The exact size of the heavy chain gene enhancer has not been delineated. The Tonegawa group finds that most of the enhancing activity is contained in a fragment of some 140 base pairs. The Zürich workers suggest that sequences needed for enhancement are distributed throughout the 300 base pairs of their active fragment. The fragments do contain the core sequences, however.

The manner in which enhancers stimulate transcription is unknown. The sequences may serve as sites of entry for the enzyme that transcribes DNA into RNA. This could be done in a relatively nonspecific way if the elements simply altered the chromatin structure in their vicinity to make it more open to the enzyme. The binding of the enzyme could be made more specific if the proposed recognition factors help to direct it in some fashion to the right gene, possibly by serving as a component of the enzyme itself.

In addition to turning on gene expression in an orderly way during development, enhancers may also do so inappropriately, perhaps leading to the development of cancer. Certain of the retroviruses can apparently activate cellular onc genes by inserting their long terminal repeats, which carry enhancer sequences, near the genes.

In tumor cells from many patients with Burkitt's lymphoma, the chromosome rearrangement characteristic of the cancer moves the cellular myc gene near the switch region for the $C\mu$ coding segment where it may come under the influence of the heavy chain enhancer. The chromosomal translocation, Khoury points out, "may have contributed a red hot transcriptional region to a gene that is either quiescent or well-regulated otherwise." However, in other tumors, such as mouse plasmacytomas, the myc gene is translocated to a new position near the $C\alpha$ segment, where there is no known enhancer. Although the presence of an enhancer there has not been ruled out, the UCLA workers did not find any enhancing activity in the DNA between the $C\alpha$ exon and its switch site.

The issue of whether the specific translocations associated with various cancers lead to the development of malignancy by causing the overproduction of a normal gene product or because the translocated gene undergoes some change resulting in an altered product has not been resolved. Perhaps both contribute.

The supposition is that other genes, in addition to that for the immunoglobulin heavy chain, have their own enhancers. There are indications that enhancer-like sequences are found in the cellular genome. Khoury and Nadia Rosenthal of NCI and Michael Botchan and his colleagues at the University of California at Berkeley have identified sequences which are structurally related to viral enhancers and which increase gene transcription. Looking for additional specific enhancers will be high on the agenda of molecular biologists. Another item to be given high priority is the development of the cell-free systems needed for establishing how enhancers work.

The research has the potential of not only providing a better understanding both of normal development and of malignancy, but may also lead to improved control of genes that are introduced into new cells in gene transfer experiments. Poorly regulated expression of such genes, those for the globin chains, for example, has been a problem. Use of appropriate enhancer sequences may improve control of the genes and perhaps facilitate development of methods for treating hereditary diseases by gene therapy.—JEAN L. MARX

Predators and Hurricanes Change Ecology

Results from direct experimentation in natural communities has reemphasized the importance of predators and climate in community organization

Ecologists are in the midst of a major—and frequently acrimonious—debate about the processes in nature that influence the structure of communities. For more than two decades the phenomenon of competition between species has been prominent—and some say completely dominant—in ecologists' thinking about the way ecological communities are shaped. Indeed, as Jonathan Roughgarden, of Stanford University, puts it, "Competition theory was the only theory on the block."

During the past several years this establishment position has come under sharp attack from several directions. On one flank a group of workers, led by Daniel Simberloff of Florida State University, has challenged the validity and interpretation of data that many ecologists claim support competition theory (see last week's issue, page 636). Attackers on the other flank proselytize experimental manipulation, as opposed to field observation, as the superior method of obtaining data that might more reliably reveal the biological processes underlying patterns in community organization. This approach, which has been inspired largely by Joseph Connell of the University of California, Santa Barbara, has highlighted the effects of predation and environmental change in determining community structure, at the expense of competition between species.

The reaction against the hegemony of interspecific competition has been accompanied by something of an antitheory shift in ecology. Donald Strong, a colleague of Simberloff's at Tallahassee, sees benefits in this movement. "The dethroning of competition has provoked a vigorous empiricism of the most productive sort." Roughgarden, however, notes in a forthcoming paper in *American Naturalist* that "There is a curious tone of righteous indignation in Strong *et al.* (1979) and of ridicule in Connell (1980) that is antitheoretical." Strong retorts, "What we want is a realistic theory, not no theory."

One reason why interspecific competition so rapidly and decisively reached its prominent position in ecological thinking was the mathematical elegance and apparent explanatory power of the late Robert MacArthur's theoretical models, which he developed during the 1960's. Like many ecologists of the time, and since, who were interested in community ecology, MacArthur studied the distribution and morphology of bird populations. Irregularities in the distribution of bird species—species A never coexists with species B, for instance—has become something of an exemplar in competition theory, but it is an exemplar over which there are now keen differences of opinion (see last week's article).

A second reason for the swift ascendancy of competition theory is rooted in the philosophically appealing notion of the balance of nature, an idea that the natural world rests comfortably at or near equilibrium. "The conception of natural systems stems in part from a world view, derived from Greek metaphysics, which proposes that nature must, ultimately, express an orderly reality, and in part from our theory, which is largely founded on equilibrium or near-equilibrium mathematics," suggests John Wiens of the University of New Mexico. "Communities were considered to be tightly integrated entities that were comprised of suites of species and that exhibited clearly defined and repeatable structure under similar environmental conditions."

Competition between species for access to resources—food and space, for example—is an inevitable corollary of an ecological community in equilibrium: but if food supply exceeds demands—that is, the system is out of equilibrium—then there is nothing over which to compete. Wiens argues that not only did the MacArthurian school of community ecology perceive interspecific competition as virtually the only significant process influencing community structure but also held it to be an incessantly acting force. The supposed dominance of interspecific competition and its putative constancy are both under challenge.

"The experimental evidence does not often reveal the well-ordered, equilibrium world of MacArthur and [Richard] Levins,"observes Robert Colwell of the University of California, Berkeley, "but rather a sometimes turbulent and bewildering place where disturbance, natural enemies, biochemistry, life histories, and behavior play leading roles, along with the original cast of competitors." If natural communities are truly not constantly at or near equilibrium, what does this imply for the status of interspecific competition?

Wiens, who set out "fervently embracing the existing views of competitively structured, equilibrium communities," has been studying breeding bird communities in the structurally simple habitats of the prairies and shrub steppe of western North America. He did not see the types of patterns normally associated with competition theory and was impressed by the fact that the populations appeared to be exposed to periods of plenty that were punctuated by occasional environmental crunches. This was clearly not a well-ordered, equilibrial world. "Our work suggests that other systems might also be nonequilibrial much of the time." Stochastic environmental effects might be very important for many communities, suggests Wiens, while interspecific competition might be rather insignificant.

Wiens does not claim that the idea of equilibrium should now be dispensed with. "Natural communities should be viewed as being arrayed along a gradient of states ranging from nonequilibrium to equilibrium," he says. "A major objective of community ecology should be to begin to place natural systems at positions along this spectrum." The presumption of equilibrium that has pervaded ecological research has inevitably shaped the methodology, says Wiens, so that ecologists are not yet in a position to be able to assess patterns in communities as a prelude to placing them at discrete points along the equilibrium-nonequilibrium continuum. "The study of community patterns and processes is not the sort of simple, straightforward matter that many avian ecologists seem to have thought."

> "Better to have your ideas knocked out by a hurricane than by someone else. It's less traumatic."

Wiens has recently been involved in an exchange of views with Thomas Schoener, of the University of California, Davis, who is closely identified with the competitionist camp. Schoener concedes that Wiens's emphasis on nonequilibrium systems is "of major importance," but suggests that "periods of equilibrium and nonequilibrium fall into a pattern, and that the pattern itself provides strong evidence for the ultimate importance of competition." Wiens wishes to avoid being labeled as a rabid anticompetitionist and stresses that "my main emphasis was on the *intermittency* of competition as contrasted with the constancy expected from prevailing arguments." The competitionist and variable-environment views are not incompatible alternatives, he says, "but are complementary, drawing attention to different aspects of the dynamics of natural systems." The natural world, as Colwell notes, is clearly a more bewildering and uncertain place than hitherto appreciated.

Adding to that uncertainty is the growing list of factors, that, together with competition, might influence community structure. Colwell, in collaboration with Robert May, of Princeton University, and British ecologists Paul Harvey and Jonathan Silvertown, characterizes succinctly the bewildering complexity of ecological systems: "community patterns may be influenced by temporal or spatial changes in the environment, or by chance events, or by competition, or by mutualism, or by parasites or predators, and in general by the complicated (not to say chaotic) interplay of all these factors."

Any particular pattern manifested within a community might be the outcome of any one of several processes, or the product of two or more interacting processes. Moreover, two processes might have opposite effects on, say, the distribution of a species; when both are operating, the patterns of distribution associated with each would be canceled by the other, and therefore no diagnostic pattern results. As ecologists must try to infer the process or processes that underlie observed patterns within communities, the complexity of it all is causing some practitioners to be cautious, not to say pessimistic, about the chances of succeeding.

Simberloff, for instance, in conjunction with Edward Connor at the University of Virginia, warns against inferring the effects of competition from perceived patterns in a community just because the patterns are consistent with those predicted by competition theory. "Since a unique cause cannot be associated with a particular class of co-occurrence patterns, it is impossible based *solely* on biogeographical evidence to infer that competition or *any* other specific cause is responsible for a particular geographic pattern." Simberloff and Connor imply that too often in the past this trap has ensnared those who uncritically accepted the supposed all-pervasive power of interspecific competition. "Without further evidence, probably of an experimental nature," they suggest, "one can neither eliminate any particular causal mechanism, nor conclude that a particular mechanism has operated."

By tradition, the MacArthurian school has tended to emphasize natural experiments, that is, observation of natural field situations, over interventionist experiments, either in the laboratory or in the field. Each approach has its advantages and disadvantages. There is a decreasing degree of control and precision as one goes from natural experiment to field experiment to laboratory experiment. But this is accompanied by an increasing degree of artificiality. Moreover, it is simply not practical to perform laboratory experiments with communities of large species. Nor, often, is it permissible, for moral or political reasons, to undertake direct intervention, such as the removal or introduction of a species, in many natural communities.

Jared Diamond of the University of California, Los Angeles, who is one of the most prominent figures among the competitionists, also considers that the results of manipulations in field experiments are inevitably rather short-term and thus possibly limited in scope. "Natural experiments have the advantage that they reveal the end results of ecological and evolutionary processes operating over long times and large areas," he says. The observer must try to control his studies by selecting two sites that differ only in one major factor so that comparison between the two will yield meaningful results. Field experimenters are more than a little skeptical that this can be achieved with any rigor. "Results of such uncontrolled experiments are far too ambiguous to be convincing," contends Simberloff. "In particular, habitats almost always differ between sites."

During the past several years there has been an upsurge in popularity of field experiments among ecologists studying community structure. This development has been accompanied by a widespread perception that results from these experiments eclipsed interspecific competition in favor of predation and stochastic environmental events. This latter trend has been viewed partly as a timely readjustment of weight attributed to competition in relation to other processes, and partly as a consequence of the nature of the systems typically studied in field experiments, namely, communities of small rather than large organisms. It turns out that, compared with other factors, competition might well be less important in such communities. Now that, in Colwell's words, "theoretical ecology is no longer the ecology of birds," a more complete picture of communities and the processes that influence them might be emerging.

Connell, the leading field experimentalist, started out in the early 1960's believing in the balance of things and believing, too, in the overriding importance of interspecific competition. He was rather quick to change his mind. "I went to Australia in 1962 to study reef and forest communities. A hurricane promptly swept through my study areas and wiped everything out." This very direct and difficult-to-ignore evidence of the impact of certain stochastic events in nature had a formative effect on Connell's thinking. "Better to have your ideas knocked out by a hurricane than by someone else," he reflects. "It's less traumatic."

Also, in the early 1960's Connell traveled to Scotland where he carried out field experiments with species of barnacle. The results conformed very nicely with competition theory. But when he tried similar experiments on the Pacific northwest coast of America he saw something quite different. "Predation kept the population below levels at which competition might arise." Through the years since those early experiments Connell has carefully devised a set of standards of evidence—derived principally from field experiment—that he considers necessary in order to draw reliable conclusions about processes occurring in communities. He has also come to view predation and certain abiotic factors, such as climate, as important influences on communities.

Atop the trophic ladder

"I'd expect competition to be more important for species-rich communities as compared with species-poor communities; more important high on the trophic ladder than low; and more important in communities subject only to modest physical disturbance. These are some of the generalizations you can make."

Strong, another enthusiastic field experimenter, also emphasizes stochastic factors and predation and downplays competition. "You see virtually no evidence of interspecific competition in [my] work . . . with insects and the work others have done with insects. Populations rarely build up to the levels at which competition becomes important." Strong considers vertical interaction through the trophic web (herbivore through to top predator) as being more significant than horizontal interactions, such as competition. The trophic web forms a very broad-based pyramid and, roughly speaking, interspecific competition becomes relatively more significant nearer the apex. "This represents just a tiny fraction of species in the world," Strong says. Small it may be, counters Roughgarden, "nevertheless, it is a conspicuous part of the animal world."

One clear product of burgeoning field experimentation has been a sharper appreciation of the importance of processes other than competition in community ecology and an acknowledgment that certain processes will be differentially influential in different types of communities. Schoener speaks for many when he says, "I'm becoming a genuine believer in the differential distribution of the importance of the different factors." The question for ecology therefore focuses more crisply than ever before on measuring the relative contributions of each process in each particular circumstance. Inevitably, this leads right back to the issue of standards of evidence and the preferred method of analysis: field or natural experiment.

Connell sees the need for far more comprehensive experimentation before anything firm can be concluded. Until that point has been reached "speculation about the importance of competition is probably premature." And Wiens considers the natural experiment approach, which is identified with the MacArthur school, to be too weak to give unequivocal answers. "The general lack of scientific rigor in the approach has left us unable to determine which patterns and which processes have real merit and which are mythological." Only by conducting manipulative experiments, long-term investigations, and concentrated studies on local assemblages will any clear answers be produced, he says.

Simberloff not only champions experi-

An environmental shift

Rising salt concentration in the soils of Amboseli, Kenya, is destroying the Acacia tortilis *woodlands, home of baboons and vervet monkeys. The community is changing through strictly nonbiological—mainly climatic—causes.*

mental manipulation as the more productive data-gathering route, but also downgrades the utility of theory. "Almost none," is his answer to the question of how much competition theory has contributed to the useful insights gained from experimentation. "Theory is a key tool in ecology," counters Roughgarden. "Experimentation by itself is not enough."

Not unnaturally, Diamond is not persuaded of the superiority of field experiments over natural experiments, nor does he accept the characterization of natural experiments as lacking in scientific rigor. "I see it as unfortunate that people push the virtues of one approach over another," he comments mildly. Some situations are, however, just not accessible to experiment, especially one that Connell caricatures as "the ghost of competition past." If competition in the past has influenced the distribution or morphology of a species A, but in recent times the competitor species B has disappeared, how does one determine what has happened? "Natural experiment is the only way in such a case," says Diamond. "Joe [Connell] would object to this, and he has a point."

When faced with ghosts or other barriers to experimentation, ecologists should not despair, urges Colwell. "Realistic experiments with primate or bird communities are not much more feasible than experiments in astrophysics," he notes, "but our curiosity about stars and starlings is not thereby lessened." "Ecology is a difficult science," offers May, "partly because evolution has only given us one world, and it is not easy to perform controlled experiments."

Field experimentation and natural experimentation are therefore proving to be somewhat uneasy, if not downright antithetical, partners in the quest to analyze community structure. The upshot is that when any protagonist puts intraspecific competition in context, the emphasis placed upon it depends very much on which technical approach is favored. Simberloff, for instance, says that "It is certainly less important than predation and effects of physical environment; certainly less important than intraspecific competition; and probably less important than parasitism." Diamond, by contrast, phrases his assessment this way: "I'd expect interspecific competition to be more important for species-rich communities as compared with species-poor communities; more important high on the trophic ladder than low; and more important in communities subject only to modest physical disturbance. These are some of the generalizations you can make."

The recent emphasis on field experimentation, in combination with keener analysis of data from natural experiments (described in last week's article), has clearly produced an intellectual shift in modern ecology. A pertinent question is, how big a shift is it?

Roughgarden, for instance, argues that "Dan Simberloff is correct in saying that interspecific competition received a lot of attention to the exclusion of other population interactions." An examination of the literature of the past several decades, says Roughgarden, "would lead one to infer that all that was happening between species was competition."

Such sentiments are to be heard frequently among protagonists in the debate. But the towering dominance of competition was not a reality for all community ecologists, and was certainly not so for British ecologists whose enthusiasm for the Hutchinson/MacArthur school was cool compared with its reception in North America. Therefore, when Diamond argues that "The suggestion that interspecific competition was the predominant interest is clearly a straw man," he might well be closer to the global truth.

The recent demonstration by Schoener, who is a competitionist, and Connell, who is not, that, contrary to a widespread perception, the great majority of published field experiments confirm the existence of some degree of competition between species is an important refinement to current debate. "Competition is alive and well," concedes Connell. Schoener concludes: "We have had a scare—what if competition cannot be detected anywhere, even where most expected?—but the scare is now ended."

So, important though the recent refocusing on a wide range of processes might be, it seems to fall short of the Kuhnian-type revolution that some protagonists suggest. Ecology, says Colwell, "is undergoing not a revolution in paradigms, but a salubrious readjustment in the balance between our increasingly detailed appreciation of nature and the domain of our theories and models."

Prominent though it was, competition theory was never a general theory of ecology in the same way that certain general theories have wide explanatory powers in the physical sciences. Ecological systems are so multilayered and complex, and differ radically in space and time, that, says Diamond, "You cannot look for overall general theories. You can look for the influences that are more important in one setting as against another." Roughgarden also sees a piece by piece approach as being the most appropriate. "We need a richer vocabulary of models that pertain to particular population processes under particular circumstances."

Ecologists recognize that such a flimsy framework would never be applied to a self-respecting physical science, and many yearn for something more coherent. "Physics-envy is misguided," admonishes Simberloff; "ecologists' proper goal should be not the approbation from physical scientists but a firm understanding of natural processes, to the point where we can predict the outcome of specified ecological processes and answer many of the specific ecological questions of direct application that currently besiege us."—**Roger Lewin**