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Disturbance, Recovery, and Stability

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Nature to be commanded, must be obeyed.
—*Francis Bacon*

Disturbance and the set of reactions that it engenders are common in nature, and the character of ecosystems results in large part from an interplay between these two forces of change. Resource managers have much to gain from understanding historic disturbance patterns, the ecological factors that act to contain and control disturbances, and the mechanisms that confer resilience (the ability to recover following disturbance). Forestry, like any renewable resource management, involves disturbing natural systems to one degree or another and has as a central objective to do so in a sustainable way. For the ecologist, by far the most reliable strategy for achieving sustainability is to understand the historic forces that have shaped ecosystems and to work within the mechanisms by which ecosystems sustain themselves.

Although most people have an intuitive sense of what constitutes a disturbance, precise definition can be elusive. Forman (1987) defines disturbances as "events that cause a significant change in the existing pattern in a system" (see also Pickett and McDonnell 1989). For foresters and plant ecologists, this often translates to stress or death of the dominant plants in numbers great enough to affect system functioning. There is good ecological rationale for this view: The dominant plants (in forests, trees) fix carbon, cycle water, build and stabilize soils, ameliorate climate, and provide the basic habitat structure for other organisms (Jones et al. 1994). However, growing knowledge of functional interdependencies in nature makes it clear that plants are not the only points of vulnerability. Ecological systems can also be disrupted by factors such as loss of large and small predators, reduced populations of mycorrhizal fungi, and spread of exotics, to name a few. Moreover, while disturbances are often thought of as dramatic events such as crown fires or hurricanes, they may also be more subtle and slower acting, as with soil compaction or the erosion of soil fertility resulting from acid rain or overly short rotations. Some changes in the existing pattern of a system may have little or no adverse impact on immediate system functioning, but increase vulnerability to future disturbances; genetic homogenization is one example of what might be termed an accident waiting to happen (Gibson et al. 1982), but it is far from the only example. Any simplification of a natural system risks eroding the system's capacity to resist and recover from disturbances, though few, if any, ecosystems are well enough understood to quantify that risk.

Recovery is another seemingly simple concept that becomes more complex with further examination. Succession is the most obvious and well-known manifestation of system recovery following disturbance. Less obvious but equally important are the many small recoveries—the controls that keep small disturbances from turning into large ones, as when particular species of mycorrhizal fungi enable their hosts to recover quickly from drought (Parke et al. 1983a) or when predators limit a growing pest population before it becomes an epidemic (e.g., Mason et al. 1983). The upshot is that, like disturbances, recoveries occur at many scales, from the small ones we never notice to the large ones that get our attention and that often come into play only when the small ones have failed. As we discuss later, these resistance and resilience mechanisms are frequently based in biological diversity.

This chapter explores these issues in more detail. We begin with the revolution in the scientific view of the structure and dynamics of complex systems (of which ecosystems are the prime example). We then move beyond these general considerations to examine more specifically what has been learned about the dynamics of disturbance and recovery in ecosystems. We close with a brief discussion of management implications.

A New View of Nature: Dynamic, Interconnected, Robust Yet Fragile

The 1980s saw the rise of what some have called the new paradigm in ecology (Pickett et al. 1992) and what we refer to as the "dynamic view." Before, the focus of community ecology was characterized by two things in particular (Pickett et al. 1992): (1) an equilibrium view, where "equilibrium" (as used here) refers to constancy in the species composition of a community (while disturbance and succession clearly alter communities, they are subordinate in the equilibrium view to the major theme of nature, which is the relatively unchanging climax community) and (2) the belief that ecosystems were self-contained, that their trajectories were determined solely by internal interactions or, put another way, that you could understand the dynamics of an ecosystem without ever looking outside its boundaries. Since the late 1970s, ecologists have increasingly focused on community and ecosystem dynamics rather than static endpoints such as the climax (DeAngelis and Waterhouse 1987). Disturbance and response to disturbance are now recognized as natural processes that lay at the core of ecosystem dynamics, a concept that plant ecologists have variously expressed as "patch dynamics" (Pickett and Thompson 1978), "the shifting landscape mosaic" (Bormann and Likens 1979), and "the mosaic cycle" (Remmert 1991). This is also known as the nonequilibrium view (DeAngelis and Waterhouse 1987), reflecting the increasing recognition that disturbances and other factors mitigate against ecological communities attaining a lasting equilibrium in species composition (though equilibria may still be attained at landscape and regional scales).

Because disturbances limit the ability of one or a few species to dominate sites, they limit the importance of competition in structuring communities (DeAngelis and Waterhouse 1987). On the other hand, the need to maintain continuity in key processes during and in the recovery stages following disturbance is hypothesized to increase the prevalence of mutually supportive interactions among species (Perry et al. 1989a, 1989b, 1992, Tilman and Downing 1994, Perry 1995a). The species diversity of a given region is strongly influenced by the interplay among disturbance (which simultaneously destroys old habitats and creates new ones), recovery (which reverses that process), and biological legacies (which act to maintain continuity of certain habitats through disturbance). Bunnell (1995) documented the relationship between disturbance history and vertebrate species composition within different forest zones in British Columbia. There, forest types characterized by small wildfires contain a higher proportion of vertebrates that breed in late-successional stages and a lower proportion that breed in early stages than forest types with a history of large fires. In British Columbia, the proportion of birds and mammals within a given forest type that use cavities drops sharply as one goes from forests typified historically by small fires to forests where large fires have been more common. However, the proportion of vertebrates that use coarse woody debris (CWD) follows the opposite trend: CWD generated by fire constitutes a biological legacy that provides habitat. In all likelihood, Bunnell's findings can be generalized beyond British Columbia.

Species diversity is generally enhanced by disturbances that occur at intermediate levels of frequency and intensity—those that do not exceed the capacity of the system to recover fully between disturbances (Petraitis et al. 1989). Diversity is reduced by disturbances to which species composing the system in question are not adapted, and also by disturbances that destroy habitats faster than they can recover (as when stands are harvested before they attain old-growth characteristics). If disturbances disrupt key processes, loss of system integrity and qualitative shifts in community type can result. The frequency and severity of disturbances on a given site are, in turn, strongly influenced by processes, both ecological and socioeconomic, that occur at the scale of landscapes, regions, and the globe.

Because natural disturbances perform critical functions that maintain ecosystem structure and processes, excluding them can lead to unforeseen and sometimes undesirable consequences. Many forest species persist only because of periodic disturbances. For example, without wind throw, which exposes mineral soil seedbeds, some northern forests convert to bogs. Some scientists believe that much of the rich diversity of moist tropical forests reflects historic patterns of shifting cultivation. Numerous forest types throughout the globe—including many pine, eucalypti, and dry tropical woodlands—are maintained by periodic fire. Fire suppression in the ponderosa pine forests of western North America provides a classic case study of the importance of periodic disturbance to stability of some ecosystems. Eliminating fire in these systems allowed late-successional trees (mostly true firs) to establish under the ponderosa pine, a dynamic that was accelerated by highgrading the older ponderosa pine. The subsequent change in forest structure from relatively widely spaced old-growth pine to densely stocked stands of younger pines and firs has increased stand susceptibility to crown fires, defoliating insects, and root pathogens (see various papers in Sampson and Adams 1995).

While the move to a more dynamic view of nature represents a significant advance in our ability to understand how natural systems function, it has yet to offer a coherent set of guiding principles to replace the equilibrium view. Consider the old idea of nature's balance. Some ecologists argue that the concept of balance as applied to nature is unrealistic and should be discarded (Botkin 1990, Pickett et al. 1992). This is certainly true if balance is interpreted as "no change." However, if we take balance to mean that some changes in the state of a system are consistent with maintaining species and processes, while other changes are not, then there clearly are balances in nature, and different kinds of disturbances can have quite different implications for the integrity of natural and managed systems. Angermeir and Karr (1994) define biological integrity as "a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates." But what is the whole? How robust are communities and ecosystems when faced with loss of species, alteration of processes, and changes in landscape and regional patterns? We must seek further understanding to guide sustainable resource management. The first step is to probe deeper into the nature of complex ecosystems. What are these unique entities that, though perhaps not organismic, are far more than the sum of their parts?

Complexity, Self-Organization, and Thresholds: The View from the Cliff

The shift among ecologists to a more dynamic view of nature is part of a larger revolution that has occurred over the past 25 years as scientists began to grapple with complexity in physical, biological, and social systems. Although a daunting subject, developing sustainable social-economic-ecological systems is unlikely to succeed without an appreciation of the nature of complexity (Levins and Lewontin 1985, Lubchenco et al. 1991, Costanza et al. 1993). It is well beyond our scope to review the subject in detail, but we summarize the basic characteristics of what scientists call complex systems:

1. Complex systems such as ecosystems are dissipative, they are maintained far from thermodynamic equilibrium by large throughputs of energy and (usually) matter (Odum 1992). Interactions among system parts include positive feedback, or what physical scientists call autocatalysis (literally, "making oneself") (Prigogine and Stengers 1984, DeAngelis et al. 1986). Autocatalysis is also referred to as "bootstrapping," after the old story of the little boy who fell in the bog and pulled himself up by his bootstraps (Davies 1983, Perry et al. 1989a, 1989b).

2. Even very simple dissipative systems (i.e., those with few parts) can exhibit highly complex and often unpredictable behavior (May and Oster 1976).

3. In a complex system, small changes in driving variables can amplify through positive feedback loops and produce large changes in system behavior. This is, by definition, chaotic behavior, often exemplified by the hypothetical (and probably spurious) example of a butterfly flapping its wings in Brazil and creating a tornado in Kansas.

4. The potential for chaotic change in complex systems is constrained by two factors: (a) the buffering effect of higher order, more stable systems (O'Neill et al. 1986, Odum 1992), such as landscape patterns (which we discuss later), and (b) internal interactions (i.e., among system components) that maintain system integrity by constraining change, a dynamic referred to as self-organizing or self-reinforcing behavior. In simplest terms, a self-organizing system is one in which the structure and the processes mediated by that structure reinforce one another: through various positive and negative feedbacks the system creates conditions that increase the probability that it will persist.

5. Self-organizing systems are stable over a range of conditions, but change rapidly when their bounds of adaptability are exceeded—a dynamic O'Neill et al. (1989) call metastability. Moreover, the change is often to a new state that is itself self-reinforcing. Note that stability as used here does not mean no change: A metastable system may be quite dynamic, but its changes are maintained within certain bounds.

While this may sound like so much esoteric gibberish, the characteristics and behaviors listed above accurately describe the world we move in every day. A system "far from thermodynamic equilibrium" is one that changes significantly when its energy source is removed: organisms, ecosystems, and processes such as the hydrologic cycle, major oceanic currents, and the earth's climate. Positive feedback is common at a variety of scales in ecological systems (DeAngelis et al. 1986, Perry et al. 1989a, 1989b), including population growth, the ubiquitous mutualistic relationships among species, nutrient cycling and other food-web dynamics, landscape and regional phenomena such as disturbance spread and the hydrologic cycle, and global phenomena such as the "Atlantic conveyor belt," a major oceanic current that influences weather globally. Moreover, complex interactions between positive and negative feedbacks create both the potential for extreme sensitivity to environmental conditions (i.e., chaos) and the evolutionary impetus to dampen that potential. Bak et al. (1988) put it this way:

> [E]cological systems are organized such that the different species "support" each other in a way which cannot be understood by studying the individual constituents in isolation. The same interdependence of species also makes the ecosystem very susceptible to small changes or "noise." However, the system cannot be too sensitive since then it cannot have evolved into its present state in the first place.

While nature is dynamic, not all changes are consistent with maintaining system integrity (Pickett et al. 1992). Numerous examples can be cited of changes in system state (e.g., species composition and processes) that are quite distinct from normal successional changes; in essence, sites convert to a new community that itself may be self-reinforcing (DeAngelis et al. 1986, Perry 1995a, 1995b, Perry et al. 1989a, 1989b, Schlesinger et al. 1990, Archer and Smeins 1991, Turner et al. 1993). Perhaps the most widely known contemporary examples are the collapse of some forests due to excessive pollution (Bormann 1985) and the worldwide desertification of arid grasslands (Schlesinger et al. 1990, Archer and Smeins 1991, Milton et al. 1994), a phenomenon underlain by loss of soil integrity due to the combined effects of overgrazing and drought, exacerbated in many cases by an intensified disturbance regime due to the spread of flammable exotic grasses (D'Antonio and Vitousek 1992). Lakes and coral reefs have also exhibited catastrophic losses of species diversity and productivity (Kaufman 1989, Knowlton 1992, Hughes 1994). Both models and real world experience show that factors other than pollution can trigger forest ecosystems into threshold transitions from one state to another (Gatto and Rinaldi 1987, Pastor and Post 1988, Perry 1988, Perry et al. 1989b, Loehle 1989, Overpeck et al. 1990).

To give an example from our own work, inability to reforest high-elevation clearcuts in the western United States has been linked to complex changes in soil structure and biology that essentially reflect a breakdown of self-organizing mechanisms (Amaranthus and Perry 1987, Perry et al. 1989b, Friedman et al. 1989, Colinas et al. 1994), the same general dynamic that underlies desertification of arid grasslands. At a much larger scale, considerable paleochemical and paleoecological data show that earth's climate is subject to rapid transitions from one state to another, at least some of which result from large-scale and relatively rapid (in less than five years, perhaps as little as one or two) reorganization of the ocean–atmosphere system (Broecker 1987, Allen and Anderson 1993, Grootes et al. 1993, Bond et al. 1993, Weaver and Hughes 1994). The geological record for the upper Mississippi basin shows that modest changes in climate can trigger large changes in the magnitude of floods (Knox 1993). Kauffman and Uhl (1990) suggest that relatively small changes in regional climate would greatly increase the probability of fire in the primary forests of Amazonia.

Threshold changes in ecological systems may be rapid, but not necessarily. In what they call the extinction debt, Tilman et al. (1994) argue that habitat losses can trigger extinctions that do not manifest for decades. The distinguishing characteristic of thresholds in complex systems is that, once the self-reinforcing mechanisms have failed, changes—whether rapid or gradual—cannot be stopped without great difficulty and expense, and in some (perhaps many) cases, not even then. Scientists working in rangelands, forests, and coral reefs have concluded that simply removing the perturbing force is unlikely to allow recovery of the original community. As Knowlton (1992) aptly puts it, once the straw has broken the camel's back, simply removing the straw does not allow the camel to rise again. A central challenge of management is to stay clear of threshold boundaries, which requires understanding and working within the natural mechanisms that buffer systems against environmental fluctuations.

New Concepts of Disturbance

Global, Regional, and Landscape Processes: No Ecosystem Is an Island

Over the past 20 years, ecologists have devoted a great deal of attention to issues of scale, or the spatial and temporal domains over which natural phenomena play out (Forman and Godron 1981, Allen and Starr 1982, Allen and Hoekstra 1991, O'Neill et al. 1986, O'Neill 1989, Franklin and Forman 1987, Urban et al. 1987, Perry 1988, Turner 1987, Wiens 1989, Levin 1992, Wiens et al. 1993, Franklin 1993). Disturbances occur at many intensities and scales, from the death of a single old dominant tree to a catastrophic forest fire to volcanic eruptions and impacts by comets, all of which are embedded within climatic cycles that may span decades to millions of years. The disturbance regime of a particular forest usually consists of a complex mixture of infrequent, large-scale events (e.g., a large fire or windstorm) and more frequent, small-scale events (e.g., small fires, the fall of a single tree). Therefore, one might draw very different conclusions about the disturbance history of a given piece of ground depending on what time period is considered. In boreal forests, for example, "few major fires that occur in extreme fire years account for the vast majority of forests burned. Sixty to 80 percent of all fires in northwest Canada and Alaska are less than 5 ha in area . . . and 85 percent of all fires in Canada between 1961–1967 were 4 ha or smaller . . . yet in severe years, individual fires can cover 50,000 to 200,000 ha" (Bonan and Shugart 1989). A similar pattern of frequent small fires and infrequent larger fires characterizes many temperate and boreal forests (Johnson 1992).

Any given disturbance may be the result of numerous, interconnected factors; moreover, the disturbance regime of a particular ecosystem cannot be understood in isolation, but rather it is tied to the systems to which it is linked and ultimately to events within surrounding landscapes, the region, and the globe (Forman 1987, Pickett et al. 1992). Climate, which strongly influences a variety of disturbances, is in large measure a global phenomenon modified by regional and local patterns of topography and vegetation. Under extreme conditions, macroclimate becomes the driving force. For example, Fryer and Johnson (1988) found that large, highly destructive fires in the subalpine forests of southern Alberta tended to occur during transitions from high-pressure systems to low-pressure systems. Hot, dry weather associated with the high-pressure system dried fuels and increased the chances of ignition, and winds associated with the incoming low-pressure system drove the fire. Johnson (1991) argue that, under such conditions, fire intensity is little affected by stand structure: "Under these conditions fires can crown in all forest types. . . ."

Disturbances at any one place may be linked through atmospheric teleconnections and global oceanic currents to events thousands of miles away (Neilson et al. 1992, Gray and Landsea 1993). Perhaps the most obvious example is climate change resulting from the buildup of greenhouse gases, which is predicted to result in more severe convective storms (thunderstorms and tornadoes) at mid and high latitudes, more severe hurricanes in the tropics (Overpeck et al. 1990), and sharp drops in available water (hence maximum site leaf area index and runoff) throughout eastern North America and interior Eurasia (Neilson et al. 1990, Neilson and Marks 1994).

However, disturbance regimes are strongly influenced by global phenomena other than the buildup of greenhouse gases. One of the more significant of these is the Atlantic conveyor belt, a massive current that flows from the North Pacific through the tropics to the North Atlantic and back (Broecker 1987). Changes in the flow of this current, which may be triggered by pulses of freshwater into the North Atlantic (Rahmstorf 1994, Weaver and Hughes 1994), are believed to influence climatic phenomena throughout the globe (Gray and Landsea 1993), including rainfall in the Sahel region of Africa, hurricanes in the Atlantic Basin, the frequency and intensity of El Niños, and multidecadal changes in global surface temperatures (Gray and Landsea 1993). Hurricanes in the Caribbean and along the U.S. East Coast have been most severe during periods of higher than average rainfall in the Sahel region of western Africa, both reflecting alterations in flow of the Atlantic conveyor belt (Gray 1990).

Excepting the ice ages, perhaps the best-known example of a link between global climatic phenomena and disturbances on land is the so-called southern oscillation, the alternate warming and cooling of the southern Pacific Ocean that produces El Niños and La Niñas and ramifies to alter climate throughout the globe. During El Niño years, spring and fall are wet in the southwestern United States, hence fire activity is low. However, the region often has severe winter and spring droughts during La Niña years, and fire activity is correspondingly high (Swetnam and Betancourt 1990). The situation is quite the opposite in the U.S. Pacific Northwest, where La Niñas tend to precede wetter than normal winters, and El Niños drier than normal winters. The latter pattern also holds in Indonesia and eastern Australia: La Niña years are accompanied by abundant rainfall, while El Niño years are drier than average. Millions of hectares burned in Australia and Indonesia during the particularly strong El Niño of 1982–1983 (Swetnam and Betancourt 1990). The strong relationship between drought and susceptibility of trees to at least some species of herbivorous insects and pathogens means that the southern oscillation (or indeed any factor that produces drought cycles) can also influence outbreaks of these disturbance agents. To complicate matters, particular sequences of wet and dry years can trigger epidemics. For example, during the past 10 years about one-half of the *Octea whitei*, a common tropical tree that grows on moist slopes and ravines, have been killed on Barro Colorado Island. Gilbert et al. (1994) traces the phenomenon to a sequence of one especially wet year, which promoted an outbreak of a native pathogen that attacks vascular tissue, followed by a severe drought (due to the 1982–83 El Niño), which killed the trees because the pathogen had reduced their ability to transport water.

Longer-term cycles of climate are known to profoundly influence fire patterns. Wildfires have been most frequent in North American forests during warm, dry periods, and less frequent but more severe during cool periods (at least in some areas). Clark (1988, 1990) used layers of charcoal buried in lake sediments to determine fire severity in northwestern Minnesota over the past 750 years. Fires were most frequent during the 15th and 16th centuries, a warm, dry period, which also saw the massive fires that established many of the old-growth Douglas-fir forests that once covered most of the Oregon and Washington Cascades. Clark found that fire frequency dropped sharply with the advent of much cooler climates beginning about A.D. 1600. Climate warmed once again during the 20th century; however, fire activity remained low because of suppression. The longevity of giant sequoia trees allowed Swetnam (1993) to study fire history in the northern Sierra Nevada as recorded in fire scars over a 2,000-year span. In that area, frequent small fires burned during a warm period from A.D. 1000 to 1300, while fires during cooler periods (A.D. 500 to 1000 and after A.D. 1300) were less frequent but more severe.

The Influence of Regional and Landscape Patterns on Disturbances

The importance of global climate in influencing disturbance regimes does not minimize the critical role of regional and local patterns of topography, soils, and vegetation. Under a given set of macroclimatic conditions, regional and local factors may be decisive in determining disturbance spread. Topography has long been known to influence stand susceptibility to fire and wind. In their study of Alberta forests, Fryer and Johnson (1988) found that "fires are oriented by wind direction, wind speed, and major topographical features. Valleys upwind of or at right angles to the fire spread are often not burned. Consequently, depending on wind direction, small valleys may escape burning largely by accident, and unless passes between large valleys are aligned with the wind and fire direction, the fire may be confined to a single large valley."

Through effects on moisture and perhaps nutrients, topography and soils also affect stand susceptibility to insects. Studies in both Quebec and Michigan found that stands growing at either end of a moisture gradient were most susceptible to spruce budworm (Hix et al. 1987, Dupont et al. 1991). Fuels generated by insect or pathogen outbreaks in turn increase susceptibility to fire (Knight 1987), and these two disturbance agents acting in concert can exert significant influence over regional forest patterns, as hypothesized by Schowalter et al. (1981) for pine forests along the U.S. Atlantic coastal plain.

More recently, attention has turned to how spatial patterns of vegetation influence a variety of ecological processes, including species interactions, regional climates, and the spread of disturbances. The growing body of work on the relation between vegetation patterns and landscape and regional processes is particularly significant for managers, who may be at the mercy of global processes and local topography, but who can directly affect vegetation patterns across landscapes.

As with global phenomena, rigorously understanding the relationships between landscape patterns and processes presents a formidable scientific challenge. These issues are not easily studied experimentally in forested landscapes (though there are a few landscape-level experiments in forests, most notably the Critical Size of Ecosystems Project in Amazonia (Bierregaard et al. 1992). Nevertheless, both experience and modeling indicate that landscape and regional patterns can profoundly influence species interactions, regional climates, and the propagation of disturbance (Turner 1987, Turner et al. 1989, 1993, Knight 1987, Perry 1988, Pielke and Avissar 1990, Franchito and Rao 1992, Mylne and Rowntree 1992, O'Neill et al. 1992, Turner et al. 1993, Tilman 1994, Castello et al. 1995, Perry 1995a).

Landscapes can have self-reinforcing patterns, that is, some landscapes tend to absorb and dampen the spread of disturbances, while other patterns magnify them, with the process reinforcing the structure in both cases. In some forest types—including Douglas-fir, ponderosa pine, and moist tropical—large intact blocks of healthy, mature forests or nondecadent, old-growth forests are less susceptible to catastrophic fires than young or fragmented forests. Landscapes dominated by these types buffer and dampen the spread of crown fires and hence preserve the forest structure (Perry 1988, Franklin et al. 1989, Kauffman and Uhl 1990). Once some threshold proportion of the landscape becomes fragmented and permeated by flammable young forests or grasses, the potential exists for a self-reinforcing cycle of catastrophic fires—an absorbing landscape crosses a threshold and becomes a magnifying one. Invasion of ecosystems by flammable exotic grasses, a growing problem throughout the world, is greatly facilitated by positive feedbacks between grass cover and landscape flammability (Hughes et al. 1991, D'Antonio and Vitousek 1992). Similarly, opening intact forests reduces their ability to buffer wind (Chen et al. 1993, 1995) and creates edges susceptible to blowdown, a self-reinforcing dynamic in which blowdown along edges creates more edge to be blown down. This happened in a portion of the Mount Hood National Forest in Oregon, where clearcut patches initiated a dynamic in which severe windstorms every several years blew down progressively more forest, resulting in an increasingly fragmented landscape (Franklin and Forman 1987).

Through albedo and transpiration, vegetation significantly influences regional climates, and even relatively slight changes in forest cover can have a pronounced effect on climate (Pielke and Avissar 1990). A particularly dramatic example of how forests can affect regional climate is provided by China's "Great Green Wall," the result of a massive tree-planting program throughout northern China beginning in the 1950s. During the 1950s, Beijing experienced 10 to 20 dust storms each spring, reducing visibility to less than 1 km for 30 to 90 hours per month; by the 1970s, Beijing had fewer than 5 dust storms each spring, with visibility below 1 km on the average only 10 hours per month (Parungo et al. 1994).

The relationship between vegetation cover and regional climate can be self-reinforcing. One of the more frequently cited examples is the Amazon rain forest, which receives roughly twice as much precipitation as can be accounted for by moisture moving in from the ocean (Salati 1987). By transpiring and keeping water in circulation, the rain forest generates the rain that supports the forest. Computer models suggest that if grasslands were to replace forests as the major vegetation type in that region, the Amazon basin would become too dry to support tree growth (Lean and Warrilow 1989, Shukla et al. 1990). This raises a question: At what point would deforestation alter the climate of the entire basin sufficiently that remaining forests could not persist? Drying related to landscape conversion would create other stresses most notably vulnerability to fire. In moist tropica forests, wildfire is a foreign disturbance to which few trees are adapted (Kauffman 1991), and extensive wildfires would almost certainly accelerate conversion of these forests to grasses, which would then perpetuate themselves through frequent burning (D'Antonio and Vitousek 1992).

Like most things in nature, the relation between landscape pattern and the spread of disturbances i complex and may vary widely depending on the disturbance under consideration (Turner 1987, Perry 1988). However, two basic principles can be identified: (1) the homogeneity of susceptible vegetation types, which creates the potential for growth and spread of disturbance, and (2) the degree to which landscape patterns provide sources of control. No surprisingly, the spread of herbivorous insects and pathogens is greatly influenced by the available food Both the eastern and western spruce budworms have been more aggressive during the latter half of the 20th century than they were in the 19th century, phenomenon that entomologists attribute to fire exclusion and high-grade logging practices that inadvertently promoted the spread of tree species susceptible to these insects (Blais 1983, Anderson e al. 1987, Swetnam and Lynch 1989, Wickman et a

1993). *Armillaria* root rot is also spreading in these forest types for the same reason (Castello et al. 1995). The spread of ash yellows, a bacterial disease of white ash, has been linked to the abundant regeneration of its host tree on abandoned farms (Castello et al. 1995). In addition to food, populations of herbivorous insects (broadly, any insect that eats plant tissues) are controlled by the combined actions of weather, plant defenses (chemical and structural), and a complex of natural enemies including vertebrates (birds and small mammals), invertebrates (e.g., spiders, ants, parasitic wasps, and parasitic flies), microbes, and viruses. It follows that landscape patterns, as expressed both in the available habitat for natural enemies and in the available refuges from natural enemies, significantly influence herbivore dynamics (Pacala et al. 1990, Comins et al. 1992, Torgerson et al. 1990, Hochberg and Hawkins 1992, Hawkins et al. 1993), a phenomenon long recognized by European foresters, who install bird boxes and cultivate habitat for small mammals. In most cases, this is a function of habitats at a landscape and regional scale, but for migratory birds, which consume large numbers of defoliating insects, the issue becomes hemispheric: Loss of habitat in the wintering grounds (for American birds, neotropical forests) weakens part of the herbivore-control complex in northern forests (Holling 1988).

Mechanisms of Resistance and Recovery

A central question facing ecologists is how complex systems maintain integrity (DeAngelis and Waterhouse 1987). For resource managers, this question translates into what types and levels of anthropogenic disturbances are most likely to maintain desired forest structure and processes in the long run. Answers to these questions, which in the final analysis are the same question, require understanding the complexity of natural dynamics. Clearly, species evolve mechanisms to persist, and ecologists increasingly recognize that such mechanisms are not solely individualistic, but involve dynamic interactions among species, other aspects of system structure (e.g., old dead wood and soils), and critical processes such as the nutrient and hydrologic cycles.

Recall that biological integrity is defined by Angermeier and Karr (1994) as "a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates." In the following discussion, we refer to the maintenance of integrity as stability, with the understanding that stability does not mean no change, but rather maintaining change within certain bounds. The issue of stability in nature is fraught with difficulty, largely because the relationship between the structure of natural systems (within and across scales) and their resistance and resilience is poorly understood. This difficulty is compounded by the fact that change at some level is common in ecosystems, including not only successional changes, but longer-term fluctuations in the relative abundance of species. No system is likely to recover to exactly the same state as existed prior to disturbance for at least two reasons: First, the longevity of trees coupled with significant fluctuations in average climatic conditions at cycles spanning decades to centuries means that in some cases the dominant species in a given locale are out of equilibrium with their current environment. Recent studies indicate this is the case in forests of southern Ontario (Campbell and McAndrews 1993). It is unknown in how many other cases this may be true. However, should climatic warming play out as predicted, the phenomenon will become more common.

Second, variation in initial conditions (e.g., type and season of disturbance, climatic factors during early recovery) may alter the initial species composition, which in turn can influence the whole successional trajectory (Drake 1990, Lawton and Brown 1992). Note that the latter case is an example of the potential for ecosystems to behave chaotically—small differences in initial conditions creating large effects. On the other hand, as we discuss later, mechanisms exist within ecosystems to constrain the chaotic potential.

Stability of What?

It is useful to distinguish three different sets to which the concept of stability can be applied (Perry 1994):

1. Species Stability: the maintenance of viable populations or metapopulations of individual species.

2. Structural Stability: the stability of various aspects of ecosystem structure, such as food-web organization, species numbers, or soils.

3. Process Stability: the stability of processes such as primary productivity and nutrient cycling.

The stability of each of the above is generally linked to the stability of the others, although the strength of the linkages is, with some exceptions, poorly understood. One case in which the link is clearly understood is in soils, whose integrity without doubt underpins the integrity of the ecosystem as a whole. Keep in mind that in all of these, but particularly the first two, stability may include considerable change (as commonly occurs, for example, during disturbance and succession). Instability results when the system crosses some threshold from which recovery to a former state either is impossible (e.g., extinction) or, if possible, occurs only over relatively long time periods or with outside subsidies of energy and matter (e.g., loss of topsoil).

Two Aspects of Stability: Resistance and Resilience

Ecosystem stability can be divided into two separate but interrelated properties: (1) resistance, or the ability of a system to absorb small perturbations and prevent them from amplifying into large disturbances, and (2) resilience or recovery, which is the capacity to return to some given system state (defined by structure and processes) following disturbance. Succession is the classic example of resilience (some of the recent thinking regarding succession is reviewed by Huston and Smith 1987, Pickett et al. 1987, and Pickett and McDonell 1989). While the state to which the stable ecosystem recovers is unlikely to be an exact replica of what existed before, it nevertheless contains the same basic elements (species richness, habitats, and soil fertility) and supports the same key processes (e.g., photosynthetic capacity and nutrient and hydrologic cycles). In other words, system integrity is maintained.

Resistance mechanisms may be thought of as those properties—of the system and of individuals—that maintain relative constancy in processes and that prevent organisms from succumbing to some stress. A common example of the latter is regulation of herbivorous insects by the combination of tree chemical defenses and natural enemies. Resilience (or recovery) mechanisms come into play when trees are weakened or killed. While succession is the most obvious manifestation of recovery, it is far from the only one. Moreover, whereas succession manifests as change in the dominant species on a site, other aspects of recovery involve constraining change, such as retaining nutrients and stabilizing mycorrhizal fungi and belowground food webs. Resistance and resilience are closely interlinked and act jointly to stabilize ecosystems. Resistance mechanisms may be thought of as filters that reduce the potential for large disturbances. If these mechanisms are weakened, the frequency of large scale disturbances increases; if disturbance frequency becomes shorter than the time required to recover, the system enters a highly vulnerable state in which threshold transitions become probable (Turner et al. 1993).

Both resistance and resilience include mechanisms that operate at the stand and landscape scales. Tree size and vigor are important stand-level components of resistance, as are stand structure and the invertebrate and microbial food webs that cycle nutrients and help control pests and pathogens. Resistance is tied to landscape patterns through factors such as the homogeneity of susceptible vegetation types, the habitat provided for natural enemies of herbivores and pathogens, and the various climatic factors influenced by vegetation. With regard to recovery, probably the most important aspect is rapidly stabilizing the soil ecosystem, including nutrients, physical structure, and food webs. However, landscape and regional patterns also contribute significantly to recovery by providing habitat refugia which serve as sources of future colonists for the recovering site (Amaranthus et al. 1994) and, again, by affecting regional climatic factors. As discussed earlier, all of these factors are embedded within and are strongly influenced by global processes.

Species Diversity and Ecosystem Function

Species diversity and ecosystem function have been a subject of much debate among ecologists. Over the past 30 years, the weight of opinion has shifted from "diverse systems are more stable in their functioning" to "diverse systems are less stable" and, most recently, back again. By Angermier and Karr's (1994) definition, loss of a single indigenous species diminishes integrity; however, without minimizing the tragic finality of any extinction, the issue of concern here is how loss of species might affect ecological functioning, including, in particular, key processes and the ability of the system to sustain remaining species. In a 1986 review, Pimm concluded that "[m]ost of the possible questions about the relationship between diversity and stability have not been asked. Those that have yield a variety of answers." Progress has been made since Pimm's 1986 review (e.g., see reviews by Pimm 1991, Vitousek and Hooper 1993, Lawton 1994), but until recently much of that has been in modeling. While ecological modeling is important to do, its value is limited unless models are verified by observation and experiments in the real world. In the latter regard, we still have a long way to go. (Pimm has a good discussion of model limitations in Chapter 16 of his 1991 book.)

Lawton (1994) lists four hypotheses concerning the relation between species diversity and ecological functioning (see also Vitousek and Hooper 1993):

1. The redundant-species hypothesis holds that most species are redundant in their ecological roles; it is only a few keystones whose presence is critical for the rest of the system (Walker 1992, Lawton and Brown 1992, Berryman 1993).

2. The rivet hypothesis takes the position that all species contribute to proper ecological function, or to use Berryman's (1993) phrase, "everything depends on everything else" (Berryman believes not). "Rivet" comes from the analogy, first used by Aldo Leopold and later by Ehrlich and Ehrlich (1981), with rivets in an airplane, each of which is presumed to be incrementally important in holding the plane together.

3. The idiosyncratic-response hypothesis holds that diversity and function are linked, but the complexity of ecosystem organization makes it impossible to predict how a given system will respond to species deletions (except in obvious cases like removing all the green plants).

4. The null hypothesis holds that species deletions or additions do not influence ecosystem function.

Although we haven't done a survey, it is probably safe to say that few, if any, ecologists would agree with the null hypothesis; the evidence for the contrary is simply too overwhelming. The idiosyncratic hypothesis certainly has an element of truth: It would be a rare field ecologist who couldn't attest to the unpredictability of nature. It does not follow, however, that valid generalities do not exist. The current debate centers largely around hypotheses 1 and 2: What level of diversity is necessary to maintain stable functioning?

Experiments on the relation between species diversity and ecosystem function have generally involved either removing a species from an ecosystem or creating systems from scratch with different species richness. Quoting once again from Pimm's (1986) review:

> Experimental studies show that few natural communities are species-deletion stable; most removals cause further species losses. The data also show wide variation in the consequences of species removals. Communities are differentially resistant. . . .

The few experiments that have been done show that primary productivity and nutrient retention are related to diversity. In Costa Rica, soils beneath diverse natural successions had higher soil nitrogen, extractable cations, and phosphorus sorption capacity than those beneath monocultures (Ewel et al. 1991). Two recent experiments (neither in forests) support what we will term the modified rivet hypothesis—which takes the middle position that, while ecosystem function (measured as the rate at which certain processes occur) may not depend on every species, it certainly depends on more than a few. Tilman and Downing (1994) found that the ability of prairie communities to sustain primary productivity during drought increased with plant species diversity up to 12 species, after which additional species had no effect. In a series of controlled environment experiments that manipulated diversity of both plants and invertebrate animals, Naeem et al. (1994, 1995) found that plant productivity and overall system carbon dioxide flux declined with declining species richness, while litter decomposition rate and soil nutrient retention varied idiosyncratically with species richness. Wood decomposition was unaffected; however, this may have been because of the short time the experiment was run (Lawton 1994).

There is considerable evidence for the modified rivet hypothesis in forests. One clear example is the ability of early successional plants to stabilize soil structure and biology, retain nutrients, and in the case of some species, restore nitrogen (Bormann et al. 1974, 1993; Amaranthus and Perry 1989a, 1989b; Amaranthus et al. 1990; Borchers and Perry 1990; Perry et al. 1989b). There are also many examples in which species richness dampens the spread of disturbances. Some species of hardwoods are relatively nonflammable and, when admixed with conifers, help protect the latter from fire (Perry 1988). In some cases, conifers are less affected by herbivorous insects or pathogens when admixed with hardwood trees or herbaceous plants than when growing in monocultures (Zutter et al. 1987; R. Gagnon, personal communication, Morrison et al. 1988, Schowalter and Turchin 1993, Simard and Vyse 1994). Atsatt and O'Dowd (1976) drew on a number of studies to hypothesize that plant species associate in defense guilds, in which each species within the guild benefits from reduced herbivore pressure. Researchers in this field emphasize that it is not diversity per se that stabilizes plant associations, but associations of species that fill specific functional niches.

Defenses that reside in plant species or guilds of plant species fall under the heading of what are called bottom-up controls, where bottom refers to the base of the food chain. Numerous studies have shown that predators also contribute significantly to maintaining herbivore populations below outbreak thresholds, a dynamic termed top-down control. Most research in forests has dealt with birds and invertebrate predators of tree-eating insects (Holmes et al. 1979, Torgerson et al. 1979, Kroll unpublished in Thatcher et al. 1980, Mason et al. 1983, Carlson et al. 1984, McClure 1986, Crawford and Jennings 1989, Torgerson et al. 1990, Way and Khoo 1992, Marquis and Whelan 1994), but even large predators can indirectly benefit tree growth by controlling herbivores, as recently demonstrated on Isle Royale National Park (Michigan), where tree growth correlates positively with the size of wolf populations (presumably because wolves control populations of foliage-feeding moose)(McLaren and Peterson 1994).

As discussed earlier, the importance of top-down controls means by extension that functional stability is influenced by the availability of habitat for predators at both the stand and landscape scales. Several researchers have identified old growth or old-growth components such as large dead wood as important habitat for the natural enemies of herbivores. Torgerson et al. (1990) argued that protecting habitat for foliage-gleaning birds and ants (e.g., large dead wood) increased the overall health of forests. Schowalter (1989) found that old-growth canopies in both the Pacific Northwest and the southern Appalachians supported a greater diversity of spiders and a much more favorable balance between herbivorous insects and their invertebrate predators than plantation canopies. He suggested that old growth serves as a source of predatory insects for plantations, which, if true, means that herbivore dynamics are influenced by the proximity of younger to older forests. Similarly, McCutcheon et al. (1993) found that, compared to young Douglas-fir separated from old growth, old trees and young trees adjacent to old trees had a much greater diversity of foliar endophytes, a microfungus that lives symbiotically in plant leaves and helps defend plants against pathogens and herbivores. In all likelihood, these observations can be traced to the structural complexity of old growth, which affords more niches for animals and microbes.

Keystones

Webster defines *keystone* as "that one of a number of associated parts or things that supports or holds together the others." In ecology, keystones are species, groups of species, habitats (e.g., large dead wood), or abiotic factors (e.g., fire) that play a pivotal role in ecosystem (or landscape) processes and "upon which a large part of the community depends" (Noss 1991). (Mills et al. 1993 discuss the need to consider keystones in management and policy decisions.) Some landscape features, such as riparian zones or migration corridors, may also be keystones. Loss of a keystone produces cascade effects: the loss of other species and the disruption of processes.

There undoubtedly are keystone species within ecosystems. Frequently cited examples include the so-called builder, or ecosystem engineer, species, such as beavers, gophers, tortoises, termites, and earthworms that, through their activities, physically modify the environment in ways important to other species (Noss 1991, Jones et al. 1994, Lawton 1994, Perry 1994). There are also keystone groups of species that perform some unique function: Walker (1992) calls these functional groups. These might include nitrogen-fixing plants, plants that provide unique food resources (e.g., nut trees and flowering plants in conifer-dominated forests), plants that provide food during otherwise lean periods (e.g., various species of figs), and epiphytes (which support a long food chain in tropical forests because their cup-like leaves catch water). There are also keystone structures, such as large dead wood. The list could go on, but the point is that critical functions exist that are filled by one or a few species or structures.

One problem with the keystone concept is that interrelationships are so complex and intertwined within ecosystems that numerous species and mutualisms might qualify as keystones; in fact, given our limited knowledge of how species function in ecosystems, it is impossible at this point to say with certainty which species are not keystones. If, to give just one example, whitebark pine is a keystone food resource for various animals, then surely Clarkes nutcracker, which distributes whitebark seeds, is also a keystone. And how about the mycorrhizal fungi and other microbes that the pine must have to survive and grow, or invertebrates that cycle nutrients? Without the tiny and unapparent residents of the soil, most or all natural ecosystems on land (certainly all forests) would collapse.

There are relative degrees of "keystoneness"—that is, the loss of some species creates a ripple, the loss of others a tidal wave. For example, extirpation of chestnut trees from forests of the eastern United States (due to chestnut blight) led to the extinction of perhaps seven species of moths (Lepidoptera). From an ethical standpoint, seven species may be seven too many; however, from a functional standpoint those seven were only 12 percent of the Lepidoptera species that fed on chestnut, no vertebrate extinctions occurred, and processes such as primary productivity, nutrient cycling, and hydrologic cycling apparently emerged intact (Pimm 1991). Loss of fig trees from tropical forests would create a much bigger wave because numerous frugivorous species depend on them. The degree to which that wave spread throughout the system would depend at least in part on secondary effects arising from loss of the frugivores. In the final analysis, the most serious keystones—the ones whose loss creates a tidal wave—are those that play a singular role in key system processes: photosynthesis, food-web dynamics, nutrient and water cycling, controls over herbivores and pathogens, and maintenance of biological legacies following disturbance.

Threads of Continuity: Biological Legacies and Guilds

Within three years after the eruption of Mount St. Helens, 230 plant species—90 percent of those in pre-eruption communities—had been found within the area affected by the blast deposit and mudflows (Franklin et al. 1985). Quoting from Franklin et al. (1985):

> Successional theory traditionally emphasizes invading organisms or immigrants . . . but this script for ecosystem recovery could be played out at only a few sites, as surviving organisms over most of the landscape provided a strong and widespread biological legacy from the pre-eruption ecosystem. In fact, essentially no post-eruption environment outside the crater was completely free of pre-eruption biological influences, although there were substantial differences in the amounts of living and dead organic material that persisted.

Webster defines *legacy* as "anything handed down from . . . an ancestor." In an ecological context, legacies are anything handed down from a predisturbance ecosystem, including green trees, surviving propagules and organisms (e.g., buried seeds, seeds stored in serotinous cones, surviving roots and basal buds, mycorrhizal fungi and other soil microbes, invertebrates, and mammals), dead wood, and certain aspects of soil chemistry and structure, such as soil organic matter, large soil aggregates, pH, and nutrient balances. Most, if not all legacies probably influence the successional trajectory of the recovering system to one degree or another (although much research is needed). That is clearly the case with surviving plant propagules, which directly affect composition of the early successional community. Other legacies may shape successional patterns in more subtle ways. For example, the composition of the soil biological community following disturbance is a legacy that potentially influences the relative success of different plant species during succession (Amaranthus and Perry 1989a, 1989b, Perry et al. 1989b, Perry 1994).

Patches of mature and older forests that survive a given disturbance may be thought of as ecosystem-level legacies that allow certain species to persist while the rest of the landscape recovers. Even small fragments of mature forest may stabilize food webs and provide refuge for some species. In a study in southwest Oregon, mature forest fragments no larger than 3.5 ha produced 30 times more truffles per hectare than plantations, and had nearly twice as many truffle species (Amaranthus et al. 1994). The difference was particularly striking in August, the height of the summer drought in these forests. Truffles, the belowground fruiting bodies of mycorrhizal fungi, are an important part of the food chain, composing a major portion of the diet for some small mammals. In maintaining truffle production during summer drought, mature forest patches provide animals such as northern flying squirrels and California red-backed voles with food that is not available in plantations—in all likelihood contributing significantly to maintaining populations of these animals during a period of food shortage. Maintaining small mammal populations increases, in turn, the chances of maintaining predator populations.

Large dead wood is one of the more obvious structural legacies of a natural disturbance, and a major reason why clearcuts are not the ecological equivalent of natural disturbance. Dead wood can influence system recovery in several ways. Standing dead trees mitigate environmental extremes within disturbed areas by shading and preventing excessive heat loss at night. Decaying logs are centers of biological activity, including not only decay organisms, but also roots, mycorrhizal hyphae, nitrogen-fixing bacteria, amphibians, and small mammals (Harmon et al. 1986, Franklin et al. 1985). After disturbance, logs reduce erosion by acting as physical barriers to soil movement (Franklin et al. 1985) and provide cover for small mammals that disseminate mycorrhizal spores from intact forest into the disturbed area (Maser et al. 1978). The sponge-like water-holding capacity of old decaying logs helps seedlings rooted in them survive drought (Harvey et al. 1987). In the Amaranthus et al. (1994) study previously mentioned, the highest truffle production occurred in older, decayed logs, in all likelihood because the logs retained water during drought.

Soil aggregates and soil organic matter are important legacies. Large soil aggregates, which are created and sustained by roots and the hyphae of mycorrhizal fungi, are essentially little packages of mycorrhizal propagules, other microbes, and nutrients that are passed from the old forest to the new (Borchers and Perry 1990). Soil organic matter in general, whether contained in aggregates or not (most is), provides a legacy of nutrients for the new stand. Depending on its origin and stage of decay, soil organic matter can either stimulate or inhibit plant pathogens (Linderman 1989, Schisler and Linderman 1989).

The threads of continuity provided by biological legacies significantly influence the diversity of animal communities during the recovery phase. In the Pacific Northwest, richness of vertebrate species differs little among successional stages resulting from natural disturbances (fire, wind), and the majority of species that have been studied occur throughout the sere (see the review by Hansen et al. 1991). Hansen concludes:

> A likely explanation for the similarity in species distribution is that structural differences among these natural forest stages are insufficient to strongly influence most species of plants and animals. The natural disturbance regime and structural legacy in all . . . age-classes provide the resources and habitats required by many species. The important conclusion is that the canopy structures, snag densities, and levels of fallen trees found in unmanaged young, mature, and old-growth stands appear to make all three of these seral stages suitable habitat for most species of forest plants and vertebrate animals.

Note that "most species" does not mean all species; some are still restricted to one or another seral stage, and the proper mix of seral stages must be maintained if the objective is to protect regional biodiversity.

A plant that survives disturbance in one form or another (e.g., thick bark, living roots, buried seeds) clearly promotes the continuity of its own genome on a site, and the surest way to eliminate a species from a successional trajectory is to eliminate its seed source (as has happened with eastern hemlock throughout much of northern Wisconsin (White and Mladenoff 1994). But one species may also provide legacies that either promote or inhibit the continuity of others. Different plant species can affect soils quite differently through the soil organisms they support, the particular array of nutrients they accumulate, their effect on soil acidity, or allelochemicals they release. Sprouters and other pioneering plants often become foci for the establishment of other plants, a phenomenon called the island effect (Perry 1994). An established plant might provide perches for birds that disseminate seeds (Nepstad et al. 1990), shelter establishing seedlings from climatic extremes and herbivores, provide nutrient-rich microsites, or support mycorrhizal fungi or other beneficial soil organisms (Amaranthus and Perry 1989a, 1989b, Perry et al. 1989a, 1989b). Whatever the mechanisms, pioneers that sprout from roots or buried seeds constitute legacies that influence the recovery of other species within the system.

One hypothesis holds that species within a given community form into guilds based on common interests in mycorrhizal fungi and perhaps other beneficial soil organisms (Perry et al. 1989, Read 1994). According to this view, early colonizers during secondary succession facilitate subsequent colonization by members of the same guild by providing a legacy of mycorrhizal fungi (and perhaps other beneficial soil organisms). Studies in southern Oregon and northern California clearly show that Douglas-fir establishes most successfully in the vicinity of certain species of shrubs and hardwood trees that support the same mycorrhizal fungi as the conifer (Wilson 1982, Amaranthus and Perry 1989a, 1989b; Tom Parker, personal communication). The beneficial effect of hardwoods on Douglas-fir has been associated in one or more studies with accelerated root tip formation, greater numbers of total and mycorrhizal root tips, shifts in mycorrhiza type, increased associative nitrogen fixation in seedling rhizospheres, increased ratios of iron to manganese in seedling foliage, and faster rates of nitrogen cycling in soils beneath rather than apart from hardwoods (Amaranthus and Perry 1989a, 1989b, Amaranthus et al. 1990, Borchers and Perry 1990).

In one Oregon clearcut, soils beneath hardwood saplings had only 10 percent as many *Streptomyces* colonies as grass-covered soils in between hardwoods. *Streptomyces*, a common soil actinomycete that is the source of the antibiotic streptomycin, allelopathically inhibits a variety of other microorganisms and some plants, and has been implicated in regeneration failures in Oregon (Friedman et al. 1989, Colinas et al. 1994b). Borchers and Perry (1990) hypothesize that hardwoods discourage growth of *Streptomyces* through their ability to concentrate manganese, a known inhibitor of streptomycin. The possibility that hardwoods are simply growing in nutrient-rich microsites cannot be totally excluded. However, all evidence points to the likelihood that hardwoods are imposing a biological pattern on soils that benefits Douglas-fir. It does not follow, though, that relationships among plants within a guild are strictly cooperative. All plants need nutrients, water, and sunlight to survive, and guild members may compete for resources as well as benefit one another. Such multifaceted interactions are probably common in nature, and the outcome of a given interaction will vary depending on specific conditions, such as what resources are most limiting, and how dense one plant is compared to another.

Some plants actively inhibit others during the recovery phase. For example, grass seeded onto sites burned by wildfire in southern Oregon inhibited recovery of the native shrub community (Amaranthus et al. 1993). Plants able to produce dense, uneven-aged stands can effectively exclude others; such is the case with the Pacific Coast shrub salmonberry, which produces pure stands of 30,000 or more stems per hectare following disturbance, and which then maintains itself in uneven-aged stands through sprouting from basal buds and rhizomes (Tappeiner et al. 1991). Once a pure stand attains a sufficiently high density, plants with the reproductive potential of salmonberry likely will persist until weakened by pathogens or insects or confronted with a disturbance for which they are not adapted. However, caution should be used in inferring long-term trends from short-term observations. Early successional stages are frequently dominated by fast-growing shrubs and trees that are replaced in time by species with slower initial growth (Oliver 1981). Moreover, there can be tradeoffs between growth and survival. For example, Berkowitz et al. (1995) found that shrubs, herbs, and grasses reduced growth but enhanced survival of planted maples, especially during a drought year. Long-term competitive exclusion is likely to occur only when one species can prevent another from establishing at all. The patchiness of natural disturbances (which translates into varied regeneration niches) and the threads of continuity provided by biological legacies act to preserve diversity in the plant community. Grazing animals and pathogens can also promote plant diversity by keeping one or a few species from dominating. Elk and deer, for example, have been shown to reduce the cover of salmonberry relative to that of Douglas-fir seedlings in early successional stands in Washington State (Hanley and Taber 1980).

In some cases, a change in disturbance regime has altered a balance and allowed one plant species (or group of species) to spread at the expense of others. A series of foreign disturbances contributed to regeneration failures in parts of Pennsylvania (Horsely 1977): Settlement and widespread forest clearing for farms led to the extirpation of large predators such as wolves and mountain lions. The loss of predators combined with abundant food on abandoned farms to produce an explosion in deer populations, and deer overgrazed establishing tree seedlings, which were also subjected to fires burning through clearcuts. Herbs, ferns, and grasses attained dominance in clearcuts and further inhibited tree seedlings through the production of allelochemicals.

Allelopathy has emerged as a common theme where one or more species begin to aggressively exclude others. In California, overgrazing by domestic livestock allowed unpalatable *Wyethia mollis* to dominate early seral stages on burned sites; *Wyethia*, in turn, excluded tree seedlings, in part at least through allelopathy (Parker and Yoder-Williams 1989). In Sweden, excluding wildfires contributed to the spread of the dwarf shrub *Empetrum hermaphroditum*, which then allelopathically inhibited tree regeneration (Nilsson et al. 1993). Allelopathy has also been linked to poor tree regeneration in the Alps (Pellisier and Trosset 1989). More than 30 years ago, Handley (1963) suggested that some plant species may serve as nurse plants for others by ameliorating the allelochemical environment in one fashion or another. In support of this, our own work in southern Oregon led us to hypothesize that the spread of allelopathic *Streptomyces sp.* in clearcuts was facilitated by herbiciding early successional hardwoods that inhibit the spread of Streptomyces through their ability to accumulate manganese (Borchers and Perry 1990, Perry et al. 1992).

When Recovery Mechanisms Break Down: Threshold Transitions

Determining ecological significance is not always straightforward in cases where once-dominant species appear to be excluded by one or more others—as when *Wyethia mollis* or *Empetrum hermaphroditum* spreads and inhibits tree regeneration, or exotic grasses dominate clearcuts. Are these temporary digressions that will eventually revert to the former successional sequences without outside subsidies? Or are they threshold transitions from one persistent community type to another? If the former is true, managers may lose time but not sites; but if the latter is true, sites will be lost, perhaps irretrievably.

As we discussed earlier, there is no doubt that threshold transitions can and do occur. Conversion of arid grasslands to desert shrublands is the clearest example on land (Schlesinger et al. 1990). However, there are also examples in forests, particularly in stressful environments (cold or dry). For example, shifting cultivation has converted large areas of dry miombo woodland in East Africa to semidesert scrub (Jummane Maghembe, personal communication). In parts of the western United States, numerous high-elevation clearcuts have been planted three to four times each over the past two to three decades, with most plantings failing. With sufficient expense, these areas might be eventually reforested, but there is little doubt that these sites are not following their historic recovery patterns. Rather, they have been converted from forests to persistent communities characterized primarily by exotic grasses and herbs.

What mechanisms underlie the degradation of forested sites? Experiments on one degraded site in southwest Oregon (Cedar Camp) showed that planted Douglas-fir seedlings would survive and grow if given 150 ml (1/2 cup) of soil from an established stand, whereas control seedlings not given forest soil died (Amaranthus and Perry 1987). A number of factors appear to be involved: Compared to control seedlings, those given forest soils form root tips faster, form more mycorrhizae, and are less needy of fertilizer (Amaranthus and Perry 1989a, 1989b, Colinas et al. 1994a, 1994b). Experiments have shown that much of the beneficial effect of forest soils was associated with invertebrate grazers (protozoa, microarthropods), organisms that occupy the top of the belowground food chain and that are critically important in the nutrient cycle. But evidence indicates that the transferred soils had other benefits as well, such as providing "safe" sites in which developing roots and mycorrhizae were protected from allelopathic *Streptomyces* (which had proliferated in the clearcut), and in reintroducing a source of microbially produced plant hormones, such as ethylene, that stimulate root and mycorrhiza formation. Whatever the mechanisms, forest soils collected from the rooting zone of vigorous Douglas-fir contained factors that Douglas-fir seedlings needed to survive and that had been lost from the old clearcut.

How is it that these fire-adapted forests cannot regenerate after clearcutting? We believe the answer lies in the destruction of biological legacies: Unlike on a site burned by wildfire, there were no snags to ameliorate the environment for establishing seedlings, a factor likely to be critically important on these high-elevation sites. Herbiciding early successional shrubs removed an important stabilizing agent for the belowground ecosystem, and, unlike the native shrubs, the exotic annual grass (cheatgrass) that came to dominate the site did not stabilize elements of soil biology and structure required by the establishing seedlings. The apparent reduction in predators at the top of the soil food chain likely reflects sharply reduced energy flow to belowground food chains accompanying the transition from forest to annual grassland. As soil biology and structure changed, seedlings were unable to form roots and gather resources quickly enough to become established before the summer drought arrived. A vicious cycle ensued in which loss of soil integrity inhibited seedling establishment and the lack of regeneration led to further loss of soil integrity (Perry et al. 1989a, 1989b).

What happened at Cedar Camp illustrates a general ecological principle that was first demonstrated experimentally more than 20 years ago at Hubbard Brook Experimental Forest in New Hampshire (Bormann et al. 1974), where clearcutting followed by herbiciding early successional vegetation led to large nutrient losses to streams. The principle, applicable to any forested ecosystem is this: Trees, along with most if not all perennial plants, divert large amounts of energy belowground, where it fuels processes that feed back positively to plant growth (Perry et al. 1989a, 1989b); the "bioregulation" of soils by plants, to use Bormann and Likens's (1979) term, acts to retain nutrients, support food chains that cycle nutrients, support microbial mutualists of plants (e.g., mycorrhizal fungi and certain types of rhizosphere bacteria), and structure soils to improve their aeration and water-holding capacity. In other words, plants and soils compose a self-reinforcing system in which energy flow from plants maintains the soil ecosystem, which feeds back to promote plant growth. This general dynamic—energy flow creating nonequilibrium pattern—can be extended beyond the plant–soil interaction to include other food chains within communities. The stability of such systems depends critically on the ability to dampen fluctuations and maintain processes within certain bounds (Prigogine and Stengers 1984, Perry et al. 1989a, 1989b). While details will undoubtedly vary from one site to another, when energy flow from plants to soils is disrupted, changes ensue in soil biology, chemistry, and physical structure that, if allowed to go too far, progressively diminish the ability of soils to support the original plant community. Sites may become dominated by annual weeds, which, because of their low productivity and life history, are likely to require less integrity in the soil system than perennials. Little is known about the potential for such changes in forests, however they are best guarded against by maintaining a cover of trees or ecologically equivalent shrubs at all times. Tree cover at the level of a traditional shelterwood is probably sufficient, though research is needed to verify this.

Cedar Camp illustrates a threshold transition resulting from the disruption of biological legacies and the consequent breakdown of key processes. Threshold transitions are also likely if seed sources are lost, or if the environment (especially climate or the disturbance regime) is altered to favor new species over the previous dominants. These factors tend to reinforce one another. In northern Wisconsin, for example, logging and slash fires (a change in disturbance regime) combined to sharply reduce the cover of eastern hemlock, which had dominated many old-growth forests of the region (White and Mladenoff 1994). Hemlock was not adapted to survive intense fires, which prior to settlement had occurred at intervals as great as 2,500 years or more (Frelich and Lorimer 1991). With the hemlock seed source gone, White and Mladenoff (1994) conclude that "[t]he pre-European settlement pattern of hemlock forests may be irretrievably lost due to the consequences of logging, fire disturbances, and regeneration failure." Similarly, factors that favor an intensified fire regime in forests (e.g., forest clearing and spread of flammable grasses in the tropics, and buildup of fuels in the dry forest types of western North America) will, unless checked, almost certainly result in threshold conversion to plant communities more tolerant of dry conditions and fire. Moreover, fires that burn too frequently may degrade soils and trigger a transition to annual weeds (Perry 1995a), a possibility that should be taken seriously both in dry forest types and in the moist tropics.

Diversity and Stability: What Can We Conclude?

Does everything depend on everything else? Intuitively it seems unlikely that an ecological system without some redundancy in key processes would persist long in the highly variable environments that characterize the real world (cf. Wilson and Botkin 1990). The loss of chestnut trees from forests of the eastern United States would seem to verify that, at least in that system, major processes were buffered against the loss of a dominant species. On the other hand, the more modest assertion that everything depends on something else seems irrefutable and can be extended without too much risk to say that everything is tied into a network of interdependence that encompasses from a few to many other species, some of which may be keystones and others members of functional groups (Berryman 1993). The glue that ties these networks together comprises the key processes—photosynthesis, nutrient cycling, hydrology, and population regulation (to name a few)—that run the system. It is the interaction between species and processes that not only creates interdependence, but defines the ecosystem, and which must be the basis of ecosystem management. Unfortunately, the scientific knowledge needed to understand the complex interactions that underpin ecological dynamics is in its infancy.

Considerable caution should be used when evaluating whether the loss of species has impacted the larger system or not. In many cases the stabilizing effect of diverse species is manifested during infrequent periods of stress: It was drought that revealed the importance of diversity in stabilizing prairie productivity (Tilman and Downing 1994) and wildfire that showed how some hardwoods shield conifers from flames (Perry 1988). Moreover, redundancy in key processes can actually mask a weakening of ecosystem buffering capacity associated with species loss—that is, the plane that loses a few rivets may fly just fine in good weather but break apart in a storm. Holling (1988) spoke to this in his analysis of whether the loss of insect-eating birds could, by itself, lead to increased insect outbreaks in North America. He concluded that resilience provided by redundancies in the controls over insect populations would prevent this from happening, and went on to generalize:

> This great resilience demonstrates a property common in ecological systems. First, the stability domains are large and the variables within them can fluctuate extensively. Second, the regulatory processes that are present are remarkably robust to external changes. . . . This is not to say, however, that ecological systems are infinitely resilient nor that loss of robustness of regulation short of producing a qualitative flip in behavior has no costs. Loss of resilience from one cause can make the system more vulnerable to changes in other events that otherwise could have been absorbed. . . . Ironically, the great resilience of ecological systems masks slow erosion of their capacity to renew and in those circumstances leave managers ill-prepared for surprises.

If it is unlikely that everything depends on everything else, it is equally unlikely that there is absolute redundancy in any process—that is, that any two species maintain the same process equally well at all times and under all conditions. A more accurate view would be relative redundancy (Perry 1994): Species within a functional group do the same job, but in different ways or at different times. The result can be a complex control structure that includes both redundancy and keystoneness. Controls over herbivorous insects provide a good example of what appears on the surface to be redundancy, but when viewed more closely is not. Berryman (1993) says that—

> populations of leaf-eating insects are sometimes controlled by guilds of insectivorous vertebrates when their densities are very sparse, by larval parasitoids if they escape from vertebrate imposed limitation, by pathogens if parasitoid regulation fails, and by competition for food in the absence of all the above.

The greatest functional diversity in nature is provided by the organisms that receive the least attention from both scientists and managers, the invertebrates and microbes—E. O. Wilson (1987) called invertebrates and microbes "the little things that run the world." Consider mycorrhizal fungi. Because each species of mycorrhizal fungi has its own set of physiological characteristics (Trappe 1987), none can be said to be strictly redundant to any other. Some may be active during cool or moist periods, others when it is warm and dry. Some are particularly effective at gathering nutrients from mineral soil, others at extracting nutrients bound in organic matter. Some thrive in large dead wood, others in humus, yet others in mineral soil. Healthy forests typically support a highly diverse ectomycorrhizal flora (Arnolds 1991, Fogel 1976, Hunt and Trappe 1987, Luoma et al. 1991, Menge and Grand 1978). To give one example, over 200 ectomycorrhizal types have been described from mature conifer and hardwood stands in southwest Oregon (Eberhart, Luoma, and Amaranthus 1995). It is highly probable that the array of functional niches provided by this diversity contributes significantly to the ability of long-lived trees to cope with fluctuating and often unpredictable environments (Perry 1995a).

Management Implications

The shift to a more dynamic view of nature has important implications for both forestry and conservation. In forestry, or for that matter any area of natural resource management, it means that, in theory at least, humans don't have to be a blight on the earth: With the proper understanding of nature's dynamics, management systems can be devised that sustain productivity and some, perhaps much, biological diversity. (It does not follow, however, that biological diversity can be sustained solely on managed lands, or that sustainability can be achieved without controlling human numbers and consumption.) While ecosystem dynamics are complex and for the most part poorly understood, the emerging scientific view has clear management implications.

1. Protect indigenous biological diversity. No forest ever has been or ever will be free from the threat of rapid swings in climate, outbreaks of tree-eating insects and pathogens, fire, wind, etc. Today's world carries new risks: widespread exotic pests, pollution, harmful levels of ultraviolet radiation, greenhouse-related climate change, and the risk of overutilization arising from population growth and an economic system that encourages consumption and rewards exploitation. From a practical standpoint, it makes no difference to managers whether the rivet hypothesis (everything depends on everything else) is false, ecologists are nowhere near being able to point to any one species and say with certainty that that one can be removed with no significant effects on the rest of the system, and ecologists won't be able to do that for a long time, if ever. Protecting biological diversity is the best insurance foresters and society can buy to protect the long-term integrity of the world's forests.

2. Protect soils. If soil integrity is lost, so is the ball game.

3. Plan at the landscape scale. No forest is an island, nor is any reserve or park. The critical role of landscapes and regions in buffering the spread of disturbances, providing pathways of movement for organisms, altering climate, and mediating key processes such as the hydrologic cycle means that the fate of any one piece of ground is intimately linked to its larger spatial context (Hansson and Angelstam 1991, Saunders et al. 1991, Franklin 1993, Pickett et al. 1992, Berg et al. 1994). One unavoidable implication is the necessity to view regional landscapes as wholes rather than disconnected pieces of different ownerships and land-use categories.

4. To conserve species in the long run, plan for the future. Once change is seen as inevitable, it becomes obvious that species cannot be preserved simply by reserving existing habitat (Franklin 1993). At some point that habitat will burn up, blow down, or be destroyed by

some anthropogenic insult that originates beyond its borders, such as pollution or climate change. Where will new habitat come from? For species that persist in early successional stages, this is not a problem—their habitat is created by disturbance. Species that require later successional stages are another matter; management strategies must provide for the development of their habitat, with or without human assistance.

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