Santa Rosalia Was a Goat

Ecologists have for two decades made assumptions about the importance of competition in community organization; that idea is now under vigorous attack

"The mission of community ecology, as of any scientific endeavor, is to detect the *patterns* of natural systems, to explain the causal *processes* that underlie them, and to generalize these explanations as far as possible." This small homily, penned recently by John Wiens of the University of New Mexico, appears simple and uncontentious in concept; but the reality behind it is a debate as acerbic and acrimonious as any that has stirred the combative instincts of academia.

The debate is many-layered and complex, but it centers on the role of competition between species in influencing the patterns observed in ecological communities. Is interspecific competition a major factor, as one prevailing notion has long contended? Or has its importance been seriously overplayed? And how can you know?

Ecologists, willy nilly, have become polarized, the discipline split in two so decisively that for some individuals reconciliation is an unlikely prospect. Both sides consider themselves embattled minorities that suffer negative discrimination over manuscript review, faculty positions, and research proposal assessment at the hands of their adversaries. Concern over attrition by five and more years of scholastic and personal confrontation has reached the point at which a group of leading ecologists is considering the need for a carefully organized conference designed specifically to heal the wounds.

At one level the debate concerns the utility of ecological theory. "Current ecological theory . . . has generated predictions that are either practically untestable, by virtue of unmeasurable parameters or unrealizable assumptions, or trivially true," contends Daniel Simberloff of Florida State University. "[T]he theory has caused a generation of ecologists to waste a monumental amount of time."

While conceding certain limitations in ecological theory, Jonathan Roughgarden, of Stanford University, retorts by saying, "I am not aware of a single finding that emerges from what Simberloff and his colleagues have written. But I am aware of a lot of bitterness it has caused." Roughgarden also expresses the hope that "the extreme antagonism in the rhetoric about theory doesn't reinforce the inherent disinclination people have to learn all that math that is so necessary in the study of ecology."

On another level the debate can be simply characterized as, on the one side, those who consider competition between species to be important in community organization and, on the other side, those who do not. But this is too simple a characterization. Yes, for certain reasons of history, the existence of competition (or lack of it) has been a common focus of many exchanges. But the real point at issue is, given the extreme complexity of ecological systems, how can one discern the processes involved, one of which might be competition? In other words, how does one deduce the process from the pattern, while ensuring that all possible alternatives have been considered?

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There has, as a result, been recourse variously to the philosophies of Karl Popper and of "common sense"; there has also been an upsurge in direct experimentation as opposed to observation as a means of collecting evidence of pattern and process.

The Popperian approach to science is, with certain caveats, proselytized relentlessly by Simberloff and his colleagues. Roughly speaking, researchers should test hypotheses not by seeking data that are consistent with them but by examining alternative explanations to the one embodied in the hypothesis. This approach goes by the slightly ambiguous title of hypothesis falsification.

The enthusiastic application of Popperian philosophy by Simberloff and his colleagues has led to a great blossoming in the literature of null models, which are meant to indicate whether observed patterns (of species co-occurence, for example) depart from random associations. If observed patterns are no different from chance associations, then there is nothing that requires biological explanation. Simberloff and his colleagues have reexamined several sets of data from which others had inferred evidence of competition and concluded, in contradiction, that the patterns were not statistically significant.

The popularity of this type of null hypothesis has been matched by vigorous criticism of the Tallahassee models, which some consider to be fatally flawed for technical reasons. "Further efforts in this direction will only sow more confusion," conclude Michael Gilpin and Jared Diamond, of the San Diego and Los Angeles campuses, respectively, of the University of California.

The language deployed in argument and counterargument between Diamond and Simberloff over this issue has often been more than a little intemperate by the standards of most scientific literature (they no longer communicate directly). That emotions should run high here is perhaps not surprising as, in many ways, the validity or otherwise of null hypotheses, or null models, in ecology is the crux of the whole debate.

A still further level of the controversy derives from social and political yearnings. "The reason for the debate is primarily for protecting and building reputations," contends Simberloff. "A lot of people want to be famous, especially in a young science, like ecology, where it is still possible to jockey for prominence. A lot of people would like to be viewed as the heir to Robert MacArthur." MacArthur, who died in 1972, was the unchallenged leader of community ecology and was largely responsible for the hegemony of competition in ecological research. To the obvious question Simberloff replied, "I don't think I should like to say; you know who they are." Diamond, who effectively was designated by MacArthur as his successor, declines to comment on this aspect of the debate.

In any event, the concentration of the "anticompetitionists" at Florida State University pitted against the "competitionist" forces deployed in the Ivy League universities in the east and in institutions of equivalent scholastic aspirations in the west has a social dynamic of its own. "We are known as the Tallahassee Mafia," says Donald Strong, a colleague of Simberloff. "The devout MacArthurians are all in powerful positions in powerful universities." Robert May, who occupies MacArthur's chair at

Princeton, observes that people often relish attacking the establishment and seeing the mighty being proved wrong; "I know I do," he says.

One reason why competition became so entrenched in ecological thinking is because it is an extremely neat and tidy explanation. Species interacting with species in a community, each potentially affecting the distribution or morphology of the other through resource and interactive competition, is in pleasing resonance with the sense of "the balance of nature." And when MacArthur generated competition theory backed up by apparently powerful mathematical models, the idea was given an extremely seductive coherence. "It was the only theory on the block," reflects Roughgarden.

MacArthur's mentor, G. Evelyn Hutchinson, had set the fuse to the explosion of competition theory in 1959 when he published his famous paper entitled "Homage to Santa Rosalia *or* Why are there so many kinds of animals?"

While vacationing in Palermo, Sicily, Hutchinson had paused outside the shrine of Santa Rosalia, whose bones were reputed to have remarkable curative powers, and collected two species of corixid waterbugs. He noticed the two species differed in size and was inspired to investigate size differences between other pairs of similar species. How close could two species be in size or in the size of their feeding structures, such as beaks in birds for instance, before competition intruded? He came up with a ratio of 1 to 1.3, a pronouncement that triggered a series of publications throughout the ecological community that presented results consistent with the "rule."

Competition theory eventually became associated with numerous models that described in quantitative terms the effect of competition on species composition within communities and on certain morphological characters of those species. The number of species that might occupy given areas is one example; another is the number of related species present in ecological communities.

Coexistence of competitors is thought to lead to evolutionary change, or coevolution, in some instances. Character displacement is a favorite phenomenon, in which similar characters or behaviors in competing pairs of species diverge as a result of competition. If one of a pair of competitors disappears from a location the remaining species may display the complementary phenomenon, character release: the character evolves toward that of the now absent competitor.

MacArthur, like many ecologists of the time interested in community structure, studied bird populations. Many such studies sought evidence of competition in the absence of, say, species A on islands where species B was present. Such irregularities in the composition of bird communities on islands of archipelagoes have become something of a touchstone of competition studies, with the finches of the Galápagos Islands being the classic case.

The coexistence, or otherwise, of similar species within communities, irregularities in the numbers of species in certain communities, and shifts in morphological or behavioral characters in coexisting species—these represent the *patterns* in nature. The *process* underlying them was inferred to be competition between species, which was considered to have wide and general application. By the mid-1970's, the ecological literature was richly served with data that appeared in healthy accord with competition theory.

and am not to this day, a rampant and unrepentant Popperian. I believe Popper is right in general, that you should try very hard to refute hypotheses. If an hypothesis cannot be refuted you should not look for confirmations of it. But it is clear that it is very hard to devise testable hypotheses in ecology. Hard, but not impossible."

Simberloff therefore began a series of reexaminations of data that purported to conform with competition theory. Step by step he concluded that the theory was largely without statistically valid support, because the patterns perceived appeared to be the result of stochastic events or because the data could not be interpreted to exclude other possibilities. Supporting evidence for character displacement fell away under close scrutiny, a revelation that Peter Grant, of the University of Michigan, had also made. Relationships, such as the number of related species possible in a community, vanished into a stochastic background.

A Galápagos finch

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Meanwhile, Simberloff, who had done graduate work with Edward O. Wilson at Harvard and had had MacArthur on his doctoral committee, moved to Tallahassee where he began to scrutinize some aspects of the competition literature. "I didn't see much direct test of the effect of one species on another," he says. "And I didn't see much consideration of alternative processes, such as habitat differences and predation." He came across several papers that lamented the lack of scientific rigor in ecology. One author, British ecologist Amyan McFadyen, urged an assault on "the tyranny of bright ideas," which was a call to arms for a Kuhnian revolution to overthrow entrenched competitionism. "I began to think, is it really this bad? And concluded that it was. I didn't see at that time a nefarious plot in all this."

Thus were sown the seeds of the current controversy. "I didn't mean to be,

And, apart from one fine study on bird-eating hawks by Thomas Schoener of the University of California, Davis, Hutchinson's size ratio now looks embarrassingly naked of unequivocal test.

In 1981 Simberloff published with William Boecklen a now famous paper entitled "Santa Rosalia Reconsidered," which was concluded as follows: "We do *not* claim that sizes are not partly determined by competition. . . . But we do feel that the evidence presented to date that sizes are competitively determined is weak, and that in particular the '1.3 rule' was probably always a red herring and has certainly outlived its usefulness to evolutionary ecologists."

With cutting reference to the tenacity of the tyranny of bright ideas, Simberloff and Boecklen began their paper with a 19th-century quotation: "When Prof. Buckland, the eminent osteologist and geologist, discovered that the relics of

St. Rosalia at Palermo, which had for ages cured diseases and warded off epidemics, were the bones of a goat, this fact caused not the slightest diminution in their miraculous power."

By now Simberloff, variously in conjunction with Strong and particularly with Edward Connor, who is now at the University of Virginia, was having a major impact on ecological literature. The Tallahassee challenges were being met with rebuttals that in their turn provoked further criticism, and so on. One of the most thoroughgoing exchanges, still current, is between Simberloff and Connor and Diamond and Gilpin. The arguments illustrate some of the core problems of constructing unambiguous models in ecology.

In 1975, Diamond published an analysis of bird species' distribution among 50 islands of the Bismarck Archipelago in the Southwest Pacific. He interpreted certain irregularities in species coexistencies as revealing, among other things, the effect of competition on structuring the communities. And he inferred a set of assembly rules from the observed co-occurrences and exclusions. It was a major piece of work in the competition literature.

Connor and Simberloff took aim at this strategic target in 1979 and concluded that "three rules are tautologies and one is untestable." They outlined a procedure—a null model—for assessing whether species' co-occurrences on islands might implicate competition, and suggested that such a conclusion would be very difficult. Diamond and Gilpin responded with scathing criticisms of the Tallahassee procedures in 1982. And both parties exchange biting remarks in a symposium volume to be published later this year by Princeton University Press.

"The 'null hypothesis' analysis by Connor and Simberloff is characterized by hidden structure, inefficiency, lack of common sense, imprudence, and statistical weakness, and ultimately by a scandalous disregard for their own procedure," write Diamond and Gilpin. "We feel the criticisms of Gilpin and Diamond are ill-founded and constitute major changes in their original arguments," came the response. "We show here that their alternate procedure is computationally impossible, ecologically unrealistic, and difficult to interpret."

Some of the substance behind these barbs is as follows. When Diamond analyzed co-occurrences of bird species he did so within guilds, that is, within assemblies of species that share similar behaviors and ecological requirements. The very reasonable assumption is that competition is likely within guilds rather than between them. When Connor and Simberloff did their analyses they included all the bird species on the islands, thus, charge Diamond and Gilpin, diluting any signs of competition there might be in a mass of irrelevant data. You should not compare humming birds with owls, for instance.

Connor and Simberloff say they did not analyze guilds because "the rules we were examining did not mention guilds." This is a disingenuous observation, says Diamond, as the word guild appears repeatedly, if not universally, in the description of the assembly rules. "Diamond considered it unnecessary to belabor this point in every possible quote about assembly rules, because it was not appreciated that anyone would be silly enough to search for the effects of competition in all pairwise combination of fauna, until Connor and Simberloff did exactly that," write Diamond and Gilpin.

"... we run the risk of submerging important biological patterns in a statistical mirage."

Connor and Simberloff counter by claiming that "confining the analysis to guilds is no trivial matter, for assigning species to guilds requires detailed data on resource use by all species in a community."

This dilution problem is one of seven "flaws" in Connor and Simberloff's approach, as listed by Diamond and Gilpin. The most fundamental "flaw" concerns the validity of the null hypothesis: is it truly null?

When Connor and Simberloff generate their random distribution of bird species on islands against which to compare the observed distributions, they constrain their data in the following ways. Each island in the model has the same number of species as in the real archipelago; the number of occurrences of a species throughout the random archipelago is the same as in nature; a species can be assigned only to those islands that contain similar numbers of species as observed in real life. Applying these constraints, Connor and Simberloff typically claim that the observed distribution does not differ markedly from the null distribution, and thus conclude that no process should be inferred from the observed pattern.

Diamond and Gilpin contend, however, that "the Connor-Simberloff 'null hypothesis' already incorporates competition through two of its three seemingly innocent constraints." The observed distribution is therefore being set against itself and, not surprisingly, is found to be similar. Robert Colwell, of the University of California, Berkeley, calls this the "Narcissus effect." And, working with David Winkler, also of Berkeley, Colwell has shown that, when a model archipelago whose species distribution is known to be affected by competition is established by computer simulation, the Connor-Simberloff null hypothesis fails to detect those effects. "The null models . . . are biased in ways that obscure or underestimate any role that competition may play," they conclude. In addition to the Narcissus effect, they note that differential dispersal abilities will serve to obscure patterns derived from competitive effects.

Diamond and Gilpin, in their Princeton chapter, conclude that even if they were to cure the other six of the list of seven "flaws" in Connor and Simberloff's approach, this seventh, the problem of hidden structure, will still be fatal to the technique. Diamond now refuses to write the term "null hypothesis" in this connection unless its uncertain status is indicated by flanking quotation marks.

In their Princeton chapter, Connor and Simberloff address the challenge of the hidden structure problem, but eschew direct confrontation. "Gilpin and Diamond present no evidence that demonstrates that the row and column sums (and incidence functions) are actually affected by competition." To the criticism about the validity of null hypotheses in general Simberloff is more direct. "We are dealing with something that is exactly analagous to chi-squared contingency tables where rows and columns are fixed and we are looking for patterns of co-occurrence—a point that is either not understood or has been deliberately obfuscated in the literature."

Simberloff readily concedes that his null model is not perfect, but he lays the blame with the nature of ecological data. "When you look at species distribution over an archipelago you have just one set of data to work with. This inevitably makes the tests less powerful than if you had several sets. We've always said this, but there still seems to be confusion in people's minds—or deliberate obfuscation—about whether anything can be done."

Strong is even more forthright in rebutting the charge that the Tallahassee null models contain competition. "That is complete rubbish. That is logically and statistically wrong." He describes the charge as "a red herring." There is no doubt that it is occupying a good deal of people's attention.

Until recently, both Simberloff and Strong insisted that their null hypothesis had "logical primacy over other hypotheses." In a paper to be published later this year in a symposium of papers in *American Naturalist*, Simberloff admits that "we were incorrect to suggest that the hypothesis of no population interactions has 'logical primacy' as a null hypothesis." He goes on to say, however, that "such an hypothesis is an apt starting point." Strong, however, maintains his position on the supposed logical primacy of null hypotheses, which he restates in his contribution to the *American Naturalist*'s symposium.

In addition to challenges over hidden structure, the Tallahassee null models draw criticism over the question of relevance. "In the Connor-Simberloff-Strong philosophy, the null hypothesis is that there are some unspecified random processes occurring in ecological communities that cause communities to be as they are," says Roughgarden. "It is not a viable hypothesis because it is not an hypothesis about any particular process." If Simberloff and his colleagues were to use their null models to test for the effects of stochastic events, such as certain climatic influences, aspects of species dispersal, and extinction in small populations, then, suggests Roughgarden, they might be onto something. "As it is, they just don't understand the concept of irrelevancy."

The real issue in testing the existence and meaning of pattern in ecological communities, therefore, distills to the question of alternative hypotheses. If the distinction ecologists had to make truly were *either* competition *or* chance association, then the business of reaching an unequivocal answer would be greatly simplified. "Unfortunately," write Colwell and Winkler, "in almost all ecological situations the alternative hypothesis is of a composite type. That is, there is an amorphous class of alternative hypotheses instead of a single, well-defined alternative." And when the alternatives cannot be defined precisely, the likelihood of reaching the "chance association" conclusion is erroneously enhanced, they explain.

Two other contributors to the *American Naturalist*'s symposium, James Quinn of the University of California, Davis, and Arthur Dunham of the University of Pennsylvania, comment on the uncertainty of null models as alternatives against which to test the impact of processes, such as competition, on community structure. "The reliability of such estimates . . . depends upon being able to state the model explicitly and estimate its parameters at least as accurately as those of the process being evaluated," they write. " 'Null hypotheses' in ecology are often unsatisfactory because they are virtually impossible to specify completely, or require knowledge unavailable directly and difficult to estimate independently of the pattern being studied."

Simberloff responds to Roughgarden's challenge about the relevance of null models by saying that "He seems generally to be arguing that a model, to be useful, must be realistic without having noticed that all models are unrealistic by virtue of being abstractions." And, as the Tallahassee school is often accused of viewing the world as devoid of competition and devoid of structure, Simberloff often feels constrained to emphasize, "I've never said that there is no competition, that competition isn't important in generating patterns in nature, even among insects. All I've been addressing is the canons of evidence."

Few would argue against this last sentiment but many have expressed themselves a mite skeptical that Simberloff is as open-minded as this statement implies. May, for instance, has said, "it is paradoxical that some of those who are most sensitively aware of the need to keep sight of alternative explanations for observed patterns in community structure seem, at the same time, occasionally to accept that there is only one True Way to do science."

Simberloff, meanwhile, is confident that his view will prevail. "I am secure that whether my reputation is besmirched or not the specific points we make are having a big effect on the way graduate research is being done. The number of papers coming out that reflect our approach shows the impact we are having."

Although there is considerable anguish over Simberloff's style, which is perceived as arrogant and combative, most ecologists, with one or two notable exceptions, acknowledge that his concern about canons of evidence is having a positive effect on the way the science is done. "The recent emphasis on the need to evaluate perceived patterns in community structure is—with hindsight—long overdue," write Colwell and May, in conjunction with British ecologists Paul Harvey and Jonathan Silvertown. "Simberloff and his colleagues have caused people to be more rigorous in the presentation of their data," says Schoener. "They have caused people to question their assumptions and to examine their procedures for handling the data. This is an excellent development."

Inevitably, the caveats come pretty strongly too. "We should apply null models with circumspection," says John Terborgh of Princeton University. "Otherwise we run the risk of submerging important biological patterns in a statistical mirage." Harvey, Colwell, Silvertown, and May caution: "Legitimate enthusiasm for sound methodology must go hand in hand with the realization that null hypotheses in ecology, as elsewhere, depend on null models, and that all models make assumptions. If these assumptions are not appropriate, or create systematic biases, no amount of mathematical and statistical precision will produce biologically valid answers. In Tukey's words, 'Far better an approximate answer to the *right* question, which is often vague, than an exact answer to the *wrong* question, which can always be made precise.' "

—ROGER LEWIN

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