Biologists Disagree Over Bold Signature of Nature

Adaptation to the different annual climatic fluctuations at low and high latitudes is suggested as an explanation for a famous, unexplained pattern of nature

BEING IN THE RIGHT PLACE at the right time can be as important for scientific insight as for making a killing in real estate. So it was for George Stevens, an ecologist who spent the summers of 1985 and 1986 teaching at the University of Alaska and the winters doing fieldwork in Costa Rica. "The contrast was dramatic," recalls Stevens. "When you travel around Alaska you are struck by how biologically very dull it is. Yes, the geology is fascinating, but there is a sameness about the fauna and flora, no matter where you are. But in Costa Rica, even with the slightest differences in terrain, you see great differences in habitat."

Faced with this very obvious contrast, Stevens was set to thinking, the result of which, he hopes, is a radical new approach to one of the longest recognized and most enigmatic patterns in the living world: for a century it has been known that as you travel from the equator to higher latitudes there is a steady decrease in the density of species per unit area. "This is the famous species-richness gradient," explains Stevens, "and if you look in ecology textbooks you can find a dozen hypotheses about it."

Stevens' hypothesis—the thirteenth in the lineup—differs from the rest, he claims, in invoking a general mechanism that applies to all latitudes, rather than being specific for the tropics or the poles, for example. "The high species richness of tropical latitudes is often assumed to be a tropical phenomenon," says Stevens, "something to be studied by tropical biologists. I see it as the outcome of a mechanism that in temperate and higher latitudes produces low species richness."

That mechanism is driven by the adaptation of species to the climatic conditions of their natural habitat: those at high latitudes must tolerate wide annual fluctuations while those in the tropics experience only a narrow range of change. One result of being adapted to these different environmental conditions says Stevens, is that "species at high latitudes can occupy broad geographic ranges while those in the tropics are much more restricted." This pattern runs parallel with the species-richness gradient. "When I realized the connection, the words just flew out of the typewriter," recalls Stevens. What emerged was a controversial paper, just published in *American Naturalist*.

Reaction to Stevens' paper is mixed. "The idea is different enough that it certainly should be out on the table for discussion," says James Brown of the University of New Mexico. "There aren't many people thinking about the big patterns and looking for underlying generalities. Stevens is going about it in an intelligent way." Dan Janzen of the University of Pennsylvania is less impressed. "Warmed-over intellectual ideas," he snorts. "He is saying what I was saying in my 1967 paper. And the data he uses don't support what he is trying to say."

"It's true that Janzen's paper touched on this theme," responds Brown. "But Stevens develops these and other ideas in an important way."

There are several reasons underlying these strong differences of opinion, the key one of which is that "this is a high-stakes issue, with some big egos involved," explains Robert Ricklefs of the University of Pennsylvania. "The species-richness gradient is *the* major, unexplained pattern in natural history, so there are big academic kudos in solving it. But it is hard to disprove any hypothesis, and people can become extremely opinionated in support of their own."

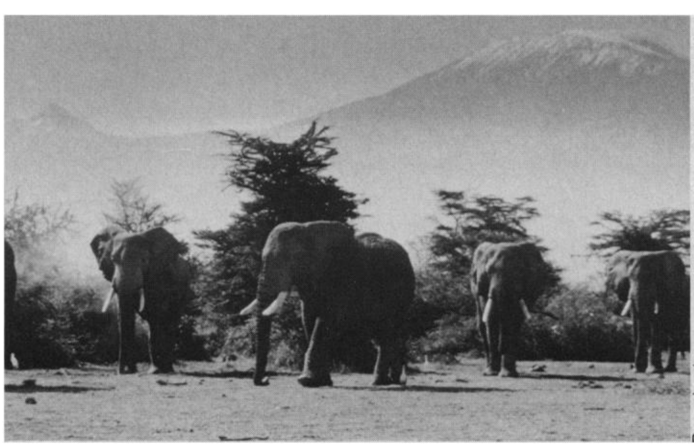
One problem here is that it is virtually impossible to think of experiments that might test some of the hypotheses that have been advanced over the years. And, comments Ricklefs, it allows researchers to support a pet hypothesis vigorously, even with only minimal of evidence in support. The species-richness pattern, so bold a signature of nature, "mocks our ignorance," he adds.

In trying to dispell that ignorance Stevens weaves together the latitudinal gradients for species richness and species range. At the core of the latitudinal gradient for species change is something of a paradox. Species that live at high latitudes and therefore adapt to wide annual fluctuation of, say, temperature are able to exist over a wide geographical range (measured in the significant north-south axis). No problem here.

For tropical species, however, adaptation to narrow environmental conditions means that straying even a few feet in elevation from their natural habitat quickly exposes them to a very different, and often unsuitable, environment. The tropics, therefore, effectively become a fine-grained mosaic of microclimates, with species being pretty well confined within or close to them. So, the tropics, that lush environment that supports so many species, also tightly constrains them.

The high species richness of tropical latitudes is, however, "due to more than just a greater variety of distinctly different habitats," notes Stevens. "In a given tropical habitat, more species coexist than in analogous extratropical sites." In other words, you have to explain how more species manage to live cheek by jowl in the tropics than in temperate latitudes. The answer, ventures Stevens, is something of a biological illusion.

"In any one habitat there are some species that are well adapted to local conditions and can thrive," explains Stevens. "In addition, there are others for which local conditions are extremely marginal, and they cannot sustain a population in the long term." This mix of successful and marginal species is the product of the mosaic of different microclimates, each supporting a core of well-adapted, successful species. "The sites where a species is successful become source areas for colonists that sometimes arrive in habitats to which they are poorly suited," says Stevens. "Populations of these poorly suited arrivals cannot be excluded through competition with better adapted locals because their numbers are constantly replenished from



The African elephant. *A wide-ranging tropical species that shares its environment with many other species.*

nearby source areas." This phenomenon is sometimes known as the rescue effect.

In temperate regions, where species' ranges are much larger, most dispersing individuals will fall within the preferred habitats, not in unsuitable habitats. As a result, the flow of colonists to marginal habitats is limited: the rescue effect is much less obvious in temperate latitudes.

In presenting data for geographic ranges of species in his paper, Stevens is quick to point out that he is building on an observation made almost a decade and a half ago by an Argentinian ecologist, Eduardo Rapoport. "I suggest that this correlation between geographic range and latitude be called 'Rapoport's rule'," says Stevens. Rapoport had made some limited observations about the geographic ranges of some subspecies of small mammals in his book, *Areografia*, published in 1975. Described by Brown as "one of the most original works in biogeography," Rapoport's book is, however, not widely known.

"I came across Rapoport's book while I was doing a literature search based on my initial findings, in May 1986," says Stevens. "I quickly found that the pattern he described for small mammals also applies to other vertebrates, to trees, mollusks, everything." It was this generality that convinced Stevens that the latitudinal pattern for geographic range might tie in with the species-richness pattern. "Stevens seems to have developed Rapoport's observations in an inventive way," comments Brown.

"Stevens has directly related something in the physical environment that leads to species diversity over the whole latitudinal range," says Ricklefs. "Many others have made connections between certain environmental conditions and *local* diversity, but none has been general throughout." Ricklefs is intrigued by the way the rescue effect is part of this overall pattern.

Faced with a problem that has frustrated biologists for generations, he would have to be incautious in the extreme who would claim to have solved it. "I certainly don't say 'this is the answer'," Stevens told *Science*. For one thing, he acknowledges, some of the relevant data on species distributions are often poor or even absent. "But there are enough there for me to be as confident as I can be that the pattern is real."

"A lot of the impact of science is not necessarily priority, who publishes an idea first," says Brown. "It often has to do with someone who pulls ideas from here and there, and takes them a step further." There are ideas here of both Janzen and Rapoport, notes Brown. But the key element is that "Stevens has taken it all a step further."

■ ROGER LEWIN

The Circle Can Be Squared!

Ask any mathematician if it's possible to square the circle, and the answer is bound to be No. Anyone claiming to have done so is rightfully disregarded as a crank, since mathematicians proved the impossibility of circle-squaring over a hundred years ago. Now along comes Miklós Laczkovich of the Eötvös Loránd University in Budapest with a claim that he can square the circle, and this time the response is enthusiastic applause. What's going on here?

The difference is, Laczkovich has solved a different, more difficult problem that goes by the same name.

The unsolvable circle-squaring problem requires a ruler-and-compass construction of a square having the same area as a given circle. The question—Is there such a construction?—predates even Euclid; the answer—No!—was finally proved in 1882. Even so, some amateur mathematicians refuse to give up. Mathematics journals still receive—and automatically reject—"solutions" to the problem.

Laczkovich's circle-squaring problem is entirely different. What Laczkovich has shown, in 39 pages of intricate analysis, is that a circle (the interior plus the boundary) can be cut up into a finite number of pieces, which can then be rearranged into the form of a square having the same area. In fact, Laczkovich has shown that almost anything can be cut up and rearranged into a square of the same area, with no gaps and no overlaps.

This version of the problem was first posed by Alfred Tarski in 1925. In 1924, Tarski and Stefan Banach proved a remarkable analog in three dimensions: Not only can a sphere be cut up and rearranged into a cube of the same volume, but it can be cut up and rearranged into a cube of *twice* the volume, or for that matter into virtually any shape of any size whatever. In fact, a solid ball can be rearranged into two solid balls of the same radius using as few as five pieces!

At first glance, the Banach-Tarski result sounds like a contradiction at the very heart of geometry. The explanation of the paradox lies in the nature of the pieces that get rearranged. The pieces are not solid chunks with nice boundaries. Instead they are so convoluted, diffuse, and intertwined that it is mathematically impossible to measure the volume of an individual piece. It's only when the pieces are put together that the resulting solid has a measurable volume—and strange as it seems, there's no contradiction in concluding that this can be done in two different ways resulting in two different volumes.

The Banach-Tarski paradox does not exist as such in two dimensions: Banach proved that any rearrangement of a figure in the plane must have the same area as the original. The reason lies in a difference between plane and solid geometry: two-dimensional objects can only rotate clockwise or counterclockwise, while three-dimensional objects have many possible axes of rotation. It remained to prove, or disprove, that plane figures of the same area could be rearranged one into the other.

Laczkovich's result goes far beyond what Tarski asked for. For one thing, Laczkovich shows that not only can the circle be squared, but so can any figure that has a suitably nice boundary. More surprisingly, he shows that it is not necessary to rotate any of the pieces—the rearrangement can be done using only rigid translations left or right and up or down. The result even applies to polygons: it is possible to take apart a triangle and fit the pieces back together as a square without rotating any of the pieces.

If you're reaching for your scissors, though, relax. As in the Banach-Tarski paradox, Laczkovich's pieces are not the sort of thing you can cut out of paper. Lester Dubins, Morris Hirsch, and Jack Karush proved in 1963 that you can't square the circle if the pieces have any kind of ordinary boundary. And even if the pieces could be cut with scissors, you probably wouldn't want to do it: Further analysis may bring the number down, but for now Laczkovich estimates that his method of squaring the circle requires something like 10^{50} pieces. ■ BARRY A. CIPRA

ADDITIONAL READING

M. Laczkovich, *Equidecomposability and Discrepancy; A Solution of Tarski's Circle-Squaring Problem* (in press).

Barry A. Cipra is a mathematician and writer based in Northfield, Minnesota.