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Ecological Disturbance and Response: Central Role of Biological Legacies

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ECOSYSTEM DISTURBANCE AND RESPONSE:
CENTRAL ROLE OF BIOLOGICAL LEGACIES

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Introduction

Our understanding of the long-term ecological consequences of ecosystem disturbances has increased dramatically in the last two decades. This expansion in knowledge has been fueled by recent large and intense natural disturbances that have provided scientists with extraordinary opportunities to thoroughly investigate impacts and recovery processes associated with such disturbances. These disturbance events include the Mount St. Helens eruption of 1980 (Franklin et al. 1984; Franklin, Frenzen, and Swanson 1996), Yellowstone forest fires of 1988 (Christensen et al. 1989), and Hurricanes Hugo of 1989 (Walker et al. 1991) and Andrew of 1992 (Pimm et al. 1994). Experiments and long-term observations by scientists at Long Term Ecological Research (LTER) sites have contributed substantially to these investigations.

A repeated lesson from these investigations has been the pervasiveness and importance of surviving organisms and organically-derived structures and patterns in the ecosystem recovery process; i.e., ***biological legacies***. Biological legacies—defined as organisms and organically-derived structures and patterns that remain following disturbances—are not really a new concept. Clements (1916) recognized the importance of surviving organisms naming them, "residuals".

Nevertheless, the importance of this phenomenon seems to have been lost from the consciousness of many ecologists. Most ecological texts and many successional papers focus on migration and re-colonization as the dominant processes in secondary succession. The two classical contrasting models of succession—initial and relay floristics—do not even recognize the concept of residual species. Perhaps the use of old fields as the model ecosystem in many early investigations of secondary succession contributed to the emphasis on ecesis rather than survival in successional studies; old fields typically have much more limited legacies—particularly structural legacies—from preceding ecosystems than do many other secondary seres.

Similarly, applied ecologists, such as foresters and range managers, have rarely considered biological legacies or their significance in sustaining important ecosystem processes and biological diversity. For example, whereas natural disturbances of forests typically generate high levels of structural legacies—such as standing dead trees (snags), logs on the forest floor, and even live trees—classical even-aged forest management regimes, such clearcutting, leave few structural legacies behind.

Biological legacies have emerged as a concept broadly relevant to a wide range of ecosystems—freshwater, inter-tidal, and marine, as well as terrestrial. The nature and importance of biological legacies in understanding disturbances and recovery processes are the subjects of this paper. We focus primarily upon compositional and structural legacies of natural disturbances at the patch level although the legacy concept is clearly applicable at larger spatial scales, as well (e.g., Turner and Dale 1998). We begin by introducing disturbances as editing processes and defining the types and roles of biological legacies. Examples of biological legacies from a broad array of ecosystem and disturbance types are than provided to illustrate the broad relevance of the concept. We conclude by discussing implications of biological legacies for ecological theory and application of legacy principles in resource management. Our goal is to stimulate a broader appreciation of the importance of biological legacies in succession and ecosystem recovery in both theoretical and applied ecology.. Much of this synthesis was developed and supported through the U. S. Long Term Ecological Research Program, including sponsorship of workshops on biological legacies in 1995 and 2000.

Disturbances as Filters

We define disturbances as editing or filtering processes that delete, transform, and add organisms, organically-derived structures, and other non-organic materials and that rearrange the spatial patterns of these elements. In doing so, disturbances create or make resources available; function as energy sources that do work; and create conditions for future disturbances. Many disturbances are abiotic, such as fire, wind, and flood. Biotic disturbances, such as pathogens, are also important and may have the unique attribute of becoming a part of the biological legacy of the disturbance that they perpetrate; i.e., they are incorporated as continuing elements of the ecosystem.

In this paper we focus on disturbances that involve major changes in the state of the ecosystem, have an external source, and are of relatively low frequency and moderate to high intensity.

As editing processes, disturbances typically leave significant elements of the perturbed ecosystem behind. What actually differentiates disturbances, from an ecological perspective, are the transformations that they achieve and the conditions that are created for the new ecosystem—not their type, intensity, or scale. Biota and biologically-generated resources are among the most important of the retained elements. These we refer to as biological legacies.

Biological Legacies Elaborated

Biological legacies are the types of organisms, organic matter (including structures), and organically-created patterns that persist from the pre-disturbance ecosystem and influence recovery and other processes in the post-disturbance ecosystem (Table 1). Also included are the organisms and organic structures moved to the site and deposited by the disturbance. These legacies facilitate the re-organization or recovery process in various ways. Some of these functional roles or modes-of-action of biological legacies (also listed in Table 1) include perpetuation of organisms, provision of refugia for other species ("life boating"), conservation of ecosystem resources ("stabilization"), and provision of habitat for re-colonizing organisms.

The types and functional roles of biological legacies are discussed below. The density and spatial distribution of biological legacies are also critical variables when assessing their potential role in a disturbed ecosystem.

Living Organisms

Living organisms survive disturbances in a variety of forms including as sexually mature or immature individuals, perenating parts (e.g., stem, root, and rhizome segments), and as propagules (e.g., seeds, spores, and resting stages). It is common for all of these forms to be represented following disturbances of terrestrial ecosystems. Indeed, all were observed within one of the most intensely disturbed regions to receive detailed study—the 600 km2 devastated area created by the 1980 lateral blast of Mount St. Helens (Figure 1).

Propagules are probably the most widely recognized form of biological legacies. We include in this category plant seeds, spores of cryptogams and fungi, eggs, and various resting stages of invertebrates and other organisms. Seed banks are an example of a legacy widely recognized by plant ecologists; these may take a variety of forms including the seed banks associated with soils and those associated with persistent reproductive structures, such as serotinous cones.

Survival of higher organisms sometimes takes unexpected forms as in the case of sexually mature trees in areas disturbed by wildfire, windstorms, and volcanic eruptions. In fact, larger trees are more likely to survive a wildfire than small trees because they are more resistant to ground fires (Agee 1993). Complete forest understory communities, including beds of tree seedlings and saplings (*seedling banks*), typically survive standreplacement windstorm events and, if sufficiently dense, may result in continuing tree dominance of the site. For example, dense stands of western hemlock developed from the seedlings and saplings present on the forest floor at the time the mature trees were blown down by a 1921 windstorm on the Olympic Peninsula. Similar seedling-bank legacies of Pacific silver fir and western and mountain hemlocks were present on subalpine forest sites that still retained snowbanks at the time of the 1980 Mount St. Helens eruption and provided replacements for the tree overstories that were destroyed by the blast (Figure _).

Sprouting from rhizomes, roots, and stumps of uprooted or decapitated trees, shrubs, and perennial herbs is another important survival mechanism for many higher plants (Perry et al. 1989). Survival of uprooted and broken trees exceeded 75 % the first year and remained above 40 % after four years in an experimental simulation of a hurricane blowdown (Foster et al. 1997; Foster and Boose 1995). Based in part this research the previously reported effects of the1938 Hurricane in the northeastern United States were reinterpreted as having been as much a consequence of post-hurricane regional salvage logging operations as the original disturbance. Sprouting from roots and rhizomes was an important survival mechanism for herbaceous species in the Mount St. Helens blast zone (Franklin, Frenzen, and Swanson 1996). Rapid recovery of leaf area and ecosystem processes was noted at the Luquillo LTER site following Hurricane Hugo in 1989 (Walker et al. 1991) due to resprouting of damaged canopy trees and accelerated growth of advance regeneration.

Significant animal legacies are characteristic of most natural disturbances although these vary greatly with disturbance type. Animals that are found in soil or sediments or are at least present there at the time of the disturbance are typical legacies. Such vertebrates were unexpected survivors of the Mount St. Helen eruptions. These included fossorial species, such as pocket gophers, as well as other vertebrate species that were below ground at the time of 1980 eruption. Similarly, amphibian species at rest in lake, pond, and stream sediments survived. Invertebrate legacies at Mount St. Helens were typically associated with protected habitats, such as soils and sediments.

Living coral are important elements in coral reef recovery following both natural (e.g., hurricane and typhoon) and human disturbance. For example, patches of less damaged corals assisted in re-population and recovery of more badly damaged adjacent coral reefs following Hurricane Hugo in the U. S. Virgin Islands (Bythell et al. 1993).

Surviving organisms and propagules are the types of biological legacies that have been most widely recognized in the ecological literature. For example, Turner et al. (1998) followed Clements in recognizing and defining "residuals" as the "organisms or propagules that survive a disturbance event".

Organic Matter

Significant organic matter persists through most natural disturbances. The major exceptions would be disturbances that effectively remove or bury all of the soil or sediments as well as the organisms and biological structures that they support. Such disturbances would include some areas affected by landslides and floods and by volcanic events that leave behind unaltered bedrock (e.g., lava flows).

The organic matter legacy may occur in a wide range of sizes, from dissolved to large and persistent, including the structures that will be addressed in the next section. Dissolved and particulate organic matter in freshwater and marine ecosystems and particulate and amorphous organic matter in soils and sediments are examples of organic matter legacies that are primarily of value as sources of energy and nutrients, rather than as structures.

The distinction between some of these materials and organic structures is somewhat arbitrary. Amorphous organic materials may contribute to the creation of structures, such as soil aggregates. Yet other materials, such as the mats of partially decomposed organic matter on the forest floor and feces, may have roles as habitat for invertebrates and other microbial organisms. For example, fecal material has been viewed and studied as a microcosm (e.g., CITATION Ecological Monographs 1943).

Organically-Derived Structures

Some organisms, such as trees and corals, create large structures that survive disturbances, albeit often in altered states. For example, disturbances such as fire and wind transform living trees into standing dead trees (*snags*) and intact and segmented boles (*downed boles*) and other coarse woody debris (CWD) on the forest floor. Such structures may be very large and persistent (see, e.g., Harmon et al. 1986 and Maser et al. 1988). These dead wood structures have diverse and important ecological roles in terrestrial, freshwater, and marine ecosystems, in addition to their value as sources of energy and nutrients. Downed boles and other woody debris can strongly influence geomorphic and hyrdologic processes, such as erosion, sediment deposition, and development of channel or bank morphology. Wood structures provide critical habitat for living organisms in all ecosystems in which they participate—e.g., as substrate, protective cover, nesting sites, and food sources. Downed boles and CWD also ameliorate microclimatic conditions on the disturbed site.

Logs and snags may play significant legacy roles in subsequent disturbance events. Partially decayed logs may survive even intense wildfires in mesic forest types because of their high water storage capacity, thereby serving as refugia for invertebrates, fungi, and other microorganisms. For example, large decayed logs—which averaged 150 % moisture content and survived a stand-destroying wildfire in an old-growth forest in Oregon—contained living mycorrhizal fungi (Amaranthus et al. 1989). Log structures created as a consequence of one disturbance will play significant roles influencing subsequent hydrologic (e.g., flood) and geomorphic (e.g., debris avalanche) events. Similarly, snags created by one fire may contribute to fire spread in subsequent fire events.

Disturbed coral reefs provide a classic example of structural legacies and strong subsequent influences on structure, composition, and recovery processes (Scoffin 1993). Hurricanes (northern hemisphere) and cyclones (southern hemisphere) are typical disturbance events (Woodley et al. 1981, Massel and Done 1993, Hughes 1994). Such disturbances are variable in their spatial intensity and impact with some areas extensively damaged and others relatively undisturbed (Scoffin 1993, Connell et al. 1997).

Structural legacies of rubble from the exoskeletons of dead corals killed by disturbances—as well as structures provided by surviving live corals—are a valuable substrate for subsequent re-colonization (Pearson 1981). Early post-disturbance colonizers include many encrusting organisms, such as some types of algae and sclerosponges that establish on coral plates and branches (Chio and Ginsburg 1983). The structural legacy also provides a range of substrate conditions that influence both the attachment of the coral larvae and the rate of recruitment of new colonies of animals. This was elegantly demonstrated in a long-term study on Heron Island on the Australian Great Barrier Reef (Connell et al. 1997). Variation in levels of legacies remaining after disturbance strongly influences the composition of coral assemblages in Caribbean reef ecosystems (Bythell et al. 1993). Pearson (1981) reviews literature indicating that coral reefs in the Caribbean were able to recover rapidly following Hurricanes Donna and Betsy because, ". . . coral larvae were able to settle on freshly exposed substrata and many broken coral branches remained alive and quickly re-established new colonies."

Other examples of large biologically-derived structures include (Table 1): accumulations of shell fragments; large soil aggregates; termite mounds and nests; and dead animal bodies. As noted, feces can be viewed as structural legacies although they are generally smaller and more transient than the other structures.

Organically-Derived Patterns in Resources

Organisms can create important and persistent patterns in resource availability through their activity (in the case of animals) or by long-term site occupancy (in the case of plants) (Table 1). These patterns often remain following major disturbance events and influence recovery and post-recovery ecosystem processes for decades or even centuries. The scale of the patterns varies widely from that of the individual plant or burrow to much larger scales, such as the scale of brush patches or aspen clones.

Patterns in Soils and Sediments. Long-lived plants, such as trees, can generate distinctive patterns in soil chemical, physical, and microbiological conditions as a result of the chemical and physical properties of the litter that they generate. Many excellent studies have been done that illustrate such effects. For example, distinctive radiating patterns in soil properties have been found with giant sequoias (*Sequoiandendron giganteum*) and other long-lived trees (Zinke 1962; Zinke and Crocker 1962). Comparative studies of soils under adjacent old western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) trees have highly contrasting soil chemical, physical and microbiological properties (Alban 1969; Turner and Franz 1985). Western juniper (*Juniperus occidentalis*) can generate strong spatial patterns in soil properties by concentrating nutrient resources and producing large amounts of organic matter (e.g., Doescher, Eddleman, and Vaitkus 1987). Plant roots and associated mycorrhizal fungi play a key role in binding small soil aggregates into larger aggregates, which, in turn, determine the pore structure of soils thereby influencing aeration, water retention, and rates of nitrogen cycling (Perry et al. 1989, Borchers and Perry 1992).

Trees and shrubs with special functional or physiological attributes are notable for generating distinctive soil patterns. Plants with nitrogen-fixing microbial associates, such as leguminous species and selected other genera, such as alder (*Alnus*) and ceanothus (*Ceanothus*), are important examples. For example, the actinorhizal shrub *Ceanothus cordulatus* generates nitrogen-enriched patches in forests in California's Sierra Nevada; these enriched soil patches persisted following moderate and intense experimental burns (Oakley, North, and Franklin 2003). Species with an affinity for calcium and other cations, such as species belonging to the Cupressaceae and Taxodiaceae (several of which were cited in the previous paragraph) provide another example. Plants that produce and incorporate toxic materials into their litter are yet another category of plants that may generate distinctive persistent patterns in either soil properties or in the composition and/or density of associated vegetation.

Uprooting of large trees creates distinctive patterns in soil properties and seedbeds. One immediate effect is creation of rootwads and pits that gradually devolve into a pit-and-mound micro-topography. The downed boles on the forest floor also can create persistent patterns in seedbed and soil properties. Where nurse logs are an important seedbed, the spatial pattern of downed boles are ultimately reflected in the density and spatial distribution of tree and other plant species within the stand, such as in northwestern North American coastal Sitka spruce-western hemlock forests (McKee, LaRoi and Franklin 1982, Harmon and Franklin 198_). The process of uprooting may, in itself, do important work in mixing soil layers and, in places like southeast Alaska, slowing the process of paludification (Bormann et al. 1995).

Animal activity in both terrestrial and aquatic environments can generate distinct and persistent patterns in environmental conditions, a process sometimes referred to as bioturbation. Development of burrows and similar structures in soils and sediments are one example. Concentrations of large terrestrial animals can generate heavily impacted localities, sometimes known as wallows or yards. Animals in the benthos can also create distinctive and persistent patterns through their feeding processes.

Patterns in Vegetation. Vegetative patterns can persist through disturbances and influence subsequent recovery processes. These patterns may result from a variety of influences including limitations in resources, such as light, the mechanical, biological, or chemical effects of dominant organisms, either plant or animal, and vegetative or asexual propagation of clones or colonies.

In forest ecosystems strong patterning often occurs in composition and density of understory or ground layer plant communities in response to overstory canopy density or other resources, such as soil moisture or nutrients. For example, the understory may be more diverse and well developed under canopy openings (*gaps*) and poorly developed and depauperate under areas with very dense canopy coverage (*anti-gaps*). In many forests much of the post-disturbance recovery is ultimately from surviving plants that were present in the pre-disturbance forest understory (e.g., Halpern and Franklin 1990). Consequently, both gap and anti-gap understory conditions may tend to perpetuate themselves in the next generation of forest; for example, tree regeneration is likely to be most successful (rapid and dense) on sites that lacked competing shrubs or herbs (i.e., anti-gaps) while microsites that had well developed understories will tend to regenerate themselves by propogating vegetatively.

Herbaceous-dominated understory communities found in Western Hemlock Zone old-growth forests of the western Oregon Cascade Range illustrate this phenomenon (Dyrness 1973; Halpern and Franklin 1990). These depauperate understories are associated with a dense overstory of western hemlock and western redcedar. Following logging, trees tend to reproduce abundantly and grow well on sites occupied by this community since competition from herbs and shrubs is minimal. The dense tree overstory then perpetuates a heavily shaded and depauperate understory.

Understory communities dominated by aggressive, sprouting species, such as dwarf bamboos and many other shrubby, herbaceous (especially rhizomatous), and even arboreal species, exemplify another important category of vegetative pattern that often persists through a disturbance to become a part of the recovering ecosystem. As will be noted below, these can play very important roles in stabilizing ecosystem processes and life-boating below-ground biodiversity. They can also slow or prevent re-establishment of tree regeneration.

Roles of Biological Legacies

The biological legacies described above play important roles in influencing patterns and rates of development in the post-disturbance ecosystem (Table 1). Many of these roles are very immediate in terms of their consequences, such as in perpetuating particular species or in stabilizing nutrient and soil resources. However, these influences continue to be consequential long after the disturbance, even through the entire sere and, as noted earlier, throughout subsequent disturbance cycles.

Perpetuating Species and Genotypes. Perpetuating species and genotypes *in situ* is the most obvious consequence of legacies of living organisms and reproductive structures. This makes it unnecessary for these organisms to migrate in from areas outside of the disturbance and that may be very distant. Surviving organisms can begin to generate propagules or progeny as soon as they are sexually mature. This may occur rapidly and in immense quantities as in the case of perennial herbaceous species, such as fireweed (*Epilobium angustifolium*) at Mount St. Helens (Franklin et al. 1985).

Presence of surviving individuals or propagules takes on special significance either when disturbances are very large or the organisms involved have poor dispersal capability or both. Density of propagules typically declines very rapidly with distance from individuals generating the propagules even for species with moderate adaptations for long distance dispersal, as illustrated by the exponential declines in seed density with distance from seed source characteristic for most forest trees. For such species, long-distance dispersal may result in low density re-colonization with further establishment delayed until initial colonizers become sexually mature. Organisms with poor dispersal capabilities may require decades or even centuries to re-colonize sites.

The survival of established plants and mature animals short-circuits the risk-prone establishment or juvenile phase of development. Plants are typically most vulnerable to adverse environmental conditions as germinants or very young seedlings; this is also a period during which high levels of herbivory may occur. Similarly, vertebrate animals are typically most vulnerable during their infancy and youth.

Legacies of living organisms can be as important in perpetuating species in anthropogenic as well as natural disturbances. The suite of forestry practices for regeneration of commercial tree species includes the use of sprouting (coppice forestry), seedling banks (advance regeneration), and seed trees (seed tree and shelterwood harvesting). Legacies of living trees have been found to play important roles in recolonization of disrupted tropical forest lands, such as on abandoned pastureland (Uhl, Buschbacher, and Serrao 1988) and sites cleared and burned for shifting agriculture (e.g., Uhl and Jordan 1984).

Lifeboating Other Species. Structural legacies have a *lifeboating* role that they fulfill by providing refugia for organisms that would otherwise disappear from the site. They do this by providing critical habitat (e.g., dens and hiding cover), substrate (e.g., in the case of epiphytes), and food sources. Structural legacies can also moderate the climatic conditions found on the disturbed area by creating localized areas where environmental conditions are within the tolerance range of survivors and re-colonizing species. An example would be the effect of surviving trees, snags, and down boles in creating shaded microsites with reduced temperature extremes in areas affected by a severe wildfire.

The protective roles of structural legacies are sometimes surprising. For example, piles of jack-strawed boles in windthrown areas make it very difficult for large ungulates to graze on the seedlings and saplings that often survive such events or develop shortly afterward. It is possible to observe this phenomenon is such disparate locations as the temperate rainforests of Sitka spruce (*Picea sitchensis*) and western hemlock on the western Olympic Peninsula in the northwestern United States and the lenga (*Nothofagus pumilio*) forests of Tierra del Fuego (Figure 2), which are inhabitated by the herding ungulates, Roosevelt elk and Guanaco, respectively. These ungulates intensively graze trees, shrubs, and herbs found in the understory of their respective forest habitats. In these forests a more intense blowdown that generates larger amounts of woody debris on the forest floor will favor survival and growth of surviving understory vegetation, including tree seedling banks, by limiting ungulate accessibility.

Species that are lifeboated by structural legacies obviously become *in-situ* sources of inocula increasing propagule density and eliminating the need for long-distance dispersal. However, it may be necessary to lifeboat such organisms for extended periods of time--even decades--for them to be effective as inocula. For example, dominant trees that survive fires, windstorms, and other disturbances often host communities of epiphytic species, including a variety of lichens. Development of suitable new host trees (trees of the appropriate species and crown structure) for these lichens may take many decades (McCune 1993). The potential effectiveness of such refugia for epiphytes is illustrated by studies contrasting forest lichen composition in stands with and without legacies [McCune et al. NEED CITATION]. Similar lifeboating phenomena apparently occur with canopy arthropod communities (Schowalter 1995a, 1995b).

Stabilizing Ecosystem Processes. Biological legacies play important roles in stabilizing ecosystem processes following disturbances such as those associated with nutrient and soil losses. The presence or rapid re-establishment of plant cover from re-sprouting survivors or seedbanks is often essential to preventing significant nutrient or soil loss from intensely perturbed sites as well as to sustain below-ground biological diversity many elements of which depend on a steady flow of high-quality energy from photosynthetic plants. Structural legacies of dead woody root systems can also be critically important in keeping soils on unstable slopes stabilized for a decade or more following a disturbance (Harmon et al. 1986).

Sprouting shrubs and hardwood trees are able to recover quickly following disturbances and play essential roles in sustaining key components of the soil ecosystem, such as mycorrhizal-forming fungi, and in retaining nutrients. Shrubs and small trees belonging to the families Ericaceae and Fagaceae provide excellent examples of plants that can lifeboat mycotrophic fungal species; individuals and patches of such plants often serve as foci for recovery (Perry et al. 1989). Many of these species are usually categorized as pioneers and dominate early in succession, many are present in both early and late successional stages of vegetation development. Some of these species, such as *Ceanothus* and *Prunus*, may maintain themselves in later stages in the form of seedbanks.

The importance of rapid vegetative responses in stabilizing nutrients after disturbance was convincingly illustrated over 35 years ago by an experiment conducted at Hubbard Brook Experimental Forest in New Hampshire (Likens et al. 1970; Likens and Bormann 1995). In this experiment nutrient losses were compared between two clearcut watersheds, on one of which vegetative regrowth was prevented by repeated plant removal. Losses of nutrients, particularly nitrogen, were much greater in the watershed where regrowth was prevented than in the other watershed.

Research conducted over the past 20 years in western North America shows that, depending on species, sprouting hardwoods may stabilize mycorrhizal fungi and other key soil organisms, cleanse soils of pathogens, and maintain soil structure (Perry et al. 1989). For example, soils beneath sprouting hardwoods in Oregon clearcuts had several distinctive chemical and biotic patterns compared to grass-covered soils, including greater mycorrhizal inoculation potential for conifers and far fewer allelopathic actinomycetes (genus *Streptomyces*) (Borchers and Perry 1990); the effect on *Streptomyces* was believed related to the effects of hardwoods on concentrations of manganese, a known inhibitor of streptomycin. Recent work on clearcuts in British Columbia shows that photosynthates flow from sunlit birch to shaded Douglas-fir seedlings through connecting hyphae of mycorrhizal fungi--threads of continuity in quite a literal sense (Simard et al. 1997). Much remains to be learned but the ubiquity of mixed hardwood-conifer forests in the temperate and boreal zones suggest that the stabilizing function of plants with evolved strategies for quick recovery is widespread.

Similar dynamics have been observed in both tropical and temperate forests affected by hurricanes. Rapid resprouting of damaged and broken trees quickly returns the leaf areas of such forests to the approximate level of the pre-disturbance forest (see, e.g., Brokaw and Walker 1991). Researchers at Harvard Forest conducted an experimental simulation of a hurricane by uprooting a large subset of canopy trees in a mature second-growth forest (Foster et al. 1997). Despite the apparent structural disruption of the experimental stand high survival and re-leafing of uprooted and broken trees resulted in tight biotic control over microclimate and such ecosystem processes as trace gas exchanges and nitrogen cycling. Indeed, Foster et al. (1997) conclude that system functions may be disrupted more in the long run by novel disturbances, such as soil warming and chronic nitrogen additions, than by physical disturbances.

Providing Habitat for Re-colonizing Organisms. Structural legacies can be very important in providing habitat needed by organisms that are re-colonizing a disturbed area. This may involve individual species as well as whole classes of organisms are eliminated from intensely disturbed regions. For example, within the Mount St. Helens devastated zone all animal species that occurred exclusively above ground, such as birds and large mammals, were killed (Franklin et al.1985). The abundant snags and downed boles present in this zone provided nesting habitat for mountain bluebirds (which needed snags) and Oregon juncos (which needed downed boles) and allowed their rapid colonization of the area. Structural legacies were also important for re-colonization by spiders and other invertebrates (MacMahon, personal communication).

Some legacies, such as snags and downed boles, may persist and structurally enrich the post-disturbance ecosystem for decades and even centuries with consequences for ecosystem development and biodiversity. Fire and wind disturbances (among others) may kill large numbers of trees but most of the organic matter remains in the form of snags and woody debris (Figure 3). The role of these structures in facilitating colonization by other organisms typically extends well beyond early stages of ecosystem recovery. For example, in northwestern North America catastrophic disturbances will eliminate or displace northern spotted owls from the mature and old-growth forest habitat that is affected. The return of the owl and one of its primary prey species, the northern flying squirrel, depends upon the presence of large snags and live decadent trees. Relatively young coniferous stands with structural legacies of large decadent trees and snags may be suitable nesting habitat for the northern spotted owl after 60 to 80 years whereas young stands lacking such legacies (such as those developed following intensive clearcutting) may remain unsuitable for a century or more.

The mountain ash (*Eucalyptus regnans*) forests found in the Central Highlands of southeastern Australia provide a very profound example of the importance of structural legacies for the survival and persistence of arboreal fauna. Nearly 100 arboreal vertebrates found in these forests, including several species of gliders and possums and many species of parrots and cockatoos, require large cavities or *hollows* (Gibbons and Lindenmayer 1996). Furthermore, the arboreal marsupials are primary prey species for several predators, including the large and wide-ranging Powerful Owl. Cavity-excavating species (e.g., woodpeckers) are absent in these forests so that cavity development depends upon several inter-related processes, i.e., microbial and termite activity coupled with incomplete plant breakage in senescing stems (Gibbons and Lindenmayer 1996). Consequently, cavities take 120 to 400 years to develop and are associated only with very large and old trees (Lindenmayer et al. 1993). The intense wildfires characteristic of the mountain ash forests typically leave behind a legacy of surviving dominant trees as well as an abundance of snags that are a continuing source of nesting and sheltering cavities. In contrast, cavity-dependent fauna are unable to persist in or re-colonize areas that are clearcut and intensely burned for timber management purposes since these areas lack the essential structural legacies (Lindenmayer 1994).

Burrows are another example of a structural legacy that can play important roles in facilitating animal colonization of disturbed regions. For example, at Mount St. Helens gopher burrows provided important refuges for amphibians attempting to disperse through sparsely vegetated areas, such as the debris avalanche; during hot, dry periods that would otherwise be fatal, dispersing individuals find can take cover and survive in burrows.

Structural legacies play comparable important roles in facilitating colonization of disturbed areas and enriching processes in aquatic ecosystems. Coarse woody debris, including tree boles, is an excellent example of structural legacy in streams and rivers (e.g., Harmon et al. 1986; Maser et al. 1988; Naiman et al. 2000). Such structures influence hydrologic processes, influence erosional and depositional processes, and provide habitat, including shaded and protected conditions, for biota. Many disturbance types, most notably floods and associated disturbances, such as debris flows, are particularly important in generating and redistributing wood structures.

The important role of surviving living corals and dead coral structures and fragments in providing substrate for recolonization of other organisms has already been noted.

Modifying Environmental Conditions. In addition to their role as habitat, biological legacies play an important role in facilitating colonization and stabilizing ecosystem processes by modifying environmental conditions. Many disturbances create a very open condition in which the extremes of the local macroclimate, such as in temperature, relative humidity, and wind, would be expected. Legacies of large, dominant plant species, such as trees, as well as large structural legacies, such as snags and downed boles, can significantly moderate environmental extremes by providing shade, moderating radiation fluxes, reducing evaporation, and reducing wind speed. Obviously, persistence or rapid regrowth of shrubs and herbs will also significantly moderate conditions at and below the soil surface as well as for many smaller organisms, such as invertebrates.

Structural legacies may also result in production of unique environmental conditions that did not exist prior to the disturbance. The mounds (initially rootwads) and pits produced by the uprooting of trees are examples of such distinctive environmental niches. The soil mixing and, particularly, shattering of important soil features, such as iron pans can result in important long-term modification of the soil environment (Bormann et al. 1995).

Providing Energy and Nutrients. All types of organic matter are obviously potential sources of energy and nutrients. Living organisms are, of course, potential sources of food for predators of various types (in the case of animals) and herbivores (in the case of plants). They can be very important in allowing survivors and early colonizing organisms of these types to persist within the disturbed area. Dead organic materials are utilized initially by detritivores and decomposer organisms; they eventually become food sources for other organisms and nutrients released through the decay processes become available to colonizing plants or phytoplankton.

Some biological legacies may be very long-term sources of energy and nutrients for the ecosystem. Coarse woody debris (including snags and downed boles) in terrestrial and freshwater ecosystems may persist for decades or even centuries, depending upon the environment, the state of the material (e.g., particulate size), and chemistry of the wood (Harmon et al. 1986).

Influencing Spatial Patterns of Community Development. The spatial pattern of biological legacies can be a powerful influence on spatial arrangements of resources, organisms, and processes in the post-eruption ecosystem. Many examples of this may be obvious to the reader based upon the preceding discussions and we will suggest only a few of the possibilities here.

Ecosystems that exhibit strong spatial patterns in structure or plant composition or both prior to a disturbance are likely to have strong spatial legacies following a disturbance. For example, plants that are form dense concentrations and persist in large numbers, such as sprouting shrubs and herbs, have a high probability of perpetuating similar spatial patterns in the post-disturbance ecosystem.

Structural legacies of downed boles and other woody debris can result in strong and persistent patterns in the composition, structure and function of terrestrial and associated aquatic ecosystems. For example, where downed boles are the primary safe seedbeds for establishment of tree seedlings or saplings (e.g., Harmon and Franklin

198_), the density and spatial arrangement of downed boles will strongly influence the density and spatial arrangement of trees in the post-disturbance stand. As noted earlier, concentrations or "jackpots" of downed boles can protect both pre- and post-disturbance seedlings and saplings of trees and shrubs from large grazing animals, such as elk, deer, and guanaco; strong spatial patterns in density, growth and composition of woody species will result.

Various spatial patterns associated with concentrated animal activity, such as beaver damns and wallows and yards, are additional examples of legacies that have persistent effects on the development of spatial patterns in the composition, structure, and functioning of the post-disturbance ecosystem.

Legacies of pathogens can have some very long-term effects on the spatial evolution of post-disturbance ecosystems. Effects of surviving pathogens will often be observed in patterns of mortality as the host species become reestablished. For example, in forest ecosystems the persistence of root rots (e.g., *Phellinus weirii*) can be observed in the development of centers of host tree mortality that gradually expand outward in a wave-like pattern (CITATIONS). Legacies of dwarf mistletoes, which are parasitic plants found in tree canopies, will similarly begin by infecting new host trees established near surviving mistletoe plants (which of course must be associated with a surviving host tree) (CITATIONS).

Cumulative Effects of Disturbances

In analyzing or predicting the effects of disturbances on biological legacies it is necessary to consider cumulative effects of multiple disturbances of either the same or other types (see, e.g., Paine, Tegner, and Johnson 1998). Different biotic components will be deleted or modified by different types of disturbances (synergisms). Similarly repetitions of the same disturbance type at time intervals shorter than time required for full recovery of ecosystem composition, structure and function can result in progressive depletion of some biological legacies.

Synergisms. Ecosystems are often affected by multiple disturbances of contrasting character. These may be part of a single episode but actually include several different disturbance types. The 1980 eruption of Mount St. Helens exemplifies this situation since it included a blast, a massive landslide, debris flows, glowing avalanches, tephra depositions, and lava extrusion (Franklin, Frenzen, and Swanson 1994). These events, some of which were repeated at short time intervals, interacted in space and time. Coupled with the diversity of pre-disturbance ecosystems and environmental conditions (e.g., presence of snowbanks at some locations) the complexity of disturbance impacts produced a complex spatial mosaic of post-eruptive conditions, including biological legacies. This complexity made the Mount St. Helens extraordinarily valuable as a laboratory for the study of disturbance impacts and recovery (Franklin and MacMahon 2000).

Contrasting disturbances may also occur over time, particularly where there are causal linkages. A common sequential example in many forest ecosystems is one in which outbreaks of bark beetles or defoliators kill large numbers of trees thereby generating high fuel loadings and the potential for an intense wildfire. Another example would be timber harvest followed by intense prescribed burning to eliminate logging slash and create mineral seedbeds. In these examples and similar disturbance sequences, each disturbance event edits out succeeding elements of ecosystem structure, composition, and, consequentially, functional capabilities.

As an example, clearcutting high-elevation forests removes the legacy of standing dead trees that, after wildfires, would have shaded the site and ameliorated climatic extremes. Herbiciding sprouting hardwoods removes a legacy with central importance in stabilizing soil biology, chemistry, and physical structure. Each alone would make conifer recovery more difficult but, together, they may make it impossible (Perry et al. 1989).

Multiple Disturbances. Repetitions of the same type of disturbance at time intervals shorter than time required for full recovery of the ecosystem can result in systematic depletion of biological legacies (as well as the physical resources of the site) and progressive changes in the pathways and rates of ecosystem recovery.

Wildfire repeated at frequent intervals in the Douglas-fir forests of coastal northwestern North America illustrates this phenomenon. While infrequent intense wildfires are characteristic of these forests biological legacies typically include live trees, which subsequently provide seed, as well as abundant snags and downed boles. Tree regeneration after a single burn is often excellent (Hoffman 1917; Isaac 1943; Gray and Franklin 1997). However, the young forest has a significant potential for a second wildfire after 20 to 40 years because of development of dense tree canopies and the presence of large fuel accumulations (i.e., the woody legacies of the initial burn) and snags, which are sites for ignition (lightning strikes) and contribute to fire spread. A second intense fire is likely to kill most young trees as well as the older trees that survived the initial fire reducing the sources of tree seed. Many shrubs and perennial herbs also respond well to the repeated fire by sprouting vigorously and offering intense competition for tree seedlings and protection for animal predators on tree seed and seedlings. Additional wildfires will continue the editing process eventually eliminating most tree reproduction and seed sources and leading to long-term occupancy of forest lands by communities of shrubs and herbs (Figure 4).

Of course, decreased frequency of chronic disturbances can also have significant effects on both the nature of subsequent disturbances and consequent biological legacies. The pine and mixed-conifer forests of western North America illustrate this phenomenon. Frequent, light to moderate intensity wildfires were characteristic of these forests and tended to maintain the forests as open stands with low densities of larger trees and understories dominated by herbs (Agee 1993). Control of wildfires has resulted in modified disturbance regimes including insect outbreaks and intense, stand-replacing fires that result in much reduced legacies of large, old trees.

Implications for Ecology Theory and Application

The concept of biological legacies has important implications for many facets of ecological theory associated with disturbances and ecosystem succession as well as for recognition of some important topical areas needing increased attention.

Influences of Legacies on Paths and Rates of Succession

Sufficient attention clearly has not been given to the role of biological legacies in the early stages of ecosystem recovery following disturbances (as well as later stages of ecosystem development), including effects on composition and structure. As noted earlier, this may be because of the early research focus in secondary succession on old fields, systems with limited organismal and essentially no structural legacies. It also may relate to the focus of much ecological theory on vertebrates, dispersal mechanisms and strategies, and ecesis.

In any case, current theoretical constructs regarding secondary succession fail to explicitly consider biological legacies. This includes the contrasting models of relay and initial floristics and mechanisms hypothesized to affect early succession, such as facilitation and competition. This despite that fact that residuals (legacies of organisms) are often major and even dominant components of many seres, such as those that follow timber harvesting on temperate and subalpine forest sites in northwestern North America (e.g., Halpern and Franklin 1990). It is very clear from the empirical data that are being collected that legacies will typically be primary factors in determining both the pathway and rate of ecosystem recovery.

Internal Points of Stability

Biological legacies provide focal points for re-organization and recovery of the ecosystem within the disturbed area, i.e., internal points of stability within what may be a relatively unstable and environmentally severe landscape. This can occur on a wide range of spatial scales, from a surviving gopher and its burrow system in the Mount St. Helens devastated zone to concentrations of coarse woody debris deposited on a flood plain. While they often provide sources of propagules these foci are at least as important in providing points within the disturbed landscape where various physical processes, such as erosion, are stabilized. Stabilized sites of this type, typically with moderated microclimatic conditions, cover, and food sources, also attract and sustain organisms migrating into the area.

The pattern of recovery in large disturbed areas is typically a process of nucleation rather than a process of gradual development from the margins. Marginal encroachment is the model one might expect for a large, intensively disturbed area such as the devastated zone at Mount St. Helens. In contrast, landscape-level recovery can result largely from the development and coalescence of numerous and distributed focal points (Turner and Dale 1998).

Considerations of Ecosystem Structure

Research on structural legacies and their multiple roles in both the short- and long-term recovery of a disturbed ecosystem is increasing our appreciation of the importance of ecosystem structure in basic and applied ecology. Structural aspects of ecosystems have probably never received an appropriate level of attention from ecologists who have generally focused on organisms and community (e.g., trophic) structure. Yet, it is the structural features of a landscape that are going to determine the types and levels of niches that are available for organisms. If structures are missing, whether as a result of absence of specific life forms or their removal by human or other disturbances, then the organisms requiring those niches and any other organisms or processes dependent upon them are going to be absent from the ecosystem.

We have provided many examples of how structural legacies provide essential functions both in initial phases of recovery (e.g., stabilization and lifeboating) as well as in structurally enriching the post-disturbance ecosystem in the long run (e.g., provision of large snags and downed boles in young and mature forests). Notably these involve systems as diverse as the ocean floor and forests (CITATIONs).

It is important to also note that sometimes it is structure itself that is important with regards to ecosystem processes rather than for some biotic or organic function that it provides. For example, it is the abundant, distributed surface area of a tree canopy that is important in condensing moisture and precipitating particulates from the atmosphere, i.e., its physical architecture and not its biological properties. As another example, it is the physical role of large woody structures that is important in influencing stream hydrology, armoring banks and river bars, and trapping sediments. As a final example, it is the architecture of tree and shrub canopies, live or dead, that is important in providing the structure required by spiders re-colonizing a disturbed region.

Considerations of Soils and Sediments in Ecosystems

Research on biological legacies is contributing to our appreciation of the importance and complexity of soil and sediment ecosystems or subsystems. Of course, ecologists have always known in at least a general sense that the organisms and processes in the substrate are important. However, the difficulty of studying these systems, particularly in non-disruptive ways, has been a significant impediment. Nevertheless, accelerating research during the last several decades has made clear the extraordinary diversity of soils and sediments in terms of organisms, structure (in all senses), and processes.

Mechanisms that sustain belowground ecosystems are an important aspect of biological legacies. The research cited earlier on the role of living plant legacies in lifeboating belowground organisms, such as mycorrhizae-forming fungi, is one example, but far from the only one. The soil ecosystem beneath a healthy plant community is a non-equilibrium system in a classic thermodynamic sense (e.g., Prigogine and Stengers 1984), maintained by large throughputs of metabolic energy from plants. Any widespread plant kill disrupts energy flow and can trigger radical reorganization of the belowground system unless the energy flow is reestablished within some presently unknown time frame (Perry et al. 1989).

Empirical and theoretical considerations of soil ecosystems—such as the preceding—are helping us to fully appreciate the powerful reciprocal relationship that exists between the belowground ecosystem and the photosynthetically active tissues that exist aboveground. What we can see is that the complex and dynamic ecosystem belowground depends as much upon the energy provided by photosynthesis aboveground as the aboveground ecosystem is dependent upon the water, nutrients, and stability provided by the soil. The implications of this reciprocity or interdependence—the need to manage aboveground so as to sustain belowground biodiversity and processes—is really only beginning to be appreciated in such diverse arenas as forest management and assessments of global change.

Implications in Natural Resource Management

Natural disturbance regimes are potential models for the design as well as evaluation of anthropogenic disturbances, including management regimes for natural resources. In fact, many techniques utilized in managing natural resources are purportedly modeled on natural disturbance regimes including those used in forestry, grazing of natural rangelands, and fishing and hunting.

Without debating the original basis of such claims, clearly our understanding of natural disturbances and how they work has been far too limited to provide adequate guidance. We have, for example, focused primarily upon sustained management of target species with limited regard for non-target species and for processes that sustain the ecosystem. Techniques have been developed to sustain high populations of target species (e.g., planting) and to assure their rapid growth (e.g., fertilization) so as to short-circuit natural processes. Moreover, our view of natural disturbances as models for management has not included biological legacies and their multiple roles in sustaining the diversity of processes and organisms.

Forest management provides an excellent example of this paradigm. Foresters frequently characterize regeneration harvest practices, such as clearcutting, as being analogous to such natural disturbances, as wildfire. The focus of such harvesting techniques was regeneration of a uniformly structured (even-aged) stand of a commercially important tree species. Planting was developed as a technique to further insure prompt and complete occupancy of the site by the desired species and even genotype. Other than nutrient capital and substrate, biological legacies are not a significant part of such management systems. Even a very abridged comparison makes clear the contrast in types and levels of legacies between clearcutting and several common natural forest disturbances (Table 2).

Understanding the nature and role of biological legacies provides a sound basis for modifying traditional forest management practices and developing new ones which have improved capabilities for sustaining biological diversity and critical ecosystem processes (e.g., Franklin et al. 1997, Franklin et al. in press). Purposeful retention of structural elements of mature forest stands at the time of harvest exemplifies the legacy lessons that are being increasingly applied in management of natural forests (Franklin et al. 1996). Typically retained structures include large and, especially, decadent trees, large snags, large downed boles, and small undisturbed forest patches (*aggregates*) from the harvested stand (Figure 5). The structures retained are used to sustain biological diversity and ecosystem processes, both above- and belowground. Decisions about the types, quantities, and spatial distribution of biological legacies are presumably based upon the management objectives and priorities for the property. Obviously there is a very broad array of management regimes and harvest (disturbance) intensities.

The concept of biological legacies has potential value in managing other natural resources, as well as assessing the effects of current practices. Grazing lands are often managed to maximize production of herbage, for example, with active efforts to eliminate shrub and tree life forms. The structural diversity represented by these life forms can be very important in maintaining the biological diversity of steppe and desert ecosystems, however. Hence, management regimes that sustain woody plants are important.

Biological legacy concepts are also useful in assessing the effects of current practices. For example, the full environmental consequences of techniques such as intensive trawling of ocean floors, which effectively eliminate structural as well as organismal legacies, can be better understood.

In fact, the principle of biological legacies has broad application in human manipulation of and responses to the natural world. These principles are relevant regardless of whether such manipulation is designed for economic utilization, conservation of biodiversity and natural ecosystems, restoration, or simply as a response to a catastrophe. Biological legacies are also a relevant consideration in assessing and designing responses to global change.

Conclusions

This review represents a significant foray into the topic of biological legacies. In it we have defined biological legacies, provided numerous examples from empirical studies, and identified some of the important roles played by such legacies in the recovery and long-term evolution of ecosystems following catastrophic disturbances.

Much work remains in enriching and systematizing our understanding about legacies of disturbances and their roles. For example, spatial aspects of legacies are in critical need of exploration. Spatial questions seem particularly relevant in the case of large disturbances—questions such as the role of foci for early recovery and the processes by which these nuclei coalesce and overall landscape integrity is restored.

Physical legacies of disturbances are an important topic that we have not considered directly in this review. Some of these, such as legacies of bedrock exposures or lava flows can be recognized indirectly through the absence of biological legacies. Of equal importance is whether the physical legacies include a rootable substrate, such as with a tephra deposition, or an essentially impermeable surface, such as a basalt flow.

We can conclude that the biotic component that remains following a disturbance is critically important in predicting the pathway and rate of subsequent recovery as well as the long-term evolution of the post-disturbance ecosystem. These important biotic components include surviving biota, biotically-generated structures, and biotically-generated patterns in resources.

It is important that we expand and further systematize our understanding of biological continuity in different ecosystems and with different disturbance regimes including, most importantly, those imposed purposefully or accidentally by man. Further, we must incorporate this knowledge into our resource policies and management practices and, most certainly in our assessments of and responses to global change.

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Table 1. Types and ecological functions of biological legacies; allocation of legacies to type categories may be arbitrary since some actually fit in two or more categories (e.g., a downed tree bole or dead animal body are legacies of both organic matter and structure). Numbers following types of legacies refer to the functional role of those legacies. Density and distribution of biological legacies are also important considerations.

Types of Biological Legacies	
Organisms (plant, animal, microbial)	
Whole organisms (sexually mature or immature)	1,2,3,4,5,6,7
Perenating parts (e.g., rhizomes)	1,2,6
Propagules (e.g., seeds, spores, and eggs)	1,6
Organic matter (broad size range: dissolved to large and persistent; primarily concerned with role as energy and nutrient source, not structural role)	
Dissolved and particulate organic matter	4,5,6
Feces	2,4,5,6
Organic Structures (also provide energy and nutrients)	
Snags (standing dead trees)	2,4,5,6,7
Logs (downed tree boles) and other coarse woody debris	2,4,5,6,7
Corals, shells, and fragments	2,4,5,6,7
Large soil aggregates	2,4,5,6,7
Termite mounds, other nests	2,3,4,5,6,7
Dead animal bodies	2,3,4,5,6,7

Beaver dams and residuum of beaver dams	2,3,4,5,6,7

Patterns (plant or animal created)

Root mounds	2,4,5,7
Burrows	4,5,7
Root channels	4,5,7
Soil chemical, microbiological, or physical patterns	7
Forest understory community patterns	7
Feeding patterns in benthos	7
Wallows, yards, and beaver harvest zones (bioturbation)	4,5,7

Functional Roles of Biological Legacies

1. Perpetuating genotype or species on site
2. Lifeboating other species (providing habitat on which they survive)
3. Stabilizing ecosystems (e.g., soils, nutrient pool)
4. Providing habitat for re-colonizing organisms
5. Modifying environmental conditions (e.g., microclimatic amelioration)
6. Supplying energy and nutrients
7. Influencing spatial patterns of community development, including re-colonization

Table 2. Partial comparison of biological legacies associated with four types of disturbances to forest ecosystems: clearcutting, wildfire, windstorm, and insect outbreak.

	Clearcut	Wildfire	Wind Storm	Insect Outbreak
Living dominant trees	None	Variable	Few	Variable
Standing dead trees (snags)	None	Abundant	Variable	Abundant
Logs on forest floors	Few	Some	Abundant	Variable
Seedling bank on forest floor	Removed	Removed	Intact	Intact

Figure 1. Biological legacies, in the form of dead organic structures and living organisms, were abundant in the intensively disturbed 600 km2 blast zone created by the 1980 eruption of Mount St. Helens.

Figure 2. Areas of blown-down tree boles may provide favorable conditions for survival and growth of seedling banks in forest types, such as the *Nothofagus pumilio* forests of Tierra del Fuego, where there are large numbers of grazing animals (guanaco in this case).

Figure 3. Natural disturbances leave high levels of structural legacies that can be utilized by re-colonizing organisms while many human disturbances leave very limited legacies. Legacies of: a) catastrophic wildfire in Yosemite National Park, CA, including large volumes of standing dead trees and logs; b) catastrophic wind storm on the Mt. Hood National Forest, OR, including logs and other organic debris on the forest floor and intact seedling banks; c) scorching at northeastern boundary of the1980 Mount St. Helens (WA) devastated zone; and d) clearcutting on the H. J. Andrews Experimental Forest, OR.

Figure 4. Repeated intense fires at this location have effectively eliminated most living tree and dead wood legacies resulting in dominance of communities of shrubs and herbs that will probably persist for at least 1 to 2 centuries (Yacholt Burn, Gifford Pinchot National Forest, WA).

Figure 5. Typical area harvested using a variable retention cutting prescription, which provides for retention of live trees, snags, and down logs, as well as other legacies (Willamette National Forest, OR).