um, so too can atomic beams diffract. To quantitatively obtain the positions of the surface atoms giving rise to the diffraction pattern, accurate calculations based on realistic potential energy curves are required. Surface scientists are studying both clean and adsorbate-covered materials in this way.

In the case of inelastic scattering, Benedek and Nicolàs García of the Autonomous University of Madrid showed last year that the shapes and intensities of the main peaks in the scattering data from lithium fluoride of Brusdeylins, Doak, and Toennies could be explained by the so-called hard corrugated surface approximation. A hard surface is one in which the repulsive part of the potential curve is approximated as a vertical line (that is, the potential rises infinitely fast). Corrugation refers to the fact that the surface is not smooth because the surface atoms occupy discrete sites. The potential energy between the atoms is slightly lower than it is over an atom.

Many authors have reported in the past year, however, that satisfactory fits to elastic, diffractive scattering require more accurate potential energy curves than the hard wall. There is considerable experimental evidence for a softer (that is, not infinitely fast rising) wall. At the surface vibrations conference, García and John Barker and Inder Batra of the IBM San Jose Research Laboratory discussed realistic potentials for helium scattering from nickel, copper, and gold. In his conference summary talk, theorist Thomas Grimley of the University of Liverpool urged his colleagues to begin a first-principles calculation of the potential energy curve and its coupling to surface vibrations, although "it may take years." The theory is only semiquantitative until this is accomplished.

Grimley also asked whether it would be possible to use atomic beam inelastic scattering to observe vibrations in adsorbed molecules. It should be feasible, he said, and could become a competitive technique with electron energy loss spectroscopy. However, in his summary talk, experimentalist Ibach, who is regarded as the father of electron energy loss spectroscopy, pointed out that the rather low energies of the atomic beams used so far (less than 100 meV) could prevent researchers from using atomic beams to look at high-energy surface vibrations. In general, vibrations in adsorbed molecules have much higher energies than the vibrations on clean surfaces.—ARTHUR L. ROBINSON

Extinction Leaves Its Mark on Ecology

In addition to energetic considerations, selective extinction helps shape the composition of living communities

Nineteenth-century naturalists argued about the most appropriate way in which to analyze the causal factors in community structure and dynamics. Today's ecologists continue the debate in vigorous manner, with a currently popular emphasis on features such as coevolution, resource partitioning, and thermodynamics. James MacMahon of Utah State University and Charles Fowler of the National Marine Mammal Laboratory, Seattle, suggest in a recent paper* that in addition to these processes ecologists should also take note of important historical effects, specifically selective extinction and speciation, both in geological and ecological time frames.

As a group, ecologists represent a broad range of scientific backgrounds, some of which embody the kind of historical perspective urged by MacMahon and Fowler. However, the main thrust of contemporary thinking, brilliantly pioneered by such figures as G. Evelyn Hutchinson and Robert MacArthur, concentrates on current ecological processes. "Historical processes are very difficult to deal with," comments Robert Ricklefs of the University of Pennsylvania. "Nevertheless, it is an important consideration to which ecologists in general have not paid sufficient attention." Peter Grant of the University of Michigan agrees that "The temporal dimension has been somewhat neglected."

Any ecological community will comprise a range of organisms of different size, habits, and abundance. Thermodynamic considerations will determine the total biomass a given area might support, but, say MacMahon and Fowler, they are less helpful in explaining the overall composition of species. Their suggestion is that since certain properties of species, such as body size, geographic range, and evolutionary plasticity affect probabilities of extinction, community composition will in part at least reflect these probabilities.

For instance, one of the substantive problems of ecology is the shape of the trophic pyramid, which goes rapidly from an abundance of primary producers at its base to a sparsity of carnivores at its apex. Why is the number of trophic levels so limited? And why is the pyramid generally so broadly based?

"There are many contending explanations," says Robert May of Princeton University. "One of them is the inefficiency of energy transfer from level to level. In this case you'd expect to see longer food chains among cold-blooded animals, which are more energy efficient than endotherms. But this is not the observed case."

MacMahon and Fowler point out that the probability of extinction of a species in a food chain is the sum of its own inherent probability and that of the levels below upon which it depends. Extinction probabilities therefore tend to increase as one climbs the trophic pyramid. The concepts of selective extinction "produces a rather simple explanation of the rather short nature of most trophic chains," write MacMahon and Fowler.

The argument can be taken further, in examining species' habits in the food chain. A specialist feeder which depends on a single food source is more vulnerable to extinction than one which has a broader resource base, for obvious reasons. This being the case, "there will be more trophic levels in communities comprised of generalist than in communities where specialization . . . [is] characteristic of the species . . . involved," predict MacMahon and Fowler.

A second property of species, but not of individuals, that bears on extinction probability is geographic range. A species with a very limited geographic range is clearly more vulnerable to extinction through local catastrophe than is a widespread species. A corollary of this is that the density of species will increase with increase in the total area of a particular environment being examined. Both these points are borne out by observation.

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The fossil record shows that species evolve at different rates: some speciate frequently while others are stable over long periods; some are apparently more susceptible to extinction than others. Again, this evolutionary plasticity is a property of species, not of individuals. The fate of any species is determined by an interaction between the environment and its innate evolutionary plasticity.

Following this line of reasoning, the theory of selective extinction provides a simple explanation of the enigma of sex. Biologists are puzzled by the popularity of sexual reproduction because it appears to be a genetic burden for the individual. But sex promotes a genetic, and therefore phenotypic, diversity at the level of the species, a property that guards against extinction in the face of environmental change.

Generation time is another factor that affects evolutionary plasticity: short generation time promotes plasticity. "Genetic plasticity may be a product of short generation times in at least two ways," write MacMahon and Fowler, "(1) the rate at which new offspring are produced, and upon which natural selection of individuals can operate; (2) the physical disruption of chromosomal material as linked to the process of cell division."

As generation time correlates with body size, one would expect higher extinction probabilities in large-bodied species. Data do show that extinction rates in mammals are significantly higher than those in invertebrates and diatoms. Even within groups of related species smallness is apparently favored. And as May has pointed out, more than 80 percent of all animals are less than 10 millimeters in length.

Properties that affect extinction probabilities interact, from which, say MacMahon and Fowler, some predictions about community structure can be made. "Generalists (species which do not trophically depend on a single species) will be common relative to specialists. Consequently, large heterotrophs, with long generation times should be generalized herbivores. Specialists must not only respond to extinction rates imposed upon them by their physical environment but must also adapt to changes in their prey or host. If the prey or host evolves rapidly, there is a possibility that natural selection will result in the prey species evading its specialist consumer. We expect, then, that specialists will have shorter generation times than the species upon which they depend. . . . These expected patterns are consistent with those in the natural ecosystems."

The question of balance also applies to body size, but here it is a balance between effects at the level of species and individuals. There are a number of reasons why being large compared with one's fellows is advantageous for individuals. This tendency is reflected in the fossil record by a recurring increase in body size through lineages over long periods of time. Why, then, are there so few species with large adult body size? "The theory of selective extinction suggests that species with long generation times (a corollary of large body size) suffer high extinction rates." MacMahon and Fowler also say that their theory predicts that large-bodied species will generally be recent lineages. Available evidence appears to support this notion.

The theory of selective extinction closely parallels species selection, an idea advanced by Steven Stanley of Johns Hopkins University and others as an important component of macroevolution. "Just as you can look at fossil assemblages as being made up of species that have survived extinction, you can say that living communities are made up of a collection of individuals from which certain individuals have been selected out," comments MacMahon. "There is a continuous process of addition of new species and an editing out of existing ones, both in local and geological contexts."

MacMahon and Fowler suggest that ecological thinking might benefit from some interdisciplinary exchange with paleontologists. Stanley, a paleontologist, welcomes this proposal. "The kinds of higher level processes with which we deal must be important in ecology."

Resistance to the idea among ecologists stems from several sources, say MacMahon and Fowler. One of these is that selection at the level of species is often misconstrued as "group selection," the idea that a species might change in response to a collective, rather than collection of individuals', benefit. "In contrast to group selection, selective extinction cannot directly determine the nature of any particular species, i.e., selective extinction only influences the properties of natural collections of species."

One can view selective extinction as a parallel to natural selection. "As a consequence . . . our thinking about groups of species, such as in communities and ecosystems, will begin to resemble our use of natural selection in thinking about the nature of individual species. We will think in terms of a relative probability that future groups of species will contain descendants of existing species."

A second problem some ecologists have with the idea of selective extinction, say MacMahon and Fowler, is that there is a tendency to believe that ecosystems can be completely described on the basis of processes, such as natural selection, acting at the level of the individual. "There is a resistance to the concept that properties of ecosystems come from the collective nature of the component species. . . . The nature of collections of species in ecosystems, communities, and the biosphere are to be viewed as products of high-level evolutionary processes of the geologic past."

MacMahon does not claim his paper with Fowler is an end point in the discussion. "It is a stage in the development of a more coherent theory of communities and ecosystems. It will allow us to erect testable hypotheses that will bring together a wide range of ideas."

—Roger Lewin

Species richness

Combined relationships between species richness, or total number, generation time and trophic level produces a three-dimensional plot. An initial increase in the number of species with respect to trophic level is possible because of risk spreading by generalist herbivores and omnivores.