they can tolerate low levels of oxygen, these bacteria may provide a means to control metal concentrations biologically in groundwater and wetland-based remediation systems.

Bioremediation is not the only way we can apply these versatile organisms. Given the wide spatial and temporal distribution of sulfate-reducing bacteria and their distinct preference for low-oxygen to oxygen-free conditions, they can also provide clues to processes that may have been more widespread in the geologic past. Modern laboratory and field studies of sulfate-reducing bacteria and their metabolic products, both inorganic minerals and organic compounds, can provide valuable information for evaluating the role these microbes may have played in the geologic past. There is a general consensus that the low-oxygen conditions dominating Earth's surface during the first ~2000 million years of our planet's history favored the proliferation of sulfate-reducing organisms and that they, in turn, controlled their environment. This implies that a single process—bacterial sulfate reduction—has been in operation from the Early Archean until today. This process is widespread in different oxygen-poor environments at variable temperatures and pressures and results in mineralization of organic matter and direct and indirect mineral precipitation. It may be possible to roughly estimate the magnitude of the environmental impact exerted by these microorganisms during the evolution of our planet, directly or indirectly through their metabolic activity.

For example, the unequal distribution of dolomite [$CaMg(CO_3)_2$] in geologic time relative to limestone ($CaCO_3$), both of which are common sedimentary rocks, has remained an enigma. Dolomite is found in far greater abundance than limestone during Earth's early history and during periods when atmospheric oxygen levels may have been low compared with modern values (*7*). In laboratory experiments at low temperatures, sulfate-reducing bacteria mediate dolomite precipitation (see the figure), implying a link between this specific microbial process and dolomite formation (*8*, *9*). Apparently, the microbes can overcome kinetic factors inhibiting dolomite precipitation during their metabolic activity. It is probably not a coincidence that dolomite is often the host rock of many Pb-Zn sulfide ore bodies. Sulfate-reducing bacterial assemblages can accumulate metals to form a valuable ore deposit while simultaneously promoting the dolomitization of the host rock.

The comprehensive study of microbial controls on geochemical cycles is a relatively new direction in the geosciences. Linking the microbial biosphere to the study of the geosphere can produce exciting new discoveries, such as that reported by Labrenz *et al.*, and lead to a better understanding of many heretofore unexplained geologic phenomena. New discoveries can be expected as geomicrobiologists probe deeper into the low-oxygen realms dominated by sulfate-reducing bacteria. A particularly challenging new microbial frontier lies beneath the sea floor, deeply buried in sediments and within the hydrothermal systems plumbing the oceanic crust.

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PERSPECTIVES: ECOLOGY

The Lion and the Lamb Find Closure

Alan Hastings

Interactions between victims and enemies—between prey and predator, plant and herbivore, host and parasite, even between host and pathogen—are a central feature of all ecological communities. Even in the earliest ecological studies of interactions between victims and their enemies, a fundamental problem emerged: As these interactions appear to be inherently unstable, how is coexistence achieved? Gause's early experiments with different species of microorganisms illustrated the coexistence problem (*1*). The enemy species would either cause the extinction of the victim species and then starve, or would reduce the numbers of the victim species to such low levels that the enemy species would starve before the victim was eliminated. Yet the world is full of enemies and victims that coexist. What is the answer to this apparent paradox? The initial mathematical models of the 1920s and 1930s developed by Lotka (*2*), Volterra (*3*), and Nicholson and Bailey (*4*) did not provide easy solutions. Not surprisingly, many seemingly quite different answers were proposed. These answers incorporated to varying degrees the parts played by interactions within and between both enemy and victim species, as well as spatial heterogeneity (the uneven distribution of species in a given area). The contribution made by Keeling *et al.* (*5*) on page 1758 of this issue demonstrates that many of these explanations arose out of a single framework based on stochastic (random) models that emphasized spatial heterogeneity.

The question of what stabilizes the interactions between enemies and their victims arises even in the simplest models. Lotka (*2*) and Volterra (*3*) developed predator-prey models describing continuous interactions between enemies and their victims. They made the following assumptions: that the victim species grows exponentially in the absence of the enemy species; that the interaction between the enemy and victim species is the result of random encounters; and that the birth rate of the exploiter (enemy) depends on the frequency of encounters whereas the exploiter death rate is a constant. This model is neutrally stable, that is, at the boundary between stability and instability. Thus, a way to find stabilizing influences is to make modifications and see whether they produce stability or instability (*6*).

Nicholson and Bailey (*4*) studied the simplest interaction—that between a host insect and a parasitoid insect where both species complete their life cycles within a single year. The parasitoid lays its eggs in the developing host, and then the young develop inside the host, usually killing the host while producing the next generation of parasitoids. This interaction has been intensively investigated by population ecologists because: it is much more common than might appear (estimates are that 15% or more of insect species are parasitoids); the specialized nature of the interaction means that often the parasitoids attack only one species; and hosts are often insects of economic importance. The simplest model in this case is unstable rather than neutrally stable as a result of the time delay introduced by the discrete generations (see the

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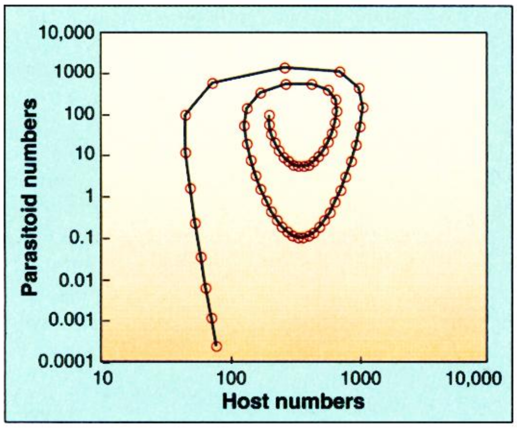

The death spiral. Dynamics of the Nicholson-Bailey model of interactions between an enemy (parasitoid) and victim (host) species. This enemy-victim interaction where the parasitoid lays its eggs in the developing host is very common among insects. The number of parasitoids and hosts over a defined time period demonstrates that this enemy-victim interaction is highly unstable.

figure). Nicholson and Bailey were among the first to look for stabilizing influences, mentioning as one possibility the importance of space (extinctions of hosts or parasitoids in one location could be compensated for by individuals at other locations).

Recent work on spatial heterogeneity in ecology has pointed out the importance of stochastic factors, in particular the dynamics that arise because the local environment faced by an organism differs from the average environment (*7*). Ecological interactions are inherently nonlinear because they depend on the combined densities of the interacting species. With spatial heterogeneity, the average of the local interactions is not the same as the interaction in the average environment. These kinds of dynamics can be easily explored by means of stochastic spatial simulations, but developing analytical descriptions of spatial stochastic models is very difficult. Similar problems arise in many other areas of biology, and have been carefully studied in the physics literature as well.

The obvious first step—taking spatial averages—yields what is known as the mean field approximation. Not surprisingly, a predator-prey version of this model does produce regional stability even if the local interactions are unstable (*8*). The next step in approximating the dynamics of a spatial model is to look at descriptions that take into account the spatial correlations of the species distributions. Unfortunately, this is a very difficult problem, and current methods rely upon approximations that are not easy to apply in general, nor easy to justify (*9*). Yet, these methods have begun to provide important ecological insight (*10*).

Keeling *et al.* begin with either of the two classic models: the Lotka-Volterra model or the Nicholson-Bailey model. They formulate equations for the dynamics of the averages of a stochastic version of the model and show that the key quantity is the covariance term describing the joint occurrence of enemy and victim. As already noted, this covariance is not a constant, but a variable whose dynamics must be included in any description of the system. Using a moment-closure approach (where the dynamics of a full spatial model are approximated by just the spatial average and variance-covariance terms), Keeling *et al.* derive approximations for the covariance term that clearly show that this term is negative. This essentially says that enemy and victim are found together less often than by chance, and therefore that this effect is stabilizing. They also show that the approximations they derive are in agreement with their simulations.

There are other interpretations of the covariance term that provide unification of explanations (both theoretical and observational) for stabilizing influences. The covariance term depends on past behavior of the system, and so it acts like a time lag. This explains observations of delayed density dependence. Alternatively, the covariance term can be interpreted as competition between parasitoids, which has been suggested as a stabilizing factor.

The Keeling *et al.* work is not the final answer, but does point the way to a better understanding of stabilizing influences in enemy-victim interactions. It also demonstrates the importance of spatial stochastic dynamics in ecology. A next step, which may require statistical advances, will be to relate work like this more closely to observations of enemy-victim interactions in large spatial scale natural systems and in smaller scale experimental work. Future progress will depend on the development of better methods for describing analytically the dynamics of spatial stochastic systems. Then, approaches like those used by Keeling *et al.* to study enemy-victim interactions can be applied to larger communities with more species, perhaps providing a better explanation of the relation between diversity and stability.

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PERSPECTIVES: APPLIED PHYSICS

Smaller, Faster Midinfrared Lasers

Jerome Faist

Semiconductor lasers are used widely as optical sources in telecommunication systems and CD-ROM and DVD optical memory drives. According to conventional wisdom, these very small, efficient devices are good for almost any task, although to date they cannot emit efficiently at very short (blue) and very long (midinfrared) wavelengths or achieve very short pulse emission. On page 1739 of this issue, Paiella *et al.* (*1*) expand the range of operation of these devices substantially by demonstrating midinfrared lasers that emit picosecond pulses at wavelengths of 5 and 8 μm. Perhaps the most interesting aspect of this work is the innovative technique used to achieve this goal.

In a simple picture, the active medium of a laser is a two-level system in which the population of the upper energy state is kept larger than the population of the lower one. Because of this population inversion, stimulated emission (transition from the upper to the lower state) is more likely than absorption. Light is amplified by passing through the active medium, resulting in optical gain. In a semiconductor laser, the active medium (the semiconductor itself) is shaped into an optical waveguide that captures and guides the light between the edges of the semiconductor. The resonant optical frequencies of this cavity are called the modes. In a mode-locked laser, the individual modes

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