cades Volcano Observatory, where many of these specialists worked side by side to capture all possible lessons of this rare event. Before 1980, some saw sharp divisions between hazards work and basic volcano research, between monitoring and geological studies, between statistics-based forecasts and process-based predictions. Today, forecasts improve as we try to marry a respect for the geologic and historical past, monitoring of the present, and fresh research into a volcano's internal and surficial processes.

Since the eruption, hundreds of volcanologists from around the world have come to study Mount St. Helens. Scientists from the United States have in turn traveled around the world to share the experience of Mount St. Helens and seek lessons from other volcanoes. The U.S. Agency for International Development (USAID) and the U.S. Geological Survey now co-fund a life-saving Volcano Disaster Assistance Program.

Mount St. Helens continues to awe and inspire those who visit. Its lessons are pillars of efforts to better understand and forecast explosive volcanism, its surprises a humbling reminder that nature's repertoire can easily exceed our imagination. Should we worry? More than 500 million people live within striking range of potentially lethal volcanoes, and the number increases by millions each year (*17*). Every success in eruption forecasting raises public expectations that the safety of these millions is assured. Forecasts are improving, but uncertainties remain high. Imagine if the next major volcanic crisis replete with uncertainty is in or near a major city, not a forest. Imagine if the trees of Mount St. Helens had been people.

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PERSPECTIVES: ECOLOGY

Messages from a Mountain

Jerry F. Franklin and James A. MacMahon

The eruptive episode of Mount St. Helens that began on 18 May 1980 created an unprecedented natural laboratory for studying the effects of large disturbances on ecosystems and the processes that affect ecological recovery. Its richness lay not only in its size but also in the complexity of the disturbance (comprising a decapitating landslide, the blast, pyroclastic and debris flows, and volcanic ash depositions) and in the interaction of subsequent eruptive events over space and time. Following the eruption, ecologists likened themselves to "kids in the candy shop" as the complexity and richness of disturbance impacts and ecological responses revealed themselves.

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Many predictions were made about the natural ecological responses expected in the gray, ash-covered moonscape visible immediately after the cataclysmic event, assuming no human intervention. According to extant theory, recovery—or "ecological succession"—would begin with the dispersal of plants, animals, and microbes into the devastated zone from adjacent unaffected areas. Hardy, specially adapted pioneer species would lead the way and create conditions that would facilitate the establishment of species characteristic of more advanced stages of succession. Recovery in the 600-km^2 area would occur primarily by migration from the edges.

Reality defied predictions. Biologists were confounded by the richly varied and often surprising circumstances that not only left organisms alive but also allowed biotic processes and structures to persist. As a result, ecosystem recovery proceeded rapidly and by diverse pathways.

Excepting only the sites of pyroclastic flows and lava extrusions, organisms survived almost everywhere as complete individuals, perenating parts (such as rhizomes or roots), seeds, and spores (*1*). Not all survivors persisted, but many did, including species representing all trophic levels, most life forms, and all successional stages—pioneer and late successional. In the soil, animals such as pocket gophers and deer mice survived; pocket gophers proved important in mixing old soil with new volcanic ash and disseminating spores of mycorrhizal fungi (*2*). Late-lying snowbanks melted away to reveal intact beds of tree saplings and shrubs that immediately resumed growth. Amphibians emerged from the sediments of lakes and ponds to reproduce.

Organisms did disperse from long distances into the devastated zone, and many established themselves. These again included species considered to be pioneers as well as those characteristic of the late-successional forest, such as Pacific silver fir and western hemlock trees. Site preparation or facilitation by pioneers did occur, as with azotobacter-hosting lupines on the pumice plain (*3*), but just as often it did not. Many solitary tree seedlings established on the pyroclastic flows, for example.

There were immense legacies of organic structures, most notably blast-flattened tree boles and standing dead trees (snags). Classical ecological theory has largely ignored ecosystem structure—the individual and collective architecture of the components—in favor of composition. Yet structural complexity is a major factor in biological diversity and ecosystem processes (*4*). Structural legacies at Mount St. Helens influenced geomorphic processes,

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such as erosion and deposition of sediments. They also provided critical protective cover, habitat, and food and nutrient sources for a variety of organisms. Re-colonization of some species depended on these structures; for example, western bluebirds and Oregon juncos require snags and logs, respectively, for nesting.

After the blast. Blown-down tree stems and standing dead tree stems (snags) in Upper Clearwater Creek, Mount St. Helens blast zone, 1980. The border of blast zone can be seen in the background.

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The devastated zone was spatially heterogeneous, reflecting the complex interactions among preeruption conditions, disturbance, and posteruption processes. This spatial complexity was often evident in the density and diversity of surviving organisms and structures. For example, areas occupied by preeruption clear-cuts and snowbanks were notable for the abundance of surviving plants. Erosion actually facilitated ecosystem recovery in some locations by removing the fresh ash cover from many buried plants and inhibited recovery on other sites where the eroded materials were deposited.

Recovery was most rapid on the numerous sites that either had concentrations of surviving organisms or represented particularly favorable microsites (such as well-watered sites), or both. Consequently, the pattern of recovery was dominated by nucleation—spreading from thousands of foci—rather than by gradual encroachment from the margins, as originally expected.

Ecologists at Mount St. Helens came to view disturbances as vast editing processes (*5*). Each disturbance event is a process in which some biotic elements (organisms and structures) are deleted (removed), some are transformed (as from live to dead), and others are left unaffected. A new term, biological legacies, was coined to describe the organisms and organic structures that survive a disturbance event. The fact is, disturbances often kill organisms—such as trees or corals—but do not consume or remove much of the structure or its organic matter. Even Mount St. Helens left most of the forest behind (see the figure).

Other large disturbance events followed on the heels of Mount St. Helens, such as the Yellowstone Fires of 1988, Hurricane Hugo in 1989, and Hurricane Andrew in 1992 (*6*). Studies of these events expanded and enriched the lessons from Mount St. Helens regarding editing processes, legacies, and heterogeneity. Important field experiments, such as the artificial uprooting of forests in a simulation of hurricanes (*7*), have followed, allowing more careful study of the processes involved in the creation of legacies and their role in ecosystem recovery.

As a result, ecologists are now actively reassessing theory and concepts related to disturbances and ecosystem recovery (*8*). Many of the findings are not really new but rather are both intuitive and evident in various forms in older literature. For example, in 1916, Frederic Clements described residuals (surviving organisms) as important elements in succession. In the 1960s, scientists at Hubbard Brook demonstrated the importance of residual vegetation in controlling nutrient losses through watershed experiments. But many modern ecological texts and teachers seem to have lost track of such lessons.

Mount St. Helens has demonstrated that disturbances are far more complex and heterogeneous than we have been prepared to acknowledge. Sound predictions about subsequent ecosystem recovery require knowledge of the kinds, quantities, and distribution of biological legacies and the roles that they may play. Understanding successional and ecosystem processes requires as much attention to structure as to composition.

We find that our predictive power is very limited. Models based on individual mechanisms such as facilitation, inhibition, and tolerance can contribute to our understanding of succession but are relevant only to specific locations in the disturbed landscape. Under the complex conditions of real disturbance, many processes are operating simultaneously, and some are the unpredictable consequences of stochastic events. In this context, reductionist approaches and an emphasis on the null hypothesis with its "either/or" outcome can be very misleading.

The lessons of Mount St. Helens and modern disturbance ecology have important applications. Natural resource management practices are purportedly modeled on natural disturbances. In fact, many favored practices—such as clear-cutting in the case of forest harvest—leave little in the way of biological legacies, because of the uniformity and frequency of the harvest and the high proportion of organic material that is lost through harvest, residue disposal, and decomposition. Hence, the notion that clear-cutting is comparable to a wildfire in its effects, including its legacies, is unwarranted.

The concept of structural legacies (living and dead) is being incorporated into new forest practices, sometimes referred to as ecosystem management (*9*). For example, retention of large trees, snags, and logs as well as patches of forest on harvested sites is a major element of the Northwest Forest Plan for federal forests. Similar practices are being adopted on forestlands elsewhere in North America, South America, Australia, and Europe, including Scandinavia.

Does Mount St. Helens have more ecological messages for scientists? Many open questions remain. Will we observe thresholds in the recovery process, with rapid and permanent transitions between states, such as from open communities to forest dominance? How will eruptive events during the next century affect the recovery process? Creating and maintaining a strong base of long-term observations on recovery processes at Mount St. Helens (as well as other disturbances) are the most important actions that we can take to ensure that we learn as much as possible from these events. For, after all, empirical data provide the only real test of ecological theory.

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PERSPECTIVES: EVOLUTIONARY GENETICS

Sinless Originals

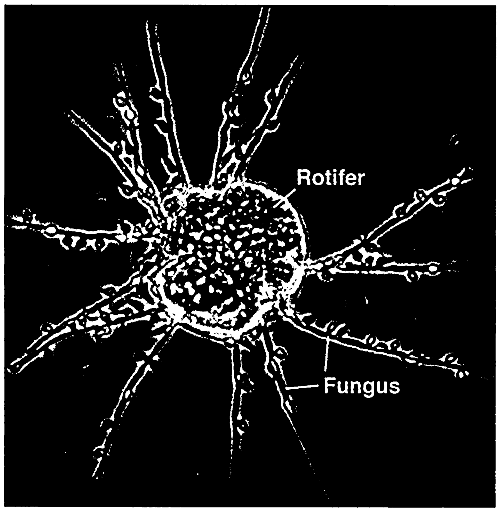
Olivia P. Judson and Benjamin B. Normark

Is it possible to live without sex for millions of years? That depends on what you mean by "sex." Certainly most organisms do fine without copulation. But if by sex you mean swapping DNA between genomes, then that is much harder to forgo. Among eukaryotes, the cycle of meiosis (in which the genome is split into random halves) and syngamy (in which shuffled half-genomes are fused into new wholes) seems to be essential. Asexual organisms—creatures in which this cycle has come to a stop—are widely thought to be doomed to a swift extinction (*1*). The apparent exceptions to this rule—those few ancient and diverse lineages of organisms in which sex is unknown (*2*)—are regarded with suspicion. Time and again, evidence of sex has been found in supposedly ancient asexual lineages (*2*), and many evolutionary biologists do not believe that any of the apparent exceptions are real (*3*, *4*).

Although evolutionary biologists agree that sex is essential, they cannot agree why. More than 20 hypotheses, ranging from the sublime to the ridiculous, have been advanced to explain why sex is crucial for evolutionary success (*5*). Two factors have abetted this exuberant proliferation of ideas. First, an evolutionary explanation for the success of sexual reproduction would bridge a huge hole in the theoretical basis of modern biology. Second, the debate has taken place in the absence of decisive data.

But help is on the way. On page 1211 of this issue, Mark Welch and Meselson (*6*) present robust evidence that the most celebrated of the apparent exceptions to the rapid-extinction rule—the rotifers of the Class Bdelloidea—are exactly what they appear to be: a diverse and successful group of invertebrates that thumb their noses at evolutionary theorists by having lived entirely without sex for at least 40 million years. At the same time, their work lays the foundations, and provides the essential tools, for two new avenues of research.

As Meselson was the first to realize, an organism that has truly been without sex for millions of years should show a distinctive and peculiar genomic structure and pattern of DNA-sequence relationships. From the moment meiosis ceases, the genome essentially freezes, with any subsequent changes arising mostly as a result of mutation. Pairs of gene sequences that were once alleles should start to accumulate mutations independently, and hence to diverge from one another. A clade that diversified after an ancient genome freeze should therefore show unprecedented levels of heterozygosity. If you pick two alleles at any locus within a single individual, the sequences should show consistent and extreme divergence, because they will have been diverging ever since the genome froze. But, curiouser and curiouser, the common ancestor of any two extant individuals will be more recent than the genome freeze. Hence, if you compare alleles *between* even very distantly related individuals, you should find that they are frequently less divergent from each other than are the two alleles *within the same individual*. This weird pattern of DNA-sequence relationships is precisely what Mark Welch and Meselson have found.



Under attack. A bdelloid rotifer (Phylum Rotifera, Class Bdelloidea) in the final stages of succumbing to attack by one of its parasites, the fungus *Harpospori-um angularis*. Parasites are thought to be one of the forces maintaining sex in populations.

In some ways a genome freeze is analogous to a genome duplication: Every copy of every gene suddenly becomes an independent locus in the sense that it evolves entirely independently of its homolog and former meiotic partner. It is possible that the results of Mark Welch and Meselson reflect an ancient genome duplication rather than an ancient loss of meiosis. But to explain their results this way you must also invoke a second hypothesis: that coincident with genome duplication the bdelloids lost virtually all heterozygosity by some unknown mechanism. In principle, complete homozygosity could be maintained by automixis (meiosis and fusion of cells from a single individual), although there is no cytogenetic evidence for that. It is even possible that the bdelloids represent the haploid phase of a life cycle whose diploid phase remains to be discovered, although such a life cycle would be unique among animals. But these are thin straws to clutch at: The striking DNA sequence relationships that Mark Welch and Meselson have discovered are exactly those predicted for an ancient asexual clade and are consistent with the often-stated a priori hypothesis that the bdelloid rotifers abandoned sex millions of years ago (*7*).

What now? The first, and most pressing, program of research must focus on the bdelloids themselves. A number of dramatic predictions that flow from the hypothesis of ancient bdelloid asexuality have yet to be confirmed: The extreme heterozygosity reported for a few loci by Mark Welch and Meselson should apply to the entire genome, such that each chromosome has a unique size and gene order (as against being one of a pair of very

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