There are immense differences between even-aged silvicultural disturbances (especially clearcutting) and natural disturbances, such as windthrow, wildfire, and even volcanic eruptions.

Threads *of* Continuity

by Jerry F. Franklin, David Lindenmayer, James A. MacMahon, Arthur McKee, John Magnuson, David A. Perry, Robert Waide, and David Foster

ON MAY 18, 1980, MOUNT ST. HELENS IN THE CASCADE RANGE OF WASHINGTON STATE ERUPTED CATACLYSMICALLY. This was a monumental disturbance event, the likes of which had not been seen since western settlement of the region. The eruption began with a massive (2.8 square km) landslide that decapitated the mountain exposing its superheated core. The ensuing explosion created a 50,000 hectare "blast zone". Superheated pyroclastic flows and numerous debris flows or lahars swept down the slopes and valleys. To the north and east of the mountain, volcanic ejecta fell over thousands of square kilometers. The scale, intensity, and synergy of these disturbances created a rich laboratory for the study of disturbance ecology (photograph opposite) (1,2).

PHOTOGRAPH BY JERRY F. FRANKLIN

TABLE 1.

SOME CATEGORIES AND TYPES OF BIOLOGICAL LEGACIES*

ORGANISMS (PLANT, ANIMAL, FUNGAL, AND MICROBIAL)
Complete organisms (varying in size and degree of sexual maturity)
Perennating parts (some roots, rhizomes, and hyphae)
Propagules (seeds, spores, eggs)
ORGANICALLY DERIVED STRUCTURES
Snags (standing dead trees)
Logs and other coarse woody debris on or near the ground
Corals and shell fragments
Large soil aggregates
Termite nests/mounds
Dead animal bodies
Feces
ORGANICALLY GENERATED SPATIAL PATTERNS
Root pits and mounds
Soil physical, chemical, and/or microbiological patterns
Root channels and burrows
Understory community patterns
Wallows and yards

** Not listed here is the general category of organic matter, which comprises a broad array of types, conditions, and sizes (from dissolved to large particulates) but is viewed primarily as a source of energy and nutrients rather than as a structure.*

Scientists expected to encounter a moonscape within the blast zone, a prediction encouraged by early television images of a uniformly gray landscape. According to traditional ecological theory, recovery would be slow: the sterilized landscape would be repopulated gradually by pioneering organisms dispersing into the blasted region. The pioneers would eventually mitigate conditions sufficiently to allow for establishment of species characteristic of later successional stages.

The reality of ecological recovery at Mount St. Helens was very different from these predictions (1,2). Surviving organisms were present almost everywhere in incredibly varied forms and circumstances—e.g., as complete animals and plants, perennating plant parts, and seed and spore banks protected within the soil and snowbanks. Included were species identified with all successional states—pioneer to climax—and of all life forms and trophic levels. Not all initial survivors persisted, of course, but many did. The diversity and abundance of survivors was notably dependent upon the site-specific combination of disturbances.

Residual organic matter provided an abundant energy and nutrient base. Moreover, much of it was in the form of large organically derived structures such as snags (standing dead trees) and logs. These structures helped retain the tephra and other sediments, modified hydrological processes in the streams, and provided protection for surviving animals.

Organic continuity between pre- and post-disturbance ecosystems was present almost everywhere—in rich and varied forms, living and dead. Throughout most of the blast zone, early ecosystem recovery was dominated by surviving organisms with surprisingly high levels of biological diversity and ecosystem function. Moreover, re-colonization occurred from multiple foci rather than incrementally from the margins of the blast zone. Although migrants have become important, even dominant, components of the blast zone in the ensuing twenty years, the contributions of the pre-disturbance ecosystem are still key.

The eruption of Mount St. Helens and other recent large disturbance events, such as the Yellowstone Fires of 1988 (3) and Hurricanes Andrew of 1989 (4) and Hugo of 1988 (5) have substantially increased our appreciation for the complexity of disturbance and recovery processes. Disturbances typically are described in terms of their type, size, intensity, frequency, and spatial heterogeneity. However, from an ecological perspective it is severity (impact) of the disturbance that is of greatest interest; and the best measure of severity may be the biological remnants.

Disturbances as Editors

Disturbances are like editors—they selectively remove or modify elements of an ecosystem while leaving others intact. As at Mount St. Helens, most disturbances leave significant elements of the preceding ecosystem behind to be incorporated into the redeveloping ecosystem, thereby enriching composition, structure and function. Heterogeneity in the editing, which is particularly apparent in large disturbances, assists greatly in this process. However, different disturbance agents—such as fire, wind, and clearcut—differ generically in their editing rules and, therefore, in biotic elements that persist.

The extent and importance of these residual elements in disturbances and secondary succession have received little attention in either basic or applied ecological texts. Similarly, discussion of categorical contrasts in these elements between different types of disturbances has not been widespread. Perhaps the focus of many classical studies of secondary succession on old fields seriously constrained the development of ecological theory on this topic. In any event—even as recognition of the role of surviving biotic elements is now emerging—generally, only living organisms are considered (6).

Biological Legacies

Webster defines a legacy as "anything handed down from an ancestor." In an ecological context, we define "biological legacies" as the organisms, organic materials, and organically-generated environmental patterns that persist through a disturbance and are incorporated into the recovering ecosystem (Table 1).

Organisms may persist as intact organisms or as seed banks, spores, fungal hyphae, and parts (such as rhizomes) with a capacity to regenerate the whole organism. Survivors provide propagules for additional establishment. Survivors may also be present in such large numbers that they dominate early successional stages and retard establishment of new individuals of the same or other species. The persistence of a dense layer of tree seedlings and saplings in areas of wind-thrown forest is a common example in temperate forests (7).

Structural legacies include dead trees, logs and other woody debris, coral, and animal carcasses. Dead wood structures (standing dead trees and logs) are particularly important legacies in forested ecosystems (8). They are not only long-term sources of energy and nutrients but also provide critical habitat for a variety of other organisms including vertebrates and invertebrates. For example, logs that persist through many disturbances are critical to sustaining populations of many red-listed species in boreal forests of Scandinavia (9). Coarse woody debris also influences hydrologic and geomorphic processes such as by trapping sediment. Because they decompose slowly, wood structures may persist as functional elements of terrestrial and freshwater ecosystems for many centuries. Carcasses of shrubs, trees, and cacti also provide structural legacies in a variety of steppe, grassland, and savanna ecosystems. Dead coral and coral remnants are good examples of structural legacies within a marine ecosystem.

Although they are often less obvious, biologically-generated spatial patterns are a third type of biological legacy. Specific biota (including plant, animal, and fungal species), plant communities, and biotic processes can generate strong and persistent spatial patterns in environmental resources, including the chemical, physical, and biological properties of soils. For example, plant species with special functional attributes—such as trees and shrubs of genera (e.g., *Alnus and Ceanothus*) that host nitrogen-fixing bacteria—generate patches of nitrogen-enriched soils. Similarly, large, long-lived coniferous tree species, such as giant sequoia (*Sequoiadendron gigantea*) and western redcedar (*Thuja plicata*) concentrate calcium and other cations in their foliage creating soil influence zones of low acidity, high base saturation, and rapid decomposition. More generically, uprooting of trees redistributes and mixes soil and results in distinctive mound-and-pit patterns.

Disturbances are like editors—they selectively remove or modify elements of an ecosystem while leaving others intact.

Strong patterns may also exist in distribution of biota, such as forest understory plants. Patterns may be associated with variation in overstory canopy density or activities of animals.

Importance of Legacies to Ecosystem Recovery

Persisting organisms, structures, and patterns can drive the rate and pathway of ecosystem recovery following a disturbance. As defined above, biological legacies can and do contribute both directly and indirectly to restoration of compositional, structural and functional diversity in the post-disturbance ecosystem (7) (Table 2). The abundance and spatial arrangement of survivors may, in fact, be one of "the pivotal factors determining how succession differs between intense disturbances of large and small extent" (6).

Survivors. Surviving organisms and propagules contribute to recovery processes within a disturbed area in several ways. Spore, seed, and seedling banks are generic examples of living biological legacies. When organisms survive and reproduce, they provide in situ inocula, rendering migration to the site unnecessary. Arboreal examples include surviving lodgepole pine (*Pinus contorta*) trees in the Yellowstone fires (6) and beds of true fir and hemlock (*Abies and Tsuga*) seedlings and saplings in snowbanks at Mount St. Helens (2). Sprouting roots and rhizomes of numerous perennial herbaceous species such as fireweed (*Epilobium*) were common at both Yellowstone and Mt. St. Helens.

Observers were surprised by high rates of survival of uprooted, wind-damaged, and even prostrate trees and the rapidity with which foliage cover was reestablished in a simulated hurricane experiment conducted at Harvard Forest (7). Forests affected by catastrophic winds also retain nearly intact understory communities, which often include abundant tree seedlings and saplings that provide for essentially instantaneous forest stand reestablishment. Vegetative survivors also avoid the risky processes of establishment and early growth from seed.

Lifeboating. Structural legacies lifeboat species that would otherwise disappear from a disturbed site by providing critical habitat (e.g., dens and hiding places), substrate (e.g., in the case of epiphytes), and food sources. Standing and down tree boles are excellent examples of such lifeboats in forested ecosystems, as are coral fragments in marine ecosystems. In a less direct manner, structural legacies (both living and dead) also promote survival and reestablishment of organisms by moderating microclimatic conditions in the disturbed area (e.g., shade and reduced temperature extremes) and providing protection from predators.

Living legacies also can play important lifeboating roles. For example, sprouting hardwood shrubs and trees, which recover quickly following a forest disturbance, can sustain important elements of the soil biota, such as the communities of ectomycorrhizal-forming fungi that otherwise might be at risk through loss of their dominant coniferous hosts (10).

Structural Enrichment. Persisting structures (dead and living) substantially increase the structural complexity in post-disturbance ecosystems for decades or even centuries beyond early stages of recovery. In other words, their contributions are not limited to the immediate post-disturbance period. For example, legacies of large, decadent trees, snags, and logs add structural richness to the young forest of uniform, sound trees that typically develops fol-

TABLE 2.

SOME FUNCTIONS OF BIOLOGICAL LEGACIES

- Perpetuation of a genotype or species
- Lifeboating of other species
- Stabilization of ecosystem processes (e.g., hydrologic or nutrient flows)
- Habitat for other organisms
- Modification of environmental conditions
- Source of energy and nutrients
- Influence on spatial pattern of re-colonization

. . .Human-imposed disturbances typically remove much more of the ecosystem, do so more uniformly, and often are repeated at more frequent intervals than natural disturbances.

lowing a stand-replacing disturbance (8,11).

This enhanced structural complexity has practical importance for recovery of species diversity and ecosystem function. Animal species dependent upon large decadent trees or snags are able to re-establish themselves in relatively young stands that have legacies of this type. Otherwise they would wait for decades or even millennia for development of such structures. For example, the presence of large surviving old-growth trees and snags allows northern spotted owls (*Strix occidentalis*) to resume residence in northwestern coniferous forests 60 to 80 years following a catastrophic disturbance, many decades earlier than would be possible without such legacies. Similarly, persistence of large cavity-bearing trees is critical for recovery of many arboreal vertebrates in burned or cutover mountain ash (*Eucalyptus regnans*) forests of southeastern Australia (12).

Patch-size Legacies and Connectivity. Disturbances create important patch-scale legacies at the landscape as well as the stand level because of their heterogeneity (13). The undisturbed or lightly disturbed patches that are part of such a mosaic lifeboat species that require a completely undisturbed patch.

Overall landscape connectivity is improved for many organisms by the combination of stand-level structural legacies, such as logs, and of lightly or undisturbed patches at the landscape level. Stand-level legacies buffer and link undisturbed patches. Ecosystem stocks of energy and materials and functional diversity also are enhanced over a broad range of spatial scales.

Both stand- and landscape-scale legacies also are powerful influences on both the pattern and rate of re-colonization. For example, the legacies provide numerous internal foci or nuclei for ecosystem recovery, negating the need for a slow and incremental process of marginal recruitment. This is particularly important in the case of large disturbances.

Natural vs. Human-caused Disturbances

Many techniques used in natural resource management are purportedly modeled upon natural disturbance regimes. For example, foresters often describe clearcutting as a practice that reproduces the effects of catastrophic wildfire. Unfortunately, such characterizations do not reflect our current understanding of natural disturbances and ecosystem recovery.

Clearly, great contrasts exist between biological legacies left behind by most natural disturbances and those left by such techniques as forest clearcutting, bottom trawling of marine ecosystems, and intensive livestock grazing on natural rangelands. These human-imposed disturbances typically remove much more of the ecosystem, do so more uniformly, and often are repeated at more frequent intervals than are natural disturbances. Consequently, biological legacies left by human disturbances are typically less diverse, less abundant, and exhibit lower levels of spatial heterogeneity than do those associated with most natural disturbances. The low levels of legacies slow or prevent recovery of compositional, structural, and functional diversity in the impacted ecosystem.

Direct human inputs into intensively-managed ecosystems can offset some of the consequences of low levels of biological legacies. For example, we are very effective at re-establishing selected tree species on harvested sites by planting; indeed, humans typically can reforest areas subject to natural catastrophes much more rapidly and thoroughly than can natural processes. Such direct efforts recover some ecosystem di-

TABLE 3.

LEGACY TYPE	FIRE	WIND	CLEARCUT
Snags	Abundant	Few	None
Logs on forest floor	Common	Abundant	Few or none
Soil disturbance	Low	Patchy*	High
Understory community impact	Heavy	Light	Heavy

** Pits and mounds associated with uprooting*

Contrasts in biological legacies among different forest disturbances; the fire is a stand-replacement fire in closed forest (e.g., Yellowstone), wind is a catastrophic windstorm that uproots or breaks most of the dominant or co-dominant trees, and the clearcut follows the classic silvicultural textbook definition, i.e., no wildlife trees or snags are retained.

versity, structure, and function—but typically in a very simplified form.

So, how can we use the concept of biological legacies to develop management regimes with a stronger ecological base? For example, how can we modify silviculture to more closely mimic the conditions associated with natural disturbance regimes? Certainly, the current dominant paradigm in forestry—clearcutting—contrasts markedly with both wildfire and windstorm in types and levels of biological legacies (Table 3).

Greater retention of structures and species during forest harvest is one important way by which timber harvesting can be made to more closely mimic natural disturbance regimes (11). The spectrum of possibilities runs from very low to very high levels of retention—i.e., from a near-clearcut where a few live trees and logs are retained to removal of scattered individual trees from an intact forest (selection). Of course, the selected level of retention depends upon the management objectives adopted by or imposed upon the landowner or managing agency.

A silvicultural prescription for retention forestry has to address the questions of *what, how much*, and *where* legacies are to be left to achieve specific management goals (11). The *what* will often be structural legacies, such as large, decadent trees, snags, and logs on the forest floor. Such structures are difficult or impossible to re-create under intensive timber management. Yet they are critical for lifeboating many organisms and processes and structurally enriching the post-harvest forest. The *what* can also include compositional legacies, such as retention of specific tree or understory species. Retaining contrasting life forms, such as some hardwood trees in a conifer-dominated forest, or a species with unusual capabilities (e.g., hosting nitrogen-fixing bacteria) are examples of compositional and functional legacies.

The question of *how much* is conceptually easy but practically difficult to answer. Obviously, legacies should be retained at levels sufficient to achieve the desired management goals! However, few guides currently exist that quantitatively relate levels of structural retention to levels of ecological function (11). Nonetheless, guidelines are emerging for some types of legacies, such as wildlife trees and woody debris, based upon research and expert opinion.

Where to leave the legacies—the spatial pattern for retention—is an intriguing question, the answer for which is often not as obvious as one might suppose. Under a dispersed approach, structures are uniformly or randomly retained throughout a harvest unit. Spatially concentrating or aggregating the structures typically involves retention of small intact patches of forest within harvest units. Both approaches can, of course, be combined as part of a single silvicultural prescription.

Both dispersed and aggregated retention have specific advantages and applications (11). For example, dispersed retention is most appropriate where ecological objectives require that structures or organisms be well distributed over the entire harvested area to provide organic matter, energy, and root strength for soils or to mitigate microclimatic conditions or hydrological processes.

Aggregated retention generally allows retention of a broader variety of tree species, sizes, and conditions than does dispersed retention, including structures that would likely not sur-

Greater retention of structures and species during forest harvest is one important way to more closely mimic natural disturbance regimes.

vive if left in isolation. Retaining aggregates also provides opportunities to maintain multiple canopy layers, undisturbed understory plant communities and forest floors, and a diversity of snag sizes and conditions. For these reasons, aggregated retention is often favored by biologists focused on lifeboating forest biodiversity (as in the case of the Northwest Forest Plan) while other specialists (e.g., hydrologists and soil scientists) often favor dispersed retention. It is important to remember that the aggregates are not intended to be mini-reserves; rather, they are integral parts of the harvested stand—not apart from it.

Variable retention harvesting is being widely applied by government agencies and private companies throughout the temperate world. For example, any regeneration harvesting on federal forest lands within the range of the northern spotted owl in the northwestern United States must permanently retain a minimum of 15% of the trees, the majority of them in the form of aggregates. In Canada, MacMillan-Bloedel Corporation began a five-year program in 1998 to phase out clearcutting and replace it with variable retention harvesting; Weyerhaeuser Corporation publicly agreed to fulfill this commitment when it purchased MacMillan-Bloedel in 1999. In the Southern Hemisphere, variable retention harvesting is being used in eucalyptus forests of Tasmania and in *Nothofagus* forests of Tierra del Fuego.

Conclusions

The catastrophic events of the Mount St. Helens eruption, the Yellowstone fires and the hurricanes of 1938, 1989, and 1992, among others, have given us important new insights into the great editing processes that we call disturbances. We now recognize much greater complexity and uniqueness in such events and subsequent recovery processes as well as some unifying concepts and themes (6). Applied ecologists (including conservation biologists) and managers of all stripes need to incorporate this new knowledge in their teaching, research, planning, and management.

A. A large blowdown in Mount Hood National Forest, Oregon. The forest floor, shrub, and herb layers, plus seedlings to regenerate the canopy, remain intact.

B. A 90-year-old Douglas-fir stand that regenerated after the 1902 Yacholt Burn in southern Washington. A scattered legacy of large, old-growth trees creates a structurally diverse stand that supports spotted owls.

C. After a wildfire in Yosemite National Park, California. Standing dead trees and down wood are left.

Biological legacies include living and dead trees and down logs left after disturbance. PHOTOGRAPHS BY JERRY FRANKLIN.

Biological legacies—structures, organisms, patterns, and processes—are the threads of continuity linking the pre- and post-disturbance ecosystems. They are critical elements in natural resource management regardless of the ecosystem type or management focus—as relevant to fisheries biologists and wilderness managers as to foresters, and to freshwater and marine ecosystems as to forests and grasslands. The concept of biological legacies can contribute to development of resource management regimes that conserve biological diversity and ecological function while allowing for economic use. The concept is also important as society and managers contemplate responses—such as rehabilitation, salvage, and restoration activities—in areas subjected to major disturbance.

What is the natural disturbance regime of the ecosystem of interest? What are the types, quantities, and spatial patterns of the biological legacies that such a regime leaves behind? What roles do they play in the recovery process? By answering these questions, the manager can begin designing management regimes that will more closely model natural disturbances. At minimum, they will better understand the limitations of intensive management regimes. ❧

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Suggested Readings

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