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PATCH DYNAMICS AND THE ECOLOGY OF DISTURBED GROUND: A FRAMEWORK FOR SYNTHESIS

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INTRODUCTION

The purpose of this chapter is to present a framework for patch dynamics and to indicate how it clarifies and unifies several of the important themes in this volume. Although disturbance is a familiar concept, there have been significant refinements to the concept since its widespread adoption in the 1970s (e.g., Loucks, 1970; Levin and Paine, 1975; Pickett and Thompson, 1978; Pickett and White, 1985). In addition, as ecologists have accumulated data on more and more kinds of ecological systems, spatial scales of study, long time spans, and kinds of disturbance events, new insights and hypotheses have emerged (Wu and Levin, 1994). This chapter will point to illustrative examples of studies that have led to new or refined insights, and combine the empirical and conceptual approaches taken, to present a contemporary view of patch dynamics which is capable of putting the ecosystems of disturbed ground in their most complete spatial and dynamic context. The differences between the contemporary perspective we present and the earlier ideas and understanding of disturbance and its effects are sometimes subtle. However, the emerging appreciation of the rich and varied role of ecosystems of disturbed ground is based on just that subtlety.

This chapter relies on the depth of empirical examples presented in the book, and emphasizes the framework rather than presenting a complete literature review. The main themes we address are:

(1) that disturbance necessarily has a spatial context in which the ecology of disturbed ground can be understood;
(2) there are limits to employing the intuitive concept of disturbance that first emerged in community ecology at other scales and in other kinds of ecological systems;
(3) added generality and comparability of disturbances and studies of disturbed systems result from a more rigorous and scale-independent concept of disturbance;
(4) structural models of ecological systems are crucial for discriminating disturbance from other kinds of alterations of ecological systems;
(5) spatial heterogeneity in disturbed ground and systems at a variety of spatial scales is functionally important;
(6) the contemporary patch-dynamics concept accommodates the foregoing insights in addition to others presented in the chapter, to enhance unity and dynamic scope in the study of disturbed ground ecosystems; and finally,
(7) we indicate the significance of the hierarchical, patch-dynamic approach to disturbed-ground ecological systems, which allows their potential contribution to stability of more extensive ecological systems to be evaluated and used in management.

DISTURBANCE AS A SPATIAL CONCEPT

Here we define disturbance and give a few examples to flesh out the abstract definition. Because disturbance is a physical force or event that disrupts the physical or biological structure of an ecological system (Fig. 31.1), there will be a geographic location where that disruption has occurred. Hence, the concept of disturbance is subtle because it implies an event, a location or affected system, and a result. At some spatial resolution, it is possible to delimit the disturbed site from the adjacent undisturbed areas. For instance, a population that has

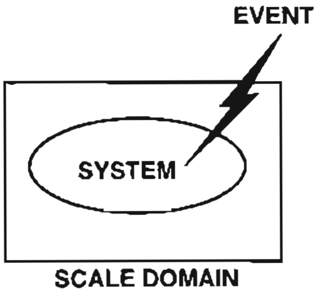

Fig. 31.1. Three crucial features to be specified in understanding the process of disturbance. The scale domain refers to the temporal and spatial extent and grain by which the system of interest is described. The event that may potentially disturb the system arises from outside of the system and its specified scale domain. Additional features are described later in association with the construction of a systems structural model to assess disturbance.

experienced disturbance may show a gap with a density of zero, surrounded by sites in which the population density remains high. Or a desert stream may exhibit some patches in which the bed has been scoured or the banks have collapsed, removing patches of stream habitat or the riparian vegetation that formerly occupied those sites (Fisher et al., 1998). Or a large tree may be blown down in a closed-canopy forest, leaving a gap in which the vertical structure of the community, from the rooting zone upwards, is now altered. As a final example of disturbance, a portion of a landscape in which humans exert energy to change the temporal pattern or frequency of fire can come, over a short time, to exhibit an altered structure.

All of these are examples of disturbance that affects a recognizable physical location, which is the basis for the focus of this book on ecosystems of disturbed ground. On the time scale at which dynamics and persistence of the system are of interest, locations have been affected by some force external to that location interacting with the structure of the system to alter the existing structure and create something new. In those new, disturbed patches, ecological processes and species composition may differ from the predisturbance conditions. In order to understand ecological systems that have been subjected to disturbance, the alterations of composition and processes by disturbance must be known. Understanding change in composition and processes has practical implications for management, conservation, sustainable use, or restoration of such systems (Hobbs, 1987; Boeken and Shachak, 1994; Arnold, 1995).

Because disturbance has spatial extent and limits, related concepts are needed to understand disturbance and the ecology of disturbed ground. These will be introduced, defined, and exemplified throughout the chapter. Here we indicate how they will be related to one another and to the central concept of disturbance. The auxiliary concepts include heterogeneity, landscape context, and patch dynamics. Disturbance creates patches recognizable at certain scales. Disturbance acts with various intensities, and hence creates heterogeneity in space. Therefore knowing the landscape context of disturbance is crucial for determining what events are or are not disturbances, how different potentially disturbing forces act and interact, how disturbance may appear through space, how fluxes of organisms and materials contrast between disturbed and undisturbed sites, and how different parts of landscapes respond to disturbance. In addressing these issues, the concept of landscape is taken in the most general sense as a criterion of observation (Allen and Hoekstra, 1992). A landscape is a heterogeneous spatial array of ecological patches at any scale. The emphasis is on heterogeneity rather than on a particular spatial scale (Turner, 1989). All of these aspects of systems that experience disturbance suggest that the emerging understanding of disturbance is more subtle than the original concept, despite the successes of that rather intuitive understanding. The final concept to be discussed below will be patch dynamics, which will be used to integrate the other concepts.

Beyond the intuitive

Disturbance is a deceptively simple and intuitive, yet important, idea. It is relevant to the ecology of the full range of Earth's biomes, but the concept originated with the experience of ecologists at the community level of organization (Watt, 1947). Community ecologists noticed sudden disruptions of community structure by powerful natural forces originating outside the community (Sousa, 1984). The impacts of disturbance were obvious because the scale of the observations at the community level are close to the human scales in time and space of decades and meters. Ecologists could literally enter the aboveground structure of many communities, especially forests and woodlands, while in other systems, such as grasslands or mussel beds, it was easy to comprehend the structure from above. The condition of the system before the disturbance, the magnitude and direction of the structural and compositional changes caused by the disturbance, and the extent of the reorganization that ensued, were

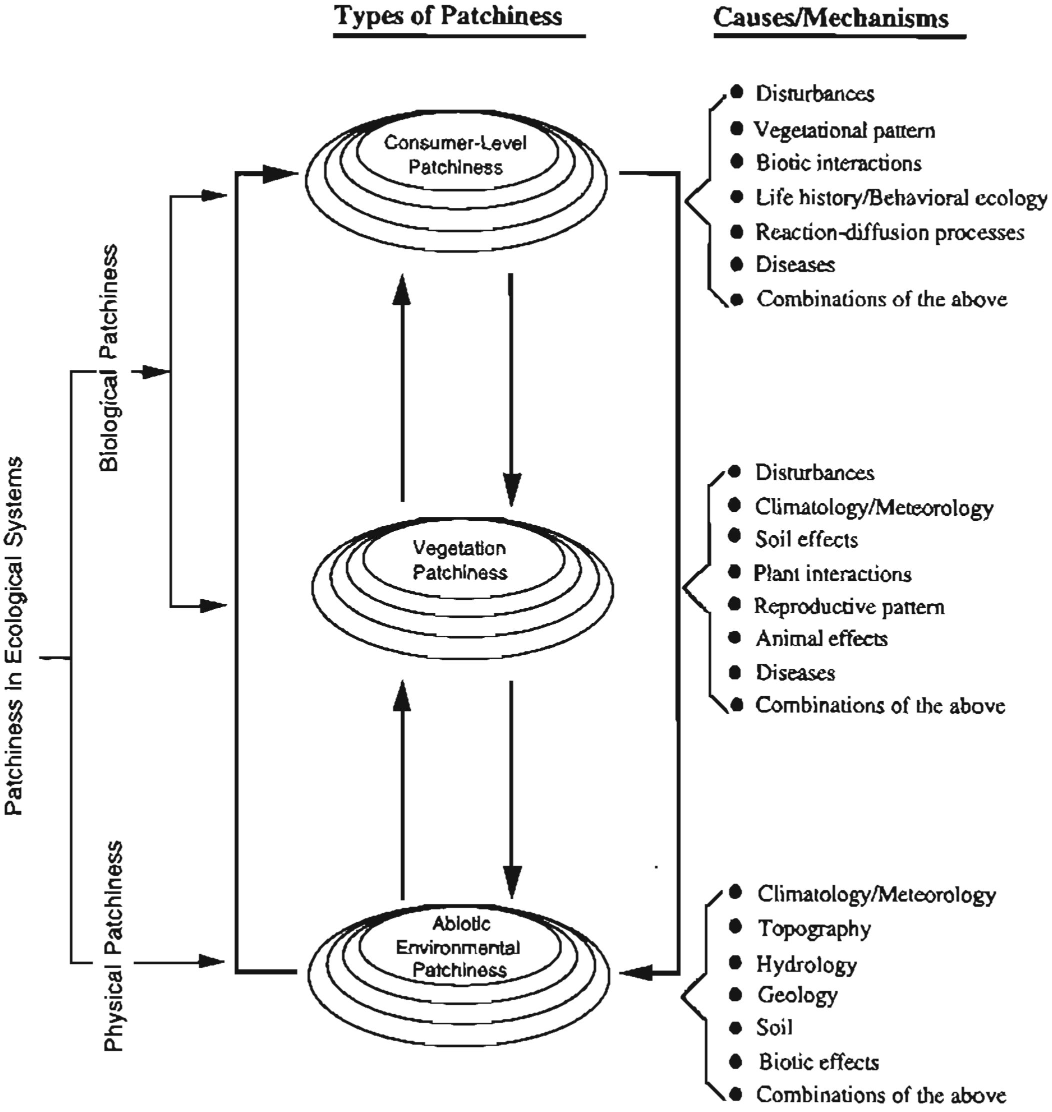

Fig. 31.2. Hierarchies of patches created by different kinds of disturbances. Patchiness is divided into physical and biological categories. Within biological patches, vegetation processes and the effects of consumers can generate patchiness. Each of the specific types of patchiness can be generated by a variety of mechanisms. The process of disturbance is not listed separately since it acts through the other specific phenomena listed. From Wu and Loucks (1995).

all obvious and intuitive. Ecologists recognized that the closed architecture and layering of organisms was functionally important, and controlled the access of different species or layers to limiting resources (Horn, 1974; Allen and Forman, 1976). Furthermore, ecologists could visit the same systems year after year, or even after decades, and observe little change. In such situations, sudden disruption of community structure was conspicuous and extreme (Falinski, 1978; Canham et al., 1990). Physical disruption of some forests, grasslands, or mussel beds, after long periods in more or less the same structural and compositional state, intrigued ecologists and required a conceptual label. This led to the adoption of a common language term – disturbance – in a specialized, technical sense (Pickett et al., 1989). The commonsense, intuitive connotations have unfortunately persisted.

When ecologists began to apply the intuitive concept of disturbance beyond the usual temporal and spatial scales of community ecology (Fig. 31.2), the need for increased rigor became apparent. If disturbance is to be truly valuable in unifying knowledge about a wide variety of ecological systems and processes, such as the breadth encompassed in this volume, the rigorous and exact aspects of the concept must be emphasized over the intuitive (Rykiel, 1985). Furthermore, disturbance must be put in a framework that shows (1) how it can interact with ecological systems observed by different criteria (*sensu* Allen and Hoekstra, 1992) or at various hierarchical levels; (2) what role it plays at various ecological scales, including large and small heterogeneous landscapes; (3) how it connects with the processes of succession; and (4) how diffuse disturbances work and how they relate to the distinct concept of stress.

Although the concept of disturbance has been most widely used at the scale of meters and years on which communities are usually studied, smaller systems can also experience disturbance (Coffin and Lauenroth, 1989; Wu and Loucks, 1995). One reason to seek increased rigor and subtlety in the concept of disturbance is that ecological systems of vastly different spatial extents and grains experience disturbance. If generality and contrast are to be discovered in the understanding of disturbed ground, the concept must be applicable across scales. One may recall that the basic definition of disturbance is the sudden disruption of the structure of an ecological system. Old-field vegetation, though not so intimately experienced by most ecologists from beneath its canopy as forests, can also undergo canopy-gap formation (Goldberg and Gross, 1988), soil turnover by frost heaving or animal activities (Korn, 1991), and so on. On still smaller scales, the structure of the canopy of a single plant can be disturbed. For example, if the nipping of buds to consume spring sap by arboreal mammals reflects outbreak levels of the herbivore population, its sudden onset and episodic pattern may make it fit the basic definition of disturbance (Pickett et al., 1989) for the array of species – the ecological system in this case – comprising a network of host-specific species or other organisms depending on that plant individual. Such alteration may make opportunities available for new epiphytes, or change the resource flux to organisms beneath the disturbed canopy. On smaller scales still, damage to a leaf by a herbivore constitutes a disturbance to the system of resident fungi. The effects of such events can also spread throughout a more extensive network of interacting species, leading to a change in structure of larger ecological systems of which individual plants or small sites are a component. The structural changes resulting from small disturbances at the individual plant level can alter resource flux in the larger system and redistribute resources. Small, inconspicuous disturbances at the individual level can propagate so that they lead to disturbances to larger systems. Keeping the concept of disturbance tied to the scale of meters and years on which ecologists typically study communities satisfies the intuitive view of disturbance, but it does not permit broad hypotheses about the generality of occurrence, control, or effect of disturbance to be tested.

Toward generality and comparability

If the ecology of systems on disturbed ground is to be fully understood, the relationships of disturbance at different scales and in different kinds of ecological systems also must be understood. Moving beyond the intuitive connotations of the concept of disturbance requires ecologists to examine how disturbance applies to other scales and kinds of systems (Petraitis et al., 1989). Disturbed ground can support all the kinds of systems exemplified in this section. It is important to recognize that focus on disturbed ground does not presuppose that one of these kinds of systems rather than the others is the object of study.

Populations are among the ecological units other than communities that can experience disturbance. The sudden alteration of population density, size, or age structure is an example of disturbance. Often patches of reduced density or with other structural changes result. The outbreak of a disease, say in a population of oaks (*Quercus* spp.), or the mortality of a band of spruce trees (*Picea* spp.) on a mountain side are population disturbances. Of course, these can also be expressed at the associated community or ecosystem realms. The mortality of seedlings smaller than a certain size threshold due to frost heaving, fire, or browsing, is a common disturbance expressed in the population realm. One may note that many disturbances in the population sphere may be seen by population and evolutionary ecologists as strong selection episodes (Endler, 1986). However, these events still encapsulate the essence of disturbance.

Ecosystem disturbances are those physical events that affect the pathways by which matter or energy flow in a system. Focusing on this criterion of ecological observation, patches appear as a result of some of the same kinds of events that drive disturbance in communities. However, the ecological structures and processes of interest in the site differ from or extend beyond those typical of community ecology. Catchment alterations, such as the experiments at Hubbard Brook (Likens et al., 1978; Likens, 1984; Likens and Bormann, 1995), change ecosystem structure in a patchy fashion, altering export of nutrients and particulates in stream or lake water. Wind-throw creates patches in coniferous-forest ecosystems in the Pacific Northwest of the United States, changing the amount of coarse woody debris on the ground and altering the decomposition rates in the ecosystem (Harmon et al., 1986). If some of the coarse woody debris created by such a forest disturbance accumulates at certain spots in a stream channel, it can act as a dam, suddenly alter the form of the channel, and concentrate sediment and organic matter, which in turn alters the ecosystem carbon budget (Hedin, 1990). An outbreak of grazing animals converts biomass in the canopy to biomass in litter, and shifts the relative roles of the detritus and grazer food chains in specific spatial locations in an ecosystem (Risley and Crossley, 1988).

The landscape criterion is one in which spatial heterogeneity is the underlying principle. One approach to landscapes is to consider them to exist primarily at physical scales where human populations, institutions, and settlements are obvious structural components. Hence, Forman and Godron (1986) defined landscapes as being kilometers wide in extent. However, that scale is only one instance of landscapes, which are spatial arrays resolvable as patches that can exist on any spatial scale. Therefore, in order for landscape theory to apply, spatial heterogeneity, expressed as a variety of patches, must be considered, as well as the processes that create and connect the patches. To ask whether a landscape has been disturbed, therefore, is to ask whether the physical structure of heterogeneity is changed. The issue is not whether a fire creates a new patch, or whether succession converts one patch type to another, which could represent the community realm. Rather, the concern is whether some event has altered the mixture of patches or the kinds of connections among them. Disturbances that can wreak such changes are alterations of the patterns or agents of patch creation, or alterations of the spatial configuration of patches.

Landscape disturbances, because they deal with mosaic structure, are likely to be of two sorts (Forman and Moore, 1992). One is the creation of barriers within the landscape. The other is the alteration of the processes that create the kinds of patches making up the landscape. The latter requires some sort of physical force originating climatically, geomorphically, or anthropogenically, and thus requires expenditure of energy or displacement of materials at various locations in the landscape (Swanson et al., 1988). Because the forces that generate patches often also appear on the community or ecosystem level as disturbances, when a large-scale landscape is considered to be composed of communities or ecosystems, then the alteration of the structure of the landscape – disturbance of the landscape – is a larger-scale disturbance made up of the pattern of the smaller-scale events that might themselves be deemed disturbances on the finer scale of communities or ecosystems nested within a landscape. The important refinement for applying the concept of disturbance to scales and criteria beyond the community is to recognize that whether an event acts as a disturbance or not depends both on the scale and intensity of the event, and on the nature of the system. We explore this relationship in the next section.

System structural models

Two important ideas emerge from the examples of disturbance at various scales and ecological realms. First, what is considered a disturbance depends very much on the nature of the system under consideration (Rykiel, 1985). Therefore, before disturbance is evaluated and studied, the system of concern must be clearly described and a model of the system structure explicitly stated (Pickett et al., 1989). A model of the system relevant to understanding whether the concept of disturbance applies to that system and event tells several important things:

(1) What are the components of the system, including physical structures and interactions among them?
(2) What temporal and spatial scale does the system occupy?
(3) What is the nature of the boundaries in the system – that is, how permeable are they, and what fluxes move across the boundaries?

It should be noted that we are referring to a static, structural model of the system to make the role of events that might be disturbances unequivocally apparent. Other kinds of models of the same system can be constructed for other purposes.

Often arguments and uncertainties about what is or is not a disturbance, and whether the disturbance emerges from inside or outside the boundaries of a system, result

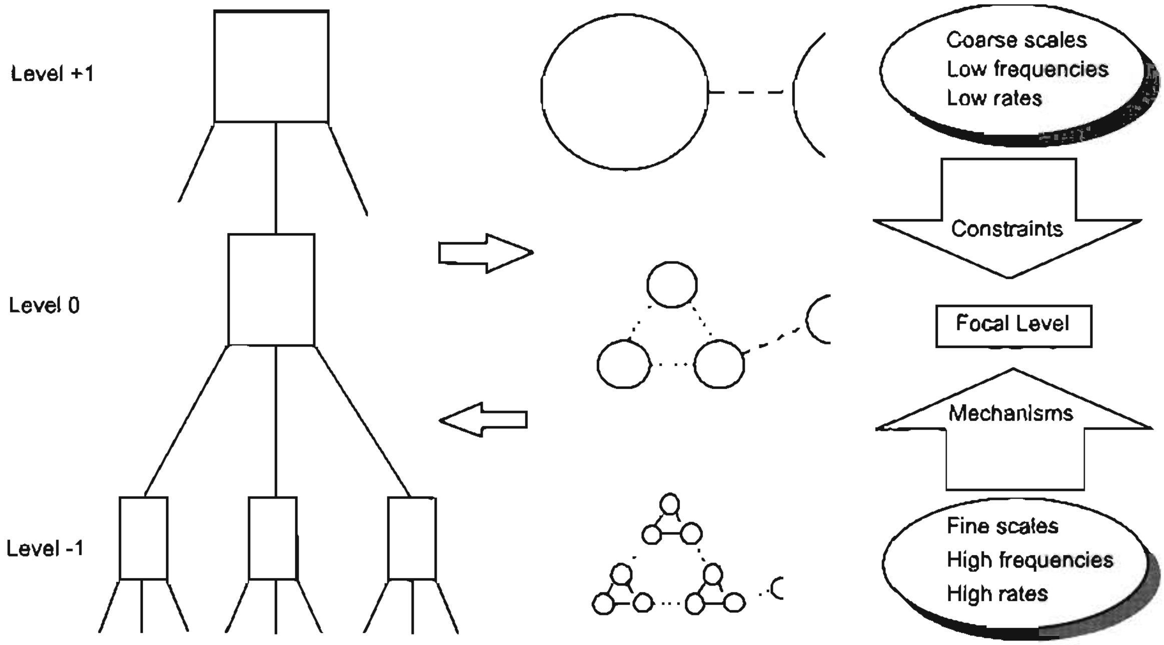

Fig. 31.3. The structure of a nested hierarchy. Because disturbance is a direct disruption of structure of a particular hierarchical level, a hierarchical conceptual model is required to assess what events are disturbances. Agents that operate with different frequencies and rates must necessarily act at different levels of the hierarchy. Stress at a lower hierarchical level may cause the physical disruption of a higher-level structure, and hence generate disturbance at that higher level. Modified from various concepts in O'Neill et al. (1986), and Urban et al. (1987).

from the error of beginning to evaluate disturbance before the model of system structure is specified and clearly stated. Whether the system model is complete, and whether it is appropriate to the research question and goal at hand, are always legitimate questions, of course. But the criteria for evaluating disturbance emerge from combining the model of the structure of the system with the fundamental definition of disturbance as a physical disruption of the structure of a system. Therefore, we can now refine the definition of disturbance by stating that it is the physical disruption of the structure of a system as specified by an explicit, if preliminary, model.

A second idea also emerges from the examples. What constitutes a disturbance at one scale or for one ecological phenomenon, may not constitute a disturbance for others (Pickett et al., 1989). Hence, disturbance for a population may be invisible to the community of which that population is a part. Disturbance to an ecosystem may be negligible to the large landscape of which the ecosystem is a part. Disturbances at finer scales or lower levels, or more specialized phenomena, often become part of the structure of the larger scales, higher levels, or more general phenomena. This phenomenon is called *incorporation of disturbance* (O'Neill et al., 1986). Arguments about whether a disturbance event is normal (i.e., has been incorporated) or not, often arise from a careless mixing of scales, criteria, or levels. Keeping such important fundamentals clear is another task that an explicit system structural model can accomplish. Indeed, linking systems models as parts of a nested hierarchy is a helpful strategy for assessing disturbances in closely related systems (Fig. 31.3).

STRUCTURAL SOPHISTICATION IN EVALUATING DISTURBANCE

Because the purpose of this chapter is to provide a conceptual framework for synthesizing key insights about the ecology of disturbed ground, we have so far emphasized ongoing conceptual clarification and rigor in applying the concept across scales and kinds of systems. In this section, we emphasize some of the insights that emerge from the empirical study of disturbed ground. We rely on the substantive review provided by the foregoing chapters, and cite only a few illustrative cases here.

Clements (1916), early in his pioneering synthesis of succession, introduced the need to understand disturbance. He called the process "nudation", and took it to be the initiation of the complex process of succession. Unfortunately, Clements's term can connote that nudation creates a uniform, blank slate (e.g., Oosting, 1956), and is therefore of interest only as the starting point for the phenomenon of restoring the vegetation climax in an area. One important feature of Clements's (1916) idea of disturbance was the recognition that events of great severity could initiate primary succession in which a biotic and soils legacy was lacking, while more modest disturbances would generate secondary successions that began with some biotic or soils capital. Of course, contemporary theory recognizes that these two processes are ends of a continuum (Miles and Walton, 1993). This section highlights insights from the concentrated study of disturbance since its widespread recognition beginning roughly in the 1970s (Loucks, 1970). That empirical effort has shown that the structure of disturbed sites is both complex and functionally significant. In general, because heterogeneity is so important to the structure and functioning of ecological systems (Chesson, 1986), especially in the maintenance of biodiversity (Huston, 1994), it is crucial to understand the pattern created, amplified, or reduced by disturbance. In fact, the heterogeneity of disturbed ground may be one of its most important ecological features.

Heterogeneity

Heterogeneity affects the role and impact of disturbance in ecological systems. Contrary to the simplicity and uniformity connoted by Clements's concept of nudation, most disturbed patches are themselves heterogeneous. For instance, burned areas at all scales, from the Yellowstone Plateau on the coarse scale (Knight and Wallace, 1989), through the pitch pine (*Pinus rigida*) plains in the New Jersey Pinelands (Forman and Boerner, 1981), to the small prairie remnant (Anderson, 1990; Collins and Wallace, 1990), are patchy. Owing to a variety of climatic and topographic factors, and to differences in fire behavior and fuel loading, there are spots that do not burn at all, or that burn with only low intensity, as well as patches in which all biota are consumed (Christensen et al., 1989). The post-fire soil conditions often reflect the heterogeneity of the burn. A particularly telling case of heterogeneity is the enormous variety of conditions and substrates created by the 1980 eruption of Mount St. Helens in Washington State (Del Moral, 1993; see also Chapter 5, this volume). The textbook definition of primary succession led many ecologists to assume that Mount St. Helens would straightforwardly illustrate primary succession. On the contrary, the area was immensely complex. There were areas of intact vegetation, mudflows, pumice plains, lake overwashes, and many other types of disturbance. The contribution of legacies and survivors was notable (MacMahon, 1982). In other volcanic situations, the flow of lava from a specific eruption rarely coats an area uniformly. Wind disturbances are also diverse in their patchiness. The damage to a forest canopy by a hurricane may vary over a matter of tens of meters only (Boose et al., 1994). The uprooting of a single tree by wind will leave a pit from which the roots were wrenched, a mound of soil wasting from the exhumed roots, and fallen trunk and branches, often with leaves concentrated in specific spots. The form of the pit and mound, and hence their suitability for different colonists, can depend on exactly how the tree was uprooted (Beatty and Stone, 1986). Other wind-throws, such as long tracks created by severe tornadoes (Peterson and Pickett, 1995) or fans created by down-drafts (Dunn et al., 1983; Nelson et al., 1994) can be quite large. Depending on the topography they cross, and the condition of the forests they encounter, there can be pits and mounds of differing sizes, fallen trunks, snapped trees, tangles of crown debris and patches of leaf litter, patches of surviving shrubs, broadleaved herbs, tree seedlings, or ferns (Peterson and Pickett, 1990). Animal-generated patches can also be heterogenous. A porcupine (*Hystrix indica*) digging in a Middle Eastern desert creates a pit, and a small mound of earth nearby (Boeken et al., 1995). Some organic matter, and even some surviving bulbs, appear in spots within the pit. Wallows of grazing animals are also not uniform across their extent.

The heterogeneity generated by disturbance and persisting in disturbed ground is important for a variety of ecological processes as mentioned above (e.g., Walker et al., 1991). Here we expand on that idea. Invasion of new propagules may concentrate in certain patches within the disturbed site (Fox and Fox, 1986). Regenerating seedlings may survive better in debris piles. Resources may only become available in some sites, such as hummocks left after wetland disturbance, which serve as safe sites for establishment. Likewise, resources may concentrate or persist only in certain sites, such as the depressions created by tree-fall. Such within-gap heterogeneity is crucial to seedling performance (Nuñez-Farfan and Dirzo, 1988). Flows of limiting resources may be profoundly influenced by the patch structure created by disturbance. The debris dams in streams already mentioned are key examples, but on various scales, the susceptibility of streams to disturbance (Reice, 1994) results in great heterogeneity. The array of sand bars, reed beds, and bank types is sensitive to disturbance, and is important for use of arid-zone riparian and stream systems by wildlife (Rogers, 1997). Stream-side habitats have conservation value for rare but relatively fugitive plants in temperate regions as well (Menges, 1990).

Diffuse disturbance

So far, we have focused on the patchiness created by disturbance. There is another way that disturbance may be manifested. Rather than being discrete and patchy *at a particular scale*, disturbance may have diffuse results. For instance, in certain sites, a hurricane may not topple any trees, yet leave the forest canopy considerably more open than before, and result in a new resource regime in the understory (Walker, 1991). Similarly, an unusual early wet snow on a deciduous forest canopy may break many branches and thin the canopy throughout the forest. Or a severe drought in a grassland may kill many plants and leave the survivors smaller than during well-watered periods (Weaver and Albertson, 1943).

All these examples – driven by such factors as wind, snow, ice, and drought – are cases of diffuse disturbance. Disturbance that increases structural heterogeneity at a particular scale *without creating discrete gaps at that scale* are called diffuse disturbances. Of course, at a coarser scale of observation, the disturbed areas that are diffuse at the finer scale may appear as patches distinct from the adjoining lands. The phrase "diffuse disturbance" emphasizes that, like so many ecological concepts, disturbances form a continuum. Disturbance, at a particular scale, ranges from discrete to diffuse. The same agents of disturbance may have diffuse or discrete effects depending on where in geographic space they occur, and the degree and spatial pattern of susceptibility of the system to the agent.

An important insight to arise from the study of diffuse disturbance is that stress can sometimes be the cause of disturbance. We fit these cases to the basic definition of disturbance because the initial cause arises as a coarser-scale event triggered from outside the area of interest resulting in structural change. For example, the structural disturbance caused by drought-induced mortality is sudden in terms of the long-term status of the grassland, and was initiated as severe stress to individual plants. This is an example of transformation of stress into disturbance. Stress refers to a factor that directly alters the function of an ecological system. The root of the stress concept in biology comes from physiology, where stress is a factor that alters the metabolic rates or physiological processes of an organism. Keeping the useful dichotomy between structure and function in place among various ecological criteria of observation, not just that of the individual organism, suggests that disturbance affects structure directly, whereas stress directly affects function. Altered structure can affect function at other scales or levels of organization, and altered function can affect structure at other scales or levels. Stress and disturbance are related, but they must not be confounded.

Landscape context

Putting disturbed sites in their landscape context indicates that disturbed patches are not isolated systems. They have the potential to interact with other patches, both neighboring and distant ones, in the landscape. In order to understand the potential for patches to interact in landscapes, their spatial relations must be described. Patches have size and shape, and these features along with what patches they abut, how far they are from similar patches, and the diversity of patch types in the landscape, determine the function of patches (Saunders et al., 1991). For example, patches of a particular composition may exchange dispersing organisms. The organisms of interest may not use patches that have some other structure. Therefore the status of that organism in the landscape depends on the spatial configuration as well as the sizes of their preferred patches. Old-field or grassland birds in primarily forested regions are a case in point (DeGraaf and Miller, 1997). Their regional demise may reflect a decrease in the number of disturbed patches and the distance between them.

Likewise, movement of materials through patch mosaics can depend on the structure of the mosaic. How materials move through patches having vastly different resistances will determine the flux of those materials through the landscape. This is generally referred to as connectivity. Connectivity may involve recognizable corridors defined by patches of the same or similar type across a landscape. Or, more generally, it may be an abstract description of the ability of a patch mosaic to facilitate or retard flow of a material from point to point in a landscape. When connectivity for one process and direction is achieved by the existence of a corridor, a flow perpendicular to it, or the flow of another material or organism, may be resisted. Hence a corridor in one direction may act as a barrier between patches arrayed in a different way in a mosaic. These phenomena illustrate the importance of accounting for the actual array of patches in a landscape in order to evaluate their function and relationship to one another.

Three-dimensional patch bodies

Patch interaction should not be thought of as though patches were two-dimensional features on maps. Although patch arrays are most often represented as simple, flat maps, patches in real ecological landscapes and mosaics have three dimensional structures (Breen et al., 1988). In fact, the contrast between neighboring patches may often be as much a matter of architecture as of species composition. Forest plantations versus forest stands that arose from unmanaged seeding are two such contrasting patch types (Bradshaw, 1992). The three-dimensional structure of patches extends both above and below the substrate. Forest and field patches may differ in the soil as well as in their vegetation canopies. The hyporhoeic zones of pools and riffle patches in streams may differ as much as the water column. The links between the two systems through upwelling and downwelling of nutrients act to enhance the stability of the larger system comprising both zones (Valett et al., 1994). The movement and retention of organisms, energy and momentum, water and water vapor, and nutrients and pollutants may be conditioned by the three dimensional structure of disturbed patches among their undisturbed neighbors.

The boundaries between patches are areas of special concern for the interaction of ecosystems of disturbed ground with neighboring patches. Apparently assuming that homogeneous areas promote the spread of disturbances, Forman (1987) stated that increasing heterogeneity in a landscape would *decrease* the permeability of the mosaic to disturbance. Fire is perhaps the best example of a disturbance agent that requires a homogeneously well-fueled matrix. Disease agents or pests with low contagion are another example. However, whether a heterogeneous or a homogeneous landscape will better promote the spread of disturbance depends on the particulars of the agent, its mode of spread, and the interaction between those features and the landscape structure.

The interfaces between neighboring patches are most often referred to in the literature as "edges". The connotation of this term is of a contact representable by a simple line on a map. A different reality is emerging from empirical studies, however (Gosz, 1993). Edges, like the patch bodies they bound, are complex, three-dimensional zones that can extend well into each of the neighboring patches (Cadenasso et al., 1997). Different factors of the physical environment show different spatial patterns across edges (Chen et al., 1995; Cadenasso et al., 1997). The physical structure and biotic composition of the ecosystem also exhibit gradients or step functions across edges (Geiger, 1965; Ranney et al., 1981; Williams-Linera, 1990). Together, the abiotic and biotic gradients and structures can act as either filters or pumps, or be neutral to flows across an edge (Pickett and Cadenasso, 1995). Much work remains to be done on this topic, but it is clear that the nature and structure of the edge between disturbed ground and its neighboring patches affects the behavior of those sites (Draaijers et al., 1994). Combining the various insights about structural heterogeneity outlined above, one may conclude that descriptions of ecosystems and communities of disturbed ground can no longer be silent about the structure of the patches or the nature of the landscape array in which disturbed ground appears.

PATCH DYNAMICS AND DISTURBANCE: CHANGE IN DISTURBED-GROUND ECOSYSTEMS

All the patterns and processes discussed above show the richness of influences that affect the structure in systems of disturbed ground. The value and utility of the knowledge of disturbed-ground ecosystems can be further increased by bringing it together in a single perspective that examines changes within disturbed ground ecosystems and the larger matrix in which they occur (Veblen, 1992). This section summarizes the current state of that perspective – patch dynamics.

There are two major causes of change affecting ecosystems of disturbed ground. First is the creation of new disturbed patches, and second is the alteration of existing patches. These two processes must be considered together to understand the patterning and function of disturbed-ground ecosystems. It is important to recognize that some of the other patches with which a disturbed patch may interact have arisen or been altered by processes other than disturbance (Frelich et al., 1993). Some patches may be relatively permanent, established by resource hot spots and geomorphic features, while others may be more ephemeral and dynamic. The fluxes from these different kinds of patches may differ, and for some may be relatively permanent, while in others the fluxes may change through time as a result of patch change. In any event, the entire landscape structure must be understood in order to determine how systems of disturbed ground function.

The landscape context suggests that in an array of patches, disturbance can be an important agent for creating new patches and altering the array. Because patches themselves can be dynamic and disturbance can act at various locations in a mosaic, the entire array may change (Remmert, 1991). This is the concept of patch dynamics, which refers to the changes in a spatial mosaic of patches over time, regardless of the scale of the mosaic, or the origin of the changes. This section will focus on disturbance as a major cause of patch dynamics in spatial mosaics, and the reciprocal effects between disturbance and patch mosaics.

The temporal and spatial pattern of the creation of new patches by disturbance is the disturbance regime. A disturbance regime describes the various kinds of disturbance agents, the size, shape, and dispersion of disturbed patches, and the frequency with which the different kinds of patches are created. More detailed characterizations of disturbance regimes can include the internal heterogeneity of patches, and their relationship to particular geographic or landscape positions. In general, disturbance regimes and patch dynamics are spatially explicit concepts associated with the landscape viewpoint of ecology.

Disturbance regimes are the spatial and temporal patterns of disturbance in specific areas. They are a key determinant of patch dynamics. Ecologists can use disturbance regimes to compare landscape dynamics across environmental gradients, or between contrasting sites. One kind of persistent spatial driver of differences in disturbance regime is the existence of local gradients of soil depth. In small desert catchments, patches disturbed by animals or better supplied with water are more common than in shallower soils elsewhere (Boeken et al., 1995). An example of the kind of comparison that becomes possible through being able to describe contrasting disturbance regimes is the different canopy structure, root architecture, and hence ecosystem functions in tropical forests exposed to different intensities and frequencies of hurricanes (Lugo and Scatena, 1996). Although few disturbance regimes have been completely characterized, especially their large, infrequent components, the recognition that a full understanding of any ecological system must include assessment of its disturbance regime is a significant advance (Denslow, 1980; Tilman, 1996). At least some sizes and intensities of disturbance occur in virtually all ecological communities and ecosystems, and there remains the need to determine how the appearance of disturbed-ground ecosystems relates to physical or biotic patterns at a coarse to medium scale.

The complexity of patch dynamics

One of the most important open questions about the landscape configuration of disturbed patches is whether the presence and configuration of disturbed ground enhances the spread of disturbance in the landscape. Cases where disturbed ground acts as an inoculum for further disturbance in an area are the propagation of insect and disease outbreaks (Nothnagle and Schultz, 1987; Knight, 1987), the spread of fire (Turner et al., 1989), and the increasing fetch around gaps that promotes wind-throw (Li et al., 1993). Sites that have been disturbed can sometimes act as firebreaks or windbreaks, however, depending on the structure of the surrounding landscape.

The distribution of disturbed-ground ecosystems is determined by the intersection of different disturbance probabilities across geographic space. The creation of patches by disturbance is intimately linked to ecological heterogeneity. At the coarser level, patch creation depends on the heterogeneity of the matrix in which disturbance acts. For example, in a large landscape, the intensity and frequency of fire depend on slope position (Hadley, 1994; Turner and Romme, 1994). More generally, specific agents that can act to disturb different ecological systems are conditioned by gradients and geographic location (Harmon et al., 1983). Earthquakes in fault zones can act as important agents of disturbance both to low-elevation estuary systems, for example the coastal Valdivian rainforests of Chile (Veblen, 1985), and in steep areas with high rainfall or where human or natural defoliation or deforestation is severe. This last situation can occur with logging or with tropical hurricanes in mountainous regions (Garwood et al., 1979; Walker et al., 1996). Differential sensitivity to disturbance in space causes certain types of disturbed ground to have characteristic geographic distributions, as illustrated by various chapters in this volume.

Internal patch change

Patches experience internal change. The most obvious internal change in patches in ecological landscapes is community succession. The arrival of different species in a patch, the growth and interaction of organisms in the patch, the alteration of resource pools and nutrient processing, and the variety of direct and indirect feedbacks among these organismal, community, and ecosystem processes change patches dramatically over time (MacMahon, 1981). It is beyond the scope of this chapter to review the richness of the literature on patch succession (Miles, 1979; Glenn-Lewin et al., 1992). However, it is one of the most powerful agents of change in disturbed patches, and hence in the larger mosaic in which disturbed patches are a part. The successional status of a patch, and of its neighbors, can determine its susceptibility to subsequent disturbance.

Human management also causes patch change. In fact, management in most patches is essentially equivalent to altering the rate or trajectory of succession in patches (Luken, 1990). Hence, most human management is a manipulation of the disturbance status and subsequent successional status of ground disturbed at some point (Pickett and Rogers, 1997). Often the disturbance associated with management will be frequent and intense. But even in less intensively managed landscapes, disturbance will often be the tool that is brought to bear, or which is prevented or altered in order to produce systems with particular characteristics (Rogers, 1997).

Finally, patch change now has a large human dimension in many landscapes (McDonnell and Pickett, 1993). Because human tenure and occupancy has spread so widely, the social and economic cycles that humans generate are now important engines of patch change (Turner et al., 1990; Cronon, 1991). On the global scale, the local intensification and spread of agricultural and extractive land uses, the spread of urban–industrial influence, and indeed the increasing spread of urban areas, including suburbs, second homes, resorts, and the like, are all generating disturbed ground over vast regions. These patches change as management tactics and intensity change, as land uses change, and as more or different people come to occupy them.

These three major classes of patch change – succession, management, and human settlement – together generate complex and dynamic mosaics of patches experiencing or recovering from disturbance, or merely moving from one type or intensity of disturbance to another. Disturbed ground is now in close proximity with less or rarely disturbed sites, and the interaction is one of the principal features of global environmental change. The dynamics within patches are ubiquitous and rapidly evolving.

Changes in disturbance regime

Disturbance regimes are not necessarily fixed through time. Like climatic regimes, they are multivariate and subject to gradual or abrupt change through time (Clark, 1988). In fact, shifts in climate likely account for most natural changes in disturbance regimes. For example, there are apparently long-term cycles in the El Niño–Southern Oscillation that alter drought and flooding intensities and intervals over much of the globe (e.g., Leighton, 1986). These climatic cycles are associated with disturbances as disparate as fires, floods, landslides, and windstorms. Migrations of species (Brown and Heske, 1990; Johnston, 1995), especially animals capable of "ecological engineering" (Jones et al., 1994), or geomorphic change are other potential causes of change in disturbance regimes. Disturbance regimes are also commonly altered by humans. Humans often interfere with natural disturbance regimes by inserting new kinds of disturbance – say, fire in systems formerly predominantly disturbed by wind. Alternatively, people and institutions can alter the frequency of disturbance agents that remain active, as in the case of changing flooding frequencies and intensities (Sparks, 1996). One of the most widespread modern alterations of disturbance regimes is the increase of energy subsidies that results from the replacement of non-industrial or locally subsidized human societies by industrial societies that draw on global markets and fossil-fuel subsidies. A complete understanding of disturbance patterns in landscapes requires knowledge of the role of various kinds of human subsidy in modifying or maintaining certain disturbance regimes. In spite of the transient nature of disturbance regimes on longer time scales, it is valuable to recognize that certain kinds, intensities, and distributions of disturbance events may, on a shorter time scale, be relatively predictable as key features of many ecological situations.

Some implications of patch dynamics for disturbed-ground ecosystems

Disturbed ground can be part and parcel of the functioning of persistent ecological landscapes. The stability of the system is the dynamic stability of a shifting mosaic of patches (Bormann and Likens, 1979). For some period of time while the climate and other forcing functions, including anthropogenic ones, remain relatively constant, the mosaic can act as a shifting steady state. This suggests that the interaction among disturbed patches, and the descendant patches of various successional states that replace them, is a key component in understanding how disturbance fits into ecological systems, and how those systems function. Focus entirely on individual patches of disturbed ground can give a misleading picture of their role in larger ecological processes or landscapes.

A hierarchical approach is required to evaluate the role of patch dynamics and metastability in system persistence. "Metastability" refers to the situation in which a system at a certain scale is stable whereas component parts of the system in fact change (Hanski, 1995). Many systems have metastability as a key feature of their persistence as a result of the widespread occurrence of disturbance regime and the patch dynamics they engender (Turner et al., 1993). Systems do not persist in the face of change by simply always resisting disturbance at a given level. Rather, many systems respond to the creation of disturbed patches through altered fluxes of materials, energy, and species (Likens, 1984). Indeed, many species take advantage of the disturbance *per se* or the changes that follow disturbance and the initial response of certain organisms and ecosystem components to it.

A system that is hierarchically divided into dynamic patches is not necessarily stable. One may witness the metapopulations that are in a transient state, with satellite populations being sinks rather than equal partners in periodically supplying colonists to other subpopulations in the system (Pulliam, 1988). An example is the bay checkerspot butterfly (*Euphydryas editha bayensis*), which has a large core population supplying a series of satellites (Noon et al., 1997). However, the question for any subdivided, hierarchically patchy system must be asked: is the system metastable?

A final value of considering disturbed ground in terms of disturbance regimes is a practical one. Because so many systems now or in the past experienced natural and non-industrial anthropogenic disturbance, disturbance is one tool available for managing wild or traditional human-dominated ecological systems (Harrison and Fahrig, 1995). Disturbance may be manipulated in many ways, including mimicking the heterogeneity and conditions created by natural disturbances, and modifying the resistance of systems to disturbance (Turner and Dale, 1990; Tilman, 1996). At the scale of large landscapes, such manipulations can affect the movement of species and materials across edges, and the function of mosaics of patches. For example, Franklin and Forman (1987) evaluated the role of different kinds of forest harvesting regimes in structuring a forest landscape, and their sustainability for resource extraction and provision of ecological services. Thus, disturbed ground and its ecological characteristics can be harnessed for restoration, production, sustainable management, and a host of other specific management goals (Pickett et al., 1997).

CONCLUSIONS

Ecological understanding of systems of disturbed ground has been enhanced by many conceptual and empirical developments over roughly the last decade. Initial research into the ecology of disturbance focused on demonstrating that the process of disturbance was ecologically significant, and on determining how widespread and frequent it was. Appropriately, the most obvious and intuitive examples, and the most highly impacted systems, were exploited in those studies. However, as knowledge has increased, and more systems have been examined, the understanding of disturbance has become more subtle and better placed in context.

Disturbance is now recognized to be a concept of much broader applicability than when it was first introduced. Rather than being restricted to a particular spatial scale or criterion of ecological observation, it can be generalized to large and small systems, and can apply to the individual, population, ecosystem, and landscape. Such generality requires recognizing the core definition of disturbance as being an event that interacts with the structure of an ecological system to change directly the structure of the system. In order to apply this more general definition to specific situations, a model of the system is required that specifies the components, interactions, and temporal and spatial scales used to describe the system.

Disturbances can be arrayed along gradients of intensity, and can have both discrete and diffuse effects at a particular scale. The gradients of intensity interact with gradients of structure in ecological systems to produce heterogeneity within disturbed sites. Heterogeneity produced by disturbance is a major cause of the variety and nature of the post-disturbance responses of ecological systems, and is proving to be a ubiquitous feature of disturbed-ground ecosystems. This realization contrasts greatly with the simplifying assumptions of early disturbance studies. Placing disturbances and disturbed sites in an explicit landscape perspective recognizes both the role of heterogeneity within disturbed sites, and the coarser-scale heterogeneity which influences sensitivity and response to disturbance. The contemporary view of patch dynamics summarizes this richness of spatial effects on and of disturbance.

As longer time series have accumulated in the study of disturbance, the variability of disturbance regimes with climate and human-accelerated environmental change has become apparent. Not only is this knowledge important in understanding the ecology of natural systems, but it is also crucial for effective management and conservation of natural and anthropogenic systems. In fact, the distinction between natural and anthropogenic systems is hard to maintain, so that management and restoration now commonly require disturbance regimes to be understood, their effects replaced, mimicked, or compensated for. Taken together, the insights summarized in this chapter show that disturbed ground is an important, vital, and dynamic part of ecological landscapes at all spatial scales.

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