Natural Processes

Courtesy National Interagency Fire Center

Biological Diversity and Heterogeneity

We had decided to look at an unusual place—an enormous blowdown in the old-growth forest in the Tionesta Scenic Natural Area in western Pennsylvania. Chris Peterson (at that time a graduate student at Rutgers University) and I were visiting Tionesta Scenic Natural Area to see if he would like to conduct the research for his doctoral dissertation there (Fig. 1). I was enthusiastic because it was a rare opportunity to study an intense, natural disturbance in a virgin forest (Peterson and Pickett 1991).

But it might be a tough place to work. It was nearly a day's drive from New Brunswick, and the tornado, estimated to have packed winds in excess of 386 kilometers per hour, had made a jumble of the forest. Many of the largest trees were between 1 and 1.5 meters in diameter and had stood more than 30 meters tall—these were now scattered like pick-up sticks. We had to make our way over the interlocking mass of downed logs; this intermittent, elevated highway of logs was the easiest way to move through the blowdown because the massive crowns of the downed forest giants made a nearly impassible tangle on the surface. The ground surface itself was now punctuated by traps and barriers. Some of the trees were uprooted, and next to the roots were the deep pits from which those roots had been wrenched. If we were lucky, we could see the pits, rather than stepping through a seemingly solid mat of leaves and branches into the soggy hole they covered. Other trees were twisted and broken, and their splintered trunks pointed at the clear blue sky. These snags became our landmarks as we navigated across the 900-meters-wide blowdown (Fig. 2).

In spite of the difficulty of working in the blowdown at Tionesta Scenic Natural Area, Chris agreed that it was a fascinating place, and over the next 7 years we came to understand this stunning place (Peterson and Pickett 1995). The piles of woody debris and leaf litter we poked through during that first visit would prove to be barriers that protected some tree seedlings from hungry deer. The pits would become ringed with ferns and mosses, and many tree seedlings would die on the dry, clayey mounds. Small clusters of American beech sprouts would turn into dense, shady patches where competition would be intense. All of these insights taught us the lesson of Tionesta Scenic Natural Area: the severe tornado of 31 May 1985 set up a patchy template of physical and biological structure, called *environmental heterogeneity*. The heterogeneity interacted with the organisms to determine how the forest would regrow, and the template itself changed with time. That lesson may sound specific to the effects of a tornado in an old-growth forest in western Pennsylvania, but the lesson is general and applies to the entire biological heritage of the United States. The diversity of organisms and of the communities, ecosystems, and landscapes in which they participate is a response to the processes that generate heterogeneity (Wiens 1977; Chesson 1985; Kareiva 1990; Caswell and Cohen 1991; Naeem and Colwell 1991; Tilman 1994). Heterogeneity appears in many guises and is generated by a handful of important ecological processes that operate everywhere in one form or another.

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Fig. 1. The intact old-growth forest at the Tionesta Scenic Natural Area, Pennsylvania. This forest, never cut, is dominated by sugar maple, American beech, eastern hemlock, and several birches.

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Fig. 2. The tornado blowdown at Tionesta Scenic Natural Area one year after its creation. Chris Peterson, now assistant professor of botany at the University of Georgia, stands on the downed and broken trunk of an eastern hemlock.

How Do Organisms Respond to Heterogeneity?

Another excursion into a different forest points to the answer. Beneath the patchy oak canopy of the last remaining primary forest in the New Jersey uplands, a population of spicebushes shows one way organisms can respond to heterogeneity (Pickett and Kempf 1980; Kempf and Pickett 1981). Walking from one bush to another, I find myself first in shade then in a bright patch of sun. I sample the leaves and figure out how much woody structure supports those leaves. The different individual spicebushes show markedly different architectural patterns—one has upright branches, reaching high into sunflecks in the forest. The leaves spiral upward around the erect shoots. But in the shadier spots, the main shoots of the shrubs lean over horizontally, and the leaf bases are twisted so that the broad blades of the dark green leaves are spread out in a plane (Fig. 3). The leaves hardly overlap at all, so there is little self-shading within a single plant, an advantage where the light level is only 1%–5% of that available in the open field next to the forest. The striking difference between spicebushes in the shade and those in brighter patches in the same forest is an example of response to heterogeneity. Differences among organisms match the contrasting environments of different patches.

Several kinds of differences among organisms permit them to respond to natural heterogeneity. Perhaps the most fundamental difference is the genetic variety so common among even individuals of a single population of plants or animals (Futuyma 1986). The genetics of an organism affect its capacity to deal with its environment, and the structure and behavior of an organism depend to some degree on its genetics. The genetic reshuffling between generations, the accumulation of mutations over time, and the natural selection among genetically different individuals are basic mechanisms that generate and reinforce inheritable differences among organisms. Of course, genetic variation itself exists in a variety of forms, ranging from the number of alternative expressions of a single gene (alleles at a locus); to differences in the genetic constitution among individuals within a population; to the division of a population into different breeding subunits; to differences between separate populations; and ultimately to the differences among species.

A given genetic type of organism can exhibit different structure or behavior, depending on its environment. The spicebushes, for example, differed in their architecture of branching and leaf display most likely because of individual flexibility, or *plasticity*, rather than genetic

Contents Article Page

differences between individuals. Although no genetic data are available on spicebush branching, such long-lived individual shrubs are likely to experience years when the canopy above them is thin and other periods when they are in deep shade. Thus, individual flexibility is the key to survival in such situations. In experiments many other organisms have been shown to exhibit genetic differences that relate to differences in environment (for example, Antonovics et al. 1987).

Organisms can also differ from one another in physiology (Bazzaz 1983). For example, the woodland herbs like those that predominate in the intact forest at Tionesta Scenic Natural Area can use low levels of light to manufacture food (Fig. 4), but they cannot tolerate bright light. In fact, full sun for prolonged periods can damage their physiological machinery or can cause them to lose so much water that they may die. In the blowdown at Tionesta Scenic Natural Area, forest herbs that were not protected by the shade of moderate amounts of debris quickly gave way to herbs such as pilewort that need bright light and cannot grow in the closed forest. Contrast in physiological tolerances between organisms of stressed and unstressed environments is common. Tolerance to salt, heavy metals, soil acidity, flooding, drought, and the like are well-known adaptations (Bradshaw and McNeilly 1981).

The timing of events during an organism's life span is another important way it accommodates heterogeneity (Stearns 1976). Contrasts in the life history of organisms appear in the potential length of life, the rate of growth, the time required to reach reproductive maturity, the investment of resources in reproduction, the sizes and number of offspring, and the degree of parental care or provisioning for its offspring. For example, the pilewort in the Tionesta Scenic Natural Area blowdown grows rapidly, matures and reproduces within one year, and produces many small seeds. It is a classic opportunist species that can take advantage of an open site and its resources before slower-growing organisms having lower resource-use rates can take over. Pilewort was shaded out over several years in the blowdown by longer-lived woody plants, some of which may become a part of the future forest canopy.

The most general answer to the question of how do organisms respond to heterogeneity is that they have contrasting capacities to deal with environmental limitations and opportunities. A basic principle of ecology is that organisms have limited amounts of energy that they have accumulated from photosynthesis or from consuming other organisms. They must divide this stored energy among all the functions they must perform, including foraging, growth, reproduction, and defense (Cody 1966; Levins 1968; Tilman 1988). Each organism exhibits a specific way to divide energy among its vital functions, but all organisms face a limit to the amount of stored energy. Each species, or often a subpopulation within a species, represents a different way to solve the universal problem of a limit to the energy that organisms have accumulated. The amount of data required to calculate the stored energy budgets of organisms is immense, but the metaphor that translates this rigorous scientific study into everyday terms is *a jack of all trades is the master of none*. So one key to understanding the processes that govern biological diversity is to appreciate that different organisms vary in their capacities to deal with their environments. Evolution has yielded a diverse array of organisms that differ in their genetic, physiological, and structural means of solving the problem of limited stored energy. What then is the nature of the environmental variety to which this array of organisms responds?

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Fig. 3. A branch of spicebush in the dense shade of a mixed oak forest. Although the leaves are attached to the twig in a spiral fashion, in the shade the leaves adjust to lie in a single plane on the horizontal branches.

Spatial Heterogeneity in the Environment

A walk along a desert hillside is an exercise in contrasts. The rock outcrops at the top of the hill are barren or support only a few shrubs in deep cracks. As I walk down a sunny south-facing slope, the environment changes. Soil appears at the horizontal joints between layers of rock or in potholes (Fig. 5). Deeper pockets of soil support many annuals after the winter rains begin in earnest. The arroyo or streambed at the base of the slope has deep, fine-textured soil and supports many plants; here there are signs of much animal activity. Amid the blooming annuals and the showy perennials in the arroyo, there is the debris of a recent flood. From the riot of wildflowers at the base of the slope, a glance up at the north-facing slope shows a greater number and size of shrubs and denser clumps of flowering herbs in the pockets of soil than on the south-facing slope. Even a small desert watershed shows great environmental heterogeneity (Inouye 1991; Shachak and Brand 1991; Fig. 6).

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Fig. 4. White trout lily. Even though this woodland herb of the eastern deciduous forest is active before the tree canopy leafs out, it has a photosynthetic capacity set to accommodate the 30% reduction in light that even the leafless forest canopy can generate compared with open adjacent sites.

This desert walk has illustrated the nature of the environment. There are physical aspects, such as the soil and rock, the solar radiation, and the rainfall and flooding. There are also biological aspects (Polis 1993), such as the shrubs and herbs, the animals whose presence may only be hinted at by burrows or tracks during a midday walk, the organic matter accumulated beneath the shrubs, and the almost invisible crust on the soil surface, which is composed of bacteria, cyanobacteria (blue-green algae),

Contents Article Page

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Fig. 5. An accumulation of soil in a pothole of a rocky desert outcrop. Runoff from the rocky area upslope of the soil pocket generates sufficient moisture to support a rich annual and perennial herbaceous community in desert areas with low precipitation. Canyonlands National Park, Utah.

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Fig. 6. A rich desert plant community in a stream valley. Such arroyo communities contrast with the relatively bare valley slopes. Canyonlands National Park, Utah.

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Fig. 7. Cryptobiotic crust in Canyonlands National Park. The apparently bare soil in this photograph is actually covered by a crust of microbes and nonvascular plants. Where the crust has been broken by the soil from the small pit, annual plants have established themselves. Soil crust is common in the deserts of the United States.

lichens, or drought-tolerant mosses (Vestal 1993; Fig. 7; also see box on Soils and Cryptobiotic Crusts in Southwest chapter.) These components of the environment are not uniform over space, even in a small desert watershed. For example, there is less solar radiation on a north-facing slope than on a south-facing one. Rainfall is converted to runoff on the bare, rocky areas, while runoff accumulates in the patches of soil just downslope of the rock outcrops; the arroyo experiences high, even catastrophic, water input compared with other sites in the area (Yair and Shachak 1987). Shade, another example of heterogeneity in the desert, is a rare commodity, found only in small patches beneath shrubs. Rodents burrow beneath only some of these shrubs, and ant mounds show a profusion of green around them. In other words, slowing down to look reveals a rich patchwork in both the physical and biological components of the environment (Polis 1993). Any environment shows such heterogeneity.

These features of the environment exhibit patterns through time as well. Over very long periods, even the rock and soil on the slope change, with periods of greater or lesser erosion and deposition. Some ant species move their nests periodically, and the seeds of annuals find more moisture and richer soil in the burrows that rodents abandon. In some extreme years, the deep soil of the arroyo may be eroded by particularly severe floods.

Environmental heterogeneity as illustrated in a desert watershed can be thought of in two complementary ways: as gradients and patches. Moving down from the crest of the divide to the arroyo takes you along an environmental gradient. Overall, soil depth tends to be greater at the base of the slope than at its top. The probability of runoff accumulation varies along the slope as well. On finer spatial scales, gradients may be observed in the soil moisture from the center to the edge of a pocket of soil in the rocky slope.

Gradients exist in all sorts of environments, not just deserts (Vannote et al. 1980; Austin 1985; Peterson and Pickett 1990; Gosz 1991; Keddy 1991). The climate changes up and down a mountainside, the salinity changes up and down a slope in a salt marsh, the air temperature changes from a field to the intact canopy of a forest, the amount of oxygen declines with depth into the water-saturated sediments beneath a stream, and bog community structure changes with moisture (Fig. 8). Some of these gradients are driven by the physical environment, but others are driven or modified by organisms or their activities. For example, the trees and understory plants along the forest edge modify the air temperature in the forest by altering solar radiation and wind input. Likewise, predators may modify the behavior of a prey organism so that, for example, the distribution and effect of deer are reduced, on average, from a forest edge to the center of a large open field.

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Fig. 8. Gradients of flooding frequency, water depth, and depth of the sphagnum moss mat control the composition and structure of vegetation in this Michigan bog. The gradient runs from the open water in the center of the bog through herbaceous, shrubby, and small tree woodlands. A forest grows in the mineral soil surrounding the lake in which the bog has grown on the expanding sphagnum mat.

Organisms are distributed differentially—or grow and survive differentially—along gradients. This pattern is especially clear when the distributions of related species are plotted in space (Austin and Smith 1989). Different species concentrate on contrasting portions of a gradient. Oaks in the eastern United States, for example, achieve dominance at different points along a moisture gradient. From moister to drier sites, ecologists expect to encounter swamp white oak, northern red oak, white oak, black oak, and chestnut oak (Fig. 9).

Animals also respond to gradients. For example, the peak densities of different rodent

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Fig. 9. An idealized distribution of oak along a slope in the northeastern United States. Although there is considerable overlap in the distributions, the peaks indicate that the species responses differ with habitat conditions (Austin and Smith 1989).

species are displaced on habitat gradients in deserts (Rosensweig and Abramsky 1986), and vole populations respond to gradients of plant cover in fields (Adler and Wilson 1989). Another example of animal response is seen in differential distribution of birds along habitat gradients (Able and Noon 1976) or resource gradients (Fleming 1992). Such differential distribution of organisms on gradients demands that the unique assemblages that appear in each kind of habitat be recognized. A hillside apparently uniformly clothed in green may be in fact a subtle array of different species from top to bottom (Milchunas et al. 1989). A given species will not appear in equal abundance throughout the gradient. In fact, depending on the environmental extent of the gradient and the requirements of the species, it may appear on only a small part of the gradient.

As important and informative as gradients are, there is another important way to view environmental heterogeneity—patches. A patch, in contrast to a gradient, has distinct boundaries and can be readily delimited on a map. A pocket of wet soil in a forest, a rock outcrop on a hillside, and a buffalo wallow are all examples of patches. When one hikes in the Pinelands of southern New Jersey, the view is usually of an open forest dominated by pitch pine with perhaps some bear oaks and an understory of leathery-leaved plants, members of the heath family. In spots, however, a group of darker green, spirelike trees will appear through a break in the pine canopy. In only a few meters, the hot, dry air of the pines becomes cool and moist, and the sandy soil blanketed by brittle pine and oak litter is replaced by a spongy carpet of sphagnum. This quick transition is a patch boundary, and the newly encountered shady patch is an Atlantic white-cedar swamp (McCormick 1979; Fig. 10). In this type of patch the delicately serrated leaves of red maple share the light with Atlantic white-cedar; the aromatic leaves of sweetbay trees are dappled in shade beneath them; and on the edges of the stream snaking its way through the Atlantic white-cedars, the tubular leaves of common pitcher-plants and the sticky, glandular leaves of roundleaf sundews await their insect prey (Fig. 11). This quick transition from dry pine forest to moist Atlantic white-cedar swamp illustrates the alternative to gradients as a way to visualize environmental heterogeneity: rapid transitions between contrasting structures or compositions appear on the landscape as patchiness. In the example of the Atlantic white-cedar swamp, a slight slope has brought the water table to the surface, changing the dominant feature of the environment.


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Fig. 10. A stream running through an Atlantic white-cedar swamp in the New Jersey Pinelands. Atlantic white-cedar swamps are the wet end of the soil moisture gradient in the Pinelands.

Patches can also be formed by biological activity. Tall goldenrod, a clonal plant that spreads by means of branching roots, can create a large clump over a few years from a single stem. Other famous patch-forming clonal plants include aspen (Fig. 12) and sumac (for example, smooth sumac). Animals can form patches too,


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Fig. 11. A roundleaf sundew plant. This species is found in open sections of gradients in Atlantic white-cedar swamps and bogs. Hairs on the spatula-shaped leaves exude a sticky substance that traps insects, which the plant then digests. Nitrogen from such insect prey is a critical supplement to the low amounts of nitrogen available in bogs and many swamps.

Contents Article Page

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Fig. 12. A patch of quaking aspen in the Rocky Mountains. Aspen clones can form large, dense patches.

by burrowing, trampling, eating, and other concentrated activities (Brown and Heske 1990; Jones et al. 1994; Fig. 13). Animal-generated patchiness appears as beaver dams, coral reefs, mussel beds on rocky ocean shores, prairie dog towns, and others. Of course, animals respond to patchiness as well as create it, and such responses are key regulators of animal populations (Wiens 1984; Ostfeld 1992).

Settled landscapes are patchy at a scale obvious to even casual observers—the old farm woodlot now surrounded by suburbs, the wetland at the edge of town, the clear-cut on the hillside, or the island isolated by the creation of a reservoir (Fig. 14). So patchiness results from the way that human society, as well as organisms, uses landscapes (Forman 1987).

In part, whether you choose to view a single phenomenon as a patch or as a part of a gradient depends on the spatial scale of the data (Allen and Hoekstra 1991). Both viewpoints are valuable and both highlight the fundamental link between environmental heterogeneity and biological diversity. Biological diversity is a response to environmental heterogeneity (Huston 1994). Heterogeneity presents the opportunity for organisms to use different resources, to be limited by different stresses, to respond to different signals, and to interact with differing combinations of other organisms, including those that facilitate and those that limit survival, growth, behavior, and reproduction (Kolasa and Pickett 1991).

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Fig. 13. Patchiness created by animal activity. The mound is an abandoned ant mound surrounded by a ring of enriched vegetation. The photograph is from the Negev Desert, Israel. Similar effects of ants or of burrowing animals such as woodrats and pocket gophers are found commonly in the United States.

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Fig. 14. A low-elevation aerial photograph of abandoned agricultural lands on the grounds of the Institute of Ecosystem Studies in Dutchess County, New York, reveals how human modification of landscapes also results in patchiness. The lines of trees and shrubs indicate stone walls erected as long ago as two centuries to delineate fields and pastures and to accumulate rocks that frost heaved out of the soil of the fields over winter.

The relation between heterogeneity and biological diversity may indicate a fixed and immutable match between organism and environment, but there is great dynamism in the relation. The dynamics of change in the environment, in the organisms, and in the relation between them is another dimension of heterogeneity that helps govern biological diversity.

Dynamics of Communities and Biological Diversity

In 1958, Murray Buell, Helen Buell, and John Small (all of Rutgers University) set up long-term permanent study plots in old fields that had just been abandoned after 200 years of row crop agriculture (Myster and Pickett 1994; Fig. 15). Ecologists had known for a long time that communities and ecosystems change through time, but most of the studies had been based on comparing similar sites of different ages (Pickett 1989).

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Fig. 15. A farm field in Somerset County, New Jersey. The farm of which this field was a part was used continuously from the early 1700's but was abandoned in 1983. Shown here in 1984, the field has since been added to the holdings of the Hutcheson Memorial Forest Center to help buffer the old-growth forest at the center from encroaching suburban development.

The basic fact of succession was not in doubt when the Buells and Small started their study. Indeed, succession is one of the most widely observed and well-accepted phenomena in the natural world (Miles 1979; West et al. 1981; Glenn-Lewin et al. 1992). Many ecologists had observed reasonably directional changes in a wide variety of communities through time (Barbour and Billings 1988). There was general agreement about the cumulative changes in species composition and community structure on sites capable of maintaining generally moderate soil moisture. In the eastern United States, bare soil was immediately invaded by an assemblage of opportunistic annuals and remnant crop weeds. The site then became dominated by

Contents Article Page


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Fig. 16. A 10-year-old-field at the Hutcheson Memorial Forest Center. The herbaceous vegetation is dominated by asters and goldenrods. The evergreen trees in the field are eastern redcedar, and the broadleaved tree is a flowering dogwood. The wedge of dense, darker-colored vegetation in the upper left of the photograph is part of an adjacent older field, with the crowns of the oaks of the old-growth forest showing slightly above the successional trees.


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Fig. 17. A meander of the Big Muddy River, Illinois. Looking down from Pine Hills this southern Illinois river channel is bounded by a dark green flood plain forest of the sort that would periodically have experienced major disturbance from infrequent floods. The annual floods would not open the stand and therefore would not be counted as a disturbance to the entire forest.

biennials such as asters, short-lived clonal perennials such as goldenrods, shrubs such as sumac, short-lived sun-loving trees such as eastern redcedar (Fig. 16), a red maple woodland and, later (presumably), the mixed oak forests such as those that had blanketed central New Jersey before Europeans cleared the land for agriculture. These trends were clear enough to provide a general understanding of the patterns of succession, and indeed, most of the dynamics of communities throughout the world had been described as a result of comparing sites of different ages to discover the trends through time. For example, the Mediterranean shrublands of the West Coast of the United States change structurally and compositionally following fire, with a conspicuous burst of annuals immediately after the fire. Coniferous forests in Yellowstone National Park after fire yield carpets of brightly flowering fireweed, grasses, and later quaking aspens and, again, the conifers. Hurricanes in New England periodically return the forests to earlier successional stages so that pines precede eastern hemlock and shade-tolerant hardwoods. Floodplain forests are occasionally opened by severe floods to reshuffle the community and allow the emergence of grape vines, poison ivy, and herbs in the understory (Fig. 17). Sand dunes are stabilized by American beachgrass (Fig. 18), which gives way to little bluestem and then to a variety of shrubs and trees such as American holly and beach plum. Even in deserts, small areas opened up by the deaths of shrubs can undergo a cycle of species composition. Ecologists, however, needed to check the assumption that substituting a comparison of spatially distinct, different-aged sites for a study of the changes in a particular site over a long period was valid. In addition they needed to know the details of change from year to year. The only way to satisfy both these requirements was to lay down permanently marked plots and to patiently study them year after year (Pickett 1989; Fig. 19).


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Fig. 18. American beachgrass colonizing the sand dunes of the southern shore of Lake Michigan. This grass species is usually the first perennial plant to establish on the dunes and thus plays a crucial role in stabilizing the dunes. American beachgrass spreads underground to send up nearby shoots.

The permanent plots established by the Buells and Small have confirmed a generally expected succession trend. There have been significant surprises, however: some species that were expected to be abundant hardly made an appearance. For example, little bluestem is present only as scattered individuals in some fields, not as the uniform cover that turns a warm reddish bronze in fall (Fig. 20). Yet some species expected to appear only later in the succession were present, though not obvious, earlier in the process (Pickett 1982). Some oaks, such as black oak, appeared within the first two decades. Herbaceous species that were common early often persisted for very long periods after they declined from prominence in the fields. This was true for even some early dominants such as the annual, common ragweed. These observations have documented that local trends and community structure are probabilistic or chancy. There is some degree of chance in exactly what species appear and become common at a particular spot. Overall, the species in a succession will divide time (as though it represented other environmental resources) and conditions, just as they divide resources and differentially respond to environmental constraints on spatial gradients (Pickett 1976).

The phenomenon of succession, which occurs in virtually every type of known


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Fig. 19. A sampling frame laid down on permanent plot markers. The plot is one of 480 used in the study of old-field succession started in 1958 at the Hutcheson Memorial Forest Center. The photograph was taken in a 33-year-old field that would have looked like the field in Fig. 15 when it was abandoned.

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Fig. 20. Little bluestem in a successional field at the Institute of Ecosystem Studies. This early fall photograph shows the grass beginning to take on the color that gives it its name.

ecosystem, suggests a caution in how we look at the natural world. People seem to have a tendency to view the natural world as static (Johnson 1995). We go to the woods and are impressed by the seeming permanence and stability implied by the massive trees and often by the very quiet and stillness of the air (Fig. 21). We sit at the edge of a waving meadow and remember that every summer we have seen the blossoms of the black-eyed susans and the purple coneflowers nodding in the warm breeze. Or we walk along the rocky seashore and peer into tide pools encrusted with layers of mussels whose armor is tried and tested by the slow-moving sea star. It was like this last year or when we were some idyllic younger age or for as long as we can remember.

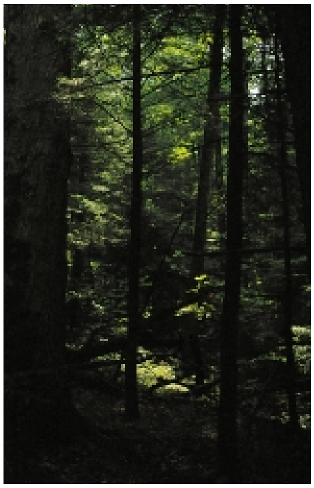

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Fig. 21. A view of the intact forest at Tionesta Scenic Natural Area.

We are tricked into viewing nature as static because so many important natural changes are slow and are not obvious in our personal experience over several decades or at the spatial scales we normally examine. It is also based on our ability to avert our view from the surprising to the familiar. Long-term studies of communities and ecosystems and precise measurement of the status of those ecological systems do not permit us these comforting biases, however. When we are forced to look long and precisely, the apparent permanence of the scene is revealed as illusion (Weatherhead 1986). The persistent scene is painted by many processes, some of which are rapidly changing, while others are slow or only periodic in appearance. Sometimes the length of time we must look has to be extended by analyzing pollen; by carefully digging, as an archaeologist would, for clues buried in the forest floor; by skimming the deeds in Dutch colonial land records; by finding a species residing in a location where conditions for its establishment are now absent; by hoping that a study we start in our middle age will be extended by a younger generation. These techniques have revealed the ubiquitous dynamism of ecological systems (Likens 1989).

Interaction among organisms is also a key to understanding biological diversity (MacArthur 1972; Begon et al. 1990; Huston 1994). Such interactions are sometimes cryptic or invisible without rigorous observation or experiments. As we snoop through a meadow with noses close to the fragrant thatch, the tunnels that voles have sculpted in the grass appear. These rodents, kin to lemmings, do not burrow belowground but rather make roofed runways beneath the grass and litter of meadows and grassy old fields. These green subways conceal the voles from predators. Voles eat the vegetation that they encounter in their runways, sometimes sampling newly emerging woody seedlings, whose stems they clip. A new seedling, too young to have set buds, cannot resprout after being damaged, and so the nipped seedlings die. In fields with moderate to high levels of vole density, the percentage of seedlings killed can be immense (Ostfeld and Canham 1993). Therefore, large vole populations can act as a brake on succession of old fields from dominance by herbaceous species to dominance by woody species; it is an important interaction influencing succession but one that is not obvious.

Not all interactions are detrimental to one or both species. Many interactions in nature are in fact mutually beneficial (Boucher et al. 1984). In many ecosystems where conifers and oaks are important, the roots harbor fungi that do several things (St. John and Coleman 1983; Read 1991). The combination of root and fungus produces a new structure, a joint fungus-root (or *mycorrhiza*, from the Greek). The tree provides carbon-based nutrition, derived from photosynthesis, while the fungus transports mineral nutrients and, in some cases, water to the tree. In particular, mycorrhizae are especially effective in searching out nutrients that do not move very much in the soil and transporting them to the plant root (St. John et al. 1983). Phosphorus is the best example of such an immobile nutrient. The fungi that participate in the complex do two things to supply immobile nutrients to plants. First, they metabolically extract the nutrients from the soil very effectively, and second, the tissues of the fungi extend far out into the soil in the form of microscopic threads. This second feature is hinted at when mycorrhizal roots are dug out of the soil. Often small aggregations of soil particles cling to the roots as a result of the net of fungal threads that hold on to them.

The mutual benefits of plants and mycorrhizal fungi are widespread. In fact, most plants are mycorrhizal, although not all have the same form of fungus; grasses, orchids, heath shrubs, oaks, and pines only begin the long list of plant groups that are mycorrhizal.

Mutualism is the general class of interaction represented by the reciprocal benefit of fungus and plant in mycorrhizae. Mutualisms are major contributors to biological diversity not only because of the obvious benefits that each partner reaps but also because the partners often become specialized to interact. Such specializations can drive diversification among organisms.

Another example of mutualism appears in pollination. Stretched out on my stomach in a grassy field, concentrating on counting herbs for a study of succession, I am interrupted by the loud buzzing of a bumble bee. The bee lands on the flag of a legume flower and deftly opens the two petals that are normally closed over the nectar and reproductive parts of the flower. Only a large insect capable of fine motor control and some learning and that possesses sufficient strength to operate the tricky door to the flower can transfer pollen from flower to flower. Less effective pollinators, such as beetles and flies, that might happily consume the nectar, simply cannot get at it. This mutualism is an example of the kind in which only a certain kind of insect can participate, and the structure of the flower is the key to the restriction (Real 1983; Fig. 22). As with the mycorrhizae, the mutualism is not obvious. The interactions in mutualisms are processes that appear only on close inspection or by using special tools for observation or experiment.

Other interactions take place in the natural world, but not all are as finely targeted as the mutualisms just discussed. In fact, many organisms are involved in some of the most important and widespread processes. An example of a widespread interaction is the phenomenon of decomposition. The decomposition of plant matter—such as the conversion of leaf litter or downed wood—is a key process that depends on organisms most people rarely see (Fig. 23). In a city park woodland, for example, earthworms are especially active in breaking down fallen leaves into smaller bits and mixing them deep into the soil where microbes rapidly turn them into organic matter—that resists further decay—and mineral nitrogen. The litter layer in these city parks is much thinner and more patchy than the litter layer in country forests only a short drive away. Fungi, which are sensitive to pollution and perhaps to the direct disruption of the litter layer in the city, are more active in the country (McDonnell et al. 1993; Pouyat et al. 1994).

What does this difference between the decomposition processes in the city parks and the country forests mean? It is too early to know, but there may be effects on water quality, tree seedling survival, and other organisms that depend on fungi for food. Inconspicuous or hidden processes involving the physical environment and chains of interacting organisms, however, are crucial to the functioning of the world around us. This wisdom has been captured in the concept of the ecosystem (Likens 1992). Organisms exchange nutrients and energy with the physical environment and interact with one another by exchanging nutrients, by transferring energy processed and stored in their tissues, by altering one another's behavior and structure, and by generating by-products and structures that become habitat for other organisms. The interactions are patchy in space and involve soil, air, and water, influencing the flows and quality of these physical components of the world. All these factors are tied together in an ecosystem—a web of processes, fluxes, and interactions. Defining an ecosystem as an interacting community and the physical environment with which it exchanges energy and matter—although correct—needs to be embellished with the reality of actual interactions seen in bumble bees and legumes, earthworms and leaves, bacteria and nitrogen, and rain and soil. The definition of an ecosystem is one of the liveliest in biology, and the interactions in ecosystems are a key to biological diversity (Schulze and Mooney 1993).

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Fig. 22. A dwarf crested iris. The view is directly downward and shows the conspicuous markings that help orient large bumble bees to the flower, which has a structure that they must manipulate in a particular way to retrieve the flower's nectar reward. Red River Gorge, Kentucky.

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Fig. 23. Fruiting bodies of wood-rotting fungus. These mushrooms emerged from an old downed log at Tionesta Scenic Natural Area. Note that one of the mushrooms has been partially eaten, undoubtedly by the mollusk that left the mucus trail on the log just above the damaged mushroom. Recycling of nutrients can sometimes be directly from dead organic matter through fungi to animals.

Disturbance and Episodic Events

The controls on biological diversity discussed previously are not all obvious, but they generally are continuous. Even ecologists have missed or undervalued some key processes, however, because these processes do not act all the time. Periodic natural disturbances and episodic events became widely recognized ingredients in the recipe for biological diversity only in the past two decades (White 1979). Understanding their effect has required that ecologists look at systems over long periods and give up the assumption that the controls on system structure and organism growth and behavior have acted uniformly through time (Pickett and White 1985).

The Impact of Hurricane Andrew on Louisiana's Coastal Landscape

Hurricanes have long affected the Atlantic and gulf coasts of North America. Return times (how frequently a hurricane strikes an area) can average from 5 to 20 years along the northern gulf coast, depending on location. Hurricanes are widely viewed as destructive agents responsible for the loss of human lives and economic disruptions, but their impact on natural ecosystems is poorly known. On 26 August 1992, Hurricane Andrew made landfall along the south-central Louisiana coast with sustained winds of 54 meters per second (about 120 mph) and a storm surge of 1–2 meters, making it one of the more powerful storms to hit the gulf coast in recent memory (Fig. 1).

Coastal Wetlands

Louisiana's coastal marsh ecosystems contain 40% of the coastal wetlands found in the United States and are the result of geomorphic processes linked with the formation and degradation of deltas associated with the Mississippi River (see chapter on Coastal Louisiana). Plant species are distributed along dominant gradients of salinity and elevation, which result in broad zones of saltwater, brackish, and freshwater marsh paralleling the coast. Previous investigations in these coastal marshes have shown intrusion of saltwater, flooding, herbivory, and disturbance as dominant variables controlling plant species richness.

Storms such as Hurricane Andrew are part of the evolution of coastal systems. Hurricanes help form and alter the shapes of coastlines and play a role in maintaining plant species diversity. Fresh and brackish marshes along the Louisiana coast appear structured, in part, by the infrequent and intense salt-intrusion events associated with hurricane storm surges. Coastal wetlands in Louisiana are also increasingly at risk from various natural and human influences. Louisiana leads the nation in wetland loss, averaging some 65.6 square kilometers lost each year. Since the 1930's, the state has lost an estimated 3,950 square kilometers of coastal wetlands; this represents 80% of the nation's total coastal wetland loss. Subsidence, sea-level rise, human activities, and erosion caused by storms have all been implicated in these high rates of loss. A storm such as Andrew can result in a year's worth of loss in a single day.

Fig. 1. Satellite imagery of Hurricane Andrew over the Gulf of Mexico.

Physical damage to coastal wetlands was evident following the passage of Hurricane Andrew. Sediment overwash, ripped and torn marsh, erosion of pond and lake margins, wrack (large amounts of plant debris) deposition, and lateral compression of marshes were common. Substantial sediment deposition was associated with the passage of the storm resulting, in some cases, in the burial of the prestorm surface and smothering vegetation. Extensive areas of marsh were pushed against firm barriers (for example, levees and firmly grounded marsh), resulting in a ridge and trough pattern with ridges 60–200 centimeters higher in elevation than the surrounding marsh surface. Areas of wrack completely buried the vegetation. Freshwater marsh species exposed to water half as saline as seawater (10–15 parts per thousand) were "burned," and the aboveground portions of these plants were killed. In scoured areas, unconsolidated or weakly rooted marsh was eroded.

No sites were without some impact. Sites that received some sediment but not enough to bury the dominant vegetation were least impacted. Hurricane Andrew created a heterogeneous landscape with different disturbance patches juxtaposed in complex configurations. These disturbance patches represented habitats for uncommon and less widely distributed plant species to invade. The relative abundances of species in the different disturbance patches also changed. Differences in vertical elevation (height above the water surface), the amount of organic material, and the amount of new sediment surface created complex gradients of soil moisture, salinity, and nutrient availability.

Marsh Vegetation

Vegetation loss and initial recovery differed in areas with different types of storm damage. At sites where prestorm data were available, one was able to see how Hurricane Andrew caused changes in the composition of the vegetation. In 1991, before the hurricane, 20 species of angiosperms were present at these sites, which were dominated by salt meadow cordgrass and American bulrush. The dominant species were distributed broadly throughout the marsh, with salt meadow cordgrass generally more abundant than American bulrush. Permanent plots sampled in 1991 before the hurricane differed in plant species composition from the same plots sampled in 1992 after the hurricane, and were different still when sampled again in 1993. Total plant cover decreased sharply in all damage categories except compressed marsh sites. The surface of the compressed marsh was elevated, creating drier and nonflooded habitat. Plant cover increased significantly there. There was, however, a shift in species composition from a community dominated by perennial grasses to one dominated by forbs (Fig. 2). Areas smothered by thick sediment deposits were quickly recolonized by short-stature wetland species, such as small spikerush, but later developed a dense plant cover as taller species became established. Plants were very slow to colonize wrack-covered areas because the wrack had to decay or be removed before plants could grow through the debris. Significant numbers of species did not become established until late in 1993. By October 1993, most damage types showed comparable levels of total plant cover except for the wrack sites. Scour areas were generally devoid of vegetation and represent permanent marsh loss. Areas where the aboveground parts of plants suffered from salt burn and died back simply regrew within weeks after the storm.

Individual plant species responded differently to Hurricane Andrew. Coverage of the dominant species showed quite different responses to each disturbance type (Fig. 3). The compressed sites were dominated by salt meadow cordgrass and creeping waterprimrose with only modest amounts of American bulrush. In contrast, wrack areas showed a slow recolonization by salt meadow cordgrass and creeping waterprimrose. Areas of thick sediment showed a strong

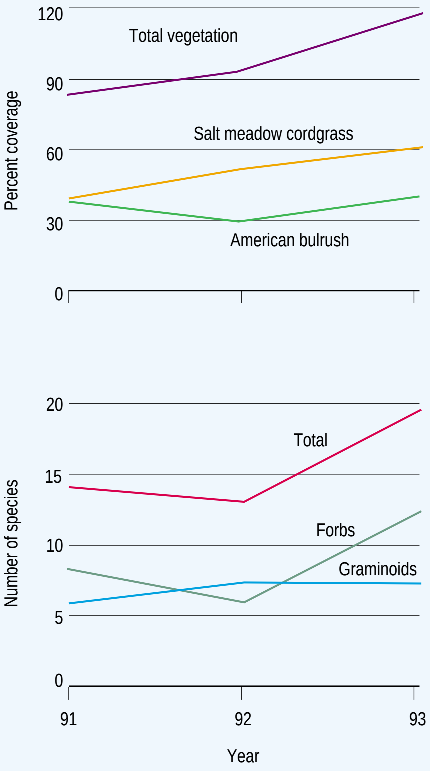

Fig. 2. Data from transects established before Hurricane Andrew at Otter Bayou, Louisiana; these transects were later located in areas of compressed marsh. Data points from 1992 are from after the hurricane. The upper figure presents data for the total percent coverage of vegetation as well as data for salt meadow cordgrass and American bulrush. The lower figure presents data on the total number of species, the number of graminoids (grasses, sedges, and rushes), and the number of species of forbs (other herbaceous species).

recolonization by salt meadow cordgrass, American bulrush, salt marsh camphorweed, and small spikerush. Least-impacted sites were characterized by nearly equal amounts of salt meadow cordgrass and American bulrush, with lesser amounts of salt marsh camphor-weed and creeping waterprimrose. Compressed marsh also provided habitat for terrestrial weeds uncommon in the coastal wetlands, and because the soils were not waterlogged, these sites may ultimately provide habitat for woody shrubs and trees more commonly found on the tops of levees.

Perhaps as important as the habitat heterogeneity created by the storm is the effect on sediment supply to coastal wetlands. Hurricanes represent an important mechanism by which coastal wetlands cut off from normal riverine sediment supplies may receive significant amounts of sediment that might partially offset the effects of coastal subsidence and marsh deterioration. Along much of the Louisiana coast, sediment accretion rates are often insufficient to maintain the elevation of the marsh surface relative to sea level. Although Andrew deposited sediment along large areas of the coast, these accumulations varied. Areas closer to the path of the storm and near a ready supply of sediments accumulated more sediment than areas distant from the track of the storm or from a sediment supply. The thickest sediments ranged from 10 to 16 centimeters and were deposited in marsh areas corresponding to the northeast quadrant of the storm track as it passed near the sediment-rich Atchafalaya River and delta. As the storm passed the delta, the accompanying storm surge mixed these sediments into the water column and deposited them onto the marsh surface. The hurricane-deposited sediments corresponded to a 100%–200% increase over prestorm deposition rates.

Barrier Islands

Andrew's impact was not confined to coastal wetlands. Barrier islands are the outermost land exposed to hurricanes and often lose significant areas of beach and marsh to erosion. Storm waves associated with tropical storms continuously alter the shape and profile of these islands. On some islands, up to 68 meters of beach were lost to erosion and significant overwashing and deposition of sand on back barrier wetlands occurred. Recent photo interpretation has documented that between 1990 and 1992 (after Hurricane Andrew passed near them), the Isle Dernieres barrier chain lost 30% of its land area. This is particularly devastating because over the past 130 years, nearly 78% of the land area in the Isle Dernieres chain had already been lost. Overwash and sand movement also damaged many island plant communities. Because plants on barrier islands are generally adapted to sand movement and salt spray, it is not surprising that despite burial by sand and exposure to saltwater, the vegetation on these islands is recovering. Changes in elevation caused by the movement and accumulation of sand, however, resulted in varying environmental conditions and a redistribution of plant species on the landscape.

Hardwood Forests

Hurricane Andrew diminished in strength after making landfall. The storm, though, passed through the Atchafalaya basin with sufficient force that more than 450 square kilometers of forested wetland were put at risk. This area contains 35% of the remaining bottomland hardwood forest and swamp forest of the Lower Mississippi floodplain. The impact of Hurricane Andrew on this forested landscape varied greatly with forest type, canopy structure, topography, and location relative to the storm's path. Most of the initial loss of tree density and canopy was restricted to bottomland hardwood forest. Stands lost between 10% and 60% of their basal area (the cross sectional-area of their trunks). Willow trees were particularly susceptible to damaging winds and in certain sites more than 85% of them were toppled. Surprisingly, baldcypress and tupelo trees were largely unaffected except for the loss of an occasional branch. The recovery of the forest will depend on the previous forest cover, the type of damage, the specific environmental conditions created, and availability of seeds and seedlings. Understory trees and saplings were unaffected by the hurricane despite the loss of canopy trees. These survivors will grow rapidly because of the removal of the

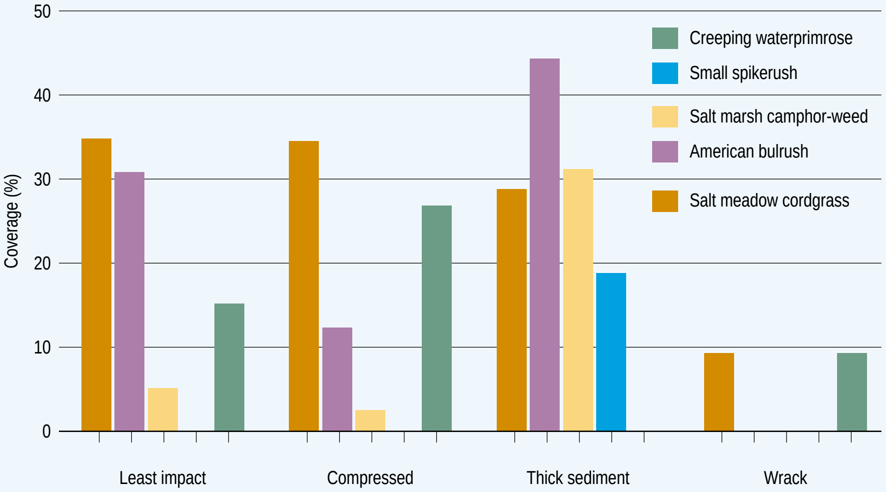

Fig. 3. Data from plots established after Hurricane Andrew struck coastal Louisiana. Species cover in 3 x 3 meter plots varied according to the type of damage sustained. See text for an explanation of categories.

canopy, which shaded them and suppressed their growth. In other cases, seeds and new tree seedlings will become established and form the new forest.

Hurricanes are a major factor affecting coastal ecosystems along the northern Gulf of Mexico. Not only are they responsible for habitat loss, but their frequent landfalls also create a mosaic of different disturbed areas resulting in a heterogeneous landscape. The plant communities that develop in the different patches are dynamic and respond to changing environmental conditions resulting from disturbance. Louisiana's coastal ecosystems are increasingly at risk from human activities. Most climate models predict a period of increased hurricane activity and a tendency toward stronger storms as we approach the new century. Continued research and monitoring are needed to determine the extent to which these ecosystems will become more vulnerable to disturbance from hurricanes.

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When I walk in an old-growth forest on a calm day, absorbed in the soft murmur of the wind in the leaves of the canopy 30 meters above and the quiet chatter of a flock of small birds, it can be a soothing experience for me. It is easy to believe that these oaks and eastern hemlocks, which have stood here for hundreds of years, are virtually eternal and the forest changeless. Suddenly, though, I freeze at the sound of an immense rumble and crash somewhere else in the forest. The reverberation is substantial enough to be felt as much as heard. It is a rare sound in the forest, and worth investigating. It was caused by the fall of a huge, old, hollow oak. The delicately lobed leaves that were exposed to the bright sun just moments before and now lie in partial shade suggest a story. Looking around the forest, I am reminded of the other, older light gaps in which seedlings of birches and red maples reach upward, spring flowers proliferate, and insects swarm. Some of the gaps appeared after violent thunderstorms or the high winds of a hurricane or after an early heavy, wet snow storm that came while the broad-crowned deciduous trees still held their leaves. These events have left downed logs scattered about the old forest floor (Fig. 24). Some of these logs end in the partially filled pits and eroded mounds where the roots were wrenched from the soil (Goodlett 1969; Fig. 25).


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Fig. 25. Wetlands and restoration ecologist Mark Gallagher stands by an upturned root mat of a downed magnolia in a forest on the inner Coastal Plain of New Jersey.

The old forest shows the work of natural disturbance. A disturbance to a community such as a forest is a sudden event, usually driven or started by some outside force that disrupts the community structure and alters the resource levels and environmental conditions at particular spots in the community (White and Pickett 1985). A fire, for example, disrupts the structure of a prairie by burning off the aboveground parts of the grasses, consuming the litter, and perhaps killing any invading trees and shrubs (Collins and Wallace 1990). Light, temperature, and nutrients are all changed by the event, and organisms respond to the changes. The surviving grasses begin to grow earlier in the next season, taking up nutrients deposited in the ash. Grazers may preferentially visit the new growth in the burned patch. Some relatively sedentary insect populations decrease for a time after the fire.


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Fig. 24. A large canopy gap in an old-growth forest in the Great Smoky Mountains National Park. The large, broad-crowned American beech was snapped off by severe winds, suddenly exposing a large area on the forest floor to a highly altered environment.

Ecosystem Recovery Following a Catastrophic Disturbance: Lessons Learned from Mount St. Helens

On 18 May 1980, the eruption of Mount St. Helens volcano removed or leveled 350 square kilometers of old-growth and younger-aged forests and dramatically altered all types of ecosystems within this area (Fig. 1). Before the eruption, this landscape was typical of those found throughout mountainous regions of the Pacific Northwest: dense, temperate coniferous rain forests, with large areas partially modified by timber harvest activity, and sparse alpine vegetation occurring at higher elevations above treeline. Crystal clear lakes and cold, fast-flowing streams were common. In contrast, the eruption created a starkly barren landscape that bore little resemblance to preeruption conditions.

Although the eruption resulted in catastrophic loss of human life, wildlife, and forests, subsequent study of ecosystem recovery has revealed important insights regarding the role of natural disturbance in regulating the productivity and biodiversity of a variety of Northwest ecosystems. The range of disturbance caused by the eruption and the resulting spatial mosaic of disturbance types provided a unique opportunity for ecologists to study how large-scale disturbances influence natural ecosystems.

Volcanism and Western Montane Ecosystems

Within the scale of a single human lifetime, the eruption of Mount St. Helens appears to be an extraordinary and unique event, a disturbance that dramatically altered the local environment but also an event so unusual that it would seem to have little relevance to understanding the “normal” processes that generally shape ecosystems of the Pacific Northwest. Closer inspection, though, has revealed that such eruptions have greatly affected ecosystems throughout the mountainous regions of the Cascade Mountains and the Sierra Nevada. For example, Mount St. Helens has erupted more than 20 times within the last 4,500 years, an average of once every 225 years (Crandall and Mullineaux 1978). Before 1980, Mount St. Helens last erupted 123 years ago. These periods are well within the 500–600 years that it takes to produce an old-growth Douglas-fir forest (Franklin and Hemstrom 1981).

Courtesy R. Emetaz, U.S. Department of Agriculture

Courtesy J. Quiring, U.S. Department of Agriculture

Fig. 1. The landscape from Bear Pass, Mount St. Helens a) before and b) after (1992) the 1980 eruption. The volcano is in the background; Spirit Lake is in the middle of each picture.

Natural Disasters, Biodiversity, and Ecosystem Recovery

The eruption of Mount St. Helens instantly created a large-scale natural experiment that ecologists could use to evaluate theoretical ideas about how entire communities recover from disturbance and the mechanisms most important in recovery. We present some examples of the lessons ecologists have learned by conducting long-term studies of both terrestrial and aquatic ecosystems after the eruption. These examples illustrate situations in which theory accurately predicted observed recovery or in which we learned something fundamentally new.

Terrestrial Vegetation

Ecologists recognize that several mechanisms may act singly or in concert to influence the development of plant assemblages. It is not always clear, though, under what conditions different processes will dominate. The eruption of Mount St. Helens had highly variable effects on vegetation. In general, both initial plant survival and rates of recovery were inversely related to disturbance intensity. It is important to recognize, however, that the dramatic visual differences between pre- and posteruption landscapes were due to the removal or leveling of a few tree species. Vegetation responses differed considerably within two distinct zones of disturbance—the blowdown zone and the pyroclastic flow zone.

In the blowdown zone, overstory trees were either blown down or snapped off, and understory species were buried under as much as a meter of ash. Wind-dispersed herbs, such as fireweeds and composites, colonized the barren surfaces of the blowdown zone during the first year following the eruption. Since then, they have spread by seeds and vegetative growth and dominated many areas within 4 to 7 years (Halpern et al. 1990). In general, this pattern fits classic ecological theory—early successional species colonize and exploit nutrient-poor, disturbed substrates that retain little water.

Not all patterns were this predictable. In several upland areas of the blowdown zone, the recovering plant assemblages are bizarre mixtures of late-successional understory and pioneering species—assemblages we never would have expected to encounter (Halpern et al. 1990; C. M. Crisafulli, U.S. Forest Service, Amboy, Washington, unpublished data). The reasons for these kinds of assemblages are related to the survival of a few late successional species and the colonization of other species. Although our initial inspection suggested that no species survived, some local patches escaped complete destruction. Four factors appeared to increase the probability that individual plants would survive in these locations: (1) patches of late-lying snow shielded some plants from the blast; (2) plants living on the lee sides of ridges were not exposed to the main force of the blast; (3) some plants survived in soils on the exposed rootwads of large blown-down trees; and (4) some plants were able to resprout from perennial root stock on steep slopes where erosion quickly cut through ash deposits (Frenzen and Crisafulli 1990; Halpern et al. 1990).

Of the individuals which survived the initial eruption, some flourished, whereas others perished quickly because of the dramatic change in conditions. Because the overstory that had formerly intercepted nearly all sunlight had been removed, surviving saplings of Pacific silver fir and mountain hemlock previously in the forest understory experienced tremendous growth and were producing cones by 1993. The survival of these few individuals will greatly accelerate the overall recovery process, because seeds will not have to arrive from distant sources beyond the disturbed area. These new conditions, though, created an intolerable stress for other survivors. Shade-adapted understory herbs, such as wintergreen and fawn lily, were unable to tolerate the posteruption conditions of increased light, temperature, and desiccating winds, and soon perished.

In contrast to the slow recovery of upland vegetation, most riparian areas recovered rapidly. Bank erosion quickly re-exposed some buried shrubs and trees such as salmonberry and willow. Fragments of some species—such as willows—were swept downstream of their original locations and then sprouted. Surviving plants quickly produced wind- and water-dispersed seeds that colonized wet shorelines.

Within the pyroclastic flow zone, no individuals survived. Considering the intensity of destruction, classical successional theory predicts a long successional recovery in which mosses, liverworts, and lichens or wind-dispersed herbs establish first, followed by shrubs and then conifers. Which species colonize and when they actually establish are theoretically governed by their dispersal abilities, subsequent alteration of the site by colonizing species, and competition among late-establishing species. Studies conducted on the pumice plain within the pyroclastic flow zone, however, show that this classical pattern of succession has not necessarily happened. Many areas within the pyroclastic flow zone remain sparsely vegetated 15 years after the eruption, and late successional species (5 species of conifers, sword ferns, and lady ferns) have colonized along with wind-dispersed herbs such as fireweed and pearly everlasting (del Moral and Wood 1993; Crisafulli, unpublished data). Still, only two main types of plant assemblages have developed here: willow–herb communities that are restricted to a few springs and seeps, and patches of lupines (C. M. Crisafulli, W. M. Childress, E. Rykiel, Jr., and J. A. MacMahon, Amboy, Washington, unpublished manuscript).

Although the prairie lupine lacks specialized structures for long-distance dispersal, this short-lived perennial herb was among the first species to arrive on the pumice plain and has profoundly influenced the first 15 years of succession (Fig. 2). A few critical attributes appear responsible for its successful establishment. First, lupine has a mutualistic relationship with a root bacteria that fixes nitrogen, and the soils of the pumice plain have extraordinarily low amounts of nitrogen (Halvorson et al. 1991). Second, because this species produces prodigious amounts of seed, populations are spreading at a rapid rate from centers of initial establishment (Crisafulli, Childress, Rykiel, and MacMahon, unpublished manuscript). When these populations are dense and growing vigorously, they inhibit colonization by other species, but once they die, they leave a nutrient-rich substrate where other species can thrive (Morris and Wood 1989).

The establishment of several species of conifers also appeared to defy conventional wisdom. Conifers are poor long-distance dispersers because they have heavy seeds, and they require the presence of symbiotic soil fungi called mycorrhizae to survive. Scientists did not believe that the barren soils of the pumice plain could support these fungi, but the fact that these species arrived and are persisting suggests that we do not fully understand either their dispersal dynamics or the conditions they require to successfully establish.

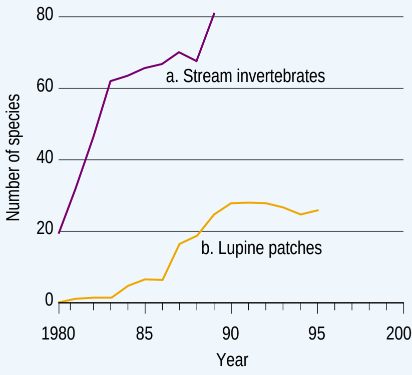

Fig. 2. Changes following the 1980 eruption in a) the number of invertebrate taxa in Clearwater Creek within the blowdown zone, and b) the number of terrestrial plant species within lupine patches of the pyroclastic flow zone.

Birds

Ecologists probably know more about birds than any other group of animals, and many ecologists would predict that two factors strongly influence the development of a bird community: structural complexity of the environment should affect species diversity, and the type and abundance of resources should influence the types of birds occurring in an area. Monitoring over a 12-year period generally confirmed theoretical predictions, although there were a few species-specific surprises. When we consider the natural history of each species, even these surprises were understandable, although not necessarily predictable.

Undisturbed forests in this area have about 15 species of birds. No bird species survived in either the blowdown or pyroclastic flow zones, so recovery of the avifauna in both areas started in the complete absence of birds. The pattern of recovery differed greatly between blowdown and pyroclastic flow zones over a 13-year period (1980–1993; Crisafulli and MacMahon, unpublished data; Fig. 3), an anticipated result considering that the two zones differed greatly in structural complexity following the eruption and recovery rates of vegetation.

The physical environment of the blowdown zone following the eruption was complex but offered few food items for birds. Habitat consisted of tangled trees and their branches embedded in a deep layer of ash and pumice. Little living aboveground vegetation existed. Bird colonization in this zone occurred in two phases. Within a year of the eruption, seven species had colonized (dark-eyed junco, white-crowned sparrow, northern flicker, hairy woodpecker, mountain bluebird, American kestrel, and Vaux's swift); these species are either ground foragers that nest on the ground or in cavities, or species that fly from perches to forage. These birds occur in open landscapes with sparse vegetation, though colonization by Vaux's swift was initially surprising, because it traditionally had been thought to occur in association with mature or old-growth forests (Manuwal 1991). Its establishment suggested that what the swifts require is snag habitat, and not old-growth forest per se.

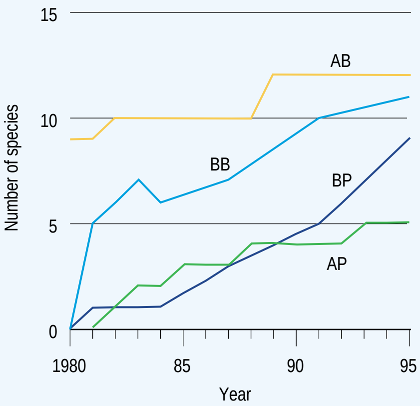

Fig. 3. Changes in number of bird and amphibian species in the blowdown and pyroclastic flow zones following the eruption. AB = amphibians in the blowdown zone, BB = birds in the blowdown zone, BP = birds in the pyroclastic flow zone, and AP = amphibians in the pyroclastic flow zone.

The second recovery phase occurred about 7 years after the eruption and was directly associated with the colonization and expansion of erect, woody vegetation (alder, willow, and cottonwood) along water courses. At this time, an entirely new assemblage of species colonized the blowdown zone, including yellow warblers, orange-crowned warblers, MacGillivray's warblers, willow flycatchers, and warbling vireos. The new species were added to those present rather than replacing them; all these species nest in deciduous shrubs and trees and forage either by gleaning insects from the surface of vegetation or by catching flying insects on the wing. After 15 years, the bird species richness was 70% that of undisturbed forest, but the species composition remains markedly different from the undisturbed forest.

Bird colonization in the pyroclastic flow zone, where no remnants of the preeruption landscape remained, was slower than in the blowdown zone (Fig. 3) and involved different species. This new landscape is stark and open, with undulating pumice hills and complex networks of rills and gullies; it presently supports bird assemblages with only 46% of the species richness of undisturbed forest. The assemblage that developed in this area was not initially anticipated, but its establishment makes sense in hindsight. These species comprised three subgroups, each with strong affinities for completely different habitat types. Red-winged blackbirds and savannah sparrows usually inhabit low-elevation wetlands or pastures; horned larks, rock wrens, and western meadowlarks are associated with shrub-steppe habitats; and gray-crowned rosy-finches and water pipits are normally found in high-elevation, alpine conditions. None of these species are normally found within montane coniferous forests, but the pyroclastic flow zone provided a new set of habitat conditions that mimicked conditions typically found in other locations.

Stream Ecosystems

Until recently, succession in stream ecosystems was thought to occur mainly in response to vegetation changes in the surrounding watersheds and riparian zones, which are known to influence both habitat features in streams and the abundance and type of food available to aquatic animals. Succession caused by competition and predation was thought unimportant since annual floods disturbed streams too frequently for biotic interactions to influence long-term successional dynamics. Research at Mount St. Helens has shown that succession in streams can be a long and ecologically complex phenomenon.

Three months after the eruption, we began an annual monitoring program of several streams in which disturbance varied from complete elimination of living things to a modest reduction in their abundance and diversity (Hawkins 1988). Data from the most severely disturbed streams show that invertebrate species richness increased very rapidly over the first 5 years following the eruption and continued to increase, though at a slower rate, up to 1990, the last year for which data have been compiled (see Anderson 1992; Fig. 2). By 10 years after the eruption, these streams had recovered about 80% of the invertebrate species typically found in an undisturbed stream.

Five species of vertebrates occurred in many of our study streams before the eruption (cutthroat trout, brook trout, shorthead sculpin, tailed frog, and Pacific giant salamander). Although at least a few individuals of most of these species were observed soon after the eruption, recovery of densities varied greatly among species (Fig. 4). In many streams, all of these animals appeared to have been completely extirpated, but within 5 years of the eruption, modest to abundant populations of tailed frog tadpoles and sculpins existed even in heavily disturbed streams. We recorded the highest densities of tailed frog tadpoles and shorthead sculpins ever reported by 4 and 5 years after the eruption (Hawkins et al. 1988; C. P. Hawkins, Utah State University, Logan, unpublished data). In contrast, the recovery of trout and giant salamanders has been slow; 15 years after the eruption, their densities are only 5% to 10% of those observed in undisturbed streams (Hawkins, unpublished data).

We believe the existence of protected refugia was largely responsible for preserving a few individuals in even severely disturbed streams. These refugia appear to be the source of the populations that established later. The eruption occurred in late May when there was still snow cover on some hillslopes and ice on some lakes. At least a few trout are known to have survived in the ice-covered lakes (Crawford 1986) that served as sources of colonists for many streams. Second, we believe that a few sculpins and adult tailed frogs survived in small springs that were also probably snow-covered and topographically shielded from the full force of the eruption.

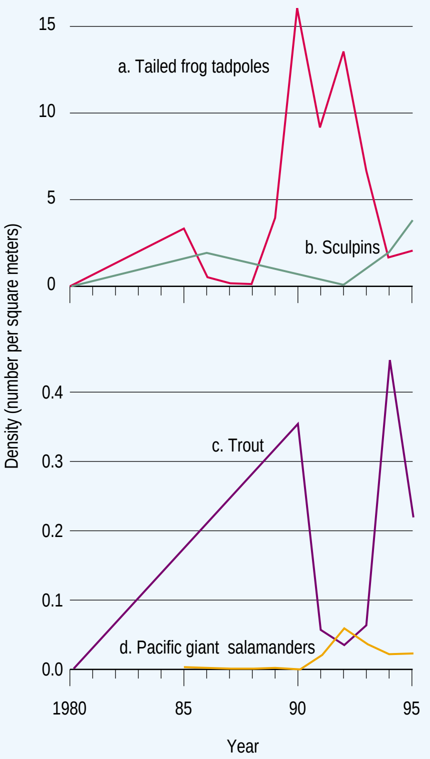

Fig. 4. Changes in densities of a) tadpoles of the tailed frog, b) shorthead sculpin, c) trout (cutthroat trout and brook trout), and d) Pacific giant salamander in heavily disturbed streams in the blowdown zone.

One clear lesson that emerged from these studies was that appearance of the surrounding landscape is not necessarily related to the quality of stream habitat. Although the floodplains and hillslopes surrounding many of these streams were still largely barren, conditions within streams quickly recovered sufficiently to support an abundant and diverse fauna (Hawkins 1988; Anderson 1992). In general, amphibians are thought to be highly sensitive to landscape alterations that affect either adult habitat conditions (temperature, humidity) or the availability of breeding sites. We thought amphibians would have been exterminated by the eruption, but we have found that many species survived and in some cases recovered rapidly (MacMahon 1982; Zalisko and Sites 1989; Crisafulli, Hawkins and MacMahon, unpublished manuscript; Fig. 3).

Aquatic species generally had higher survival rates than terrestrial species, and among aquatic species, pond breeders fared better than stream dwellers. At the time of the eruption, aquatic species were present as both terrestrial adults and aquatic larvae. Because ice, snow, and cold water buffered the aquatic biota in many high-elevation lakes and streams from the impact that devastated neighboring terrestrial environments, some individual animals that were in water or under snow survived (frogs and toads that were hibernating, tadpoles of the tailed frog, and larval and neotenic salamanders). We think these individuals served as a source of colonists to lakes and streams at lower elevations where aquatic biota appeared to have been completely extirpated. Dispersal of colonists therefore appears to have radiated from epicenters of survival within the blast zone rather than from distant, unaffected populations.

One of the most astonishing events that we observed was that four species of frogs and toads and one species of pond-breeding salamander had colonized all available lake habitats within 5 years of the eruption even though absolutely no dispersal corridors existed between lakes. These animals were dispersing great distances over nonforested, barren pumice substrates. Another surprise was that the eruption may have actually created more aquatic habitat than existed before the blast.

In contrast to the aquatic species, three species of salamanders in the family Plethodontidae, which is a largely terrestrial family, seem to have been eliminated from the entire disturbed landscape. The only species of this family to survive was a semiaquatic species. Because all three of the extirpated species are thought to have low mobility and require mesic forest conditions, we expect these species to be absent from this landscape for decades or centuries.

Not only has the eruption of Mount St. Helens provided many insights into the vulnerability of many types of plants, animals, and ecosystems to a catastrophic disturbance, but it has also shown us that many of our ideas about succession and the factors that influence the colonization and establishment of species need refinement. In almost every case in which we were surprised at a response, we had lacked sound information on the basic biological attributes of a species. If nothing else, the study of biotic recovery at Mount St. Helens has convinced us that we must continue to describe, document, and quantify the basic biological features of this nation's flora and fauna.

See end of chapter for references

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The blowdown at Tionesta Scenic Natural Area is another example of a natural disturbance—a particularly large and spectacular one. Similar large disturbances have occurred elsewhere. The famous fires in Yellowstone National Park in 1988 are an example, and the history of that landscape reveals that such fires have been a periodic occurrence (Romme 1982; Turner and Romme 1994). The effects of Hurricane Hugo in 1989 (Walker et al. 1991) and the eruption of Mount St. Helens in 1980 (del Moral 1993; also see box on Mount St. Helens) are also notable examples. Other landscapes, such as the boreal forests of the Boundary Waters Canoe Area Wilderness, the coastal sage shrublands of California, and the Pinelands of Long Island, have a history of periodic fire (Fig. 26). Forests of the Midwest and Southeast are affected by tornadoes, some leaving swaths of downed trees up to 1.6 kilometers wide (Pickett and White 1985).

There are many other kinds of natural disturbances; some are restricted to particular landforms. Flooding reworks the channels in broad, seemingly slow-moving rivers, in small brooks, and in desert arroyos (Fisher et al. 1982). Floods lay down new surfaces, uproot or bury existing plants, and bring new seeds. The animal communities of streams can be severely affected as well, with populations of insect

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Fig. 26. A burned pitch pine resprouting after a fire. Pitch pine is one of the few pine species capable of resprouting from root crown and stem, contributing to its dominance in frequently burned pinelands and barrens in the eastern United States. The other woody species in this community in the New Jersey Pinelands, such as bear oak and the heath species, are also capable of resprouting after fire.

larvae swept downstream and fish displaced (Fig. 27). Landslides and snow avalanches can affect mountainous regions. Sometimes mass movements of soil and rock or of snow can be set off by earthquakes, heavy rains, or by instability in the mass itself. Diseases and herbivorous insects can occasionally open gaps by causing mortality of the largest organisms in a community (Knight 1987; Pacala and Crawley 1992). So the range of events and the variety of sizes of the openings they create in communities are large. Patches of early successional communities, open space, and resource-rich patches often owe their existence to natural disturbance. Thus, disturbance is a widespread, if periodic, source of some of the heterogeneity to which biological diversity is a response (Pickett 1976; Huston 1979).

Disturbance can also be generated as a result of long-standing natural stresses in a community. For example, long periods of drought can ultimately lead to the deaths of many individuals in an ecosystem, create openings in the community, and alter the availability of other resources such as nutrients. The dust bowl of the 1930's is an example of disturbance in a human-managed system triggered in part by extreme climatic fluctuation. Of course, that natural stress would not have had such severe effects without the intense human use of the systems. However, even in unplowed prairie, the extreme droughts of the 1930's had significant ecological effects by changing the proportions of the species in the communities (Weaver and Albertson 1943). Such disturbances can be thought of as diffuse compared with the precise opening of a community by, for example, a lightning strike.

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Fig. 27. A creek in the Inner Bluegrass region of Kentucky. Although calm when this photograph was taken, the stream is subject to intense flooding during the spring freshet and after particularly heavy thunderstorms in summer. Such intense floods scour the channel and greatly alter the community of stream invertebrates. The altered sediment conditions can also affect algae and diatoms that grow on the rock surfaces.

An important characteristic of disturbance remains to be explored here. Disturbances of a particular type have a generally characteristic distribution through time in a specific system and climate. Larger, more intense events (Fig. 28) are less frequent in time, ranging from many centuries to a millennium for huge blowdowns at a spot in eastern forests (Pickett and Thompson 1978; White 1979). In contrast, single tree gaps are formed on average about every 120 years in moist eastern deciduous forests. Large, lasting floods are less frequent than small, temporary spates. Huge crown fires are low-frequency events because of their dependence on high fuel accumulations and extremely dry weather.

The mixture of disturbance types, their characteristics, and their temporal and spatial patterns in a particular landscape and climate, can be defined as a disturbance regime. Disturbance regimes are complex because they have so many aspects. A disturbance regime is characterized by the spatial and temporal distribution of type, size, shape, and temporal frequency of disturbance. The term regime should not be taken to mean that the patterns are rigid. Rather, the patterns are probabilistic—distributed with some unpredictability in time and space. Exactly when a given spot on the ground will experience a disturbance of a certain kind and intensity is somewhat unforeseeable. What is absolutely certain, however, is that such natural disturbances will occur (Bormann and Likens 1979; Denslow 1980; Bazzaz 1983).

The pattern of natural disturbance molds the biological diversity of a region. Plants and

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Fig. 28. A false-color infrared aerial photograph of a portion of the tornado blowdown at the Tionesta Scenic Natural Area, Pennsylvania. This photograph was taken by U.S. Forest Service personnel 2 weeks after the tornado in 1985. The red color indicates intact and healthy plant canopies. Careful examination of the photograph reveals the spiral pattern of downed logs within the blowdown, reflecting the rotary motion of the tornado winds. The tornado began to touch down just to the left of the frame of the photograph.

animals must respond to the disturbance regimes in the areas they inhabit. In fact, the assemblage of organisms in a region reflects the disturbance regime to a large extent (Denslow 1980). A large or permanent change in the disturbance regime is expected to alter the kinds and numbers of organisms in a landscape (Clark 1986). This is one of the key insights of ecology, indicating that biological diversity depends on processes rather than just static conditions (Loucks 1970; Reiners 1983; Walker 1989). In fact, static conditions are rare or nonexistent.

Very severe disturbances can reduce biological diversity. Likewise, disturbances that promote the establishment of invasive exotic species that in turn reduce native biological diversity have a negative influence. Very frequent disturbances tend to reduce the number of species, because few species have the short life span and rapid growth to be able to respond within the intervals between disturbances. Nevertheless, ecologists must understand how disturbance fits with the other ecological factors that affect biological diversity. This view of organisms and the assemblages and ecosystems of which they are a part—responding to ever-changing landscapes—can be summarized as patch dynamics (Pickett and White 1985). The natural world is punctuated by disturbances and other episodic events, creating patches in which environments differ from their surroundings. Different organisms die, leave, survive, or invade at characteristic rates in the opened patches, and the assemblages in those patches change through time, undergoing succession (Whittaker and Levin 1977; Bormann and Likens 1979). Organisms may migrate between patches, exploiting those that match their requirements or offer them shelter from predators and other consumers. Organisms may avoid or be extirpated from those patches that do not satisfy their requirements or where the successional change in the patch moves the environment beyond the range of tolerance of the organisms.

Patchy landscapes can be reflected in the structure of populations. Populations can be subdivided into units that occupy separate patches, and migration among the patches may be an important feature in the persistence of the entire population. Geographically subdivided populations that are connected by migration, either directional or reciprocal, are called metapopulations (Pulliam 1988). Metapopulations can function in several ways (Pulliam 1988; McLaughlin and Roughgarden 1993; Harrison 1994). One mode is for the whole array of patches to serve as a joint, interconnected reservoir of organisms. Alternatively, some of the patches can act as sinks, siphoning individuals from more suitable patches. Finally, there can be a persistent core that supplies satellite populations. Patch dynamics can interact with all of these subdivided population structures. Knowing the nature of patch dynamics and the degree and nature of population subdivision is necessary for successful management or maintenance of biological diversity (Heinselman 1973; Gilbert 1980; McNaughton 1989; Menges 1990).

Homogenization

So far, the processes and patterns in nature that contribute heterogeneity to physical and biological aspects of the environment have been presented. Heterogeneity is the primary ecological filter that enhances biological diversity. The rich history of evolution has generated a diverse array of organisms that can respond to the heterogeneity of the natural world. Many features and behaviors of organisms create additional heterogeneity. But biological diversity is not only the result of processes that generate heterogeneity—homogenizing forces play a role too, but a negative role (Huston 1979; Pickett 1980). Homogenization reduces the number of opportunities for different species to exist in an area, thereby counteracting the generation and maintenance of heterogeneity. To fully understand biological diversity, the relative balance between homogenizing and diversifying forces must be assessed (Huston 1994).

There are natural and human-generated processes that cause homogeneity in nature. The natural force behind homogeneity that has been most often demonstrated by ecologists is competition. Competition is the joint use by two or more organisms of the same resource that is in short supply. If two competitors are unevenly matched, the one that captures the most of the resource in a place and over some interval will "win." The winner will displace the less effective exploiter of the resource. This observation has been generalized as the *competitive exclusion principle* (Hardin 1960; Aarssen 1983; Tilman and Wedin 1991): within an environment that supplies a uniform amount of a limiting resource, two competitors for that resource cannot coexist at equilibrium. There are many ways to state this important principle, but they all involve the assumptions that organisms are not perfectly matched in their competitive relations, that the competitive relations are direct, and that the environment is uniform in resource supply and the environmental factors that affect resource use by the organisms.

The competitive displacements suggested by the competitive exclusion principle are observed in many situations. One compelling example is in succession. The sequence of species reflects a ranking of competitive ability for one or more resources with the more effective competitors becoming important in older communities (Bazzaz 1987). For example, successional turnover can be seen as reflecting different demands for light (Horn et al. 1989). The species that are important early in succession require high levels of light. In turn, the species that become important later in succession can tolerate lower levels of solar radiation. Thus, light becomes, in effect, less limiting to the plants. At the same time, other resources such as nitrogen build up in the soil. Therefore, the identity of the limiting factors shifts through succession, and the changes in species composition reflect the shift because species that are better competitors for light give way to species that are better competitors for nitrogen (Tilman 1988). The physiological, morphological, and architectural trade-offs mentioned in the first section of this chapter (explaining why organisms respond to heterogeneity) underlie the successional and competitive replacements. A species cannot effectively use the contrasting resource levels that appear in early versus late successional communities. Such trade-offs are universal features of organisms and drive competitive displacement.

Another factor that can drive homogenization—under certain specific conditions—is consumption. Predation, herbivory or browsing, and parasitism are three main ways consumption is expressed in nature (Fig. 29). If a consumer tends to use prey indiscriminately, then consumption can reduce diversity because all prey in an area are equally targeted and equally susceptible. In such a situation, all species are reduced in numbers, and the rare ones may be extirpated because they are all consumed, they exist in such low densities that they are unable to find mates, or because unpredictable variations in the environment kill them all.

Some disturbances can reduce biological diversity through homogenizing the environment—for instance, very large or very frequent disturbances. In the case of extremely large disturbances, especially those that are quite intense, environmental conditions can be made uniform over a large area. A relatively few species may find such sites suitable. Likewise, very frequent disturbances can exclude many species that take a long time to grow and mature. The high frequency of disturbances synchronizes an area so that few species match the conditions there.

The processes tending toward homogenization in nature are rarely unopposed (Denslow 1985). The fact that they are counteracted by a variety of physical and biotic interactions is what keeps our world so interesting, diverse, and functioning in a sustainable way. The homogenization that results from monotonous succession, competitive displacement, indiscriminate consumption, or large, frequent disturbances is opposed by a variety of processes. Fine-scale and moderate disturbance (Loucks 1970), differential predation and herbivory on the dominant or most abundant organisms (Petraitis et al. 1989), and the basic variability in the physical environment (Chesson 1985) counteract the tendency toward uniformity. The factors that generate homogeneity and the types and natures of the factors that oppose them are specific to an environment and time. Whether a factor shows up in the homogenizing or in the diversifying side of the ledger depends on the species that are present in the system, the resources available in the system, and possibly the role of humans. Let me give some examples.

The dominant organisms—the ones that give the conspicuous structure to the community—can be struck down in patches by wind and fire or by herbivore outbreaks. American beech, which casts a shade that most other tree species cannot tolerate, is toppled by a severe windstorm after having stood in the canopy for perhaps two centuries. Suppressed saplings of other tree species take advantage of the light, water, and nutrients released in the gap. The dense, aromatic canopy of chaparral shrubs, which has been inhibiting the germination of wildflower seeds, is burned by the first severe fire in as much as 40 years (Fig. 30; also see California chapter). The next growing season, there is a raucous bloom. On a rocky seacoast, a dense, thick bed of mussels is battered and partially removed by a log carried in a storm surf. A variety of algae and sessile invertebrates, which had been excluded from the spot for years, now can attach to the rock and exploit the light or consume the plankton carried in by the tide. Rabbits that had been excluded from a formerly rich grassland are reintroduced, and species not seen for years now prosper and flower. All these types of heterogeneity—and many others—interact so that homogenization is foiled at every turn. The twists, convulsions, and surprises in nature generate opportunity for diversity.


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Fig. 29. A tree felled by beaver, illustrating plant consumption, a factor that can drive homogenization.


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Fig. 30. Recently burned chaparral in southern California.

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Fig. 31. Plumed seeds of little bluestem. These seeds are awaiting dispersal by the wind, a biotic factor that can contribute to heterogeneity. Although the seeds are light and copiously plumed, most of them fall within a few meters of the plant that produced them.

Other biotic factors can contribute to heterogeneity as well. Dispersal might be thought of as a uniform, unrestricted phenomenon in nature. However, the patchiness that results from gravity, from the narrow focus of dispersing animals, or from the vagaries of wind and water flow, means that few organisms are distributed evenly in nature. For example, fish larvae, although microscopic and buoyant, can be captured in eddies, or the light, plumed seeds of many plants can be blown away in a single concentrated gust (Fig. 31). In short, dispersal is a chancy and nonuniform business in nature (McLaughlin and Roughgarden 1993).

But there is another source of homogeneity that is, in many cases, as strong or stronger than the ability of nature to generate variety. Human sources of homogeneity are many and pervasive (Goudie 1990). They include novel disturbances and stresses, alterations of natural disturbance regimes, and changes in the structure of landscapes, among others. They work on many scales, as well, from the global to the backyard.

Consider the backyard: the unbroken neighborhood lawn, one of the unique contributions of American landscape architecture and regional planning, is a potent force for homogeneity. The ideal lawn has been viewed as one comprising one or a few species—often Kentucky bluegrass—maintained at great investment of cost, energy, and chemicals (Bormann et al. 1993). The lawn may be bordered by a small number of evergreen shrubs, either cultivated varieties of natives or, more likely, exotic species. Perhaps in spring, bulbs of plants bred from ancestors in the Middle East—tulips and daffodils—will appear. But most of the growing season, there is an unremitting carpet of uniform green. Looking up the street, we shift to a coarser scale but still see a landscape of a homogeneous grid of blocks that disregards natural topography and hydrology (Fig. 32). Modifying the grid into sweeping suburban curves and quiet cul-de-sacs is no more biologically heterogeneous than the ancestral grid inherited from the Roman Empire.

Other examples of human homogenization abound (McDonnell and Pickett 1993). Parks bristle with tree species from Europe and Asia, resound with the songs of exotic birds, and burble with fountains supplied from reservoirs hundreds of miles away. Our farm fields grow perhaps one or two of the handful of cultivated species that feed most of the people on Earth, and they are laid out in huge uniform rectangles convenient to mammoth plows and combines. The hedgerows (Fig. 33), which may have harbored native plants and animals, have retreated to the house, where they persist as islands of shrubs and ornamentals in which domestic cats stalk and a mongrel dog lounges. Hilltops are shorn off to make way for houses and so reduce topographic heterogeneity, while interstate highways shrink the distances between ecologically different climatic regions. And indeed, in many places, the homogeneous farm fields give way to even more homogeneous parking lots for malls. Large clear-cuts are cleaned up so they look nothing like the regrowing biotic jumble at Tionesta Scenic Natural Area, and they are filled from the top to the bottom of their slopes with seedlings of the same tree species. The annual pulse of streams—rising in spring and falling in summer, with variation from year to year—is smoothed out to provide reliable navigation, water supply, and electrical power. Landscapes are manicured to maintain the same view year after year.

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Fig. 32. A portion of the city of Poughkeepsie, New York. The regular grid has cut through hills and obliterated the valley of a small tributary to the Hudson River.

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Fig. 33. A hedgerow bordering a farm field in central Illinois. Agglomeration of family farms into larger units often is associated with the removal of hedgerows, which are corridors for the movement of wildlife and habitat for a variety of species. Hedgerows can also affect the flows of nutrients and water in landscapes.

The lesson is clear. Industrial agriculture and forestry, uniform town planning, accidental or intentional transport of species, provision of energy, and expansion of the land base for housing are all homogenizing influences. Of course, all the services and amenities that these homogenizing processes generate are widely desired.

Biological diversity is a net outcome of processes favoring heterogeneity and processes favoring homogeneity (Pickett 1980; Huston 1994). Much of what humans do, either intentionally or accidentally, shifts the balance toward homogeneity and thus decreases biological diversity. Biological diversity is a nonrenewable natural resource in the short term of human resource exploitation. Can human activities enhance or preserve heterogeneity? Can human land uses mimic better the heterogeneity that is such a key part of the natural world? Can development plans become more appropriately *patchy*? These questions emerge from the ecological understanding of the natural processes that determine biological diversity.

Research Needs

Understanding the natural processes maintaining the biological diversity of the United States may at first glance seem to require little additional work. The scientific literature provides a good basis for the overall picture of diversity as a net response to the processes generating heterogeneity on the one hand and those that reduce the crucial heterogeneity of the environment on the other. There is, however, need for much better knowledge about the subject of biological diversity itself, the processes affecting it, and the relation between the two (Pickett et al. 1994).

The most basic research need is to deepen the understanding of the biological diversity of the United States. I have taken the evolutionary richness of biological diversity as a given, but the biological diversity we see today is, in fact, a part of an ongoing evolutionary process. The ecological understanding summarized in this chapter rests on where the biological diversity has originated and how it has changed in time and space. The knowledge of evolutionary relations, geographic patterns, and the physical, chemical, and behavioral characteristics of organisms is the very foundation for conservation and use of the wild living resources of the United States. Improving the understanding of the basic raw material of biological diversity will require sustained research into the systematics of organisms. The needs are particularly pressing for taxonomic groups for which experts are few or collections of specimens are sporadic. Even in the case of well-known groups, the collections must be well-maintained in museums and herbaria and the catalogs made available to digital networks. Thus, a priority for best understanding the natural processes underpinning biological diversity is the health of modern biosystematic research and curation of specimens.

A second major need is the better use of quantitative data in understanding the patterns and changes in biological diversity in the United States. Quantitative measurement of the heterogeneity of the environment needs to be more extensive and must involve a greater variety of spatial scales. For example, how regional and local processes interact in determining the biological diversity of particular areas is still an open question for most taxonomic groups and sites. In addition, measurements of the characteristics of biological diversity must be made both in areas that are relatively pristine and in those that have been extensively modified by humanity. Measurements in a broad array of situations will allow the relations between various amounts of spatial heterogeneity and biological diversity to be statistically evaluated. Examining situations in which homogenizing processes are also at work to varying degrees is necessary to complete the quantitative models suggested by the overview presented here. In particular, the agents, intensities, frequencies, and spatial extents of natural disturbance regimes and their modifications by humans need to be measured. Infrequent events and episodic processes require special focus because they are likely to be missed by short-term or casual observation.

A range of reference sites and situations for biological diversity must be amassed. The array of sites must include not only those of unusual composition and aesthetic merit but also representatives of more common assemblages and ecosystems. These are needed to assess intentional and unintentional changes in biological diversity caused by human activities; they are also needed to inform realistic goals for restoration and management. Existing sites that have suffered relatively less from human effects as well as historical reference sites whose past environmental controls can be determined are required. Historical and paleoecological analyses are both required for successful establishment of benchmark natural systems.

Biological diversity exists in both a naturally and a human-generated changing environmental context. Natural climate change has been a major control of biological diversity, albeit with the flexibility allowed by evolution and migration. Therefore, the climate changes predicted as a result of human-generated changes are a special concern for the future of biological diversity. Long-term ecological studies, retrospective studies, and intelligent monitoring are all required to document the changes in the systems and to determine what the causes may be. To begin to determine causes of changes in biological diversity in particular areas, small-scale experiments and concomitant measurements of environmental resources, stresses, and disturbances must be made.

It is clear that biological diversity and ecosystem and landscape function are related, because the elements of biological diversity are the elements that compose these other kinds of ecological systems. There is, however, an urgent need to quantify the linkages between biological diversity and functional attributes of various ecological systems and to conduct experiments on the relationships. In the past, biological diversity and ecosystem research have intersected rather little, given the importance of the linkage.

The Flux of Nature

I have presented an overview of the key ecological processes that maintain biological diversity by generating natural heterogeneity. I close with two images of modern ecology to summarize these processes. One is of a simple graph showing how biological diversity is the outcome of the opposing processes that generate heterogeneity and homogeneity (Fig. 34). Throughout nearly the entire history of the Earth, that battle has been fought without a human referee. Even when humans were part of the game, until the invention of hydraulic agriculture or the massive use of fire, the ecological game swirled about them, little perturbed by their presence. Now humans are referees and coaches, seeming to favor the processes that foster homogeneity (Turner et al. 1990). Some of this is inevitable and desirable, while some of it is avoidable and perhaps even unnecessary. These issues deserve careful consideration in the public sphere. The science is clear: biological diversity is part of the machinery of this planet (Wilson 1992). It is the result of a trade-off between factors that promote heterogeneity and factors that promote homogeneity; the natural world is overwhelmingly heterogeneous. When the mix of homogenization and "heterogenization" is altered, biological diversity is altered. The awkward word in the previous sentence has a point: there is no readily available, simple, and familiar term for the process of creating heterogeneity. Heterogenization—or some better, simpler term capturing this idea—needs to be a part of our everyday language if we are to better deal with our national heritage of natural biological diversity.

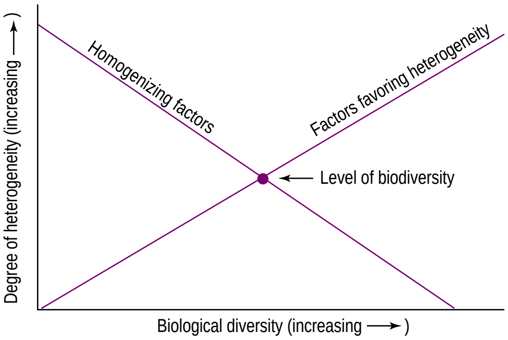

Fig. 34. A conceptual model indicating the opposing influence on biological diversity of factors that generate heterogeneity and those that generate homogeneity. The level of biological diversity is a net result of the factors that make opportunities available for different species, as opposed to those that remove opportunities. The introduction of aggressive exotic competitors that are more generalized and can preempt the place of more specialized or limited native species or the introduction of disease or consumer organisms that directly remove the native species from the systems because of deaths can cause additional deficits in diversity beyond those reflecting loss of heterogeneity.

The second image that emerges from the insights reviewed in this chapter is the one of the natural world as dynamic. Successions wax and wane; natural disturbances punctuate the lives of organisms and the structures of communities, ecosystems, and landscapes; and climate change and migrations move organisms and change the rate of transforming matter and energy in ecosystems. Many of the important interactions that are key parts of this machinery are usually hidden from us because they depend on microbes or tiny organisms in the soil. Many of the processes become obvious only when we examine systems for long periods or delve into their long histories. Nevertheless, whether invisible or infrequent, such processes and organisms are as much a part of the systems that sustain us and provide important services as are the more obvious and sometimes seemingly static structures.

This view of the natural world is of ecological systems in flux. The flux has some components that are continual, while others are episodic; some components of flux are obvious while others are subtle. But, to echo the words of the ancient Greek philosopher Heraclitus, all is flux. Rather than envisioning the natural world as being in simple balance, which unfortunately connotes stasis and permanence, the persistence of natural systems is founded on flux. So the flux of nature is an ecologically appropriate metaphor (Pickett and Ostfeld 1995). If there is a balance, it is a dynamic and changeable balance derived from the interaction of fluxes that generate heterogeneity and the opposing fluxes that generate homogeneity. Biological diversity is founded on dynamics yielding heterogeneity, and this is the key to understanding our natural heritage. Maintaining the heterogeneity on which natural diversity is founded while preventing the extreme homogenizing tendencies of humans is the key to maintaining that nonrenewable natural heritage.

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