

Researchers have dug up some surprising evidence casting doubt on the long-held belief that microbes are impervious to geographic constraints

Biogeography: Is Everything Everywhere?

How would the world look if marsupials, instead of being confined to the sanctuary and prison of Australia, had been forced to confront every other carnivore, tree-climber, burrower, and grazer on the planet? Our ideas about ecology, evolution, and history would be quite different had they been derived from studying animals that had crossed oceans, mountains, or deserts to seek out suitable environments. Polar bears in the Antarctic? Penguins in Alaska? Chimpanzees in Amazonia? Kangaroos on the Serengeti?

The picture seems far-fetched. Yet for about a century, microbiologists have believed that the organisms they study are unhindered by geographic boundaries, traveling the world and thriving wherever they find their preferred environment—be it hot springs, freshwater ponds, or rotting fir trees. That view gives researchers who study microbes a rather different perspective on the world. As the Dutch biologist Lourens Bass-Becking put it in 1934: “Everything is everywhere; the environment selects.”

Or maybe not. In the past few years, many microbial ecologists have come to believe that microbes are not infinitely mobile. Bass-Becking’s dictum is really only “an assumption,” says Jessica Green of the University of California, Merced. “It’s based on a confusion of hypotheses for facts.”

DNA studies have given us a more detailed picture of microbial diversity that, argue some, demands a more nuanced view of

microbial ecology. Those nuances have spawned a debate over what the DNA data actually show, and how a molecular view of microbial diversity can be compared with our species-based view of plant and animal ecology. Answering those questions, in turn, will help scientists better understand the crucial role played by microbes in keeping our ecosystem livable.

On Priest Pot

Bland Finlay of the Centre for Ecology and Hydrology (CEH) in Dorset, U.K., has spent a quarter of a century building up evidence to sup-

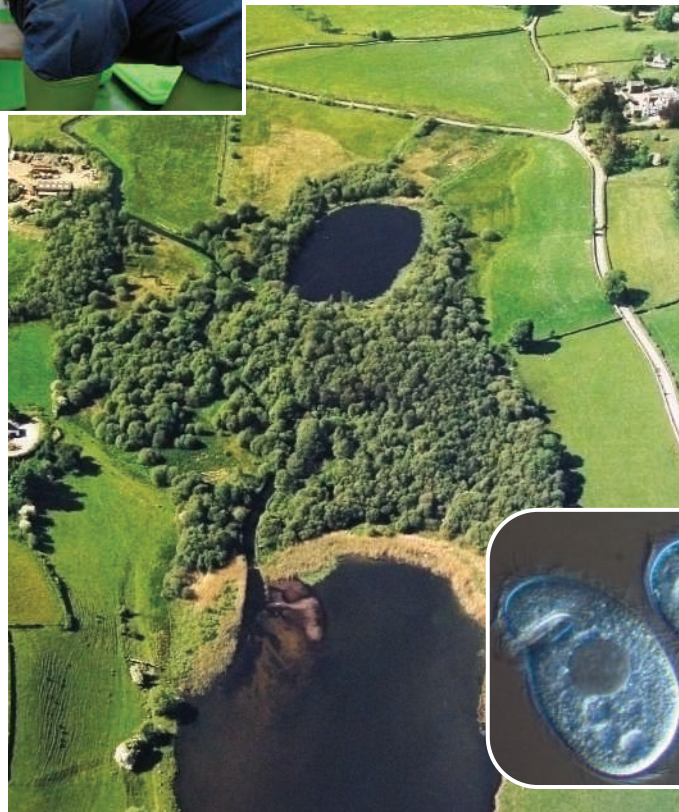
port Bass-Becking’s view of microbial ubiquity, much of it gathered in a small lake in northern England called Priest Pot. For example, he has found that a mere 25 microliters of sediment from Priest Pot contains 40 of the world’s 50 known species of the protozoan *Paraphysomonas*. What’s more, each species’ abundance in the sample matches its abundance worldwide. Everywhere he goes, Finlay finds identical ciliates: “There’s no convincing evidence for endemic species,” he says. “I see the same ones in Scotland, New Zealand, and central Africa.”

The main cause of microbes’ ubiquity is their vast populations, says Finlay. Although a specific ciliate is extremely unlikely to make a long journey, there are so many of them that some inevitably will hitch a ride via wind, water, a bird’s foot, or a clump of floating vegetation. Many can tolerate a wide range of environments—salt- and freshwater, for example—and they have an astonishing ability to hunker down in harsh environments until their moment arises.

Cultured in its native conditions, a gram of Priest Pot sediment yields 20 species of ciliate protozoan. But when Finlay’s team tested that sediment in the lab under different conditions—altering salinity, temperature, illumination and so on—it found 137 species. And the total keeps rising. He thinks those findings argue strongly for

the idea that the lake contains not only all the species adapted to its conditions but also a “seed bank” of many others that have arrived and survived, but not thrived. Everything seems to be everywhere, even if it is not immediately obvious.

“There is no biogeography for anything smaller than 1 millimeter,” he says.



Lake effect. Bland Finlay has plumbed Cumbria’s Priest Pot for a quarter-century of discoveries involving ciliate protozoa.

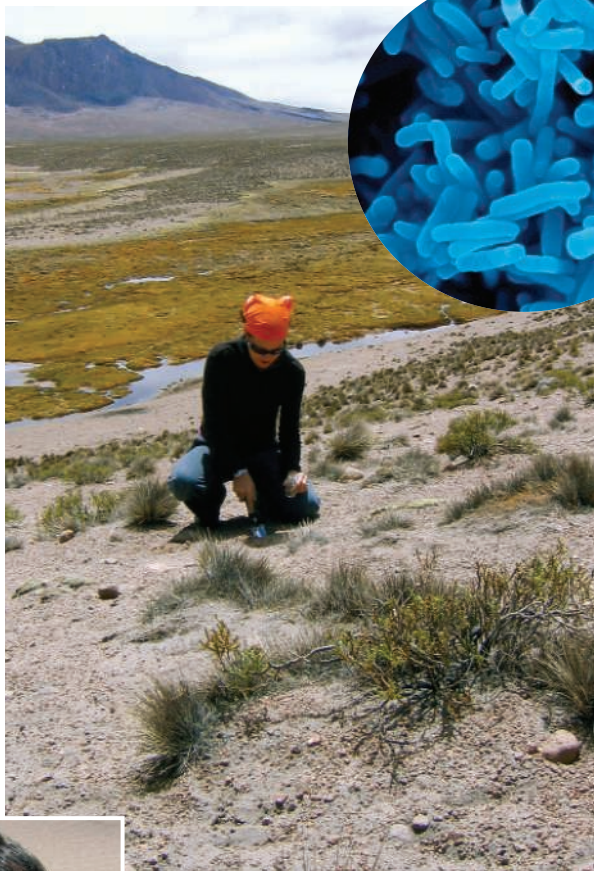
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But Green believes that our understanding of microbial diversity is too sketchy to support such statements. “[Finlay] has shown that there’s similarity at certain points, but the sampling effort on a global scale isn’t enough to make these sweeping generalizations,” she says. Green is one of a wave of researchers using molecular studies to probe the patterns in microbial diversity. The ability to sequence DNA samples from the environment has allowed scientists to detect far more than the 1% of microbes that can be cultured in the laboratory. It has also revealed how they vary from place to place.

Studying ascomycete soil fungi in the Australian desert, Green and her colleagues have found that the genetic differences between fungi from different locations increase with distance. Others have found that archaea of the genus *Sulfolobus* living in the hot springs of Yellowstone and Lassen U.S. national parks, for example, are more similar to each other than to those found on Russia’s Kamchatka peninsula. “We are beginning to see biogeographic patterns in microorganisms,” says Claire Horner-Devine of the University of Washington, Seattle, lead author of a study of New England salt-marsh bacteria with similar results. “There will be organisms that are global and can get anywhere, and you’ll also find ones that don’t have those ranges.”

Biologists studying plants and animals realized 150 years ago that the number of species found in a patch of habitat climbs as the area of the patch increases, a biogeographic pattern called the species-area relationship. A CEH team led by Christopher van der Gast recently argued that the same held for the bacteria living in oil-filled sump tanks in engineering machines and in water-filled tree holes in Amazonia. This seems to contradict the “everything-is-everywhere” view, in which the relationship between a place’s area and the microbial species it contains is essentially flat.

One complication is that limited dispersal is not the only thing that could create geographic variation in microbes. A big challenge is to separate the effect of environmental heterogeneity—which everyone accepts will cause biological differences—from divergences caused by dispersal. Finlay and his colleague Tom Fenchel of the University of Copenhagen, Denmark, have argued that van der Gast’s tree-hole study found more diversity in larger sites because larger sites are environmentally more heterogeneous, not because they are easier to disperse into or harder for



Digging in. Jessica Green pursues *Nitrosomonas* bacteria at two high-altitude locations in Chile.



populations to go extinct in.

“The next frontier is to figure out whether the patterns are due to environmental selection or to evolution and diversification,” says Jennifer Hughes of Brown University. She says a handful of published studies so far show geographical patterns when environmental differences are controlled for.

Phenotype matters

More vexing is the issue of how to make sense of the molecular data themselves. Some believe that microbes seem ubiquitous because our view of them is blurry. Many studies assign microbes to different species if their ribosomal DNA is less than 97% identical. If that were done with animals, Green points out, all primates from humans to lemurs would likely be lumped into one category—creating a group with far more cosmopolitan distribution and habits than any of the species erected by traditional naturalists. What’s needed, she says, is a study that would detect whether and how the patterns in microbial diversity compare with those seen in plants and animals—at scales from a cubic centimeter to intercontinental. She aims to do this for the bacteria in Mediterranean-

type ecosystems in Chile, California, and South Africa.

But Fenchel believes that simply comparing DNA sequences misses biological reality. Microbial species tend to be very old, he says, and have accumulated a lot of “neutral” genetic variation that has no evolutionary effect. If you look hard enough, he argues, every individual will be different.

Fenchel favors classifying microbes by what they look like and what they do. “The molecular data are super, but you shouldn’t forget the phenotype—and some of the molecular chaps do,” says Fenchel. “A couple of years ago, people thought genetic analysis was the bees’ knees and that it would clear up all the questions,” adds Finlay. “I don’t think this is true at all.” And many microbiologists believe that the ability of distantly related bacteria to swap DNA may further confuse our picture of

their diversity and distribution.

The debate about microbial biogeography is about more than how many bacteria can dance on the head of a pin. Microbes support the visible living world and provide trillions of dollars’ worth of ecosystem services for free, cleaning air and water and keeping soil fertile and healthy. They are a critical component of efforts to restore degraded ecosystems. As pathogens, they help regulate the populations of plants and animals, and their absence may be one factor behind the success of invasive species.

To understand these processes, says Horner-Devine, we must understand microbes’ ecology and how they will respond to stresses such as climate change and pollution. “To know how we’re affecting these communities, we need to know what the patterns in spatial and temporal variations are,” she says. Such knowledge will help build a biology that applies to all life on Earth.

“Comparing microorganisms with plants and animals will highlight where we see patterns and processes that could be the same for all domains of life,” says Horner-Devine. “That would be pretty phenomenal.”

—JOHN WHITFIELD

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