

---

A Succession of Paradigms in Ecology: Essentialism to Materialism and Probabilism

Author(s): Daniel Simberloff

Source: *Synthese*, Vol. 43, No. 1, Conceptual Issues in Ecology, Part I (Jan., 1980), pp. 3-39

Published by: Springer

Stable URL: <http://www.jstor.org/stable/20111524>

Accessed: 30/11/2009 00:43

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=springer>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



Springer is collaborating with JSTOR to digitize, preserve and extend access to *Synthese*.

<http://www.jstor.org>

DANIEL SIMBERLOFF

A SUCCESSION OF PARADIGMS  
IN ECOLOGY: ESSENTIALISM TO  
MATERIALISM AND PROBABILISM

1. THE MATERIALISTIC REVOLUTION  
IN EVOLUTION AND GENETICS

Lewontin (1974a), in his provocative essay 'Darwin and Mendel – The Materialist Revolution,' suggests that by the time *On the Origin of Species* was published in 1859, the notion of evolving species was already firmly established in both lay and academic circles. Embedding the evolutionary species concept in a matrix of new evolutionary thought in many areas of the arts, natural sciences, and social sciences during the late eighteenth and first half of the nineteenth centuries, he points to a different significance of the Darwinian revolution. The emerging evolutionary worldview was incompatible with the philosophical tradition, stretching back to the Greeks, which, although patently metaphysical, still dominated nineteenth century thought: viz. Platonic idealism and Aristotelian essentialism (Popper 1961, 1963). Idealism views the material objects of the world as imperfect embodiments of fundamental, unchanging essences or ideal formal structures. Plato drew the analogy of shadows cast on a cave wall for the imperfect reflections which constitute the objects we can perceive with our senses, although Aristotle sought his version of essential forms within particulate matter, and not in some spectral transcendental realm. Lovejoy (1936), Wiener (1949), Peckham (1959), and Ghiselin (1969) suggest that the nascent evolutionary worldview engendered a reaction to metaphysical essentialism, especially in politics and economics, which eventually paved the way for the Darwinian revolution.

Lewontin observes that a necessary consequence of Greek metaphysical philosophy is that differences between objects belonging to the same type have a different ontology and ontogeny from those of differences between the types themselves. The former are

'noise' or disturbance beclouding the latter, and can only confound our attempts to see the essential or ideal structure of the universe. The goal of philosophy and science, in this view, is to see through this variation and to try to understand the ideal forms. Mayr (1963) outlines the domination of biology, particularly systematics, by typological thought and how this outlook retarded our understanding of the most dramatic evolutionary event, speciation. For if species correspond to types, essences, or ideals, which were by definition eternally unchanging, then how could evolution occur at all, much less result in the production of a new species (type)? The 'type' specimens of taxonomy are, of course, a legacy of typological thinking, and epitomize the difficulty in defining species which such a philosophy imposes on us.

So long as evolutionists were tied to a typological universe, they were confronted with an insoluble problem: what mechanism could produce a type *de novo* (Ghiselin 1969, Lewontin 1974a)? Two solutions are possible: either an individual must change type or an individual (or individuals) of one type must produce offspring of a different type. Both solutions were proposed before *The Origin*. Lamarck suggested the former, with the specific mechanism that use or disuse of particular organs could cause an individual to change type; his giraffe example is well known, with necks (and therefore types) gradually changing. Geoffroy St. Hilaire adopted the latter, with dramatic and discontinuous change in type said to occur at reproduction. But neither solution was accepted, and Lewontin argues that they failed because they rested on inferred but unobserved entities or forces. Lamarck's theory of inheritance of acquired characteristics was not founded on observations from nature, and though Geoffroy's proposal of saltational speciation could have adduced as evidence the rare occurrence of unusual variants among offspring of normal parents, it did not. Instead, he posited unobserved changes in type. Both ideas, therefore, were easily and persuasively dismissed by the ant-evolutionist Cuvier, who won a widely publicized debate with Geoffroy. The revolution of Darwin and Wallace consisted precisely in examining the individual variation which had previously been discarded as "noise," rather than types, essences, or ideals. Instead of viewing this variation among in-

dividuals as a hindrance, they took it to be the proper focus of study. Variation between individuals and variation between species were no longer distinct, but rather were causally connected. In short, the differences between individuals within a species were converted to differences between species. And the mechanism of conversion rested on a trivial syllogism plus three easily observed, material properties of individuals. The syllogism, of course, was that of Malthus (1798), and that it independently inspired Wallace (Ghiselin 1969, McKinney 1972) precisely as it did Darwin is a reflection of a widespread replacement of Greek metaphysics by materialism in all areas of human thought (Barzun 1958) which was intricately intertwined with the burgeoning of evolutionary notions alluded to above. The Darwinian revolution was to become the leading edge of this rise of materialism, and it is appropriate that Malthus's consummately materialistic formulation, resting solely on the requirement for food and sex, should be at its root.<sup>1</sup>

The three observations on individuals in nature which Darwin and Wallace required for the Malthusian syllogism to produce evolution were:

1. Within a species, individuals vary in morphology, physiology, and behavior.
2. Different variants produce different numbers of offspring.
3. The variation is at least partly heritable.

All are apparent from even a casual observation of animal and plant breeding. The Darwinian mechanism requires no divine or vital forces or essences, as do orthogenetic interpretations, nor the unobserved events of Lamarck's and Geoffroy's explanations. Lewontin notes that the Darwinian revolution was even more revolutionary than the earlier Newtonian one, for it lacked hypothetical constructs such as Newton's ideal bodies following ideal trajectories from which individual material objects varied somewhat.

Darwin's subsequent difficulty in defending his evolutionary mechanism of natural selection lay in the nature of points (1) and (3) above. It was required that, whatever the mechanism of heredity, it must allow both the production of variant offspring and the similarity of parent and offspring (the functional definition of 'heritable').

Futhermore, the variation itself, once produced, must be heritable. The problem which Darwin and all other nineteenth century biologists but one never satisfactorily resolved was to find a genetic mechanism capable of producing both similarity and difference. The irony, according to Lewontin, is that Darwin's failure can be attributed directly to his not applying to genetics the materialistic outlook which served him so well for evolution. He believed, as did other nineteenth century naturalists, that inheritance was generally blending, with the characteristics of offspring a blend of their parents' characteristics; this belief is readily traced to Darwin's attachment to essentialist, typological thought (Ghiselin 1969). This mode of inheritance boded ill for Darwin's notion of natural selection of variants within a population, for it meant that all new variation, however it arose, would be lost, or at least vitiated, through blending with the traits of the 'normal' mate. Mutants (called 'sports') were not viewed as an important source of variation, since they were only recognized when they were grossly abnormal (and usually poorly fit); in any event, their origin and significance were unrecognized before the rise of genetics in the twentieth century.

Darwin was increasingly concerned with this apparent gap in his theory. Whereas the first edition (1859) of *The Origin* stressed the evidence for evolutionary change and the operation of natural selection, the fifth (1867) and sixth (1896) editions betrayed an overriding desire to account for the variation, and did so primarily through an explicit acceptance of inheritance of acquired characteristics, the very doctrine which the first edition discounted! Darwin produced no new material evidence to support the Lamarckian view, and perhaps the most poignant manifestation of the crisis in which the Darwinian paradigm found itself was Darwin's 'Provisional Theory of Pangenesis' in *The Variation of Animals and Plants under Domestication* (1868). Pangenesis, dating back at least to Nathaniel Highmore (1651), and in outline to Hippocrates (400 B.C.), postulates tiny entities (Darwin called them 'gemmules') that arise in particular parts of the body, and confer the characteristics of the part in which they arise. Darwin hypothesized that at reproduction the gemmules are carried from the different body parts to the reproductive organs, there to be

packed in sperm and eggs. This mechanism allows the inheritance of acquired characteristics for it provides a means by which environmentally induced changes in somatic cells can be transmitted to gametic cells.

Though Darwin came to view pangenesis as both his favorite hypothesis and his salvation (Irvine 1955), and Ghiselin (1969) defends it as a reasonable hypothesis, in the light of nineteenth century knowledge, to explain certain empirical observations, Lewontin perceptively observes that it was a retreat to idealism or essentialism, the unseen gemmules constituting egregiously ideal essence-conferring entities. More remarkably, Darwin made a number of material observations which had already led Mendel to a solution to Darwin's dilemma, yet failed to recognize their significance. He recorded that inheritance need not be blending but rather that traits may contrast sharply, that one trait may be dominant over the other, causing the second to manifest itself only after two generations of interbreeding (Irvine 1955), and even an approximate 3 : 1 ratio of two flower types in the second generation of interbreeding between two varieties of snapdragons (Lewontin 1974a). His failure, and those of others doing similar breeding experiments,<sup>2</sup> Lewontin attributes to a Platonic idealism, focussing on groups of offspring as wholes rather than on the physical variation among the component individuals. Such a focus proceeded logically from a world view of types (ideals) and individuals imperfectly reflecting these types. Further, a concomitant of this view was the attempt to seek the causes of differences between the types separately from the causes of variation within the types (species). Group statistics, particularly means, were routinely reported as type descriptions, precluding an examination of intraspecific variation.

Mendel alone realized that both similarity and variation are produced by the same mechanism, and by concentrating on the variation among individual offspring of the same cross he deduced that inheritance is particulate, not blending. Key to this deduction was his emphasis on individual differences. Lewontin observes that Mendel nowhere characterized separately the average appearance of offspring and their variation. The mean, as a summary statistic of a cohort, had no place in Mendel's scheme. Further, he kept offspring

of different crosses separate, even when the parents had identical appearance. Both of these techniques were in contradistinction to those of biometricians such as Galton, whose use of group characterization led him to a blending theory of inheritance. That Mendel's two papers (1866, 1870) lay utterly unrecognized until 1900 reflects the truly revolutionary nature of his materialistic focus on individuals and differences or discontinuity. Just as surely, his simultaneous and independent discovery in 1900 by DeVries, Correns, and Tschermak demonstrates in the largest sense the progress of the ongoing materialistic revolution in all disciplines, and more directly that the sort of research being done on heredity inevitably led to the recognition that inheritance is particulate and to the basic mathematics of genetic segregation. In their papers in the *Reports of the German Botanical Society* Mendel's three discovers all credited him with primacy in this recognition, but it is transparent that he really had no effect at all on the revolution that bears his name. Merton (1973) discusses his retreat from research after failure to receive credit for his discovery.

## II. PROBABILISM AND THE NEO-DARWINIAN SYNTHESIS

The materialist revolution in evolution and genetics was not quite completed with Mendel's rediscovery. I would argue that three further developments were required, two of them technical advances within genetics, the other a permeation of biology by an aspect of the broadly based rise of materialism which I have not yet discussed.

First, the 'factors' of Mendel (called 'genes' by Johannsen in 1903), although subsequently shown by geneticists (primarily Boveri, Sutton, Morgan, and Bridges) to be material bits of observable chromosomes, were still ideal constructs or essences for Mendel and his three adherents, insofar as they could only infer the existence of such entities by looking at morphologies of living organisms. Only with Sutton's insight (1903) that the chromosomes of the cytologists were (or bore) the genes of the geneticists was the materialist revolution in genetics beginning to be firmly grounded in physical observation. Even this insight did not completely put genetics on a materialistic basis, for starting with Johannsen's distinction (1903, 1909) between

'genotype' and 'phenotype' came a growing recognition that the morphology, physiology, and behavior which we observe are not a direct, one-to-one translation of the genes, but rather the product of a complex and fundamentally inseparable interaction between genes and environment. Waddington (1957, 1974, 1975) did most to elucidate this interaction, and his and other work, summarized by Lewontin (1974b, particularly chapter 1), indicates that in every generation there are four transformations determining the genotype and phenotype. Two of these are steps between genotype and phenotype; even more important (a point to which I will return soon), none of the four involves a completely specified, deterministic outcome.

The second technical advance required for the Darwin-Mendel revolution to be both complete and unified was an understanding of how the particulate and ultimately material genes could produce the continuum of physical traits that was observed in nature, and on which Darwin claimed that natural selection acts. This is still an area of active research, and many means are known by which discrete genes are translated into continuous variation: polygenicity, position effects, operators and repressors, and the interaction of genes with environment during development, just discussed, are a few. But the first clear demonstration that continuous variation is compatible with Mendelian genetics was by Morgan and his colleagues in the first thirty years of this century.

Even more fundamental than these technical advances to the completion of the materialistic revolution in genetics and evolution was the recognition that evolution, and its underlying population genetics, are stochastic and not deterministic processes. Statistics, a mathematics of variation and indeterminism or probability, developed late in comparison with other branches of mathematics (Robbins 1974) and was, until recently, a scientific stepchild. This is not surprising, in view of the apparent success of the Newtonian revolution with its deterministic calculus. When Newton's ideal trajectories and forces seemed to accord so well with nature, why focus on individual variation? It should be very clear that statistics is inherently materialistic and anti-typological, since it takes the 'noise' as its object of study, and not the type. Its two sixteenth century beginnings (Robbins



1974) – an attempt to increase gambling success, and the collection of data on population, wealth, and industry of a state – are as materialistic as can be. That it was an explicit denial of typological thought accounts for its meager success in permeating the various intellectual disciplines until this century. An ideal or essential universe is *ipso facto* a deterministic one.

The nineteenth century was dominated by a deterministic mechanics (Kac 1974, Robbins 1974), hypostatized by twin hypothetical ideal beings, Laplace's Demon and Maxwell's Demon. The former could predict in Newtonian, cause-and-effect, action-reaction fashion the complete state of the universe, given knowledge of the positions and velocities of all its particles for a single instant. The latter could violate the second law of thermodynamics, and in so doing, construct a perpetual motion machine. Kac (1974) dates the beginning of the revolution against determinism in 1859, with Maxwell's observation that the velocities of gas particles are distributed according to a statistical law. It is almost superfluous to observe that 1859 was the year of *The Origin*, and that Barzun (1958) views it as the signal year in the materialist revolution, with Marx's *Critique of Political Economy* and Wagner's *Tristan and Isolde* combining with *The Origin* to signify the overthrow of idealism in the arts and social and natural sciences.<sup>3</sup> Maxwell's observation extends the revolution to the physical sciences, and it was in the physical sciences that an explicit recognition of the probabilistic nature of the universe led to the exorcism of the demonic reifications of typology, essentialism, and idealism. Aspects of this exorcism have been treated by Brillouin (1962), Ehrenberg (1967), and Klein (1970). The key tools were:

(1) Einstein's Special Theory of Relativity (1905, *cf.* Lanczos 1974), with its consequence that a measurement (such as those by the demons) would necessarily affect the object measured.

(2) Heisenberg's Uncertainty Principle (1927), which states that an inherent property of matter precludes either demon from simultaneously measuring both velocity and location of even a single particle, much less all of them.

(3) An information theoretic analog of the second law of thermodynamics enunciated first by Szilard (1929), and elaborated by

Shannon (1948, *cf.* Tribus and McIrvine 1971) and Brillouin (1962), which states that Maxwell's Demon must have information in order to sort fast and slowly moving particles (and so to violate the second law), and that the minimum amount of energy which it will need to get the information enabling it to do its sorting will be more than it can possibly derive from the ordered state which the sorting would produce.

These generalizations from the physical sciences, plus two counter-intuitive theories – Planck's Quantum Theory (1900, *cf.* Wilson 1944) and Bohr's Complementarity (1928) – destroyed the Victorian optimism, engendered by the success of the Newtonian Revolution, that an improved technology would allow an infinitely close approach to true, precise, and readily understood knowledge of the physical world. One might be tempted to emphasize the essential pessimism wrought by this overthrow of Newton, and to point to Gödel's Theorem (1931), that any logical system, including the Greek hypothetico-deductive one, contains unprovable assertions, as the crushing, crowning blow. But my purpose is better served by observing the *form* of statements allowed by the three exorcising tools. In each instance, the most complete statement which can be made about the state of the world is a probabilistic one: a distribution of probabilities of states of the physical universe (or some part of it), or a specified statistical distribution of possible outcomes of some event. Dirac (1977) sketches the replacement in this century of an ideal, deterministic physics by a probabilistic one based on observable quantities.

This probabilistic and pessimistic aspect of the materialistic revolution spread beyond the physical sciences. Robbins (1974) argues that it has finally caused us to think statistically about all aspects of our day-to-day existence. The key figure in transferring probabilistic thinking from the physical sciences to the biological sciences was Quételet (Singer 1959, Robbins 1974) and though his attempt began in earnest in 1853, I would argue that its culmination did not occur until the Neo-Darwinian synthesis of 1917–1930 (Provine 1971, Allen 1976) which wedded Mendelian genetics to Darwinian evolution. The main architects of this union, Fisher, Haldane, and Wright, working quite independently produced a probabilistic conclusion very much in the

spirit of the concurrent victory of probabilism in the physical sciences. That this should be so is, in retrospect, not surprising, since Mendel's results were themselves statistical in nature. His ratios of traits in second generation progeny of a varietal cross were never *exactly* 3 : 1; rather for all seven traits they deviated slightly from 3 : 1. Mendel was not misled by this deviation; focussing on the exact numbers of each kind of offspring, as stated above, he clearly interpreted his results as the outcome of events which happen with fixed probability; the variation was not 'noise,' but expected. He did *not* postulate an ideal ratio, and the probabilistic interpretation was a necessary consequence of the materialistic outlook.<sup>4</sup> The Neo-Darwinian synthesis, in brief, concluded that the best we can do is to specify some distribution of probabilities of gene and genotype frequencies, given certain underlying (and themselves probabilistic) constraints on production and survival of gametes and zygotes, and on unions of gametes. Thus ended forever the notion that evolution can be orthogenetic, at least with much precision at the level of genes. For *one* of the major forces which the synthesis demonstrated to affect the gene and genotype frequencies – genetic drift – even the direction of frequency change cannot be predicted, and the firmest statement we can make is that the magnitude of the change after a specified number of generations will *probably* fall within a specified range. The major thrust now, as stated above, is to determine the rules (doubtless also probabilistic) by which the genotype and environment interact to produce a phenotype. Whatever is learned about these rules, we can say that the Neo-Darwinian synthesis sounded the death-knell for Newtonian cause-and-effect determinism in biology as surely as did relativity and complementarity in the physical sciences, at almost the same time. Further, the synthesis was a development in the ongoing materialist revolution. Thomas Pynchon's *Gravity's Rainbow* (1973) has as two antagonists Roger Mexico, apostle of the new physics, and Pointsman, the 'Antimexico,' 'left only with Cause and Effect.' Mexico propounds the utility of the Poisson distribution and characterizes himself by the equation for the normal curve. The metaphoric significance of these characters, representing the shift in human thought which I have outlined, is

transparent in Mexico's manifesto:

...there's a feeling about that cause-and-effect may have been taken as far as it will go. That for science to carry on at all, it must look for a less narrow, a less...sterile set of assumptions. The next great breakthrough may come when we have the courage to junk cause-and-effect entirely, and strike off at some other angle.

### III. THE RISE OF PROBABILISM AND MATERIALISM IN ECOLOGY

Ecology has undergone, about half a century later than genetics and evolution, a transformation so strikingly similar in both outline and detail that one can scarcely doubt its debt to the same materialistic and probabilistic revolutions. Many major events in this transformation have been described by Ponyatovskaya (1961) and McIntosh (1975, 1976), but the relationship to developments both inside and outside biology seems not to have been noticed. An initial emphasis on similarity of isolated communities, replaced by concern about their differences; examination of groups of populations, largely superseded by study of individual populations; belief in deterministic succession shifting, with the widespread introduction of statistics into ecology, to realization that temporal community development is probabilistic; and a continuing struggle to focus on material, observable entities rather than ideal constructs; all parallel trends which I have described for genetics and evolution.

Ecology's first paradigm was the idea of the plant community as a superorganism, propounded by Clements in the first American ecology book (1905) and elaborated by him in numerous subsequent publications. The crux of this concept was that single species populations in nature are integrated into well-defined, organic entities, and key subsidiary aspects were that temporal succession in a sere is utterly deterministic, analogous to development of an individual, and leads inevitably to one of a few climax communities. The relationship between the stylized, integrated superorganism and the deterministic successional development producing it is organic and fundamental, as pointed out by Tansley (1920): "When we have admitted the necessity of first determining empirically our natural units, we have to find ways of grouping them. This way we can only find in the concept of development. Development of vegetation is a concrete fact equal with

its structure.” McIntosh (1975, 1976) illustrates the extent to which this paradigm dominated ecology until recently with a series of well-chosen quotes and an analysis of ecology texts.<sup>5</sup> Suffice it here to cite Shelford (1913), one of the leading animal ecologists of the first half of this century:

Ecology is the science of communities. A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to the natural phenomena of its habitat and community... is not properly included in the field of ecology.

Although the superorganismic community concept with its deterministic succession arose in plant ecology almost as a logical consequence to de Candolle’s pioneering descriptions of plant formations, it quickly won acolytes among zoologists (*e.g.*, Shelford) and limnologists (*e.g.*, Naumann). Allee as early as 1931 had aligned his work on animal symbioses with the superorganismic paradigm, observing “. . . a more or less characteristic set of animals which are not mere accidental assemblages but are integrated communities.” Emerson’s similar focus also led him to the notion of an ‘integrated ecological community’ (1939). Thienemann described a lake community as “a unity so closed in itself that it must be called an organism of the highest order” (*fide* McIntosh 1975). Probably even more important than this zoological and limnological support in solidifying the superorganism concept as a paradigm was Elton’s description of the food chain as a conduit for community energy flow. Although Elton himself was not an adherent of the superorganism view, his discovery provided such a diagrammatic analogy to the physiology of an individual organism that it was readily incorporated as an integral part of the superorganism, in fact, one of the forces giving it organismic cohesion. Citing Elton (1927), Clements and Shelford (1939) stress that trophic structure studies “can be utilized to reveal the significance of each process in the working of the community as a whole.” Further, “the universal role of coaction [including trophic interaction] is to be seen in the integration of plant and animal relations to constitute an organic complex, which is characterized by a certain degree of dynamic balance in number and effects.”

That a formulation almost identical to Clements' appeared in Russia (Sukachev 1910, 1915, 1931, in Ponyatovskaya 1961) at almost the same time as in the United States, and that it achieved comparable paradigm status (McIntosh 1975), also suggests that its sway is not to be attributed simply to the force of Clements' personality or the persuasive prose and prodigious volume of his publications. Similarly, the appeal of the superorganism concept outside ecology (*e.g.*, Smuts (1926) states that his philosophy of holism was inspired by Clements) argues that larger philosophical forces militated for its acceptance. Perhaps the strongest evidence to this end is that the superorganism paradigm had, from its inception, eloquent critics – notably Gleason (1910, 1917, 1926, 1939) in this country and Ramensky (1910, 1925, in Ponyatovskaya 1961) in Russia, but also including Lenoble and Negri in Europe – whose work was uniformly dismissed or ignored until 1947 (Kormondy 1965, McIntosh 1975).

Surely the ultimate philosophical basis for the superorganism paradigm is Greek metaphysics, and this explains its strong appeal in the face of data-based objections by Gleason and others. For the superorganism, one of a small number of distinct climax communities, is an explicitly typological construct which allows immediate classification of an observed community into an already described category. Differences among individuals within that category are viewed as less important than the similarities which cause them to be classified together, and are ontogenetically different from differences between categories. The latter are viewed as a reflection of different organizing relationships (such as the 'multiple stable equilibria' (Sutherland 1974) in a currently popular incarnation of the superorganism concept (*cf.* Holling 1973)). The former, as in pre-Mendelian genetics, are rather viewed as 'noise,' probably the result of minor differences in physical environment, like soil chemistry, during development. And the deterministic path of succession in the strictest Clementsian monoclimate formulation is as much an ideal abstraction as is a Newtonian particle trajectory. There is a tidiness, an ease of conceptualization, to well-defined ideals moving on perfect paths that is as appealing, both aesthetically and functionally, in ecology as it was in genetics and evolution. Unfortunately, it is as poor a descrip-

tion of ecological as of evolutionary reality. That the superorganism paradigm did not lead to mechanistic understanding of the operation and structure of nature is not surprising. As MacFadyen (1975, and references therein) points out, in many sciences it has proven possible to treat emergent features of a higher level deterministically while recognizing that the underlying, component phenomena are stochastic; it is in this spirit that the deterministic superorganism held out the promise of an adequate description of the almost unimaginable complexity of natural communities. But the underlying supposition of rich and omnipotent connectedness and interaction precluded an understanding of low-level, probabilistic mechanisms, a danger in treating any field holistically: "Those who are obsessed by the interactions of everything with everything else...are of necessity diffuse. Practical conclusions are not drawn from the holistic contemplation of totality" (Pirie 1969).

The watershed year for the materialistic and probabilistic revolution in ecology was 1947, in which three respected plant ecologists (Egler, Cain, and Mason) all published papers in *Ecological Monographs* forcefully attacking the Clementsian paradigm and citing Gleason's 'individualistic concept of plant association' as the first articulation of their view (McIntosh 1975). The formal analogy to Mendel's resurrection is patent, but even more enlightening is an examination of the specific reasons given for this dramatic change. Egler cites Raup (1942) and Cain (1944) to the effect that the Clementsian assumption of cause-and-effect in community development is an *a priori* explanation, rather than an empirically derived mechanism, and he claims that his own extended observations on a series of Hawaiian communities are completely in accord with the individualistic concept of Gleason's 'all but forgotten paper.' Cain avers his interest in "actual, concrete, specific communities on the ground," and scorns the 'hypothetical' Clementsian community. Later he suggests that the monoclimate theory as originally stated was wrong, had subsequently become a panchreston, and that focus on local studies will demonstrate the correctness of Gleason's individualistic hypothesis. In a 'heretical' section entitled, 'Does the Association Have Objective Reality?', he bases his negative answer on materialism ("Species are

facts, ...Environments are facts.") while lambasting the "pre-conceptions of the reality of the association in the abstract." He is at pains to stress that a specific stand, having material existence, is real, while the association, only a hypothetical ideal, is not. In the final analysis, for Cain, the superorganism is a fictitious construct because 1) unlike a species, it has no continuity by descent, and 2) there is no objective criterion for determining when two stands are similar enough to belong to the same association. Mason also stresses that genetic continuity renders the species population a real entity, and lack of it renders the community a fortuitous abstraction, limited only by the 'coincidence of tolerance' of environmental factors by its component species. He, too, credits Gleason as the first proponent of this notion.

The spate of ecology texts early in this decade (Colinvaux 1973, Collier *et al.* 1973, Krebs 1972, Poole 1974, etc.) all agree that, twenty-five years after its rehabilitation, the Gleasonian paradigm had overthrown the Clementsian one (McIntosh 1975). If one asks why the revolution occurred when it did, two convergent lines of research appear to have necessitated it. First, the facts that real stands generally *lack* well-defined boundaries, and when such boundaries do exist they are frequently associated with abrupt changes in the physical environment, were often noted by Gleason and Ramensky, but by 1947 constituted an intolerable contradiction of dogma by observed fact. Egler, Cain, and Mason all attack the superorganism paradigm on this basis using data from field studies. This type of observation was greatly extended in the next decade by two independent groups; Curtis' 'vegetational continuum' (Curtis and McIntosh 1951, Curtis 1955, 1959) and Whittaker's 'gradient analysis' (1956, 1967) both describe the spatial distribution of plants as a consequence of the individual, relatively uncoordinated responses of individual species to gradients in the physical environment, without need to invoke groups of species' persisting or dying as a unit. It may be observed that this work also demonstrates that discrete populations acting individually produce a community continuum (whatever statistic is used to characterize communities) much as the Morgan group's understanding of polygenicity, position effects, etc. resolved



the apparent Mendelian paradox that phenotypes are, for the most part, continuous while the alleles of a gene are discrete.

The second line of research which, I would argue, contributed to the demise of the superorganism was a shift in emphasis within the study of animal and microbial populations which led, inevitably, to focussing on individual populations as proper objects of study, or at most two or three of them together, rather than the entire community in which they are embedded. The failure of Haskell in 1940 to attract interest in a hypervolume concept of the species' niche (McIntosh 1976) is a reflection of the lack of interest in studying populations *per se*. That Hutchinson's identical suggestion in 1957 has generated an enormous literature on niche parameters and relationships is an indication of the extent to which the plant population research by Egler, Cain, Mason, Curtis, and Whittaker and animal population studies by Nicholson and Park (*i.a.*) had legitimized the population or few-species interaction as an object of study, independent of the community. Experiments on real populations were key to this shift of focus from community to population.

Population ecology had its own origin in ideal abstractions. The progenitor of the deterministic logistic equation, which has dominated population ecology right into this decade, was a paper by Verhulst (1838) communicated, ironically enough, by Quételet, the seminal figure in introducing statistics into biology. The irony, of course, is that the logistic curve is as much an ideal description of population growth as a Newtonian trajectory is but an idealization of particle movement.

The logistic model of single population growth was virtually ignored until the early twentieth century, when it was simultaneously exhumed and exploited by Lotka (1907, 1925), Pearl and Reed (1920), Pearl (1925), and Volterra (1926, 1928); the first and last authors even became eponyms for the equation, which they elaborated into a pair of equations to describe predator-prey or parasite-host relationships. Gause (1934) performed interspecific competition experiments on microorganisms (ultimately his basis for Gause's Law, or the Competitive Exclusion Principle) which he believed were satisfactorily explained by a two-equation system based on the logistic. The logical

and complete conclusion to this proliferation of logistic based population descriptors did not come until 1968, when Levins' community matrix attempted to describe and predict the workings of an entire community, based on the assumption that all species populations adhered to the ideal logistic law modified only by equally ideally characterized pairwise interactions.

But long before this conclusion, criticism of the logistic had set in, based on material properties of living organisms, as opposed to abstract, reproducing particles. Gause himself (1934) was an early doubter of the predation version of the logistic, and attributed his discrepancies between experimental results and equation predictions to a failure of the mathematical model adequately to describe the biology of a particular pair of species. But Nicholson (1954b) makes a more cogent and, from the standpoint of the underlying shift in thought which I am describing, suggestive analysis of the discrepancy. He demonstrates that the equations can only represent a mean result of an interaction between two large populations ("these equations represent the statistical effects of the interaction of large numbers of individuals operating in adequate space") and that Gause's experiments were too small to display with high frequency the statistical expectation. Observe that variation among populations or replicates had as little place in logistic formulations as variation among individuals had for the pre-Mendelians.

Nicholson's own work (1933, 1947, 1954a, b, Nicholson and Bailey 1935) was even more severely critical of Lotka-Volterra type models. His early two and three-species models of insect host-parasite systems, and more importantly his later experiments and models of single species populations of *Lucilia cuprina* (the sheep blowfly), all emphasized that logistic formulations did not and could not (because they contain too few parameters) realistically represent any populations but those of the simplest microorganisms. In particular, the invariant carrying capacity, the fact that the equation is continuous while organisms occur as discrete individuals, the non-decaying asymptote, and the lack of lag factors all render the logistic the most aseptic of ideals, cleansed of many of the most interesting (and 'noisiest') biological properties. Nicholson noted that, aside from the

inappropriateness of the logistic as a model even for a laboratory population (such as his blowflies) in a controlled environment, it took no account of climatic, edaphic, biotic, and evolutionary influences. In his own mechanistic models, Nicholson attempted partially to account for these more idiosyncratic factors, sacrificing generality for realism and achieving an impressive match to population data in certain instances. Interestingly, in light of his discussion of Gause's results, Nicholson's models were always deterministic; variance was never calculated, nor confidence limits given for goodness-of-fit of any real data. Nevertheless, by his focus on single or few populations, and partial success in modelling them, Nicholson could only damage the claim of the superorganism supporters, quoted earlier, that "ecology is the science of communities." By the nature of his models, he also began to break the hold of Greek metaphysics on population ecology.

Park's flour beetle research (1948, 1954, 1962, Park, Leslie, and Mertz 1964) had an even greater impact. The primary emphasis was not on modelling ideal population trajectories, but rather on examining how physical environmental factors affect the *outcome* of competition between two populations and on the precise physical mechanisms (such as cannibalism, poisoning of the medium, etc.) by which the outcome is achieved. The most revolutionary aspect of Park's work, however, was the discovery that under certain environmental conditions a specific outcome could not be predicted; the process was stochastic, and the best prediction one could possibly make, very much in the neo-Darwinian mold, was a probability that a given species would win. It is significant that Park published on this aspect of his work with Neyman, the statistician (Neyman, Park, and Scott 1956), for this was one of the first inroads of statistics into population ecology, and constituted an explicit recognition that processes on the population level are not deterministic.<sup>6</sup> Park's stochasticity was a breakthrough, and his success on the population level could only aid the shift from superorganismic communities to populations as an object of study.

A measure of the impact of Park's indeterminate outcome is the disproportionate emphasis placed on this aspect of the *Tribolium*

work (Mertz 1972). Virtually every subsequent ecology text cited this result, and Mayr's review of the nature of biological causality (1961) adduced it as an example of indeterminacy caused by the extreme complexity of ecological interactions (it is notable, however, that this two-species laboratory competition must be among the simplest ecological phenomena). Further, a major effort was mounted (*e.g.*, Hardin 1960, Lerner and Dempster 1962, King and Dawson 1971) to demonstrate that the indeterminacy was illusory and could be accounted for by uncontrolled variation in Park's experimental conditions. Lerner and Dempster, for example, were at pains to show that genetic differences among the cultures could account for contrasting outcomes in different 'replicates.' Two points require comment here. First, increased genetic uniformity greatly reduced, but did *not* completely eliminate, unpredictability in outcome of competition between supposedly uniform strains (*cf.* Table 2 of Lerner and Dempster 1962). Mertz, Cawthon, and Park (1976) show that demographic stochasticity is also important. Second, from the standpoint of populations in nature, some degree of genetic heterogeneity must be considered a universal premise; attempting to explain away observed different outcomes on these grounds is analogous to seeking the reasons for a Poisson distribution of raindrops in buckets in the specific determinants of the trajectory of each drop. Of course such determinants exist and in principle could be found (at least to the limits imposed by the uncertainty principle). But the information we are likely ever to have available renders rainfall patterns the epitome of a stochastic process, and viewing it in this light will serve us well and allow sufficient predictions. I would argue that the genetic composition of natural populations will be as elusive as the physical forces acting on precipitation, and our understanding of population phenomena will require stochastic treatment.

I do not wish to imply that the new interest in single species populations was to the exclusion of concern with community properties. Rather the growing conception of the community as a collection of species, rather than a superorganism, led in some quarters to an analytic rather than synthetic mode of community research: community properties were approached through assembly of populations

and pairwise population interaction which were ostensibly well studied first. Mertz (1972) gives many instances of this tack from the *Tribolium* literature; two further examples will suffice here. First, the determinants of community stability have long been sought as a matter of both practical and theoretical interest. Clements (1936) ascribed the increasing stability of successional stages in a sere to an increasingly tight organization and integration of community components. More recently, interest has focused on another community attribute, species diversity, as possibly conferring stability. Goodman (1975) suggests that this hypothesis in its simplest form is disproven (but cf. McNaughton 1977)), but even while other community level attributes are sought as potential determinants (e.g. May's (1973) discussion of properties of the community matrix), a reductionist explanation was proposed by Frank (1968): the *population* characteristics of one or a few critical species determine whether the community as a whole is stable, by whatever statistic one wishes to characterize stability. Goodman (1975) strongly supports this notion, that a community property is a fortuitous consequence of properties of one or a few component species.

Horn's attempt (1975) to study succession as an exponentiation of a matrix of transition probabilities between individual tree species not only reduces successional phenomena to the level of populations, but explicitly introduces stochasticity as a fundamental successional property, the antithesis of deterministic succession leading to a superorganismic climax. Similarly conceived treatments are by Stephens and Waggoner (1970), Waggoner and Stephens (1970), Leak (1970), and Botkin, Janak, and Wallis (1972). Other detailed observations at the population level have also suggested that succession is truly a population phenomenon (Drury and Nisbet 1973), largely determined by the effects and tolerances of a few critical species. Needless to say, the work of Curtis and Whittaker discussed earlier supports this view.

#### IV. THE CURRENT STRUGGLE

Finally, one ought not to be left with the feeling that the materialistic,

probabilistic revolution in ecology is a *fait accompli*. Essentialism, idealism, and determinism are, if not dominant, still rampant (Slobodkin 1975). Their persistence is partly a reflection of ecologists' diffidence because of the apparent sloppiness of their field compared to the physical sciences; "physics-envy is the curse of biology" (Cohen 1971). The large scatters of points and jagged trajectories which typify ecology (e.g., the colonization cruves for new island communities (Simberloff and Wilson 1970) and the dispersion of the number of herbivores on different plant species (Strong and Levin 1977)) seem to foster the view that ecology is not quite so scientific as chemistry and physics, and militate for a search for more ideal models, often from the physical sciences themselves. For example, a topical endeavor during this decade has been the erection of deterministic rules for packing species into communities, as if some clearly and permanently bounded physical entity could be denoted 'community' and studied in isolation. In MacArthur's summary work (1972), he presents an analogy of species-packing to crystal packing, suggested by Gordon Lark, a biochemist. Such an ideal, deterministic approach appears to be symptomatic of a wide variety of proposals on species-packing, and May (1974, *fide* McIntosh 1976), a physicist-turned-ecologist who has quickly become the leading figure in analytic ecological modelling (e.g., May 1973), raises the metaphor to an even higher level, envisioning the eventual establishment of many 'perfect crystal' models in ecology and the consequent emergence of ecology as co-equal to "the more conventional (and more mature) branches of science and engineering. . . ."

The crystal-packing and related models for species-packing, however, do not appear to have been strikingly successful; certainly they constitute a retreat to idealism. The community matrix of interaction coefficients from the deterministic logistic equations (Levins 1968) is still used to characterize communities and to explain community properties (e.g., Culver 1975). May's treatment of the matrix, and the community in general (1973), appears to be revolutionary since it incorporates statistical noise to produce a stochastic neighborhood outcome of community dynamics, rather than a single deterministic point. But the underlying equations are distressingly

ideal, and the noise distribution is an *ad hoc* suggestion. MacArthur's quadratic form  $Q$ , which he claims competition minimizes (1969, 1970), is not only a deterministic consequence of logistic equations, but as metaphysical an entity as Darwin's gemmules, Maxwell's Demon in statistical mechanics, and Adam Smith's hidden hand in economics. Surprisingly, it is condoned by Lewontin (1969). Limiting similarity  $L$  of coexisting species was calculated from logistic equations by MacArthur and Levins (1967); despite a data-based, mechanistic demonstration of its incorrectness by Dayton (1973) and a cogent, damning theoretical treatment by Heck (1976) it is still cited as a possible characteristic of nature (*e.g.*, Fraser 1976). Neill's experiments showing that the multispecies form of the logistic model rests on untenable assumptions (1974) seem not to have been heeded. MacFayden (1975) deplores the autonomy and independence from the biological world which the essentialist strain in ecology appears to have achieved, but his explanation – frequent failure to propose truly testable hypotheses – is only the proximate cause. The ultimate difficulty is the tenacity of the Greek metaphysical worldview.

Another manifestation of this tenacity is the relative independence of the nascent stochastic school of population and community ecology, discussed above, from the mathematical school epitomized by logistic-based differential equations. A striking text of ecology from the probabilistic viewpoint was produced by E.C. Pielou in 1969, and though it attracted generally favorable reviews and a few new adherents to the stochastic cause (*e.g.*, Wangersky 1970), its ideas and methods are given short shrift by the logistic-oriented texts which dominate American ecology in this decade; earlier stochastic treatments by Chiang (1954, 1968), Skellam (1955), Bartlett (1957, 1960), Bartlett, Gower, and Leslie (1960), Leslie and Gower (1958), and Leslie (1958, 1962) were even more summarily consigned to oblivion in these quarters. Systems analysis ecologists were not more enthusiastic than mathematical ones. For example, Watt (1968) predicts that stochastizing systems models of communities and large populations will not appreciably improve their performance.<sup>7</sup> Cohen's review (1970) of Pielou's text states, "This book should liberate those who assess work in mathematical ecology according to its projection along an

axis from Princeton to Davis by informing them in the very substantial efforts, accomplishments, and opportunities in orthogonal directions.”<sup>8</sup> The liberation is still in the future, and will come only with the completion of a materialist revolution in ecology. Recent papers by Tiwari and Hobbie (1976a,b) stochasticizing differential equations which describe a simple aquatic ecosystem may be in its vanguard.

The unease of ecologists vis-à-vis physics and the zeal with which they seek deterministic physical science models are misplaced. What physicists view as noise is music to the ecologist; the individuality of populations and communities is their most striking, intrinsic, and inspiring characteristic, and the apparent indeterminacy of ecological systems does not make their study a less valid pursuit. Mayr (1961) suggests that the uniqueness of biological entities and phenomena constitutes one of the major differences between biology and the physical sciences, and that this difference makes it particularly difficult for physical scientists to understand biological concerns. There are three types of indeterminacy at issue here. One is at least as fundamental to ecology as Heisenberg’s uncertainty is to physics, and is in fact grounded in the latter. Perhaps the most elegant expression of this sort of indeterminacy in ecology is Lerner and Dempster’s example (1962) of the potential effect of a random mutation in a flour beetle: “A molecular accident could, conceivably, affect slightly the stimulus threshold of a neuron, in consequence of which the path taken by a beetle in its wanderings through the medium may be modified, and perhaps deflected from an egg that otherwise would be eaten.” Such molecular indeterminacy, as Lerner and Dempster indicate, is intrinsic to ecological systems but unlikely to be critical to the outcome of a particular event, like competition between populations of two species. A second form of apparent indeterminacy has only recently been addressed (May 1974, Oster 1975, Poole 1977), and takes the form of ‘chaotic’ behavior of populations governed by certain non-linear, apparently quite realistic, systems of difference equations. Despite the fact that the underlying equations are completely deterministic, the resulting trajectories may be so complex as to appear random, and Oster (1975) suggests that it may be impossible



with biological data to distinguish among true stochasticity, experimental error, and complex flows of a deterministic model. However, similar situations arise in meteorology (May 1974) and even in that quintessential physical ideal, the Newtonian billiard table (Oster 1975), so ecology can hardly be relegated to the status of second-rate science on these grounds.

The third type of ecological indeterminacy is probably most foreign to the physical sciences and is the primary cause of ecologists' defensiveness. This is apparent indeterminacy engendered by the enormous number of entities even in simple ecological systems themselves rather than by the form of the equations describing the systems. Further, these entities may be interacting, and the interactions are often subtle. Whether we believe with Mayr (1961) and Wangersky (1970) that this complexity will forever preclude completely deterministic ecological description or feel, more optimistically, that better and better instrumentation and effort will bring us to within Heisenberg's limits of a perfect description of ecological systems (Holling 1966), we must agree that we will not, in the near future, have sufficient information or insight to produce equations as predictive as those of most physicists and engineers. On the other hand, neither are meteorologists able to predict weather patterns with remarkable precision, and the amount of money and manpower committed to the study of single ecological systems pales compared to the effort involved in, say, scooping up a few moon rocks. With sufficient resources ecologists have been notably more successful and precise in their predictions; many examples are given by DeBach (1974) for biological control. In any event, the nature of genetic systems of living organisms and the fact that evolution constantly occurs insures a certain amount of variability in the outcome of ecological events (Pimentel 1966), and this variability is among the most interesting aspects of ecological phenomena. Further, the amount of variation itself can be predicted, as in Schaffer and Elson's study of salmon life history phenomena (1975). Finally, as discussed early in this paper, a certain amount of variability is evolutionarily adaptive; consequently variability *per se* is selected for, and manifests itself in the workings of ecological systems. In sum, that

variability typifies ecological systems because of their complexity does not render their study less worthwhile than the study of physical systems; rather it suggests different mathematical approaches and criteria for success, "rather than attempting to force biological phenomena into a mold created by hydrodynamics, economics, physics, or what have you" (Slobodkin 1975). The policy instituted by *Ecology* in 1963 of not publishing extensive tabular data symbolizes such an attempt, coming in the midst of new interest in logistic-based, ideal characterizations of populations and communities; increasing recognition of the stochastic nature of ecology demands a re-evaluation.

I end this section on the status of the materialistic revolution in ecology with the observation that the first ecological ideal, Clements' superorganism, is not dead, but rather transmogrified into a belief that holistic study of ecosystems is the proper course for ecology (Watt 1966b, Levins 1968, Lane, Lauff, and Levins 1975, Johnson 1977, Odum 1977; cf. McIntosh 1976). Odum (1964) views the ecosystem as bearing the same relation to ecology as the cell does to molecular biology, a clearly superorganismic conception. Patten (1975) sees the ecosystem as a "holistic unit of coevolution," and argues that ecosystems evolve toward linear good behavior: "Nonlinearity is a mathematical property, not an ecological one, and no ecosystem process is nonlinear until someone writes a relation that describes it so." Aside from the fact that linearity is as much a mathematical property as is nonlinearity, the well-behavedness is an artifact of Patten's convention of defining an ecosystem out of existence when it is egregiously ill-behaved; Holling (1973) views the same behavior as evidence for multiple domains of attraction in the same system. The true measure of the validity of the holistic, well-behaved ecosystem concept is whether it provides insight into community mechanisms, and its record here is equivocal (Mitchell *et al.* 1976, Auerbach *et al.* 1977). Well known instances of abrupt fluctuations in single populations are ignored, yet Preston (1969) gives sufficiently many examples that one might reasonably claim that poor behavior characterizes nature. The widely cited, dramatic increases of *Acanthaster planci* in the Pacific (Branham 1973, Glynn 1974) and

*Sphaeroma terebrans* on Florida mangroves (Rehm and Humm 1973) are two more recent examples of ill-mannered ecosystems.

One may ask why focus on ecosystems has seduced so many ecologists in the face of its failure to add substantially to our understanding of the workings of nature. Indeed, even when this failure is noted, it is ignored or explained away, as Kuhn (1970) suggests is typical for a paradigm before it is finally overthrown by a scientific revolution. Admitting the predominant failure of the U.S. International Biological Program (I.B.P.), the most massively supported American ecological effort and one wholly conceived in a holistic, ecosystem vein, Odum (1977), a leading ecosystem adherent, suggests that it is not the paradigm which is faulty, but rather the consistency with which the paradigm was used in organizing research. In short, the I.B.P. effort was not holistic enough!

One suggestion for the apparent paradigmatic status of the ecosystem concept in the face of conflicting data is that it provides support for the notion of self-regulatory powers inherent in unfettered capitalism (Leigh 1971). For if a community of organisms, naturally selected each to maximize the representation of its own genes, can be shown to be analogous to a single organism whose parts all work to a common purpose, so ought a competitive capitalism to produce a unified whole which benefits all. This is an old notion; Adam Smith's metaphor was that of a hidden hand converting the profit-maximizing activities of individuals into the good of the whole. That this should be true for ecological systems is questionable on both evolutionary grounds (Levins 1974) and the grounds of observed ecological irregularity described above. Even *were* it true for ecology, I suspect that it is not the primary attraction of the ecosystem paradigm; but one ought always to recognize the strength with which a basic philosophy, even an economic one, structures our perception of apparently unrelated phenomena. Perhaps the most convincing argument that the main attraction of holism is not as a subtle justification of capitalism is that it has adherents with long-standing, impeccable Marxist credentials (e.g., Levins 1968, Lewontin and Levins 1976).

McIntosh (1976) documents the transformation in the 1950's and 1960's of American ecology into a big-money operation, the era of

'Grant Swinger,' without observing that the big money is primarily in the area of ecosystems. For example, the I.B.P. was followed by the creation of a new program, Ecosystem Studies, in the National Science Foundation. Currently this program has over twice the annual budget of the General Ecology Program, and fewer than half the proposals. Consequently awards in excess of \$100,000./yr. are common in Ecosystem Studies and unusual in General Ecology. To the extent that grant funding is an important determinant of academic advancement, and economic well-being a general goal (Storer 1973, Merton 1973), one might reasonably argue that the ecosystem paradigm is seductive on economic grounds alone, independent of either philosophical or biological considerations.

Yet another attraction of the ecosystem is that it lends itself to cybernetic interpretation *via* systems analysis, a vogue vocation in the United States for about two decades (McIntosh 1976). Indeed, the primary thrust of ecosystematists has been systems analysis (Patten 1959, 1971, Watt 1966a) and the glamor of turning ecology into a space-age science, replete with the terminology of engineering and physics, must itself have been a powerful inducement of the ecosystem approach, fitting hand-in-glove with the economic appeal. The concurrent rise of computer technology further augmented the appeal of a systems analytic study of ecosystems, and though McIntosh (1976) observes that the tide appears to have crested, nevertheless this aspect of ecosystem research remains a powerful force in ecology today. Odum's (1964) analogy, cell:molecular biology = ecosystem:ecology, may be relevant not only for the light it throws on the relationship of the ecosystem concept to metaphysical thought and its intellectual debt to the superorganism concept, but also as an expression of the desire of ecologists to achieve the respectability, even glamor, of molecular biology in its heyday, when Odum wrote.

But I suggest that the chief reason for the persistence of the ecosystem paradigm is that it accords with Greek metaphysics. The attractiveness of holism, the notion that 'everything affects everything else' (Watt 1966a), includes not only its tidiness but its determinism, for if all components are included in the system and linked to all others by deterministic equations, then no exogenous, random input is

possible.<sup>9</sup> The myth of the balance-of-nature persists in the popular consciousness, and takes systems ecological form in Barry Commoner's condensation of all ecology into 'You can't change just one thing' (1971); Colwell (1970) also notes the identity of the ecosystem paradigm and the balance-of-nature. That an idea so readily accepted by the lay public attracts professional adherents as well is not surprising, particularly when the idea has 2000-year old roots. Even Albert Einstein, a founder of stochastic quantum mechanics, viewed it only as an instrument for dealing with atomic systems, not as a true representation of the universe: "I am absolutely convinced that one will eventually arrive at a theory in which the objects connected by laws are not probabilities, but conceived facts. . . ." (Born 1949). That Einstein's objection to a 'dice-playing God' was irrational, however, he readily admitted: "I cannot provide logical arguments for my conviction, but can only call on my little finger as a witness, which cannot claim any authority to be respected outside my own skin" (Born 1949). Small wonder that Greek metaphysics continues to influence ecologists! Certainly there is something profoundly disturbing about a nature in which random elements play a large role. Just as much of the opposition to Darwinian evolution powered by natural selection was engendered by the large role assigned to chance, so the idea of an unbalanced, stochastically driven natural community inspires distrust.

The ecosystem paradigm purports to have corrected the superorganism's shortcomings, primarily by explicitly noting that succession need not always lead to the same climax and by focussing on certain individual characteristics of ecosystems. But its most fundamental features are determinism and interest in a high-level ideal entity; in these it is squarely in the camp of the essentialists. The success of the materialist revolution in other disciplines, particularly evolution and genetics, augurs well for ecology, but Greek metaphysics will not vanish easily.

## ACKNOWLEDGMENTS

I am grateful to Donald R. Strong, Jr. for numerous specific suggestions on all aspects of this manuscript, as well as for a long-standing, freely discussed interest in the history and philosophy of science. Edward F. Connor, Frances C. James, Eugene F. Kaelin, David B. Mertz, Alexandra Radbil, and Edward O. Wilson provided both discussion and several key references.

*Department of Biological Science*  
*Florida State University, Tallahassee*

## NOTES

<sup>1</sup> Malthus stated his syllogism thus:

"First, That food is necessary to the existence of man. Second, That the passion between the sexes is necessary and will remain in the present state.

.....

"Assuming then, my postulata as granted, I say, that the power of population is indefinitely greater than the power in the earth to provide subsistence for man.

.....

"This implies a strong and constantly operating check on population from the difficulty of subsistence. This difficulty must fall somewhere and must necessarily be severely felt by a large portion of mankind."

<sup>2</sup> Seton and Goss, Knight, Gaertner, Vilmorin, Naudin, Verlot, Haacke (Olby 1966)

<sup>3</sup> Wiener (1949) develops the related idea that the increasing recognition of the role of chance and the consequent use of statistical approaches in a number of disciplines, plus the emphasis on evolutionism and the individual in *The Origin* and Mill's *On Liberty* (also published in 1859!), led directly to twentieth century American pragmatism.

<sup>4</sup> It is ironic but appropriate that the integrity of Mendel's reports be thrown into doubt by R.A. Fisher, this century's foremost statistician and one contributor to the Neo-Darwinian synthesis. Fisher (1936) noted that Mendel's ratios were, as a group, too close to the hypothetical ones for the deviations to be caused by chance alone, even given that the underlying probabilities are as Mendel suggested. Perhaps Mendel can be excused this disturbing anomaly on the grounds of the novelty of statistics in his field!

<sup>5</sup> The power of the paradigm was such as to preclude gathering of data oriented toward individual species. Margaret B. Davis, in her long-term studies of long-term vegetation changes, has been frustrated by this lacuna: "We do not know what the virgin vegetation of the pioneer days was like because all the ecologists were so busy looking for a non-existent climax that they forgot to record what was actually growing there" (Colinvaux 1973).

<sup>6</sup> Gleason adumbrated this discovery, as he did so many others, when he wrote of 'fortuitous immigration' (1926) and plants' being distributed "in accordance with the laws of probability and chance" (1929). But statistics was in its infancy in biology, as described above, and Gleason's insight was imprecise. A literature on the spread of epidemics as a stochastic process was also extant at the time of Park's work (e.g., Bailey 1957, Bartlett 1956, 1960), and Kendall had published a formal statistical treatment of population growth (1949), but this work was not integrated into ecological thought.

<sup>7</sup> He quotes Beverton and Holt (1957): "Considering population change as a stochastic process... often gives results appreciably different from those obtained with deterministic models... especially for the prediction of critical phenomena such as total extinction of the group. It is our belief, however, that, except in particular instances... the multiplication of effort both in deriving the stochastic equations and in computing them would not have been justified when the standard of accuracy of our data, the complexity of the biotic system with which we are dealing, and the order of magnitude of the expected discrepancies are all taken into account."

<sup>8</sup> Princeton, the institution of Robert MacArthur, was widely viewed as a center of mathematical ecology, while the University of California at Davis housed K.E.F. Watt's leading ecosystem systems analysis group.

<sup>9</sup> A witty, widely circulated but unpublished manuscript 'On the Tendencies of Motion' by R. Lewontin and R. Levins (under the pseudonym 'Isadore Nabi') lambastes the stochastic approach on grounds of both messiness and tunnel vision. A bogus experiment on motion of apples, cannonballs, etc. with massive amounts of data is described, and the subjection of the data to multiple regression, factor analysis, and analysis of variance results in a series of nonsensical conclusions without leading to Newton's laws.

#### BIBLIOGRAPHY

- Allee, W.C., *Animal Aggregations. A Study of General Sociology*, Univ. of Chicago Press, Chicago, 1941.
- Allen, G., 'Genetics, eugenics and society: Internalists and externalists in contemporary history of science', *Soc. Stud. Sci.* **6** (1976), 105-122.
- Auerbach, S.I., R.L. Burgess, and R.V. O'Neill, 'The biome programs: Evaluating an experiment', *Science* **195** (1977), 902-904.
- Bailey, N.T.J., *The Mathematical Theory of Epidemics*, Hafner, New York, 1957.
- Bartlett, M.S., 'Deterministic and stochastic models for recurrent epidemics', in *Proc. Third Berkeley Symp. on Mathematical Statistics and Probability*, Vol. 4, Univ. of California Press, Berkeley, 1956, pp. 81-109.
- Bartlett, M.S., 'On theoretical models for competitive and predatory biological systems', *Biometrika* **44** (1957), 27-42.
- Bartlett, M.S., *Stochastic Population Models in Ecology and Epidemiology*, Methuen, London, 1960.
- Bartlett, M.S., J.C. Gower, and P.H. Leslie, 'A comparison of theoretical and empirical results for some stochastic population models', *Biometrika* **47** (1960), 1-11.

- Barzun, J., *Darwin, Marx, Wagner: Critique of a Heritage*, 2nd ed., Doubleday, Garden City, New York, 1958.
- Beverton, R.J.H., and S.J. Holt, 'On the dynamics of exploited fish populations', *Fish. Invest.* (ser. II) **19** (1957), 1-533.
- Bohr, N., 'The quantum postulate and the recent development of atomic theory', *Nature* **121** (1928), 580-590.
- Born, M., *Natural Philosophy of Cause and Chance*, Oxford University Press, London, 1949.
- Botkin, D.B., J.F. Janak, and J.R. Wallis, 'Some ecological consequences of a computer model of forest growth', *Journ. Ecol.* **60** (1972), 849-872.
- Branham, J.M., 'The Crown-of-thorns on coral reefs', *BioScience* **73** (1973), 219-226.
- Brillouin, L., *Science and Information Theory*, 2nd ed., Academic Press, New York, 1962.
- Cain, S.A., *Foundations of Plant Geography*, Harper, New York, 1944.
- Cain, S.A., 'Characteristics of natural areas and factors in their development', *Ecol. Monogr.* **17** (1947), 185-200.
- Chiang, C.L., 'Competition and other interactions between species', in O. Kempthorne, T.A. Bancroft, J.W. Gowen, and J.L. Lusk, editors, *Statistics and Mathematics in Biology*, Iowa State College Press, Ames, Iowa, 1954, pp. 197-215.
- Chiang, C.L., *Introduction to Stochastic Processes in Biostatistics*, Wiley, New York, 1968.
- Clements, F.E., *Research Methods in Ecology*, University Publ. Co., Lincoln, Nebraska, 1905.
- Clements, F.E., 'Nature and structure of the climax', *Journ. Ecol.* **24** (1936), 252-284.
- Clements, F.E., and V.E. Shelford, *Bio-Ecology*, Wiley, New York, 1939.
- Cohen, J.E., Review of *An Introduction to Mathematical Ecology* (E.C. Pielou), *Amer. Sci.* **58** (1970), 699.
- Cohen, J.E., 'Mathematics as metaphor', *Science* **172** (1971), 674-675.
- Colinvaux, P.A., *Introduction to Ecology*, Wiley, New York, 1973.
- Collier, B.D., G.W. Cox, A.W. Johnson, and P.C. Miller, *Dynamic Ecology*, Prentice-Hall, Englewood Cliffs, New Jersey, 1973.
- Colwell, T.B., 'Some implications of the ecological revolution for the construction of value', in E. Lazlo and J.B. Wilbur, editors, *Human Values and Natural Science*, Gordon and Breach Sci. Publ., New York, 1970, pp. 245-258.
- Commoner, B., *The Closing Circle*, Knopf, New York, 1971.
- Culver, D.C., 'The relationship between theory and experiment in community ecology', in S.A. Levin, editor, *Ecosystem Analysis and Prediction*, SIAM-SIMS, Philadelphia, 1975, pp. 103-110.
- Curtis, J.T., 'A prairie continuum in Wisconsin', *Ecology* **36** (1955), 558-566.
- Curtis, J.T., *The Vegetation of Wisconsin*, Univ. of Wisconsin Press, Madison, Wisconsin, 1959.
- Curtis, J.T., and R.P. McIntosh, 'An upland continuum in the prairie-forest border region of Wisconsin', *Ecology* **32** (1951), 476-496.
- Dayton, P.K., 'Two cases of resource partitioning in an intertidal community: Making the right prediction for the wrong reason', *Amer. Natur.* **107** (1973), 662-670.
- DeBach, P., *Biological Control by Natural Enemies*, Cambridge Univ. Press, London, 1974.



- Dirac, P.A.M., 'Heisenberg's influence on physics', *Commentarii* 3 (14) (1977), 1-15.
- Drury, W.H., and I.C.T. Nisbet, 'Succession', *Journ. Arnold Arboretum* 54 (1973), 331-368.
- Egler, F.E., 'Arid southeast Oahu vegetation, Hawaii', *Ecol. Monogr.* 17 (1947), 383-435.
- Ehrenberg, W., 'Maxwell's Demon', *Sci. Amer.* 224 (Nov. 1967), 103-110.
- Elton, C., *Animal Ecology*, Macmillan, New York, 1927.
- Emerson, A.E., 'Social coordinations of the superorganism', *Amer. Midl. Natur.* 21 (1939), 182-209.
- Fisher, R.A., 'Has Mendel's work been rediscovered?', *Annals of Science* 1 (1936), 115-137.
- Frank, P.W., 'Life histories and community stability', *Ecology* 49 (1968), 355-357.
- Fraser, D.F., 'Coexistence of salamanders in the genus *Plethodon*: A variation of the Santa Rosalia theme', *Ecology* 57 (1976), 238-251.
- Gause, G.F., *The Struggle for Existence*, Williams and Wilkens, Baltimore, 1934.
- Ghiselin, M.T., *The Triumph of the Darwinian Method*, Univ. of California Press, Berkeley, 1969.
- Gleason, H.A., 'The vegetation of the inland sand deposits of Illinois', *Bull. Ill. State Lab. Nat. Hist.* 9 (1910), 21-174.
- Gleason, H.A., 'The structure and development of the plant association', *Bull. Torrey Bot. Club* 44 (1917), 463-481.
- Gleason, H.A., 'The individualistic concept of the plant association', *Bull. Torrey Bot. Club* 53 (1926), 1-20.
- Gleason, H.A., 'The significance of Raunkiaer's law of frequency', *Ecology* 10 (1929), 406-408.
- Gleason, H.A., 'The individualistic concept of the plant association', *Amer. Midl. Natur.* 21 (1939), 92-110.
- Glynn, P.W., 'The impact of *Acanthaster* on corals and coral reefs in the eastern Pacific', *Environm. Conserv.* 1 (1974), 245-304.
- Gödel, K., 'Über formal unentscheidbare Sätze der Principia Mathematica und verwandter systeme. I', *Monatshefte für Mathematik und Physik* 38 (1931), 173-198.
- Goodman, D., 'The theory of diversity-stability relationships in ecology', *Quart. Rev. Biol.* 50 (1974), 237-266.
- Hardin, G., 'The competitive exclusion principle', *Science* 131 ((1960), 1292-1297.
- Haskell, E.F., 'Mathematical systematization of "environment," "organism," and "habitat"', *Ecology* 21 (1940), 1-16.
- Heck, K.L., 'Some critical considerations of the theory of species packing', *Evol. Theory* 1 (1976), 247-258.
- Heisenberg, W., 'Über den anschaulichen Inhalt der quantentheoretischen Kinematik und Mechanik', *Zeitschr. F. Phys.* 43 (1927), 172-198.
- Holling, C.S., 'The strategy of building models of complex ecological systems', in K.E.F. Watt, editor, *Systems Analysis in Ecology*, Academic Press, New York, 1966, pp. 195-214.
- Holling, C.S., 'Resilience and stability of ecological systems', *Ann. Rev. Ecol. Syst.* 4 (1973), 1-23.
- Horn, H.S., 'Markovian properties of forest succession', in M.L. Cody and J.M.

- Diamond, editors, *Ecology and Evolution of Communities*, Harvard Univ. Press, Cambridge, Mass., 1975, pp. 196–211.
- Hutchinson, G.E., 'Concluding remarks', *Cold Spring Harbor Symp. Quant. Biol.* **22** (1957), 415–427.
- Irvine, W., *Apes, Angels, and Victorians: Darwin, Huxley, and Evolution*, McGraw-Hill, New York, 1955.
- Johannsen, W., *Über Erbllichkeit in Populationen und in reinen Linien*, Gustav Fischer, Jena, 1903.
- Johannsen, W., *Elemente der exakten Erblchkeitslehre*, Gustav Fischer, Jena, 1909.
- Johnson, P.L., editor, *An Ecosystem Paradigm for Ecology*, Oak Ridge Associated Universities, Oak Ridge, Tenn., 1977.
- Kac, M., 'The emergence of statistical thought in exact sciences', in J. Neyman, editor, *The Heritage of Copernicus: Theories "More Pleasing to the Mind"*, M.I.T. Press, Cambridge, Mass., 1974, pp. 433–444.
- Kendall, D.G., 'Stochastic processes and population growth', *Journ. Roy. Statist. Soc., Ser. B*, **11** (1949), 230–264.
- King, C.E., and P.S. Dawson, 'Population biology and the *Tribolium* model', *Evol. Biol.* **5** (1971), 133–227.
- Klein, M.J., 'Maxwell, his Demon, and the second law of thermodynamics', *Amer. Sci.* **58** (1970), 84–97.
- Kormondy, E.J., *Readings in Ecology*, Prentice-Hall, Englewood Cliffs, New Jersey, 1965.
- Krebs, C.J., *Ecology: The Experimental Analysis of Distribution and Abundance*, Harper & Row, New York, 1972.
- Kuhn, T.S., *The Structure of Scientific Revolutions*, 2nd ed., Univ. of Chicago Press, Chicago, 1970.
- Lanczos, C., *The Einstein Decade: 1905–1915*, Academic Press, New York, 1974.
- Lane, P.A., G.H. Lauff, and R. Levins, 'The feasibility of using a holistic approach in ecosystem analysis', in S.A. Levin, editor, *Ecosystem Analysis and Prediction*, SIAM-SIMS, Philadelphia, 1975, pp. 111–128.
- Leak, W.B., 'Successional change in northern hardwoods predicted by birth and death simulation', *Ecology* **51** (1970), 794–801.
- Leigh, E., 'The energy ethic', *Science* **172** (1971), 644.
- Lerner, I.M., and E.R. Dempster, 'Indeterminism in interspecific competition', *Proc. Nat. Acad. Sci. U.S.A.* **48** (1962), 821–826.
- Leslie, P.H., 'A stochastic model for studying the properties of certain biological systems by numerical methods', *Biometrika* **45** (1958), 16–31.
- Leslie, P.H., 'A stochastic model for two competing species of *Triobolium* and its application to some experimental data', *Biometrika* **49** (1962), 1–25.
- Leslie, P.H., and J.C. Gower, 'The properties of a stochastic model for two competing species', *Biometrika* **45** (1958), 316–330.
- Levins, R., 'Ecological engineering: theory and technology', *Quart. Rev. Biol.* **43** (1968), 301–305.
- Levins, R., *Evolution in Changing Environments*, Princeton University Press, Princeton, New Jersey, 1968.
- Levins, R., 'Evolution in communities near equilibrium', in M.L. Cody and J.M.

- Diamond, editors, *Ecology and Evolution of Communities*, Harvard University Press, Cambridge, Mass., 1975, pp. 16–50.
- Lewontin, R.D., 'The meaning of stability', in G.M. Woodwell and H.H. Smith, editors, *Diversity and Stability in Ecological Systems*, Brookhaven Nat. Lab., Brookhaven, New York, 1969, pp. 13–24.
- Lewontin, R.D., 'Darwin and Mendel – the materialist revolution', in J. Neyman, editor, *The Heritage of Copernicus: Theories "More Pleasing to the Mind"*, M.I.T. Press, Cambridge, Mass., 1974a, pp. 166–183.
- Lewontin, R.D., *The Genetic Basis of Evolutionary Change*, Columbia University Press, New York, 1974b.
- Lewontin, R.D., and R. Levins, 'The problem of Lysenkoism', in H. Rose and S. Rose, editors, *The Radicalisation of Science*, Macmillan, London, 1976, pp. 32–64.
- Lotka, A.J., 'Studies on the mode of growth of material aggregates', *Amer. Journ. Sci.* **24** (1907), 199–216.
- Lotka, A.J., *Elements of Physical Biology*, Williams and Wilkins, Baltimore, 1925.
- Lovejoy, A.O., *The Great Chain of Being, A Study of the History of an Idea*, Harvard University Press, Cambridge, Mass., 1936.
- MacArthur, R.H., 'Species packing, and what interspecies competition minimizes', *Proc. Nat. Acad. Sci. U.S.A.* **64** (1969), 1369–1371.
- MacArthur, R.H., 'Species packing and competitive equilibrium for many species', *Theoret. Pop. Biol.* **1** (1970), 1–11.
- MacArthur, R.H., *Geographical Ecology*, Harper & Row, New York, 1972.
- MacArthur, R.H., and R. Levins, 'The limiting similarity, convergence, and divergence of coexisting species', *Amer. Natur.* **101** (1967), 377–385.
- MacFadyen, A., 'Some thoughts on the behaviour of ecologists', *Journ. Anim. Ecol.* **44** (1975), 351–363.
- Malthus, R.R., *An Essay on the Principle of Population as it Affects the Future Improvement of Society*, Johnson, London, 1798.
- Mason, H.L., 'Evolution in certain floristic associations in western North America', *Ecol. Monogr.* **17** (1947), 201–210.
- May, R.M., *Stability and Complexity in Model Ecosystems*, Princeton Univ. Press, Princeton, New Jersey, 1973.
- May, R.M., 'Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos', *Science* **186** (1974), 645–647.
- Mayr, E., 'Cause and effect in biology', *Science* **134** (1961), 1501–1506.
- Mayr, E., *Animal Species and Evolution*, Harvard Univ. Press, Cambridge, Mass., 1963.
- McIntosh, R.P., 'H.A. Gleason – "Individualistic Ecologist" 1882–1975: His contributions to ecological theory', *Bull. Torrey Bot. Club* **102** (1975), 253–273.
- McIntosh, R.P., 'Ecology since 1900', in B.J. Taylor and T.J. White, editors, *Issues and Ideas in America*, Univ. of Oklahoma Press, Norman, Okla., 1976, pp. 353–372.
- McKinney, H.L., *Wallace and Natural Selection*, Yale Univ. Press, New Haven, Conn., 1972.
- McNaughton, S.J., 'Diversity and stability of ecological communities: A comment on the role of empiricism in ecology', *Amer. Natur.* **111** (1977), 515–525.
- Mendel, G., 'Versuche über Pflanzenhybriden', *Verhandlungen des naturforschenden*

- Vereines in Brünn* 4 (1866), 3–47.
- Mendel, G., 'Über einige aus künstlicher', *Verhandlungen des naturforschenden Vereiner in Brünn* 8 (1870), 26–31.
- Merton, R.K., *The Sociology of Science*, Univ. of Chicago Press, Chicago, 1973.
- Mertz, D.B., 'The *Tribolium* model and the mathematics of population growth', *Ann. Rev. Ecol. Syst.* 3 (1973), 51–78.
- Mertz, D.B., D.A. Cawthon, and T. Park, 'An experimental analysis of competitive indeterminacy in *Tribolium*', *Proc. Nat. Acad. Sci. U.S.A.* 73 (1976), 1368–1372.
- Mitchell, R., R.A. Mayer, and J. Downhower, 'An evaluation of three biome programs', *Science* 192 (1976), 859–865.
- Neill, W.E., 'The community matrix and interdependence of the competition coefficients', *Amer. Natur.* 108 (1974), 399–408.
- Neyman, J., T. Park, and E.L. Scott, 'Struggle for existence. The *Tribolium* model: biological and statistical aspects', *Proc. Third Berkeley Symp. on Mathematical Statistics and Probability* 4 (1956), 41–79.
- Nicholson, A.J., 'The balance of animal populations', *Journ. Anim. Ecol.* 2 (1933), 132–178.
- Nicholson, A.J., 'Fluctuations in animal populations', *Rept. Austr. N.Z. Ass. Adv. Sci.* 26 (1947), 134–148.
- Nicholson, A.J., 'Compensatory reactions of populations to stress, and their evolutionary significance', *Austr. Journ. Zool.* 2 (1954a), 1–8.
- Nicholson, A.J., 'An outline of the dynamics of animal populations', *Austr. Journ. Zool.* 2 (1954b), 9–65.
- Nicholson, A.J., and V.A. Bailey, 'The balance of animal populations', *Proc. Zool. Soc. Lond.* 3 (1935), 551–598.
- Odum, E.P., 'The new ecology', *BioScience* 14 (1964), 14–16.
- Odum, E.P., 'The emergence of ecology as a new integrative discipline', *Science* (1977), 1289–1293.
- Olby, R.C., *Origins of Mendelism*, Schocken, New York, 1966.
- Oster, G., 'Stochastic behavior of deterministic models', in S.A. Levin, editor, *Ecosystem Analysis and Prediction*, SIAM-SIMS, Philadelphia, 1975, pp. 24–38.
- Park, T., 'Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst', *Ecol. Monogr.* 18 (1948), 265–307.
- Park, T., 'Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of *Tribolium*', *Physiol. Zool.* 27 (1954), 177–238.
- Park, T., 'Beetles, competition, and populations', *Science* 138 (1962), 1369–1375.
- Park, T., P.H. Leslie, and D.B. Mertz, 'Genetic strains and competition in populations of *Tribolium*', *Physiol. Zool.* 37 (1964), 97–162.
- Patten, B.C., 'An introduction to the cybernetics of the ecosystem: the trophic dynamic aspect', *Ecology* 40 (1959), 221–231.
- Patten, B.C., editor, *Systems Analysis and Simulation in Ecology. Vol. 1*, Academic Press, New York, 1971.
- Patten, B.C., 'Ecosystem linearization: an evolutionary design problem', *Amer. Natur.* 109 (1975), 529–539.
- Pearl, R., *The Biology of Population Growth*, Knopf, New York, 1925.

- Pearl, R., and L.J. Reed, 'On the rate of growth of the population of the United States since 1790 and its mathematical representation', *Proc. Nat. Acad. Sci. U.S.A.* **6** (1920), 275–288.
- Peckham, M., 'Darwinism and Darwinisticism', *Victorian Studies* **3** (1959), 19–40.
- Pielou, E.C., *An Introduction to Mathematical Ecology*, Wiley-Interscience, New York, 1969.
- Pimentel, D., 'Complexity of ecological systems and problems in their study and management', in K.E.F. Watt, editor, *Systems Analysis in Ecology*, Academic Press, New York, 1966, pp. 15–35.
- Pirie, N.W., 'Gardylloo', *The Listener* **82** (1969), 331.
- Ponyatovskaya, V.M., 'On two trends in phytocoenology' (trans. by J. Major), *Vegetatio* **10** (1961), 373–385.
- Poole, R.W., *An Introduction to Quantitative Ecology*, McGraw-Hill, New York, 1974.
- Poole, R.W., 'Periodic, pseudoperiodic, and chaotic population fluctuations', *Ecology* **58** (1977), 210–213.
- Popper, K.R., *The Poverty of Historicism*, Harper & Row, New York, 1961.
- Popper, K.R., *Conjectures and Refutations: The Growth of Scientific Knowledge*, Harper & Row, New York, 1963.
- Preston, F.W., 'Diversity and stability in the biological world', in G.M. Woodwell and H.H. Smith, editors, *Diversity and Stability in Ecological Systems*, Brookhaven Nat. Lab., Brookhaven, New York, 1969, pp. 1–12.
- Provine, W., *The Origins of Theoretical Population Genetics*, Univ. of Chicago Press, Chicago, 1971.
- Pynchon, T., *Gravity's Rainbow*, Viking, New York, 1973.
- Raup, H.M., 'Trends in the development of geographic botany', *Assoc. Amer. Geogr. Ann.* **32** (1942), 319–354.
- Rehm, A., and H.J. Humm, '*Sphaeroma terebrans*: a threat to the mangroves of southwestern Florida', *Science* **182** (1973), 173–174.
- Robbins, H., 'The statistical mode of thought', in J. Neyman, editor, *The Heritage of Copernicus: Theories "More Pleasing to the Mind"*, M.I.T. Press, Cambridge, Mass., 1974, pp. 417–432.
- Schaffer, W.M., and P.F. Elson, 'The adaptive significance of variations in life history among local populations of Atlantic salmon in North America', *Ecology* **56** (1975), 577–590.
- Shelford, V.E., *Animal Communities in Temperate America*, Univ. of Chicago Press, Chicago, 1913.
- Simberloff, D.S., and E.O. Wilson, 'A two-year record of colonization', *Ecology* **51** (1970), 934–937.
- Singer, C., *A History of Biology*, 3rd rev. ed., Abelard-Schuman, 1959.
- Skellam, J.G., 'The mathematical approach to population dynamics', in J.B. Cragg and N.W. Pirie, editors, *The Numbers of Man and Animals*, Oliver and Boyd, Edinburgh, 1955, pp. 31–46.
- Slobodkin, L.B., 'Comments from a biologist to a mathematician', in S.A. Levin, editor, *Ecosystem Analysis and Prediction*, SIAM-SIMS, Philadelphia, 1975, pp. 318–329.
- Smuts, J.C., *Holism and Evolution*, Macmillan, New York, 1926.
- Stephens, G.R., and P.E. Waggoner, 'The forests anticipated from 40 years of natural

- transitions in mixed hardwoods', *Bull. Conn. Agric. Exp. Stn.* **707** (1970), 1-58.
- Storer, N.W., Introduction to R.K. Merton, *The Sociology of Science*, Univ. of Chicago Press, Chicago, 1973.
- Strong, D.R., and D.A. Levin, 'Species richness of plant parasites and growth form of their hosts', *Amer. Natur.* **114** (1979), 1-22.
- Sutherland, J.P., 'Multiple stable points in natural communities', *Amer. Natur.* **108** (1974), 959-873.
- Sutton, W.S., 'The chromosome in heredity', *Biol. Bull.* **4** (1903), 231-251.
- Szilard, L., 'Über die Entropieverminderung in einem thermodynamischen System bei Eingriffen intelligenter Wesen', *Zeits. Physik* **53** (1929), 840-856.
- Tansley, A.G., 'The classification of vegetation and the concept of development', *Journ. Ecol.* **8** (1920), 118-149.
- Tiwari, J.L., and J.E. Hobbie, 'Random differential equations as models of ecosystems: Monte Carlo simulation approach', *Mathematical Biosciences* **28** (1976), 25-44.
- Tiwari, J.L., and J.E. Hobbie, 'Random differential equations as models of ecosystems. II. Initial conditions and parameter specifications in terms of maximum entropy distributions', *Mathematical Biosciences* **31** (1976), 37-53.
- Tribus, M., and E.C. McIrvine, 'Energy and information', *Sci. Amer.* **228** (Sept. 1971), 179-192.
- Verhulst, P.F., 'Notice sur la loi que la population suit dans son accroissement', *Corresp. math. phys.* **10** (1838), 113-121.
- Volterra, V., 'Fluctuations in the abundance of a species considered mathematically', *Nature* **118** (1926), 558-560.
- Volterra, V., 'Variations and fluctuations of the number of individuals in animal species living together', reprinted in R.N. Chapman, *Animal Ecology*, McGraw-Hill, New York, 1928.
- Waddington, C.H., *The Strategy of the Genes*, Allen & Unwin, London, 1957.
- Waddington, C.H., *The Evolution of an Evolutionist*, Cornell Univ. Press, Ithaca, New York, 1975.
- Waggoner, P.E., and G.R. Stephens, 'Transition probabilities for a forest', *Nature* **255** (1970), 1160-1161.
- Wangersky, P.J., 'An ecology of probability', *Ecology* **51** (1970), 940.
- Watt, K.E.F., editor, *Systems Analysis in Ecology*, Academic Press, New York, 1966a.
- Watt, K.E.F., 'The Nature of systems analysis', in K.E.F. Watt, editor, *Systems Analysis in Ecology*, Academic Press, New York, 1966b, pp. 1-14.
- Watt, K.E.F., *Ecology and Resource Management*, McGraw-Hill, New York, 1968.
- Whittaker, R.H., 'Vegetation of the Great Smoky Mountains', *Ecol. Monogr.* **26** (1956), 1-80.
- Whittaker, R.H., 'Gradient analysis of vegetation', *Biol. Rev.* **42** (1967), 207-264.
- Wiener, P.P., *Evolution and the Founders of Pragmatism*, Harvard University Press, Cambridge, Mass., 1949.
- Wilson, W., 'Quantum theory', *Encyclopedia Britannica* (1944), vol. **10**, pp. 814-827.