Ecological Studies 12

Perspectives of Biophysical Ecology

Edited by David M. Gates
and Rudolf B. Schmerl

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Springer-Verlag
Berlin · Heidelberg · New York

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Springer-Verlag Berlin · Heidelberg · New York 1975

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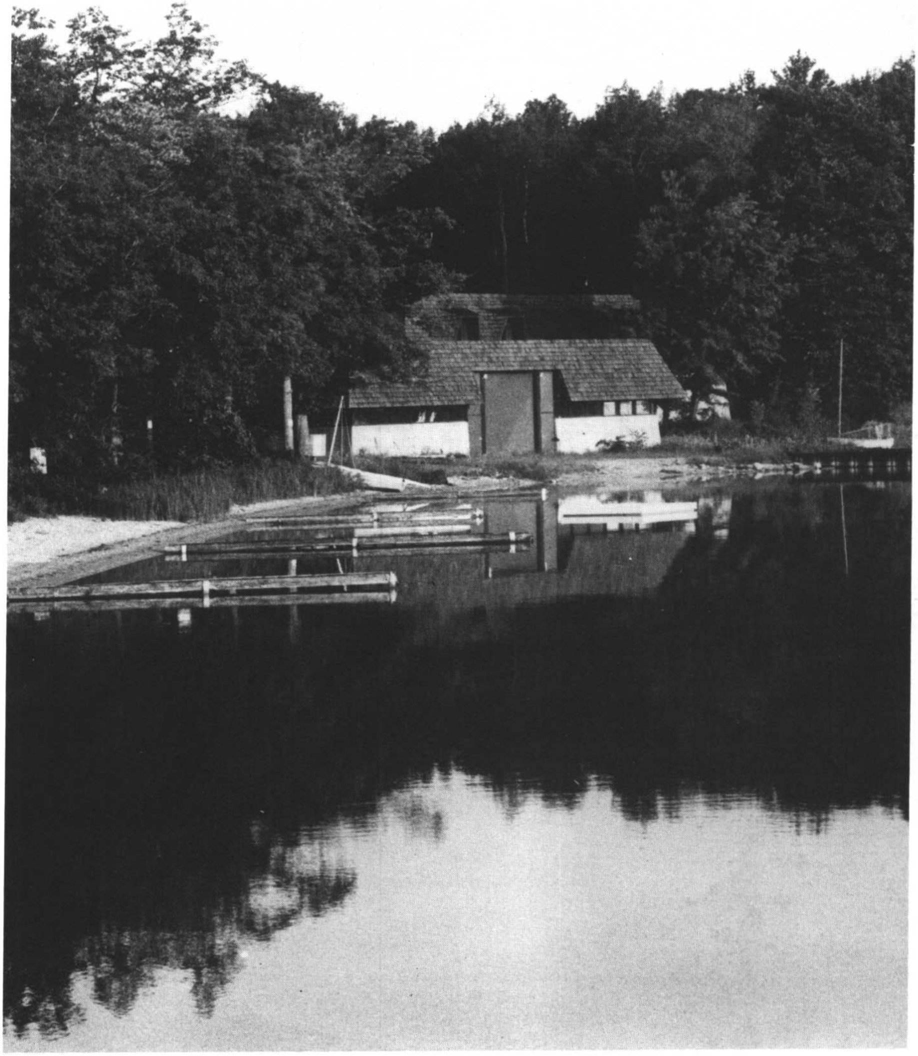
Library of Congress Cataloging in Publication Data

Main entry under title:
Perspectives of biophysical ecology.
(Ecological studies, v. 12)
Papers presented at a symposium held at The University of Michigan, Biological Station, Aug. 20–24, 1973.
Includes bibliographies.
1. Ecology—Simulation methods—Congresses.
2. Biological physics—Congresses. I. Gates, David Murray, 1921- ed. II. Schmerl, Rudolf B., ed.
III. Michigan. University. Biological Station.
IV. Series.
QH541.15.S5P47 574.5 74-17493

Printed in the United States of America.

ISBN 0-387-06743-4 Springer-Verlag New York · Heidelberg · Berlin
ISBN 3-540-06743-4 Springer-Verlag Berlin · Heidelberg · New York



Alfred M. Stockard Lakeside Laboratory, The University of Michigan Biological Station on Douglas Lake, Pellston, Michigan

(Photograph courtesy of Gary R. Williams)

Preface

A symposium on biophysical ecology was held at The University of Michigan Biological Station on Douglas Lake August 20–24, 1973. Biophysical ecology is an approach to ecology which uses fundamental principles of physics and chemistry along with mathematics as a tool to understand the interactions between organisms and their environment. It is fundamentally a mechanistic approach to ecology, and as such, it is amenable to theoretical modeling.

A theoretical model applied to an organism and its interactions with its environment should include all the significant environmental factors, organism properties, and the mechanisms that connect these things together in an appropriate organism response. The purpose of a theoretical model is to use it to explain observed facts and to make predictions beyond the realm of observation which can be verified or denied by further observation. If the predictions are confirmed, the model must be reasonably complete except for second or third-order refinements. If the predictions are denied by further observation, one must go back to the basic ideas that entered the model and decide what has been overlooked or even what has been included that perhaps should not have been. Theoretical modeling must always have recourse to experiment in the laboratory and observation in the field.

For plants, a theoretical model might be formulated to explain the manner and magnitude by which various environmental factors affect leaf temperature. A theoretical model might explain how wind, radiation, and air temperature affect the rate of water loss from a leaf or precisely how photosynthesis depends upon carbon dioxide concentration for a given light intensity, air temperature, wind speed, and relative humidity. A theoretical model might be formulated to explain how various environmental factors such as wind, air temperature, radiation intensity, and humidity affect the temperature of an animal. The intent in biophysical ecology is to obtain not simply a qualitative description of cause and effect, but a precise quantitative relationship between the final event and the causative factors.

As a general rule, it has been extremely difficult for the person trained primarily in biology to engage in theoretical analysis or modeling based on mechanisms from physics and chemistry. The biologist is usually more thoroughly trained in chemistry than in physics and, unfortunately, often lacks adequate advanced training in mathematics. The physicist or chemist often has little interest in a biological problem, and, when there has been interest, it has been at the molecular or cellular level. To fulfill the needs of the science of ecology, one must work with whole organisms and with the full scientific spectrum of significant factors, features, and mechanisms. This requires knowing biology well, but also knowing quite a lot concerning physics, chemistry, and mathematics. To achieve this, we have tried to find biologists with a facility for physics and mathematics and to lead them into the field of biophysical ecology. This has not been easy to do. Very few people trained in biology are able to originate and advance new methods of theoretical analysis. We have also tried to interest people trained primarily in physics and mathematics in the problems of ecology, and this also has not been easy. It is often difficult for such people to understand the biological problem, particularly the more subtle aspects of a problem, and to see the directions they should go in ecological science to work on significant and not on trivial matters. The dichotomy that continues to exist among people trained in the biological or the physical sciences is truly amazing. Yet to address certain questions in modern ecology, one must, as much as possible, be the complete scientist.

The purpose of the Biophysical Ecology Symposium held at Douglas Lake was to review our achievements to date in this field and to determine in which directions we should go to advance the state of the science as rapidly as possible. To do this, we brought together most of the Ph.D. students and post-doctorates who had trained with me during the last decade. To this group we added two others: a group of physiological ecologists who had a strong interest in the methodology of biophysical ecology, and a group of graduate students who have a serious interest in the subject. During the symposium the plant and animal papers were alternated in sequence. Nearly everyone in attendance participated in the entire set of presentations. During the last day the symposium participants formed four workshop groups, two around problems of plant ecology and two around animal ecology. The four groups met in working sessions and were asked to formulate recommendations for future work in biophysical ecology. These recommendations are summarized at the end of the book.

Not all the papers presented at the symposium were strictly biophysical ecology. Many were standard observational, empirical plant or animal ecology or physiological ecology. Some of the papers had nothing to do with modeling or analysis but formed significant contributions in terms of data. All the papers contributed ideas of importance to those working in biophysical ecology.

The symposium was supported by funds generously made available by The University of Michigan's Institute of Science and Technology, and the publication of this volume has been facilitated by funds from the Class of 1962–Institute of Science and Technology Publishing Fund. The Institute's Director and Assistant Director, James T. Wilson and Jay Katz, deserve special thanks. The staff of the Biological Station was responsible for transportation, housing, and commissary arrangements for all guests at the Station, and did a superb job. I am deeply grateful to all who participated in this symposium for their contributions.

David M. Gates

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Introduction: Biophysical Ecology

David M. Gates

Prefatory Remarks

Biophysical ecology, a subdiscipline of ecology, uses an analytical approach involving the laws of physics and chemistry to understand the mechanisms by which plants and animals interact with their environment. Ecology is the study of organisms and their interactions with their environment and with one another. Taking the first part of this definition, one recognizes that we are dealing with the interaction of biology with the physical world. If ecology is to be done well, the biological aspect of the science must be understood well and the physical aspect must be understood equally well.

Biological and physical sciences each have had their descriptive phases, but the physical sciences have been more amenable to incorporating mathematical analysis. Mathematics abbreviates the lengthy thought processes involved in logic and extends these thought processes to extrapolation and prediction. It is for this reason that mathematics is applied as an analytical tool in the solution of biological problems.

Not only do all organisms live in a physical world; in every respect, they utilize basic physical mechanisms for their viability and reproducibility. As remarkable as the biological world seems to us, I do not believe that its workings are more than an incredible number of physical mechanisms interacting in a large number of subtle combinations. The complexities involved are enormous and our ability to understand these is limited. Nevertheless, certain mechanisms, forces, and processes may dominate the performance and behavior of organisms. Our task in the study of biology is to understand these and to recognize those of primary importance first, then those of secondary or tertiary importance. This viewpoint does not deny that every possible kind of cell-to-cell, organ-to-organ, or organism-to-organism interaction may exist. A community of organisms has many remarkable properties, some of which may not be characteristic of any other kind of assemblage in the universe.

A reductionist approach to biology, or specifically to ecology, by no means excludes a holistic viewpoint. I am convinced that a great deal of biological understanding will be achieved through analysis based on mechanisms; at the same time, other approaches are worthwhile and necessary.

My initial approach to the subject of biophysical ecology was strongly microclimatological, as shown by the references given in Gates (1959). Because of my training in physics and my work in atmospherics from 1947 through 1959, I was not familiar with the literature of biological science, except superficially. The 1959 article, given as an address at the Semicentennial Celebration of The University of Michigan Biological Station, was largely concerned with the radiation environment of plant and animal habitats. My interest in this subject and my feeling that it was of great importance to ecology was evident in a much earlier publication by Gates and Tantraporn (1952), concerned with the infrared reflectivity of vegetation. During the intervening years, I often thought about the problems challenging ecologists, e.g., problems of adaptation, productivity, succession, competition, and distribution among organisms. Concern with these problems had been firmly imprinted on my mind by my many years as a youth at the Biological Station and close association with my ecologist father, Frank C. Gates, and his colleagues. My interest in biology was intensive at that time, but I wished to work in a branch of science more analytical than biology then appeared to be. Physics was compatible with that desire and, as is clear in retrospect, was an excellent route to ecology. I had the good fortune to learn a good deal about biology from close association with the many great biologists at the Biological Station.

I spoke of the dichotomy between physical and biological sciences in my Semicentennial Address in 1959 and suggested some means to close this gap in the training of students. Some changes have occurred in university curricula in this respect during the last 15 years, but the changes are not nearly sufficient. Once again I wish to emphasize that to do the science of ecology well, one must do the biological and the physical sciences related to it equally well. Usually the training of ecologists stresses biology very heavily and neglects the physical sciences. This is not adequate preparation for a subject inherently extremely difficult. Relatively few people have come to grips with the most difficult and challenging ecological problems. For the most part, they have been satisfied with the qualitative aspects of ecology, or with the quantitative aspects in terms of numbers and rates. The new, extremely worthwhile work concerning systems ecology provides insights to the interrelations among many components of ecosystems. Yet within such interrelations of trophic levels, the flow of energy, the flow and cycling of minerals, and the gains and losses of biomass are the fundamental mechanisms that control, regulate, and influence them. These fundamental mechanisms are physiological and physical; they involve organisms and their environment. Once the coupling mechanisms between an organism and its environment are thoroughly understood, an extremely critical domain of physiological ecology will still remain to be worked out. This domain is in the biochemistry of metabolism and growth, resistance to heat and cold, fertility, germination, and a whole complex of important biological events. Many of these events are mediated through enzymes, and the incredible number of complex, closely related, biochemical reactions staggers the imagination.

Yet eventually the ecologist must confront these problems and bring as much biochemistry as necessary into the analysis of organisms and their interaction with their environment.

The process of understanding the interactions of plants and animals with their environment and their response to various factors involves every aspect of the organism and the environment. No scientific problem could be more difficult or more challenging, yet modern science is fully capable of addressing it. The analysis of this problem involves taxonomy, systematics, physiology, biochemistry, biophysics, physics, meteorology, climatology, mathematics, engineering, and other disciplines. Clearly a single investigator cannot learn all these things well, but given the proper initial training, one can do much to address the problems of autecology rigorously and competently, and this must be done if ecology is to advance rapidly as a modern science.

Organism–Environment Interaction

An organism interacts with or is coupled to its environment through the exchange of energy and materials, but also through sensory perceptions of sight, sound, touch, taste, and emotion. Only a few of these processes are addressed in this volume. The problem we face when attempting to understand the interactions of organisms with their environment is to choose where to begin. This choice may be made on the basis of the most dominant or first-order factors, or it may be made through some other rationale. Since any event that involves life requires the expenditure of energy, I decided some years ago that I would approach the problem first through the flow of energy. Once I understood energy exchange, I would concentrate on understanding mass exchange, and finally become involved with the internal physiology and chemistry of the organisms. However, energy and mass exchange are closely related, and one cannot deal with the one without immediate involvement with the other.

I also made another choice very early. Given a choice of working with either plants or animals, I decided to work with plants first. Not only are plants the primary producers, but in many respects they are easier to work with than animals. They do not bite, their metabolic rates are relatively low, they do not move about very much, and for the most part they have a more agreeable odor.

Energy exchange between an organism and its environment may involve radiation, convection, conduction, evaporation, and chemical reactions. Each of these is fairly complex and must be dealt with in detail. The flow of energy between an organism and the environment is time-dependent and often involves rather rapid rates of change. Amid frequent and irregular variations of energy flow are periods of steady state when an organism is neither gaining nor losing a net amount of energy. With full recognition of the ubiquity and importance of time-dependent energy flow, I made an early decision to solve the steady-state problem first. To approximate time-dependent or transient events, one can consider a series of incremental changes in steady-state energy flow. But beyond that approximation, one must come to grips with the complete time-dependent analysis to realize as accurately as possible how the real world of plants and animals works in response to environmental factors.

The temperature of a plant or an animal is a manifestation of its energy state, which in turn is determined by the rate of flow of energy between the organism and its environment. Many physical and physiological events that occur in organisms, such as metabolism, water loss, mobility of ions, fluidity of fats, permeability of membranes, and gas exchange, depend upon temperature. Hence the temperature of a plant or an animal, and precisely how the environment influenced it, were of primary interest in our initial research.

Without going into great detail here, I shall summarize the advances made by our research group during the past 15 years. A complete bibliography concerning this work is included. References in this paper to publications of our research group are in this list. A separate bibliography is attached for references to papers published outside our group.

Plants

Since the temperature of a plant is a measure of its energy status, which is the result of energy exchange between the plant and its environment, my first major effort was to identify the mechanisms involved in the exchange of energy. Once this was accomplished, a research program evolved which led to the explanation of many ecological events involving plants.

The energy budget of a plant leaf in steady-state condition is written in the form

$$Q_a = \varepsilon\sigma T_l^4 + H(T_l - T_a) + LE + P \quad (1)$$

where Q_a = amount of radiation absorbed
P = energy consumed by photosynthesis
ε = emissivity of the leaf
σ = Stefan–Boltzmann coefficient for blackbody radiation
T_l = leaf-surface temperature
H = convection coefficient
T_a = air temperature
E = amount of water consumed by transpiration
and L = heat of evaporation (about 580 cal g^{-1} at 30°C) and converts the rate of water loss in grams to energy units (actually, L is a function of the leaf temperature)

All terms in Eq. (1) are expressed in cal cm^{-2} min^{-1} or ergs cm^{-2} s^{-1}. The photosynthetic term is negligible for most heat-budget calculations, and only in rare cases, such as with some of the arums, does the respiration rate have a significant effect on plant temperature. In Eq. (1) all surfaces of the leaf are considered at the same temperature, and heat exchange by conduction is considered negligible.

These are clearly approximations that may be more or less true, depending upon the particular leaf. For most thin, broad leaves, these approximations are very good. For a thick leaf or, for example, the blade of a prickly pear cactus, the upper and lower surface temperatures are usually very different, and heat is exchanged between them. Equation (1) is not adequate when considering heat flow in stems, branches, trunks, etc.; other terms, mainly conduction, must be added.

The rate of evaporation of water from a leaf is determined by the amount of energy available and by the presence of a water-vapor gradient between the leaf and the air. The rate of water loss by transpiration is given by

$$E = \frac{{}_sd_l(T_l) - (\mathrm{rh})\,{}_sd_a(T_a)}{r_l + r_a} \tag{2}$$

where ${}_sd_l(T_l)$ = saturation water-vapor density of the air in the mesophyll of the leaf as a function of the leaf temperature

${}_sd_a(T_a)$ = saturation water-vapor density of the air beyond the leaf and its boundary layer and is a function of the air temperature

rh = relative humidity of the air

r_l = diffusion resistance for water vapor in air within the stomatal cavity of the leaf and neighboring passages

r_a = diffusion resistance for water vapor in air in the boundary layer adhering to the leaf surface

In retrospect, the energy-budget relationship given by Eq. (1) and the water-vapor exchange concept as expressed by Eq. (2) are very obvious formulations, but at the time, first in Gates (1959, 1961) and then in Gates (1963), the ideas were new to me. My first papers dealt primarily with radiation in the environment and its importance as an environmental factor. In fact, quite early I published a paper concerning the infrared reflectivity of vegetation (Gates and Tantraporn, 1952) which became the primary reference in this area. Raschke (1955, 1956, 1958, 1960) had also developed in considerable detail the concepts of energy and gas exchange for a leaf. When I first worked out my ideas, I was not aware of Raschke's papers. Only when I presented a paper on this subject to the Denver meeting of the American Association for the Advancement of Science in 1961 were these called to my attention, by James Bonner. I had been working for 15 years in physics and had not been reading the biological journals. My first ideas concerning energy exchange were influenced considerably by a paper of Budyko's (1956) and by discussions with him during a visit I made to Russia in 1958.

To apply Eq. (1) effectively to the determination of leaf temperatures and transpiration rates, one must solve it simultaneously with Eq. (2), and the various coefficients and parameters in each equation must be known accurately for the particular leaf. For example, the following parameters are required: leaf absorptivity to sunlight, absorptivity and emissivity to thermal radiation, actual surface area of the leaf, effective areas for the absorption of solar and thermal radiation and for the emission of thermal radiation, leaf width and length (which enters the convection coefficient), the diffusion resistance to water vapor within the leaf (i.e., the stomatal and substomatal resistance), and the diffusion resistance of the