured the essentials of the growth of populations of organisms but also could be generalized to include the growth of an individual organism, understood as a population of cells.

The other main player on the mathematical side of ecology in this period was Vito Volterra, an Italian mathematical physicist. Volterra (1926) independently came up with equations describing the behavior of two interacting species in response to a problem posed by his son-in-law regarding cycles in the Italian fishery industry (see Kingsland, pp. 106ff.). Using his background in physics, Volterra also looked for equations that would represent the laws governing changes in population sizes, in this case involving predator-prey relations between different species of fish. In the work of both Lotka and

Volterra, we see the influence of scientists working outside of ecology in providing a mathematical framework based in the physical sciences for research in ecology.

The early emphasis on interpreting the equations of population ecology as the fundamental laws of ecological theory has given way to mathematical modeling and references to ecological mechanisms. While debates about the status of laws in ecology continue today (see Turchin, 2003, pp. 19-26; Colyvan and Ginzburg, 2003), much (perhaps the overwhelming majority) of the work of ecologists takes place in the absence of any explicit concern with uncovering ecological laws. Ecologists are typically interested in developing mathematical models that can be used to characterize and predict the behavior of ecological systems of study. This applies both to the fields of population ecology (initiated by Lotka, Volterra and others) and ecosystem ecology (an area of ecology which focuses on functional assemblages of populations of different species). The shift away from laws in ecology is replaced with a shift toward "mechanistic" models, models that capture in a mathematical form the underlying mechanisms driving the behavior of ecological systems. As evidence of this shift, I focus on the work of Paine and Levin (1981) on intertidal communities and Tilman et al. (2003) on plant communities. This shift highlights the need for a satisfactory understanding of the concept of a mechanism as it applies to ecological systems (see Machamer, Darden, and Craver, 2001, for a starting point). Ecologists use the term 'mechanism' regularly to characterize their research; thus, ecology provides a useful forum for evaluating and perhaps extending recent work by philosophers in developing a useful concept of a mechanism.

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