Competition and Theory in Community Ecology

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COMPETITION AND THEORY IN COMMUNITY ECOLOGY

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This essay is about competition as an ecological and evolutionary force, and about theory in community ecology, particularly competition theory. It responds to Connell (1980), Strong et al. (1979), and Connor and Simberloff (1979) (who criticize the evidence for competition, and the theoretical attention that competition has received.) These criticisms imply that competition theory, including its extension to the coevolution of competitors, is irrelevant to natural processes and is unworthy of testing regardless of whether the testing is feasible. As someone active in community theory, I wish to explain why these criticisms are unfounded and what the nature and function of theory is in community ecology.

The essay is in three parts. The first is philosophical and concerns how one establishes an empirical fact in science. The essay begins with a philosophical discussion because the criticisms spring from what I feel are untenable positions in the philosophy of science. The second part details some serious technical flaws in the proposals of the critics. The third is an account of what theory in community ecology is, what it is trying to do, how it should be judged, and what some of the sources are of misunderstanding between theoretical and empirical points of view.

PHILOSOPHY

Some Initial Propositions

Consider some propositions about how facts are established in science. They provide a point of departure for evaluating philosophical aspects of the papers by Connell (1980), Strong et al. (1979), and Connor and Simberloff (1979).

We establish an empirical fact in science in the same way that we establish ordinary empirical facts during our everyday lives.

The way we establish an ordinary empirical fact is by building a convincing case for that fact.

In our everyday lives we rarely abide by formal rules to tell us how to build a convincing case; we use our native abilities, common sense, and experience in building a case for, and evaluating, claims of fact.

As scientists, we rarely abide by formal rules in establishing scientific facts. To

establish a fact, we develop a case for that fact by appealing to the common sense and experience of people, most of whom are other scientists. Whether a case is convincing depends both on what is in the case, and on the knowledge, bias, and dispositions of the people to whom it is submitted. A finding is accepted as fact only as long as, and to the extent that, people remain convinced. Acceptance is neither complete nor eternal for a factual claim.

The truth of a factual claim is eternal; it either did or did not rain in Rome on the Ides of March in 100 B.C., and grassquits either did or did not eat the same types of food as anoles during the dry season of 1981 on St. Eustatius. In accepting or rejecting such claims, we evaluate the evidence offered on their behalf. Yet the degree to which we are convinced by the evidence depends on our experience at that time, and can change as our experience changes.

Any belief that scientists establish facts with more certainty than we can in our everyday lives is a delusion. Our distinctive activity as scientists is that we encounter and experience phenomena that are remote from our everyday lives, or that are overlooked during our everyday lives; but the way we try to understand these phenomena is with abilities whose credibility originates in everyday circumstances.

As scientists we use experimental setups, specialized equipment, and statistical techniques more often than we do in our daily lives; but all this is a matter of degree, not kind. In our daily lives we test the speed limit, sample clothes, alter recipes, and so forth; all activities with parallels in the practice of scientific inquiry.

I am not saying that the practice of scientific research is identical to what we do in our everyday lives. For example, as scientists we usually try to be more careful in our investigations than we might be about matters of casual and nonprofessional interest. Yet, the credibility of our reasoning and of our approach, as scientists, rests on their being referable to some analogous nontechnical situation in our everyday lives.

There can be a sense of uneasiness about the idea that scientists evaluate claims of fact with their common sense abilities rather than by applying some set of rules. It may seem that common sense is no more than uninformed prejudice, and that people come to conclusions about matters of fact in their everyday lives without being thorough, and by uncritically including evidence of dubious quality and relevance. But this is all part of the human condition; we cannot escape our humanity by passing laws against sloppiness and irrelevancy. Instead, we must remain free to evaluate such laws themselves against our experience and common sense.

This view of what scientists do is close to that of Huxley (1894) and also consonant with contemporary philosophers of science who emphasize the multiplicity of criteria used in the evaluation of scientific claims, as reviewed, for example, in Suppe (1977).

No Proof for Competition and Coevolution

In contrast with scientific findings, a proof that is valid according to formal rules eternally establishes a new theorem in logic and mathematics. Constructing the

proof is a creative human activity, but acceptance is based on whether formal rules of validity have been correctly applied in the proof.

Connell (1980) presents a table of experiments that he insists be followed in order to determine whether the coevolution of competing species has led to niche separation. Connell (1980, p. 135) writes that the experiments are "it seems to me, both necessary and sufficient" to demonstrate that competition is present and that the niches of each species have a genetic basis. The meaning of this justification is unclear. The "it seems to me" might legitimately indicate what Connell would personally find convincing. The "both necessary and sufficient" misleadingly suggests, first, that there is an element of logical certainty compelling the acceptance of a conclusion based on Connell's protocol (sufficiency), and second, that no other protocol is satisfactory (necessity).

Following the formal rules of logic and mathematics actually guarantees both that a theorem is valid and that the theorem is accepted as valid.

In contrast, there is no table of experiments, no matter how well thought out, which, when followed, guarantees that competition actually occurs in a system and also that the finding will be accepted. At best, following a table of experiments would produce a case convincing to many people. Even here we reserve the right, for each situation, to make our own reasoned evaluation of the appropriateness of the protocol and of the clarity of the experimental results before accepting the conclusion.

A Litmus Test for Competition or Coevolution?

Nonetheless, perhaps following a general protocol could produce a case that is convincing to virtually all reasonable people. If we insert litmus paper into a solution, any solution, and it turns pink, then we conclude the solution is acidic. It is conceivable, however, that the paper is defective or that there is pink pigment in the solution to begin with. If so, then the conclusion that the solution is acidic may be incorrect. Yet without any evidence that something is amiss, it would be unreasonable to withhold agreement that the solution is acidic.

Could we devise a similarly general protocol to detect competition and coevolution, a protocol whose results are not necessary and sufficient, in a deductive sense, to guarantee the existence of these processes, but whose results are conclusive in a practical sense? I think not, but it is too early to tell. The circumstances seem too varied. The mechanism of competition varies as does the population structure that those mechanisms must affect.

No Logical Primacy to Null Hypotheses

Connor and Simberloff (1979) and Strong et al. (1979) propose procedural rules for the study of competition. They insist that scientists begin by defining many alternative hypotheses for the thesis they are investigating. For example, if one is investigating whether the coevolution of competitors has led to niche divergence, various alternative hypotheses are that predation somehow causes the divergence (e.g., the prey are evolving a size escape in opposite directions), that divergence results from a pleiotropic correlation with the evolution of other aspects of

the phenotype, and so forth. Second, they insist that a special alternative hy-
pothesis be singled out as the "null" hypothesis. The main feature of the "null"
hypothesis is a proscription against population interactions. Third, they insist that
the "null" hypothesis be falsified first (in time) before moving on to consider the
alternative hypotheses that do include population interactions other than competi-
tion, finally ending up with a direct look at hypotheses involving competition
itself.

There is certainly no objection to considering alternative hypotheses. The need
to do this is obvious, and does not require a sophisticated philosophical
justification. The objections are to a rigid sequencing of research activities accord-
ing to rules, and to singling out a special alternative hypothesis as the "null"
hypothesis.

Strong et al. (1979, p. 910) misuse philosophical jargon; they write, "we pro-
pose another possibility with *logical primacy* over other hypotheses . . . this is the
null hypothesis that community characteristics are apparently random [my ital-
ics]." This is not logic; this is simply an unjustified assertion.

The "null" hypothesis of these critics is not simply the negation of the hy-
pothesis being investigated. Clearly, establishing strong interspecific competition
is equivalent to falsifying the absence of strong interspecific competition. If one
calls the negation of a claim a "null" hypothesis, then, by this definition, to
establish a claim one must falsify a "null" hypothesis. This is a trivial tautology.
In contrast, the null hypothesis in Strong et al. (1979) is that there exist
unspecified random processes in ecological communities that cause communities
to be as they are.

In evaluating philosophical claims about how to do scientific research, it is
helpful to return to everyday circumstances. Suppose you are sitting by a window
in your living room with a guest. You can see your driveway through the window
while your guest cannot. Your guest says, "I see the shadow of a car on the lawn,
so your car is parked in the driveway." Obviously, this statement jumps to a
conclusion that is not fully warranted by the data. Yet the conclusion may be true
nonetheless, and the data that are cited may actually be enough to convince you.
One alternative hypothesis is that you parked your car at the front curb. If you
were not convinced, however, and wanted to verify the conclusion, you would
first look directly at the driveway. You would not avert your eyes from the
driveway in order to begin with an inspection of the front curb. Clearly, one is not
logically compelled to start with an alternative hypothesis before getting around to
the claim that is at issue.

Furthermore it is preposterous to single out one of the possible alternative
hypotheses for special attention by calling it the "null" hypothesis. What is our
null hypothesis here: that you have no car; that there is no car in the driveway;
that there is no car on earth; that shadows flicker across the lawn by chance
alone? There has to be an independent justification for the selection of a null
hypothesis. Simply declaring some hypothesis to be logically prior is a presump-
tion.

Moreover, logical priority has nothing to do with temporal priority. Logical
priority does not, even when justified, imply that people should investigate the

logically prior hypothesis before investigating other hypotheses. The temporal sequence of investigation is a practical matter, not a matter of logic.

The Popperian Alignment is Unjustified

Connor and Simberloff (1979) and Strong et al. (1979) are explicitly philosophical in proposing their rules. They claim to be descendants of the philosophy of Popper (1968). In brief, the philosophical idea is that one cannot directly confirm a scientific claim; instead, one concludes that a claim is true only after falsifying alternatives to the claim and failing to falsify the claim itself.

The critics do not present a clear and cogent justification for this philosophical alignment. Strong et al. (1979, p. 909) offer only the statement that modern science "has made much of its progress by attempting to disprove universal hypotheses like competition." What is not clear is whether Strong et al. (1979) find an inherent problem with experiments that directly detect competition, or whether they believe that progress will occur faster if scientists investigate alternative hypotheses before getting around to the principal thesis of interest. The latter position is philosophically innocent, and probably false. The former position is philosophically dubious.

More fundamentally, Connor, Simberloff, and Strong are attentive to their philosophical alignment during the course of their scientific research. I feel that this can lead both to bad science and to an abuse of philosophy.

Philosophy is an ongoing field; the perceptions of philosophers change as thought accumulates on research issues in philosophy. The important early research of Karl Popper is not necessarily among the best thinking currently available in the philosophy of science, a field that is just beginning to understand the differences among the various natural sciences (see, e.g., Beckner 1959; Hull 1974; Suppe 1977). It seems premature to adopt a philosophical alignment in this area of philosophy.

Some philosophy identifies and clarifies the main ideas in a subject; this is a "foundational" inquiry. It has little impact on the practice of the field being investigated. Research on the meaning of the infinitesimal does not affect the utility of the formula for the derivative of a polynomial in science and engineering,

$$d(x^n)/dx = nx^{(n-1)}.$$

Philosophical research is not irrelevant to this formula; it may lead to a different (and better) interpretation of its meaning, to a generalization of the concept of a derivative, and so forth. Yet it is a mistake in a scientific paper to fail to use this formula in a standard way because of a philosophical position on the meaning of the infinitesimal. Similarly, it is a mistake to act in ways contrary to good judgment when investigating a scientific claim because of an alignment with a position in the philosophy of science.

Popper's philosophy seems to be prescriptive; not about how scientists do work as much as about how they might work. Popper and others writing earlier in this century were interested in whether the certainty of scientific findings could ap-

proach those of mathematical findings. This may be interesting, although unnecessary. The potential danger, however, is that following Popper's dicta may lead to results that do not speak to the concerns of the actual scientists who have to be convinced.

Perhaps the most difficult issue facing both philosophers of science and interested scientists is to explore the role of the philosophy of science vis-à-vis science itself. Is the philosophy of science a metascience? By adopting alignments are scientists unwittingly participating in an experiment on how to do science? Is the best alignment to be gauged by the amount of scientific progress it produces? If so, the experimental design needs further thought.

If the philosophy of science is not a metascience, what is it? This question has been faced before in another guise. Here is Wittgenstein (1958), a giant in twentieth century philosophy, writing about the relation between formal logic and the natural language that people actually use for reasoning and for communicating with one another.

> In philosophy we often *compare* the use of words with games and calculi which have fixed rules, but cannot say that someone who is using the language *must* be playing such a game. —But if you say our languages only *approximate* to such calculi you are standing on the very brink of a misunderstanding . . . as if it took the logician to shew people at last what a proper sentence looked like." [Paragraph no. 81, p. 38, with original italics.]

> Philosophy may in no way interfere with the actual use of language; it can in the end only describe it. For it cannot give it any foundation either.
> It leaves everything as it is. [Paragraph no. 124, p. 49.]

Thus philosophy may also be descriptive; about how scientists do work, how they draw conclusions, what they count as evidence, whether the findings are self-consistent, whether its language contains terms that can be operationally defined, and so forth. We are the source material for this type of inquiry. We compromise ourselves when we abandon our natural talents in adhering to a philosophical alignment.

TECHNICAL CRITIQUE

Connell's Protocol

Connell's (1980) paper concerns whether coevolution between competing species is common and important. Connell wants the demonstration of coevolution between two competitors to consist of: (1) evidence of evolutionary divergence of the two competitors from the fossil record or other historical sources; (2) experimental evidence for present-day competition between the coevolved species based on observation of niche compression/expansion in a scheme of transplant/removal experiments; and (3) experimental evidence for a genetic basis to the species differences that are also based on observations of niche compression/expansion in a scheme of transplant/removal experiments. I do not think Connell's table of "necessary and sufficient" experiments is workable, convincing, or even on the right track.

A. If coevolution does occur between competing species, then divergence

through time is only one possible outcome; indeed, a rather unlikely one. According to the theory being tested, whether this possibility is realized depends on the initial condition. Consider an island with one species, and visualize a resource axis of one dimension. In sufficient time the niche position of the species should shift to the point corresponding to the peak of the carrying-capacity function. Now consider an invader and suppose its initial niche position is to the right of the resident. If it is sufficiently far to the right, then both species will shift to the left. Then they may equilibrate, with the original resident located to the left of the peak position and the invader to the right of the peak position, although not as far to the right as the position at which it originally invaded. Only if the invader enters very close to the resident's niche position will there be a divergence such that the resident shifts to the left while the invader shifts to the right. A position close to an established resident, however, is an unlikely place for a successful invasion. In the more probable scenario, the fossil record would indicate a parallel evolution of both members. (Of course, the argument is the same with the directions reversed if the invader enters at the left of the resident.)

B. Connell's protocol focuses on observation of niche compression and expansion. The relationship of these observations to shifts in niche position is unspecified. Hence these observations are possibly irrelevant to the hypothesis being tested.

C. In the special case when competition does produce divergence over evolutionary time, the case that Connell is trying to find, the residual competition after divergence is low and hence should necessarily tax the resolution of his experimental system. Thus, Connell, himself, must detect the "ghost of competition past" if he is to follow his own protocol. Hence this recommendation is unworkable. An unworkable recommendation biases the protocol against the hypothesis being tested and might be taken to imply that the hypothesis itself is not testable; but it is the protocol that is flawed not the hypothesis.

D. Simple transplant/removal experiments hardly begin to assess whether there is a genetic basis for the difference between two populations of the same species that are sympatric and allopatric, respectively, with a presumed competitor. The important issue is whether there is variation that is heritable, i.e., capable of responding to directional selection (see Boag and Grant [1978] and Van Noordwijk et al. [1980] for examples of how the heritability of ecologically interesting traits in natural populations has been determined). Alternatively, a selection experiment could be conducted on the relevant traits to see if they do respond to selection. Indeed many selection experiments for size traits have been done over the last 50 yr with generally positive results.

The Context of Connell's Protocol

Connell's (1980) paper places too much faith in the conclusiveness of certain field experiments for studies of population dynamics. The general problem !in interpreting experimental results from the intertidal systems that Connell cites is that interindividual interactions are detected, but the population-dynamic consequences of these interactions are unknown. Many sessile marine invertebrates

have a population structure involving a long-lived, pelagic, larval phase. The range of the population may be very large. Data on the interactions of individuals at a few study sites within the species' range, and observed within a scale of a few square meters, have an uncertain connection to population and community processes. This connection needs to be investigated with other methods, including the use of biogeographic and distributional data.

Connell's recommended field experiments are biased toward the detection of interference mechanisms between individuals. It may seem that experimental studies of competition tend to establish the existence of interference mechanisms and fail to provide evidence of exploitative mechanisms. To the extent this is true, it is an artifact of studies focused on the observation of interindividual interactions. The existence of interference mechanisms does not rule out the presence of exploitative mechanisms as well. To the contrary, exploitative competition should cause the evolution of interference mechanisms. Without reference to some exploitative basis, it is difficult to explain why two species should actively interfere with each other at all.

Connell (1980, p. 136) maintains a view downgrading the importance of competition in nature that does not make sense. He believes that, under "benign" physical conditions, "natural enemies (predators, parasites, herbivores) tend to be more effective so they keep the populations below the level at which they compete." [Parentheses in original source.] It is not clear how this hypothesis could apply to all trophic levels at the same time.

Suppose there are two prey species, A and B, and a predator, P. Suppose that if P is removed, A causes the extinction of B. Next, with P present, suppose that P has no preference for either A or B; it eats both in proportion to their relative abundance. In this situation, B may still become extinct; it is because there is no differential effect of the predator on either prey species. Here is it fair to say that competition is unimportant? No, because it is the competition that may determine which species becomes extinct. Alternatively, suppose P has a preference for A, the superior competitor. In this situation B may coexist with A when P is present. Is it now fair to say that competition is unimportant? No, because B is influenced by its competitor, A, and this influence would be especially large should P be perturbed by pollution or some other factor. Thus, it does not make sense to downgrade competition as an important contributor to community structure solely because there are effective "natural enemies" in the system.

Connell (1980) concludes that the results of coevolution are likely to be restricted to systems of low dimension. (Here, the dimension of a system means the number of species in it.) I tend to agree, but for different reasons. Connell feels that in systems of high dimension, the species will not co-occur enough either in space or time for the potential interactions among them to yield evolutionary results. This may be true in some circumstances; no one knows. My studies of the theory for the coevolution of competing species show that even when species are assumed to be co-occurring, the coevolutionary process slows down as the dimensionality of the system increases (Roughgarden et al. 1983a; Rummel and Roughgarden 1983). There are two reasons. First, as more species are added to the system, the net selection pressure favoring any particular coevolutionary change

diminishes. Consider several species on a resource axis. If one species moves, say to the left, it reduces competition with the species on its right, but adds to the competition with the species on its left, thereby reducing any net advantage to such a shift. Second, the species in a high-dimensional model affect one another through very long feedback loops, most of whose individual links are weak, causing the system to equilibrate only after a very long time. For example, consider again a species added to a place on a resource axis. It evolutionarily affects a species that is not adjacent to it primarily by influencing an adjacent species which, in turn, passes the effect on, though with diminished strength.

The tone of Connell's point is negative, as though a localization of the effects of coevolution to low-dimensional systems somehow negates the importance of coevolution as a process. To the contrary, although Connell dismisses the possibility, it remains extremely important if large-dimensional systems are decomposable into many coevolutionarily shaped low-dimensional subsystems within each of which strong interactions occur, but among which the interactions are weak or absent. It is not clear how large-dimensional systems can exist to begin with if they are not compartmentalized, because there is serious difficulty in achieving coexistence among a great many strongly interacting populations. The low-dimensional subsystems that probably exist within large-dimensional systems are excellent candidates for evidencing the results of coevolution. Furthermore, even if coevolution is slow in large-dimensional systems, some large-dimensional systems may exist in habitats that are permanent enough for the process to have attained noticeable results.

Connor, Simberloff, and Strong's Null Models

The basic error in the papers of Connor and Simberloff (1979) and Strong et al. (1979) is that the "null" hypotheses are empirically empty. No biological processes are exhibited that produce the distributions predicted by the null models. Hence, we do not learn anything by "falsifying" these hypotheses. These null hypotheses are irrelevant to whether competition influences natural communities.

The null models are stated as though based on sampling theory. Actually, the data analyzed are not a sample drawn from a population of data in the usual sense. Typically one would regard the data taken on an island as a sample of what was actually on the island. Then confidence limits would be applied to these data based on statistical sampling theory. Instead, island data, assumed error free, are regarded as a sample of some faunal source pool. Islands do not reach into urns and draw out their species. There are real processes that bring species to islands. It is these processes that must be modeled to determine what distributions of data are expected in the absence of competitive interactions among species.

Fabricating random communities by sampling with replacement from some source fauna does not bear the relation to ecology that the neutrality hypothesis does to population genetics. The neutrality hypothesis is about real processes. Genetic drift is a real process whose workings have been demonstrated in the laboratory and in the field. Similarly, natural selection is known to be a real process. What is being claimed by the neutrality hypothesis is that selection is

largely a "purifying" selection as distinct from various schemes of "balancing" selection. The neutrality hypothesis in genetics has empirical content.

I stress there is no disagreement about the usefulness of considering alternative hypotheses. The point is that null models fabricated by rearranging species lists, and indices of species morphology, are not viable alternative hypotheses. Indeed, the biological stochastic processes of dispersal combined with population extinction do offer viable hypotheses for the formation of island faunas and these hypotheses are alternatives to those postulating a key role for population interactions during faunal buildup. But null models are not about processes at all, and so remain irrelevant to the study of how island faunas are formed, regardless of how well or poorly they compare with data. Moreover, following upon the philosophical discussion earlier in this essay, hypotheses based on stochastic processes of dispersal and population extinction share the same logical status as other hypotheses, and no methodological rule requires that stochastic models be investigated before any of the other hypotheses.

Null models misrepresent the concept of a null hypothesis in statistics. A null hypothesis in a statistical test is a model, that is, a simplified picture, of how data are taken and what they are taken from. In developing a statistical test, one calculates what data are anticipated from this model. If the actual data are sufficiently different from what is anticipated, then the null hypothesis is rejected. Statisticians justify the null hypothesis in a statistical test by referring to the actual sampling practices of people who gather data, and by developing theorems, like the central limit theorem, that describe the characteristics of the populations being sampled (often a population of sample statistics). In fact, different formulas are available for placing confidence limits on population size estimates from mark-recapture data based on different pictures of the sampling process that is occurring when people conduct mark-and-recapture work under field conditions. A null hypothesis in statistics is a justified model of a sampling procedure. It is not a hypothesis that the world has no structure.

Strong et al. (1979) imply that one must investigate pattern before one is licensed to pursue research into the processes that may have caused the pattern. This is a fallacy. Sometimes it is obvious that a process is occurring. Knowledge of that process may aid in discovering its consequences.

Grant and Abbott (1980), Hendrickson (1981), and Diamond and Gilpin (1982) have shown that the null models lack statistical power (inability to distinguish the "checkerboard" pattern) and suffer methodological irregularities (the "dilution effect" and the incorporation of competition-dependent information). The inclusion of competition-dependent information in a noninteractionist model is not necessarily fatal, however, provided the degrees of freedom for the model are correspondingly reduced.

Strong et al. (1979) confuse the character displacement possibly resulting from the coevolution of competitors with the niche separation resulting from selective invasion at niche positions where competition is relatively low. These processes are quite different. The morphological data are taken solely from continental birds, and yet are applied to species lists from the Tres Marias islands. Obviously, these data cannot speak to whether species have changed after arriving on the

islands. These data may not even be relevant to selective invasion if some of the early invading species changed substantially before the more recent invasions.

The Conservative Posture

The papers of Connell (1980), Connor and Simberloff (1979), and Strong et al. (1979) are biased against the existence of competition. They offer no justification for this bias. In any particular field system, there are two possible errors of assertion. First, one may assert that there is competition when in fact there is not (a type I error), and second, one may assert that there is no competition when in fact there is (a type II error). The critics are severely biased in favor of committing a type II error in order to avoid a type I error. To justify this bias, the critics should exhibit that a far greater harm results if we accept the presence of competition when it is really absent, than if we reject competition when it is really present. Still another approach would be to withhold judgment until the case is more complete.

The Case for the Coevolution of Competitors

How, then, are we to determine if the coevolution of competitors occurs? We see if we can build a convincing case. If we cannot build a convincing case in some system or a close analogue then we should dismiss the matter in that system. Better yet, if competition is unimportant it would be more informative to find out what is. A convincing case should include on-site experiments, together with biogeographic and distributional data, and data addressing viable alternative hypotheses. An analysis of morphological data and species lists may suggest the presence of competition. It is better, though, to regard morphological data and species lists only as a description of what is to be explained rather than as evidence of any particular process.

The mark of a convincing case is that the proposition of interest has been examined fairly from every angle. The case must be thorough, and yet balanced, with no particular angle pushed to the point of overkill.

The case should be evaluated on the basis of its content and not on the basis of philosophical and methodological doctrine.

THEORY

Something of a tone of righteous indignation in Strong et al. (1979) and of ridicule in Connell (1980) seems to tinge the antitheoretical rhetoric. Strong et al. (1979) assert that textbooks have uncritically accepted an interpretation of community structure based on competition theory as a "paradigm" (p. 909) and that the "enthusiasm" (p. 897) for this paradigm is so strong that alternative explanations and contradictory evidence are ignored. They claim there is a "lack of reciprocity between material and theoretical effects" in the study of competition (p. 909). And Connell (1980, p. 132) writes, "Despite all the theoretical attention it [the coevolution of competitors] has received, there remains a real question as to

how much this notion applies to real communities." Has competition theory really escaped from biological control?

To begin, many authors of ecology texts in North America, Europe, and Australia hardly embrace competition theory. Most textbook authors view competition theory with a wary eye, if at all. Furthermore, the frequency and skill with which field experiments are done in community ecology is continually increasing and important alternative hypotheses are being addressed in such studies. It would be a clear disservice to students in ecology today if textbooks failed to mention: (1) the phenomenon of resource partitioning; (2) the "checkerboard" distribution pattern of species of the same body size; (3) the regularity of the degree of difference in body size among the species who do coexist; and (4) that a possible explanation for these facts is provided by competition theory.

Perhaps more to the point, what is the purpose of theory?

Characteristics of Theory

The purpose of most models in community ecology is to simplify.

Making a simplifying model typically involves three steps. First, we agree to consider a subset of what is known about a system. Second, we fill the gaps in the simplified description with assumptions that may actually be false if taken literally, but which are hoped somehow not to be too misleading. Also, even the simplified description may contain points that are too complicated to deal with and so are replaced by other statements that are more tractable. Third, we derive predictions. Sometimes the derivation serves only to show that some features of the simplified description follow from others. In this context the derivation reveals interrelationships among the features of the system. Other times the derivation leads to a new proposition that no one has considered before. The simplified description of the system, together with the predictions, comprise a model. A set of models sharing many assumptions in common is a theory.

Why would someone want to develop a simplifying model? Because experience shows this is useful. In school we learned the concept of mechanical advantage from the study of simple machines like the frictionless pulley. Anyone who has hoisted the engine from a car knows that as the number of pulleys increases, the length of rope that must be pulled also increases, but the strength needed to pull the rope decreases. Moreover, when the pulley is well oiled, the model of a frictionless pulley is actually quite accurate. Similarly, network theory, the most important theoretical tool in electrical engineering, is based on simplified models of electrical components. Experience shows that, although simplifying models incorporate dubious assumptions, like that of no friction, they are useful as aids to understanding what is going on and often serve as guides to the quantitative description of systems.

A simplifying model is vulnerable. It differs from a summarizing model whose purpose is to include everything that is known about a system and that is continually updated as more is learned. One cannot falsify a model that is continuously updated; it has, so to speak, no degrees of freedom.

The predictions of a model are robust if, as a historical accident, they happen to

have been derived from premises that later research shows were unnecessarily restrictive.

In fact, most theoretical results are derived for the first time in models that have been unnecessarily simplified. How do we know to what extent results are robust? This is very difficult. The mathematical approach is, first, to try to generalize the original derivation somewhat and, second, to bound the robustness by developing mathematical counterexamples. The empirical approach is, to me, more interesting and it consists of deliberately looking for the prediction of a model in a situation that is known to be somewhat different from what is described by the assumptions of the model. If the predictions check out, then we have a clue that they may be more robust than originally believed.

The results of a model are structurally stable if they change quantitatively in proportion to quantitative alterations to the premises. The idea is that a small change in the premises produces a correspondingly small change in the results. Some technical criteria are available for ascertaining structural stability. For example, it is known that if the dimensionality of a dynamical model is high, then the global flow of the trajectories is not likely to be structurally stable; but the flow of trajectories in the neighborhood of a locally stable equilibrium usually is structurally stable.

Theory of Interspecific Competition

Niche theory offers a simplified picture of how competition can produce and maintain a pattern of resource partitioning among coexisting competing species. It also addresses the phenomenon of zonation, including the length of the overlap zone near the borders of species that replace one another along geographical gradients. Its results for low-dimensional systems are structurally stable and moderately robust from a mathematical standpoint. At present, niche theory offers very few predictions concerning large-dimensional systems (see review in Roughgarden 1979).

The research of Diamond (1975), so strongly criticized by Connor and Simberloff (1979), remains a very important exploration of the possible consequences of competition in high-dimensional systems. His study, and others, do not directly test or support competition theory as much as offer suggestions of what to look for as possible predictions from high-dimensional theory when it is developed. Such suggestions are essential if theory is to present results of biological relevance. Most of Diamond's suggestions about how competition causes patchiness have been sustained by an analysis of the competition equations themselves (Roughgarden 1978). Other suggestions, including the possible existence of assembly rules and forbidden combinations of species are clearly relevant to the multiple, simultaneously stable, boundary equilibria that are possible in high-dimensional systems with strong competition.

Testing Theory

Summarizing models are tested by direct comparison with the data being predicted. If the model parameters are estimated from, say, the data of the last 5

yr, then the model is used to predict the new year's data return. If the new data are impressively different from the predictions, then the model itself is reworked, or at least the parameter estimates are redone. Meanwhile the outdated model is automatically discarded. Testing a model in this sense is called validating a model.

For simplifying models the matter is more subtle. A simplifying model must be somewhat unrealistic to begin with; simplification is what it is all about. It must remain somewhat unrealistic if it is to continue being a simplification rather than a summary. Arriving at an acceptable degree of simplification involves human judgment.

Testing a simplifying model means establishing whether the picture supplied by the model is, by and large, a correct account of what is going on in a system.

There are three reasons why a simplifying model may fail to provide a correct account of what is going on in some system. (1) The model may be about processes that do not occur in the system. (2) It may be about processes that do occur, but that are relatively unimportant when compared to other processes that have been omitted from the model. (3) The model may be about processes that do occur, but may provide a severely distorted characterization of those processes.

A model is biologically general if the picture it presents is correct for many systems. Biological generality rests on either a universal mechanism (as in Mendelian inheritance) or on the existence of a large variety of mechanisms that work in the same way.

The fate of a simplifying model is determined by people's interest. Does a model help in planning research or in understanding results, or even in understanding other models? If not, the model does not hold the interest of active scientists and falls into disuse. A similar fate awaits empirical findings that, although correct, turn out to be inconsequential.

It is a distraction to focus on the model rather than on processes in an actual system. For example, on the island of St. Maarten there is strong present-day competition between two species of lizards, *Anolis gingivinus* and *A. wattsi*. I hypothesize that the absence of *A. wattsi* from sea-level habitat on St. Maarten represents competitive exclusion by *A. gingivinus*. The Lotka-Volterra competition equations help us to visualize how competitive exclusion occurs as a population process, and thereby aids in planning the research to determine if this hypothesis is true. However, what we are testing is not so much the Lotka-Volterra model, but whether there really is present-day competition strong enough to cause competitive exclusion on St. Maarten. The empirical issue, and not the model, is what is significant. If indeed there is competitive exclusion on St. Maarten, then we will have a key point to the discovery that the coevolution of competitors can lead to extinction. Such a discovery would show that the coevolution of competitors may not necessarily lead to character displacement with an accompanying reduction of competition, as is widely believed. Furthermore, it was the mathematical theory for coevolution that sensitized us to this possibility.

Theory does not substitute for the knowledge of actual systems any more than architectural drawings substitute for a house. Yet we cannot build a house without architectural drawings.

Nonetheless, today we do plan and carry out almost all field research without aid of the insights that simplifying models provide. This, however, may be a transient state in the history of ecology. With more experience in using theory we may come to ask questions about processes that now seem hopelessly complicated and may come to devise more informative experimental designs than we presently envision.

Living with Theory

There is antagonism among many ecologists toward theory, and some of it arises, I suspect, from the fear that ecological theory is considered the "foundation" of ecology. Some sciences, like physics, are hierarchical, and physicists speak of theoretical axioms, laws, and of "truths" that have been derived from such theory. In a hierarchical field, it is conceivable that a misdirected theory could divert the entire field away from a commonsense evaluation of its own empirical findings; if so, this is a legitimate fear. Ecology does not have such a hierarchy now, I doubt it ever will, and hope it never does. It is difficult to imagine what could ever qualify as a "law" in ecology. Ecological theory is no more than a collection of tools. A useless model should be discarded like a broken chisel.

Another source of antagonism toward theory springs from a conflict between the ethic of perceptiveness among naturalists and the need to simplify among theoreticians. Among naturalists, failure to note detail is, in the extreme, equated with a lack of perceptiveness. In this context, simplification becomes synonymized with sloppiness, and with impatience, as of a novice who jumps to conclusions before a phenomenon has been thoroughly observed. On the other hand, the steadfast refusal to simplify ultimately leads to a glorification of the particular, to a celebration of the personality of each species and their interactions in each habitat.

There is a craft to developing theory. Solving for equilibria, for example, tells one about the mathematical structure of a model. In solving for equilibria, one is not saying the world is constant. To the contrary, one way to model environmental stochasticity is to introduce stochastic variation into the parameters of a model that was originally solved using parameter constants. Similarly, it is good practice to explore the premises of a model one by one and not to jump in with all of them at once. Doing so gives the appearance of leaving out important factors. The early analysis of a model is often sufficiently interesting to warrant publication in a theoretical journal, thereby giving the impression of completion. Still more discord sounds when someone's cherished fact is not incorporated into a simplifying model.

Theoretical research has an integrity of its own; it does not march in lock-step with empirical research. Nonetheless, theoretical ecology is ultimately valued by its utility in understanding ecological processes in nature.

There is a problem, though, that is more than a misunderstanding of the nature of the craft. It is that, for a theoretician, the natural object of study usually corresponds to only one of many hypotheses for a phenomenon. Suppose one is interested in what causes the observed body sizes of male lizards. There are

several hypotheses to consider, involving resource use, sexual selection, mechanics of body growth, to name a few. Each hypothesis may require separate theoretical development, and they may not be equally tractable. A theoretician may think his job is done when one of these is satisfactorily modeled, that to take up another hypothesis is to take on another job. From an empirical standpoint the job is to build a fair case about the phenomenon itself. And if the hypotheses have received unequal theoretical treatment it is hard to develop a case that is fair to all reasonable hypotheses. The same problem exists when the hypotheses differ in their tractability for testing in the field. In short, it is hard to build a fair case when some hypotheses are easier to study, or are more studied, than others.

If there is any villain on the scene, it is the set of popular impressions about "what theory says". These impressions are always naive and usually incorrect concerning what theory actually does say.

The place of ecology within the sciences depends on the perception by scientists from other fields and by the public that progress is being achieved in ecology. This perception becomes the basis for science policy decisions concerning faculty billets and research support. The advance of theoretical ecology during the 1970s is an important event in contemporary science; it has begun to attract serious attention from other areas of science and from mathematics; and it has contributed to enhancing the stature of ecology as a result. This growth of theory, together with the increased use and understanding of experimental methods under field conditions, and the determination of biogeographic patterns to community structure, are evidence of substantial progress in community ecology during the last decade.

Theory in the 1980s

Where does community theory go from here? The theory of the 1970s explored models formulated in the 1960s and earlier. The theoretical content of these models and their relationships to one another and to models in population genetics were largely unknown at that time. During the 1980s the challenge is to formulate new models that can serve as useful simplifications for community processes in systems to which current theory is largely irrelevant. Hickman (1979) has eloquently called for such theory in annual plant communities. The rocky intertidal and herbivorous insect communities merit similar attention.

Another challenge is to extend local community theory to take account of migration-coupling among habitats. The number of species at a local site, especially on continents, often cannot be explained by observations taken within that site. Instead, the local species diversity reflects an interaction between the regional habitat diversity and the degree of habitat segregation practiced by the species. The habitat segregation that evolves probably depends on the geometry of the habitats available in the region, and on the long-term temporal stability of those habitats.

Still other important topics include the specialization of coevolutionary theory for the systems in which coevolutionary phenomena are readily studied, the incorporation of size and age structure into models of density-dependent population dynamics, the development of mechanism-based submodels for the parame-

ters in population models and for the constraints used in optimization models, and the exploration of how population interactions can theoretically control ecosystem processes.

CONCLUSION

This essay was provoked by the insistent claims of Connell (1980), Connor and Simberloff (1979), and Strong et al. (1979) that competition and the coevolution of competitors are not real and important processes in nature, and hence, that theory for these processes is not worthy of testing. These authors are wrong. Both competition and coevolution among competitors occur, and are extremely important in some systems.

The genus, *Anolis*, contains 5% to 10% of the lizard species in the world today, and about half of all anole species reside in the West Indies. Anoles are very common; 0.5 to 2 individuals per m^2 is typical. They substitute for ground-feeding insectivorous birds, and, as major consumers, probably determine the abundance of many arthropod species, and probably set the flow rates for matter and energy through their terrestrial ecosystem.

Collaboration with S. Pacala, J. Rummel, and others has established experimentally that there is strong present-day competition between the two *Anolis* lizard populations on St. Maarten (see Heckel and Roughgarden 1979; Roughgarden et al. 1981; Pacala and Roughgarden 1982b; Roughgarden et al. 1983a, 1983b; Pacala et al. 1983; Pacala and Roughgarden 1983; Adolph and Roughgarden 1983; and Roughgarden et al. 1984). Excellent indirect evidence existed by 1977, but now both the effect of *A. gingivinus* against *A. wattsi* and the reciprocal interaction have been demonstrated with repeated experiments. Studies of physiological ecology and microclimate ruled out an alternative hypothesis involving thermal requirements. From a comparison with St. Eustatius, the magnitude of the competition has been experimentally shown to vary with the difference in body size (the more similar the body sizes, the stronger the competition). Also, the possible importance of predation and competition from birds and other taxa has been studied. The pair of species on each island bank with two species has been together at least since the Pleistocene, and all the anole populations in the Lesser Antilles have evolved taxonomic endemism. It is now practically certain that anoles in the Lesser Antilles have coevolved as competitors with one another.

Mathematical theory for the coevolution of competing species provides a picture of the process of faunal buildup on islands. This theory seems to account for the regularities and also for all exceptions in the pattern of species diversity and body sizes for anoles throughout the eastern Caribbean (Pacala and Roughgarden 1982a; Roughgarden et al. 1983a; Rummel and Roughgarden 1983). This theory is about real processes. It provides a genuinely useful simplified picture of what may be happening in the *Anolis* system of the eastern Caribbean.

Baxter, Michael Bratman, Paul Ehrlich, Anne Harrington, Richard Holm, Kent
Holsinger, Harold Mooney, Stephen Pacala, John Rummel, John Thomas, and
James Watanabe. I also thank Deborah Rabinowitz for showing me the reference
to Huxley (1894).

POSTSCRIPT

The original draft of the essay above is now over two years old. Circumstances
have changed for the better since it was written. Joe Connell's contribution
reveals that the existence of competition, and, to a lesser extent, the coevolution
of competitors is accepted for some natural communities. I agree with Don Strong
that competition seems unlikely to be important in the many arthropod systems he
cites, and repeat my original call for the development of models that offer useful
simplifications for systems to which existing community theory is irrelevant.
Concerning competition theory, I can vouch for its utility in at least one system,
and there is literally a world of difference between a theory that applies to one
system and a theory that applies to no system. Moreover, George Salt's remarks
testify to an increasing appreciation of theory as a tool to aid in ecological
research; its track record, even in community ecology, perhaps the most difficult
area in which to test theory, is slowly but steadily improving. I still part company
with Dan Simberloff both on philosophical issues and on whether his null models
can be counted as viable alternative hypotheses. Our differences notwithstanding,
it is clear that we now know much more about ecological communities than we did
a decade ago, and ecological theory has contributed to this progress. (J. R., May
6, 1983).

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