BOOK REVIEWS

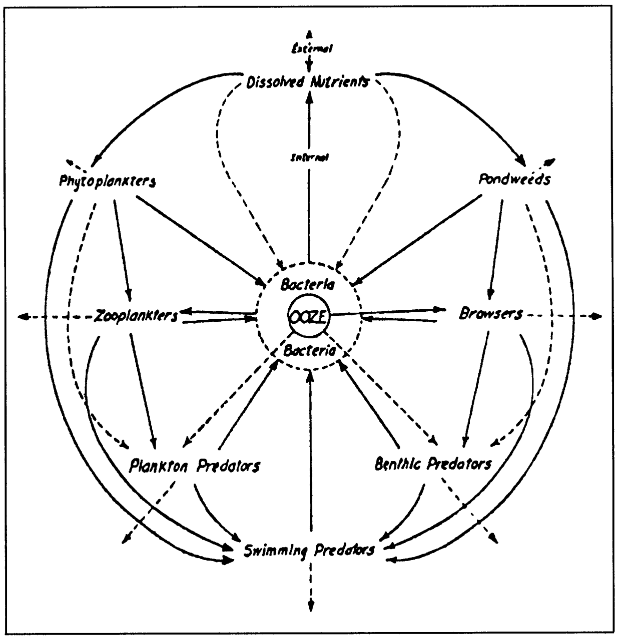
Ecological Comprehensiveness

A History of the Ecosystem Concept in Ecology. More than the Sum of the Parts. FRANK BENJAMIN GOLLEY. Yale University Press, New Haven, CT, 1994. xviii, 254 pp., illus. $30 or £25.

The term "ecosystem" originated out of controversy over the use of a metaphor and over the failure to recognize the influence of both abiotic and biotic factors on the structure of plant associations. Ecosystem ecology is in turn controversial because research has failed to develop a theory associated with whole systems rather than their component parts. Frank Golley's historical analysis recounts these controversies and reminds ecologists of the value of ecosystem studies. Golley begins with an account of why the term was first used and reviews the subsequent growth of ecosystem ecology as a discipline. Much of the book is devoted to discussion of what Golley considers effective and ineffective ecosystem research, as judged by success or failure in measuring whole-system parameters. The book is written from an insider's viewpoint. Golley is an ecosystem ecologist; he was a member of the U.S. International Biological Program committee and for four years was Director of Biotic Systems and Resources at the National Science Foundation.

Sir Arthur Tansley proposed the term ecosystem in 1935 to describe units of the environment in which a stable dynamic equilibrium exists between the organisms and their abiotic environment. Henry Clements and John Phillips had argued for the primacy of biotic interactions underlying the progression of taxonomic changes in plant succession. This emphasis on biotic interactions led them into a metaphorical description of the climax stage as a "complex organism." Tansley made two points in his critique of their ideas. First, he believed that both biotic and abiotic factors were critical in the development of the climax and suggested the term ecosystem to distinguish his concept from Clements's concept. Second, he strongly opposed the use of organismal metaphor to describe these whole systems.

According to Golley, at the time of Tansley's paper studies of ecosystems lacked a framework for integrating the components of whole systems. Raymond Lindeman's classic study of the trophic dynamics of Cedar Bog Lake, Minnesota, in the early 1940s provided the needed framework. Lindeman applied Tansley's concept of the ecosystem by integrating solar radiation and nutrient cycles with energetics in a study of the lake. Lindeman's contribution, stimulated by his work at Yale with G. Evelyn Hutchinson, was to categorize organisms of the ecosystem into feeding groups or trophic levels and to substitute a common currency (caloric energy) for biomass. He then



Raymond Lindeman's diagram (1941) of a food cycle in Cedar Bog Lake. [From *A History of the Ecosystem Concept in Ecology; American Midland Naturalist*]

estimated the amount of energy transferred between levels and calculated conversion efficiencies or the gross production efficiency for each trophic level. In the late 1950s, Howard T. Odum published similar studies of energy dynamics in whole ecosystems that included more precise methods of measuring production and respiration. These studies provided the first integrated analyses of whole ecosystems.

One conclusion of these ecosystem studies was that transfer efficiency, the gross production efficiency of energy transfer between trophic levels, was similar from ecosystem to ecosystem, varying within a range of 5 to 15 percent. This similarity suggested to Odum and Lawrence Slobodkin that ecosystems might have energetic constraints. Slobodkin later abandoned this conclusion, arguing that it is not possible for maximum or minimum rates of energy transfer between trophic levels to be selected for. However, the apparent similarity became an important theme in ecology in the 1960s and 1970s.

By the mid-1960s, ecosystem ecology was very popular in the United States, and it became the major theme of the International Biological Program (IBP). The IBP was originally proposed as a five-year study of human health and the environment, with government funds from each participating country. Growing concern about environmental pollution persuaded the member committees to select ecology as a major theme.

The U.S. part of the IBP attempted to bring together concepts of species diversity and energy flow dynamics in specific biomes (broad ecological assemblages such as tundra or desert) to find general rules applicable to all ecosystems. The program was divided into biome groups, each consisting of a team of scientists that was to define trophic-level interactions and measure primary and secondary production. The massive data set for each site was to be synthesized in a systems model, with theory to emerge from this synthesis.

Golley provides exceptional insight into the problems encountered with this approach. He focuses on the Grassland Biome modeling efforts and describes in detail why they failed. The primary outcome, he believes, was a series of component models (for "productivity, cycling, and species impacts") rather than a model that could test ecosystem theory. Golley is forthright about the criticisms of IBP that he suggests have fueled the controversies surrounding ecosystem ecology.

Golley counters criticism of the IBP with a comparison of the more effective studies at Hubbard Brook in New Hampshire. The research at Hubbard Brook, designed and directed by F. Herbert Bormann and Gene Likens, measured the impact of forest clearance on the biogeochemistry of a watershed. This study showed that the chemistry of rainfall could have major impacts on forests and that the chemistry of water leaving the watershed was modified by plants and by exchange processes in the soils. The significant conclusions were drawn from analysis of the whole system. The Hubbard Brook study also showed that ecosystem-level research, focused on a small watershed, could attract independent researchers who could contribute to an understanding of the whole without the need for large budgets.

This review of the events leading to acceptance of ecosystem ecology as a discipline, the shortcomings of the IBP studies, and the emergence of new approaches in the study of ecosystems ends with the middle 1970s. The final chapter of the book examines why ecosystem studies took different directions in Europe, Japan, and the United States and critiques reductionism in ecology.

Golley's historical account is fascinating and effective. It provides perspective on a time when theoretical and experimental studies were increasing, partly because of emerging environmental problems. An emphasis on large field studies by groups of scientists is needed for the study of global environmental problems, which makes Golley's review a timely one. By setting forth the strengths and weaknesses of the IBP and other ecosystem studies, he provides us with a historical perspective and guidelines to make future research more effective. The book is also a timely reminder of Tansley's concept of the ecosystem. Organismal metaphors (environmental "health," for example) are still commonly used in ecology. Their use glosses over concepts that are difficult to define and in the process impedes the building of theories.

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Vignettes: Dire Predictions

The control of the beastlike in human nature is sometimes said to be a matter of species survival. Here is a characteristic sentence from Carl Sagan: "There is today in the West (but not in the East) a resurgent interest in vague, anecdotal and often demonstrably erroneous doctrines that, if true, would betoken at least a more interesting universe, but that, if false, imply an intellectual carelessness, and absence of toughmindedness, and a diversion of energies not very promising for our survival." . . . He goes on to enumerate astrology, flying saucer accounts, modern prophecy, and other efflorescences of popular antirationalist belief. Sagan as scientist shows a bit of siege mentality here: dissent from the rule of scientific reason, even on this small scale, risks apocalypse, the destruction of the species.

—*Alan G. Wasserstein*, in *The Literature of Science: Perspectives on Popular Scientific Writing* (Murdo William McRae, Ed.; University of Georgia Press)

Mathematical studies on the disappearance of rare family names date back to the nineteenth century. Statisticians rigged up a properly simplified model—later called a *branching process*—and derived from it that every family name would inexorably have to vanish sooner or later. This was a heraldic counterpart, so to speak, to the *Würmertod* (heat death) which the contemporary physicists prophesied for our passing world—a disconsolate perspective for a century hooked on progress. Both results turned out to be wrong, by the way. The *Würmertod* is out, like the same physicists' *ether*—today's cosmologists have other fates in store for our world. And the apparently inescapable extinction of family names was based on a simple miscalculation; but it took a long time to discover the error.

—*Karl Sigmund*, in *Games of Life: Explorations in Ecology, Evolution, and Behaviour* (Oxford University Press)

Intergradations

Hybrid Zones and the Evolutionary Process. RICHARD G. HARRISON, Ed. Oxford University Press, New York, 1993. x, 364 pp., illus. $65 or £45. Based on a symposium, College Park, MD, July 1990.

Interest in the causes and consequences of hybridization between genetically differentiated natural populations remains strong in evolutionary biology, both because new molecular and statistical methods make multifaceted studies feasible and because refinements in hybrid-zone theory now provide a richer perspective on thinking about fundamental issues of adaptation and speciation. This compilation provides a timely update on many theoretical issues and includes examples of long-term multidisciplinary studies.

The first four chapters review conceptual issues and practical concerns for field studies. Those unfamiliar with hybrid-zone issues will find chapters 2 through 4 useful. In chapter 2 Barton and Gale describe models used to estimate cline shape and width, linkage disequilibrium between unlinked markers, and the assumptions and limitations of each model and then show how the models are used to estimate the strength of selection maintaining a zone, the number of loci differing between hybridizing populations, dispersal rates, and the facility with which alleles introgress. A fundamental distinction is made between selection maintaining a zone due to extrinsic factors (where fitness varies along an environmental gradient) and the existence of a "tension" zone in which selection acts against hybrids (intrinsic).

In chapter 3, Howard provides a useful definition of reinforcement (that is, prezygotic barriers to gene exchange improved by natural selection in response to selection against hybridization) and a possible consequence, reproductive character displacement (RCD; a pattern of greater divergence of an isolating trait in areas of sympatry and hybridization between closely related taxa than in areas of allopatry). Several theoretical objections have been raised regarding the importance of these processes, but most empirical studies cited as failing to support RCD were not originally designed to critically test reinforcement hypotheses.

The last chapter of this section (Rieseberg and Wendel) summarizes much of the literature on plant hybridization and suggests that many plant systems are suitable for studies of the transfer of adaptations once molecular markers have been linked to adaptively significant traits.

The remaining chapters summarize data on a variety of different hybrid zones that display a remarkable diversity of characteristics. Moore and Price describe an extremely broad, ecotonal contact on a continental scale between two subspecies of northern flicker (*Colaptes auratus*), whereas extremely narrow zones are described for two complexes of grasshoppers (*Caledia*, Shaw *et al.*; and *Chorthippus*, Hewitt) from Australia and Europe, respectively, several species of *Iris* from the southeastern United States (Arnold and Bennett), Amazonian butterflies of the genus *Heliconius* (Mallet), European toads of the genus *Bombina* (Szymura), European mice and shrews (*Mus* and