13 Coexistence of Species

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Introduction

Part of the charm of science is its unpredictability. And one characteristic of the history of ecology is that students tackle completely new and unexpected problems rather than tidy up those left by their teachers. Hence, as a teacher charged with guessing the future of ecology, I begin with two strikes against me. But the science of ecology finally has some structure, even if not a very orderly structure as yet, and it is from the shortcomings of its present structure that we can make the safest predictions of the future. I will analyze these shortcomings in some detail and hazard guesses as to the difficulties in overcoming them.

Since my task is to predict the future, I shall not review details of the past here. The empirical and theoretical background of this chapter is discussed in a book that I wrote last summer: *Geographical Ecology*. Harper & Row, New York. 1972. 287 p.

Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true, as Eddington pointed out, that it is best not to put too much faith in facts until they have been confirmed by theory. This is why scientists are reluctant to believe in ESP in spite of indisputable facts. This is also why group selection is in such dispute among evolutionists. Only when a reasonable theory can account for these facts will scientists believe them. Ecology is now in the position where its facts are confirmable by theory and its theories at least roughly confirmable by facts. But both the facts and the theories have serious inadequacies providing stumbling blocks to present progress.

Present State of Knowledge of Coexistence

It is a platitude to say that species do coexist in nature. What is slightly less commonplace is that both early theory and early bottle experiments suggested that coexistence should be difficult. Darwin had resolved the difficulty before it ever arose by noticing that more similar species should compete more and find it harder to coexist. The theory and bottle experiments had treated either very similar species or ones in environments where their differences could not be shown.

The main progress in recent years has been the slow unravelling of the limiting similarity of coexisting species. Even the theory was hard to work out; in its present form, it can be stated in two ways: 1) In an unchanging environment, an arbitrarily large number of *appropriately* selected species could persist (up to the point where some were so rare they went extinct for random reasons). But the closer the species are packed, the more careful must be the choice of new species. A randomly selected one would likely not succeed when packing was close. In these tightly packed communities, all sorts of unexplored phenomena should exist. For instance, there should be cases of "domino extinction" in which elimination of one species results in the loss of a sequence of other species. 2) In a fluctuating environment, there is a distinct limit to the similarity of coexisting species, and it is a limit that is not too dependent upon the degree of fluctuation. Roughly speaking, species cannot be packed much closer than one standard deviation of the utilization curves of separate species.

Our empirical knowledge comes mostly from birds. Closely related species are often found to be doing just one thing different. For instance, pairs of species often forage in the same places and in the same way and differ only in size and, hence, in the size of food or diameter of twig they can perch on. In such pairs of species, the larger one is usually about twice the weight of the smaller. Alternatively, we can sometimes find closely related species that differ not in size but rather in height above the ground at which they forage. Such species usually differ in mean foraging height by about a standard deviation as the theory suggests.

Why are these data largely confined to birds? Partly because birds are easier to census and observe. Perhaps, also, birds are different—maybe they have packed their environment more fully, so that patterns of species packing are more evident. Only time will tell.

Shortcomings of Our Present Knowledge

First, and most interesting, there will be new patterns discovered and described by theory. The present structure is not complete enough to allow any prediction of what patterns these will be. But it is certain that the existence of undiscovered patterns, rather than the beauty of the already elucidated ones, should lure new talent into a field. It is paradoxical that so much talent goes into physics, with its glorious past and uncertain future, when ecology, with a certain future, gets far less talent.

From a view of present theory, it is clear that we know more about overlap of species than we do about their degree of specialization. In the jargon: Why is one species "broad niched" and another "narrow niched"? And why are some species able to adjust niche widths rapidly when put in a new situation while others are rigid? This will certainly be one of the problems occupying critical attention in the future.

Ecology is supposed to be concerned with relations between organisms and their environments, but most ecologists were trained as biologists and have been reluctant to tangle with the complexities of an environment. This has two consequences. First, many ecologists tried to avoid studying the environment by standardizing it in a laboratory situation, and usually by putting organisms into a homogenous medium and, thereby, removing the environmental structure. In these homogenized media, it proved almost impossible to get animals to coexist, in marked contrast to nature. The moral, of course, is that the complex structure of a real environment is essential to the coexistence of species. Therefore, field ecologists must become more concerned with the structure of the environment, and laboratory experiments will more and more be concerned with the effects of different spatial and temporal patterns added to their bottles or cages.

A primary aim of education is to train the student to distinguish the trivial from the profound. The educated theorist thus learns to tell an "interesting" theory from a "trivial" one although the distinction is not easy to spell out. Most interesting theories of coexistence have four shortcomings: 1) The mathematics have a simplified functional form, usually with some linear expressions. Often the equations are explicitly linear and, hence, only valid near equilibrium. 2) They describe populations in a single patch of environment but seldom tackle populations that trickle back and forth between patches. 3) They assume all individuals of a species are identical. 4) They neglect temporal variations in the environment.

These difficulties, coupled with the manifest complexity of nature, have led some good ecologists to doubt that a satisfying theory of ecology is possible. These are largely self doubts. Difficulty in imagining how theory can adequately describe nature is not a proof that theory cannot. People used to believe organic chemicals were too complex to synthesize in the lab on exactly the same grounds.

Philosophical Difficulties

Words are used in two contexts in science. First, when motivating research, or discussing it, or introducing it, one often uses words in a vague but suggestive way to help formulate ideas. When actual data are presented or theories formulated, these vague notions have no place, and all notions must have clear and public meaning. Ecologists have often confused these two uses and tried to give prematurely precise definitions of terms only used in the vague context. At best, this is harmless, while at worst, it is quite misleading. For example, ecologists are quite properly interested in the stability of ecological systems. But there are many different precise meanings for stability, some of them quite inconsistent with others.

The word "niche" is another example. From examination of the theory of species competing along a single resource dimension, it is clear that some definition of niche will be relatable to competition and coexistence, and the word is useful in the vague motivational context. I also believe no present precise definition can be related to competition and that the current precise definitions are premature.

What will the future bring? Clearly it will bring precise definitions of terms like "niche" but only when the time is ripe. Perhaps niche will turn out to be a concept that requires some subdivision into several precise definitions.

Here is a difficulty of another kind.

Ecology stands at a curious crossroads. As a science it is dedicated to reason, the enlightenment it produced, and even to the technological apparatus that make observations and interpretations easier. Yet the "Ecology Movement," to which most scientific ecologists are dedicated, is certainly anti-technological and often in fact anti-intellectual as well. Although individual ecologists resolve the dilemma by one decision or another, the movements do seem to have a fundamental opposition. Unbridled growth of science is certainly correlated with destruction of the environment, and unbridled "ecology" in the popular sense would promote anti-scientific outlooks.

A Long Range Prediction

What I have said so far involves only the short term predictions that can be made with some certainty by examining the weaknesses of present ecology. A longer range prediction must involve more than just the study of species' coexistence, because the long range goals of each ecologist involve the unravelling of a network of relations spanning the whole of ecology. Here I attempt my own prediction of how ecology, especially the ecology of coexistence, will develop; if this deters anyone from following an alternate approach, I will have failed, but if it stimulates people to think about the future without blindly following any course, I will be content.

I predict there will be erected a two- or three-way classification of organisms and their geometrical and temporal environments, this classification consuming most of the creative energy of ecologists. The future principles of the ecology of coexistence will then be of the form "for organisms of type A, in environments of structure B, such and such relations will hold." This is only a change in emphasis from present ecology. All successful theories, for instance in physics, have initial conditions; with different initial conditions, different things will happen. But I think initial conditions and their classification in ecology will prove to have vastly more effect on outcomes than they do in physics. Furthermore, there are many ecologists who, in their education, have been only exposed to one successful bit of science—the DNA, RNA story that proved essentially the same from viruses to mammals. These ecologists are often misled into thinking that viruses and mammals can be utilized equally well to elucidate the same principles of ecology. I will give some examples. First, it seems very clear that predators are very important in intertidal communities and not in terrestrial bird communities. The intertidal is essentially a simple surface, and is easy for a starfish to search effectively; a forest has a very much more complicated geometry, and it would be far more difficult for a hawk to cover it thoroughly. Hence, plausibly the intertidal falls into a classification of environment that tells us to pay special attention to predators, while in the forest community, we pay more attention to competition. Again, bird censuses in a habitat in successive years or in similar habitats in one year are usually very similar, while insect censuses (to the extent they can be taken) seem often to differ dramatically from place to place and year to year. Thus, plausibly in our classification, insects, at least of some kinds, will go into a non-equilibrium category and birds into an equilibrium category. But the classification will be more pervasive than these examples suggest; many morphological, behavioral, and genetic parameters will probably be included.

There has been a biological tradition of searching for the best organism to solve a problem—like Drosophila for chromosome genetics and viruses and bacteria for aspects of molecular genetics. The ecologist should resist this temptation. This is not to say he should not be selective about what he studies—of course he should. Rather, it is to suggest that competition and coexistence must be studied under a very wide spectrum of conditions before we can make the classification. A study of competition in micro-organisms is in no sense the slightest substitute for a study in vertebrates —or conversely.

The Training of Ecologists

Ecology as a science is almost always taught in biology departments, giving a natural priority of the organisms over the environment in ecological training. Although most ecologists are exposed to a spread of biological education from biochemistry through subjects closer to their preference, they are seldom exposed to the wide array of subjects that would be much more useful to them than most of biology. How many ecologists have had graduate level training in meteorology and climatology for instance? Or even a respectable training in geology? The cure here is easy: Ecologists should urge their departments to allow the option of substituting, say, geology for biochemistry in an ecologist's education.

But there is another aspect whose treatment is not so clear. How does the ecologist learn what science is? At the undergraduate level, he gets no clear picture from his biology courses, and at the graduate level, he may seldom see his major professor doing research. From the viewpoint of the subject of ecology, it is probably best for a variety of ecologists, with widely divergent backgrounds, to participate, but an open-minded student, wishing the education most likely to be successful, requests a more specific program. What should he be told? As an undergraduate, if he has the talent, I think he should be urged to take several physics courses. Although the actual material may not be applicable to ecology, and physics is not a perfect paradigm for ecology, it provides training in scientific thinking that can hardly be provided in any other way. The problem is more severe for graduate students. I think there is no systematic answer. When many graduate students are good, they reinforce each other.

Ecology has several "schools," at least as recognized by some people. This is all to the good, and we can hope all thrive. Unfortunately, there are propaganda efforts by insecure members of the various schools aimed at others, and it would not be the first time in history if one of these efforts succeeded in temporarily putting one school out of favor. To the extent that the propaganda is positive, it is harmless enough, but most insecure people get their kicks out of attacking others, usually pretending to be logical about it. In the interests of freedom and diversity, even these destructive attacks must be tolerated, but it is well to recognize that they tell us more about the attacker than the attacked. However, it is a pity that several promising young ecologists have been wasting their lives in philosophical nonsense about there being only one way—their own way, of course—to do science. Anyone familiar with the history of science knows it is done in the most astonishing ways by the most improbable people and that its only real rules are honesty and validity of logic, and that even these are open to public scrutiny and correction. For the future, we can hope that fewer ecologists waste their lives.