Ecology for Tomorrow

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Physiology and Ecology Japan
Volume 27, Special Number
March 1990

Physiol. Ecol. Japan, 27 (Special Number):199-205. (1990)

14. Three Interconnections of Ecology

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INTRODUCTION

Higashi and Burns (1990) argued that three perspectives are currently of great importance to ecological study, particularly on the ecosystem-community level of organization. Those are the network perspective (Higashi and Burns 1990), hierarchical perspective (O'Neill *et al.* 1986) and evolutionary perspective (Burns, Patten and Higashi 1990). Among these three, the network perspective is the most fundamental, providing the basic modelling framework. The other two perspectives supplement the first by increasing the efficiency and effectiveness of modelling; specifically, the hierarchical perspective distinguishes multiple scales, whereas the evolutionary perspective introduces the powerful dimension of time into the whole picture. The network perspective utilizes the *interconnections* existing among objects of concern as the main ingredients to discover "structure", the context in which ultimate factors can be better perceived and their significance understood.

We observe that many, and virtually all, of the papers presented in the symposium are concerned with interconnections of some sort. We may conveniently distinguish the following three categories of interconnections. The first category is for interconnections among the components that constitute an ecological system of concern. The second category of interconnections are methodological ones; namely, the interconnections among different but related approaches in ecology, which are desirable but in practice very weak in current ecology, and those that ecology should make with other related fields of science. The third category is for the interconnections that ecology should have with the resolution of practical problems of social interest, particularly the environmental problems that threaten in various ways and scales all of the life on earth including *Homo sapiens*.

INTERCONNECTIONS AMONG COMPONENTS OF AN ECOLOGICAL SYSTEM

Ecology is the biology of interdependence. A pair of action and reaction between two objects makes up a feedback loop, which provides a novel mechanism for generating self-regulatory or self-amplifying behavior, of the objects involved in the loop, depending on whether the loop represents a negative or positive feedback (DeAngelis, Post and Tribus 1986). A classic example of this is Clements'(1936) idea of succession. As Burns (this volume) pointed out, it was unfortunate for Clements to use the term "super-organism" for his conception of communities as a *system*. This is not only because the terminology misleads those who, forgetting the fact that "an analogy is an analogy", tend to rely too much on analogies, but also because the justifiable negative reaction to his idea obscures an important point in his original thoughts: the explicit recognition of the action-reaction pair, which makes up a feedback cycle, and its role and significance as a driving force for the succession of an ecological system.

The "Gaia", which was proposed by Lovelock (1979) and presented in the paper by Hinkle and Margulis (this volume), is a modern version of Clement's super-organism. This notion represents a perception of the global geosphere-biosphere complex as a cybernetic system incorporating stabilizing negative feedbacks. Although it is thus an application of the general notion of ecosystems (Higashi and Burns 1990), the extremely global scale to which it is applied generates a fresh image. But, one must be careful in further investigations of the Gaia, not to rely too much on the analogy between the Gaia and an organism or a cell, avoiding the repetition of the mistake that Clements made by overextending the notion of super-organism.

When we obtain a means to detect chemical signals that cannot usually be sensed, the world must appear to be filled with a much denser network of ecological interactions. Yamaoka (this volume) shows that chemical media are available for complex networks of information transmission among individual organisms in the same and different species. Because information affects the behavior of organisms, it alters the manner in which organisms or species interact with each other, resulting in an increase in the complexity of interaction networks.

The network of interactions among species, which may contain feedback loops, has more recently found its relevance to, and even its important role in, biological evolution (Burns, Patten and Higashi 1990). Endler (this volume) emphasizes that the interactive connections, in the context of which each biological species is placed, are crucial when one studies the evolution and natural selection that a species experiences in the wild.

INTERCONNECTIONS AMONG DIFFERENT APPROACHES

Species-population approach and ecosystem-process approach

Ecology has been the study of biological species, their life histories, population dynamics and social structures, on the one hand, and the study of ecosystems, their energy and matter processing and sustainability, on the other. Also, it has pursued the origin and evolution of species in diverse environments. But, a review of recent studies on communities, the intermediate levels between the population and ecosystem levels, reveals a discrepancy or gap between these two research foci, population and ecosystem ecologies, or more specifically, species-population approach and process-functioning approach (O'Neill *et al.* 1986). This gap or separation has resulted in several shortcomings, which in turn suggest important research areas and themes that new research should address.

Among those the most important in our view is the deficiency in understanding the relationship between the macroscopic functioning of an ecosystem, in terms of energy and nutrients processes, and the spatiotemporal dynamics and fate of species-populations, as well as their biotic interactions (predation, competition and mutualism etc.) within the ecosystem. The importance of understanding the interplay between these two subjects is increasing in the context of the potentially great contributions of ecology to several global environmental problems, i.e, *globally distributed* problems, such as greenhouse effects, acid rain, and *globally shared* problems, such as the drastic reduction of biodiversity.

The separation of research efforts has caused, on the part of population/community theory, the neglect or underestimate of the decomposer and detritus components and also the nutrient and energy cycling processes in communities and food webs. The explicit addition of these missing ingredients to the population/community interaction model may make a quantitatively and quantitatively significant difference in the theoretical conclusions on community stability, food web structure and development, and species coexistence and diversity.

On the part of ecosystem theory, the same separation has caused the neglect of the life history, spatial heterogeneity and social structure of biological species when studying ecosystems. The lack of an evolutionary perspective in past ecosystem study seems a natural concomitant of this neglect of species' ecological traits, though community and food web theory from species-population approach has not fully incorporated an evolutionary perspective either. The explicit addition of these missing ingredients to the ecosystem model may reveal the causes and effects of disturbance (particularly biological disturbance due to invasion, introduction, or extinction, and deletion of species), spatial heterogeneity, and dynamic features (such as catastrophic changes, succession and evolution) of ecosystems.

Perhaps a more serious problem from the separation into two approaches is that most of the important theoretical problems have not been considered from both points of view at once or from an integrated view of species-populations and ecosystem-processes. This is the case even with those problems that by definition involve these two aspects, such as the relationship of stability (in the multiple senses of resistance, resilience, persistence etc.) and species-diversity to the energy and nutrient supply regime (total supply level and patterns of resource-supply paths, both spatiotemporally variable) of a food web (ecosystem), and further, the trend in these properties during long-term dynamic processes on time-scales of ecological succession and evolution. New insights into these theoretical issues should improve our understanding of the impacts made by various disturbances upon natural ecosystems, and thus contribute to environmental management and policy making.

Interface between population ecology and behavioral ecology

The main objective of population ecology is to identify and explain a wide variety of observed patterns of population fluctuations. In particular, the last three decades have seen the population regulation by density-dependent feedback mechanisms be debated. In spite of a number of long-term population studies in various taxa, no consensus on population regulation has been attained. Rather, most of these studies have remained at a level of phenomenological descriptions of temporal population fluctuations. The lack of consensus is largely due to the method that the conventional population study has adopted, which compares demographic parameters at the population level among different species. This comparative approach is less effective for drawing general conclusions from such complex observations, where the magnitude of population fluctuations, population densities and degree of density-dependence often differ from one locality to another even in one species.

An alternative approach should thus emphasize underlying mechanisms governing essential processes responsible for population fluctuations (Ohgushi and Sawada 1985, Schoener 1986). When we consider underlying mechanisms of population dynamics, *average* parameters of demography will no longer be appropriate. Instead, we should focus on ecology at the individual level, such as behavior, physiology, and morphology, associated closely through survival and reproductive processes with the components of demographic parameters.

Conventional population ecology has ignored, however, population consequences of the properties of individuals. This comes from the long accepted assumption that *all members within a population are identical in terms of survival and reproductive processes.* Population ecologists, based on this assumption, have long estimated the average values of demographic parameters, and tried to relate, using a regression method, these average values to those of population densities that are often defined ambiguously. However, regression analysis tells us nothing about the causal mechanisms generating various types of temporal variation in population density.

Once we look at the behavior or physiology of individual organisms, we must examine how the properties at the individual level are translated to demographic parameters at the population level. We thus need to know much about demographic variation within a single population. Demographic variation within a population comes from two different sources: exogenous and endogenous agents. The former involves spatiotemporal heterogeneity of resource availability, predation pressure, and habitat structure. Even when these agents remain constant in space and time, demographic variability derives from endogenous variations in phenotypes or genotypes associated with each demographic parameter.

The mechanistic approach based on characteristics at the individual level also contributes to understanding the consequences of evolutionary changes for population dynamics. For instance, an increase in frequency of individuals with a more efficient trait in resource use will increase population density relative to resource abundance (Endler, this volume). An understanding of this connection requires examining how changes of individual characteristics are related to changes in survival and reproduction. In studying natural selection in the field, the life-table approach, which has been widely used in population studies, provides a powerful tool for estimating not only lifetime fitness, but also the variability and intensity of selective agents when the information available in a life table is used to trace the fate of individuals and detect natural sources of mortality throughout the life cycle of an organism.

Ecology as a synthesizer of diverse fields of science

The papers in this volume, those in Part II in particular, represent interdisciplinary extensions of ecology. Endler (this volume), which offers a summary of his view on natural selection, shows interconnections that ecology has with genetics and evolutionary biology. Yamaoka (this volume) presents his own study on ant interactions by means of chemical "signals", along with a concise review of recent developments in chemical ecology, a new area of ecology growing in the interaction between ecology and biochemistry. Hinkle and Margulis (this volume) provide us with an introduction into global ecology, another new area of ecology emerging through interconnection with earth and space sciences. Oikawa (this volume) presents a study on forest carbon dynamics using mathematical simulation models, demonstrating an area in ecology that has been developed through the interconnections with mathematical sciences.

This list is enough to suggest at least a potential that ecology has for continuous growth and expansion through interactions with other fields. But, beyond that, when one considers the complexity of any ecological system, involving physicochemical and biochemical processes of great diversity, it is clear that ecology has to employ every available means, regardless of which field they belong to. This collaboration with other fields makes ecology a natural "synthesizer" of all these related fields of science.

INTERCONNECTIONS WITH PRACTICAL PROBLEM SOLVING: TWO-WAY INTERACTIONS

Complementary to and combined with rapidly advancing molecular and cellular biologies, which aim at understanding the whole complex system of biochemical interactions taking place inside organisms, ecology, which studies the complex system of interactions among organisms of diverse biological species, points to a more complete understanding of life and the fundamental logic of life-sustaining mechanisms. Just as basic research in molecular and cellular biologies are indispensable to remedy complex diseases such as cancer, basic ecological research provides firm ground on which to fight against complex global environmental problems. Ecology is a constant and primary source of ideas on how to recover and maintain nature's "life-support system."

Several papers in this volume, those in Part III in particular, provide examples for the interconnections that ecology has with practical problems of social concern. Orians (this volume) takes conservation biology and shows the interconnections of ecology with an applied field of science that is concerned with the preservation of biological species. Tundisi (this volume), dealing with the problem of "Ecology and development", provides overall perspectives and specific suggestions on how one can utilize and incorporate ecological results and knowledge in the processes of decision-making for regional developments and for solving environmental problems, demonstrating clear interconnections between ecology and environmental issues.

Since we already have in this volume these excellent reviews on the subject of the relationship between basic studies in ecology and practical problem solving, we merely make a few remarks. It is important to recognize the possibility for a mutually enhancing relationship between basic ecology and applied problem solving, even though it is harder for ecology to contribute to applied problem solving than it is for ecology to be enriched by practical problem solving (Orians, this volume). It is interesting to note that because there are no territorial boundaries in natural phenomena *per se,* practical problem solving not only enhances the basic study of ecology, but also demands that ecologists collaborate with each other and with researchers in other fields, promoting the synthesis of those related fields.

Thus, the interconnections of ecology with practical problem solving serves as a bridge connecting different approaches in the basic study of ecology, which should in turn enhance the understanding of the complex networks of nature. Believing that the better is a theory the more useful it is, we envision the "Ecology for Tomorrow" will be more useful in managing many threatening environmental problems.

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