

DISTURBANCE IN TERRESTRIAL ECOSYSTEMS: SALIENT THEMES, SYNTHESIS, AND FUTURE DIRECTIONS

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INTRODUCTION

Disturbance has become a leitmotif of contemporary ecology. It affects all terrestrial biomes and may play a critical role in determining key structural and functional aspects of many ecosystems. Theories of disturbance have changed the way that ecological systems are viewed; rather than static entities, landscapes comprise patches affected by various disturbances and undergoing temporal changes as a consequence of succession (i.e., they are shifting mosaics). Simple equilibrium approaches may be inadequate; models that incorporate meta-stability, chaotic behavior, or complex-system perspectives may be more useful. Recognition of the non-equilibrium or dynamic nature of ecosystems is especially important because humans, as potentially intense agents of disturbance on a global scale, are effecting changes in structural and functional aspects of ecosystems, as well as modifying disturbance regimes to an extent to which few species are adapted. Understanding the ecology of disturbed ground, and how to manage heterogeneous and increasingly fragmented landscapes effectively, while balancing concomitant needs of human societies, may become the greatest challenge in the next century. Success at meeting this challenge will require the dedicated efforts and cooperation of the scientific establishment, governmental and private agencies, and local populations throughout the world.

In the following section, we summarize fourteen recurrent themes that appeared throughout the chapters of this volume, and are pertinent to understanding disturbance ecology and management. We do not extensively survey other disturbance literature, but instead refer the reader to the extensive literature citations in the preceding chapters. In the second part

of this chapter, we present two models that crystallize our current understanding of the relationships between disturbance and ecosystem response as mediated by patch dynamics and successional processes. We also suggest future directions for research on disturbance ecology and management.

SALIENT THEMES

Of the recurrent themes that emerged from the diverse contributions to this volume (Fig. 33.1), perhaps the most important is the interaction between disturbances. The various elements of a disturbance regime are not independent or random in occurrence; rather, particular agents related to earth, air, water, fire, or the biota form an interacting network of correlated disturbances (Walker and Willig, Chapter 1). Directly or indirectly, such disturbances result in spatial heterogeneity and temporal variation in ecological characteristics of sites. In view of this, we focus on interactions early in our exposition, followed by a consideration of spatial heterogeneity. Aspects of the physical environment which cause heterogeneity (e.g., slope, aspect, elevation, geological characteristics) combine with the disturbance regime to produce a geographic mosaic of patches which differ to various degrees in abiotic and biotic features. Equally important, post-disturbance changes in the ecological characteristics of sites occur as a result of dynamic interactions among the surviving biota, immigrating taxa, and the disturbance regime, continually changing the abiotic and physical characteristics of sites. Taken together, these changes represent ecological succession. After considering the importance of disturbance regime,

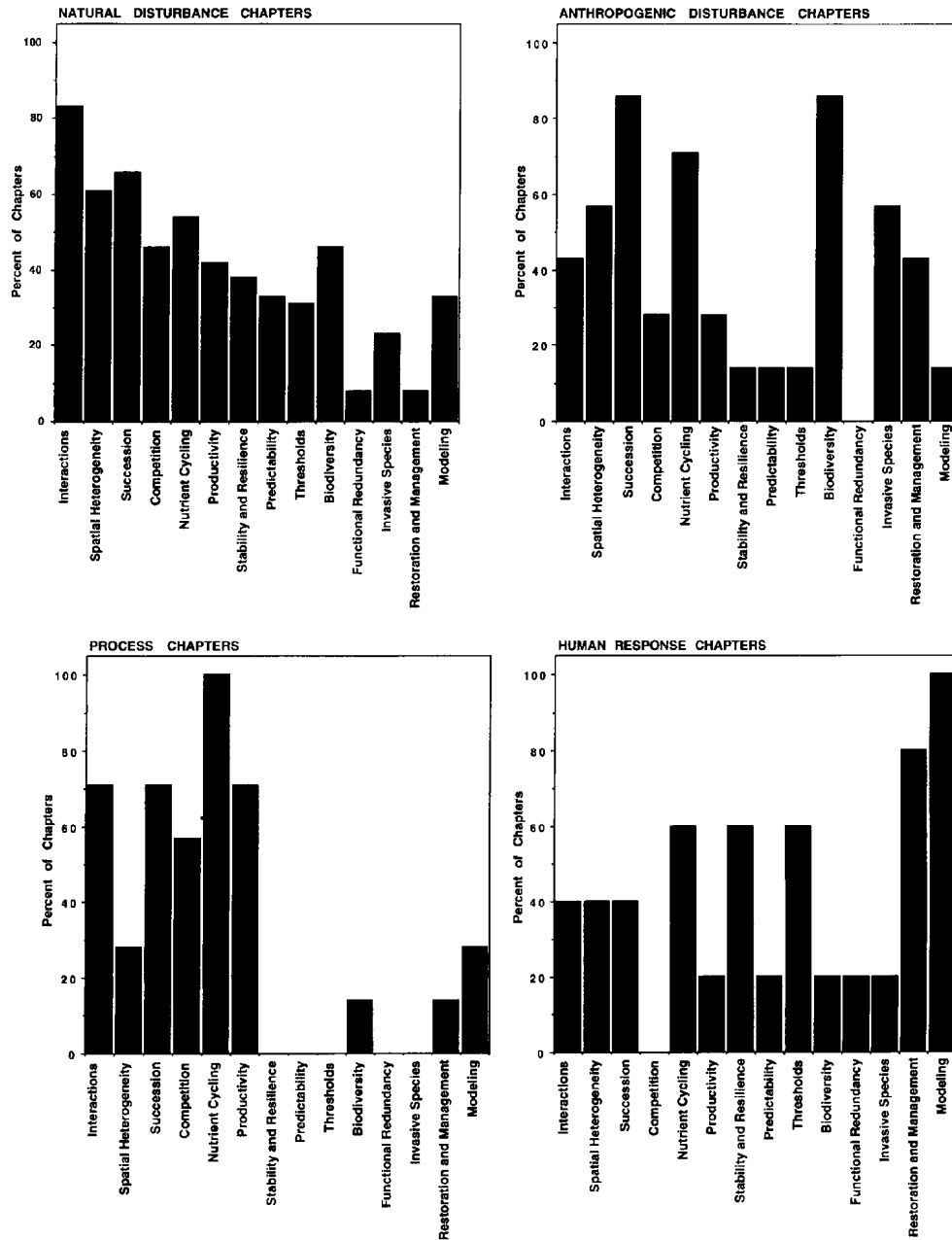


Fig. 33.1. Major themes of the chapters in this volume include interactions, spatial heterogeneity, succession, competition, nutrient cycling, productivity, stability and resilience, predictability, thresholds, biodiversity, functional redundancy, invasive species, restoration and management, modeling. The proportion of chapters [excluding the Introduction (Chapter 1) and the current chapter] in each of the four sections of the volume (natural disturbances, $n = 12$; anthropogenic disturbances, $n = 7$; natural processes, $n = 7$; and human responses to disturbance, $n = 5$) that consider each theme in a substantive manner is indicated by the height of bars in the corresponding diagram. Table 1.2 (p. 14) identifies which of these themes are discussed in a particular chapter.

spatial heterogeneity, and ecological succession, we continue our discussion by focusing on disturbance-related characteristics of systems: nutrient cycling and productivity, stability and resilience, predictability, and threshold effects. Thereafter, we address two interrelated themes of disturbance ecology (biodiversity and invasive species) at the level of populations and communities, which are particularly important from the perspective of conservation biology, and we follow with a consideration of restoration and management. We address modeling as an integral part of synthesis, and conclude with a suite of recommendations for areas of research that will advance the conceptual development of the ecology of disturbance.

Interactions

Disturbance regimes include a number of interacting elements and are illustrated for the tabonuco (*Dacryodes excelsa*) forest in Puerto Rico (Fig. 33.2). Some disturbance elements are much more likely to trigger others (e.g., in Puerto Rico, hurricanes may induce drought, flooding, tree-falls, and landslides, and even affect forestry practices). Conversely, some disturbance elements are predisposed to occur as a consequence of previous disturbances (e.g., in Puerto Rico, herbivory may be stimulated as a consequence of stress on plants induced by hurricanes, droughts, tree-falls, forestry practices, road construction, or landslides). Clearly, the occurrence of a particular disturbance modifies the likelihood that at least a subset of the elements in the disturbance regime subsequently will impinge on the same area.

From a biogeographic perspective, interactions are pervasive and characterize the disturbance regimes of all biomes. Consequently, interactions are considered in many of the chapters in this book (Fig. 33.1). Indeed, the interactive nature of these elements contributes to the difficulty of associating particular abiotic and biotic effects unequivocally with their causal agents. For example, anthropogenic activities in Los Angeles enhance the dry deposition of nitrogen in portions of the eastern Mojave Desert (Rundel, Chapter 10). Enhanced levels of nitrogen then facilitate expansion of cover by annual grasses, the dead stalks of which subsequently act as kindling for fire. Fire is then fueled by annuals between desert shrubs, which were previously outside the range of this disturbance. Finally, declines in the abundance of shrubs may have concomitantly facilitated the invasion of the exotic

herb *Erodium cicutarium* in regions of the western Sonoran Desert, especially during wet years. Clearly, disturbances can interact in complex fashions, and their effects are often synergistic rather than additive.

From an applied perspective, chapters dealing with restoration (Hobbs, Chapter 29) and environmental policy (Barrow, Chapter 28) clearly recognize the interactive nature of disturbance. In fact, they consider wise management policies and activities to be predicated on understanding how human intervention (or absence of it) interacts with natural disturbance regimes to attain desired goals. Humans, as agents of disturbance, are unique in having the ability consciously to modify the frequency, extent, and intensity of their own activities in order to minimize or maximize the severity of their effects on populations, communities, or ecosystems. Humans may be equally unique as biotic agents of disturbance which have the potential to jeopardize their continued existence. Especially as a result of recent technological advances, humans have become an invasive species with the capability to cause severe disturbances threatening the continued existence of many species, the structure of communities, and functioning of ecosystems.

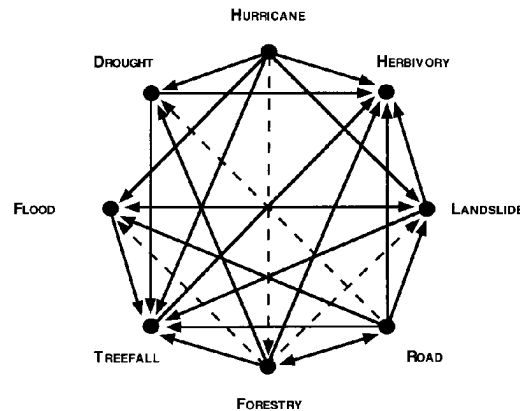


Fig. 33.2. The disturbance regime of an area comprises a number of interacting agents. For example, in the tabonuco forest of Puerto Rico, hurricanes, herbivory, landslides, roads, forestry, tree-falls, floods, and droughts affect the structure and function of the forest. The occurrence of one agent of disturbance (e.g., a hurricane) may enhance the likelihood of subsequent disturbances to various degrees, with stronger enhancements indicated by solid arrows (e.g., herbivory, landslide, tree-fall, and drought) and weaker enhancements indicated by dashed arrows (e.g., forestry). Some agents of disturbance have reciprocal effects, indicated by double-headed arrows (e.g., landslides enhance the likelihood of flooding, and flooding enhances the likelihood of landslides).

Spatial heterogeneity

The disturbance regime of an area comprises different agents (e.g., herbivore outbreaks, tree-falls, hurricanes, droughts, termite mounds, anthropogenic activities). As a consequence, the effect of a particular disturbance (e.g., hurricane) on the structure and function of a biological system, at the population, community, or ecosystem level, depends on the distribution, intensity, frequency, and extent of each agent; their degree of spatial and temporal correlation; their synergisms; and the current status of the biological system upon which they impinge (see Figs. 33.3 and 33.4, and the discussion on pp. 760–765). Given the variety of agents of disturbance that can affect any system, and the complexity of their interactions, it is often difficult to predict with reasonable confidence the severity of effects. Disturbance regimes, by their very nature, inject heterogeneity to the landscape at a variety of spatial and temporal scales. Ecological succession superimposes additional heterogeneity on the system, as disturbed patches change in biotic and abiotic characteristics over time.

Early views of disturbance (White and Pickett, 1985) emphasized its discrete nature in time and space, as well as the production of patches with discrete boundaries (e.g., a landslide). That view has evolved and gained considerable sophistication during the past decade (Pickett et al., 1994; see also Pickett et al., Chapter 31), and now recognizes that disturbances may be characterized along a gradient from highly discrete (e.g., a tornado) to diffuse (e.g., a drought). The characterization of a disturbance along the gradient from discrete to diffuse is predicated on the particular scale at which heterogeneity is manifested in the landscape. To the extent that a disturbance alters heterogeneity at a particular scale, without creating discrete gaps at that scale, it is diffuse in nature. Moreover, a disturbance must be defined within the context of the system of interest (Pickett et al., Chapter 31). Explicit delineation of a preliminary model of that system (structural components and their interactions) aids in distinguishing disturbances from other ecological “forcing functions”. Nonetheless, clear and unambiguous definition of a system model is not associated frequently with ecological studies of disturbance, and may at times contribute to controversy (e.g., compare Schowalter and Lowman, Chapter 9, with Willig and McGinley, Chapter 27).

Although many of the chapters in this book address

issues of patch-formation and spatial heterogeneity (Fig. 33.1), few provide a comprehensive description of patch dynamics for any particular system or an explicit conceptual model. Indeed, such coverage is beyond the scope of each chapter and likely is unavailable for many if not most ecological systems. Broad landscape-level heterogeneity in abiotic and biotic conditions is a consequence of some disturbances, as illustrated by the following examples. Volcanoes create a variety of sterile patches (lava, pyroclastic flows, and most lahars) on which primary successions proceed, as well as patches containing some biotic elements (thin tephra and some lahars) on which secondary successions proceed (del Moral and Grishin, Chapter 5). Large-scale differences in the frequency and intensity of fires exist among boreal regions, which in part affect differences in species composition and life history characteristics (Engelmark, Chapter 6). For example, forests with intense fires often have patches comprising even-aged stands of the dominant trees, whereas in areas with less intense fires the stands of dominant trees are more mixed in age structure. Winds create gaps of various sizes both in temperate forests (Webb, Chapter 7; Binkley, Chapter 18) and in tropical forests (Whigham et al., Chapter 8; Hartshorn and Whitmore, Chapter 19), as well as in polar regions (Komárková and Wielgolaski, Chapter 3), and in wetlands (McKee and Baldwin, Chapter 13), creating a mosaic-like structure across the landscape. In general, the size of the patch and the grain of the organismal unit (*sensu* Kolasa and Rollo, 1991) affect the severity of response, whereas the size and the dispersion of the patches affect predisposition to subsequent disturbance.

Reiterating the major premises of Schowalter and Lowman (Chapter 9) and Willig and McGinley (Chapter 27), many of the chapters focusing on a particular biome identify animals as important agents of disturbance through patch-generating activities, sometimes accelerating and at other times retarding rates of succession. In boreal ecosystems (Engelmark, Chapter 6), beavers (*Castor* spp.) are keystone species, creating discrete patches with regard to canopy structure, the distribution of woody debris on the forest floor, and the distribution and extent of wetlands. Reindeer (*Rangifer*) and moose (*Alces*) have more diffuse effects through their selective foraging behavior. Insect outbreaks are also important in boreal forests. Relatively regular outbreaks of spruce budworm (*Choristoneura fumiferana* (spruce budworm)) in balsam fir (*Abies balsamea*) forests have a dramatic effect

on the structure of the canopy: mild infestations of budworms favor fir, whereas intense infestations favor spruce (*Picea*) (Baskerville, 1975; Holling, 1992; Morin, 1994). In contrast, outbreaks of spruce beetle (*Dendroctonus rufipennis*) are episodic and cause large canopy gaps in forests of the Rocky Mountains of the western United States (Veblen et al., 1989). In temperate forests, overgrazing by deer (*Odocoileus virginianus*) causes considerable loss of understory plant species and alteration of vertical structure, which in turn, modify the response of the system to other disturbances (Webb, Chapter 7). Insects may also indirectly initiate diffuse disturbances by acting as vectors of plant pathogens such as “blue stain” fungus (*Leptographium engelmannii*, carried by the bark beetle *D. rufipennis*) and exotic Dutch elm disease (caused by *Ceratocystis ulmi*, carried by the exotic bark beetles *Scolytus multistriatus*) in temperate regions of North America (Binkley, Chapter 18). Large patches denuded of vegetation (“eat-outs”) are created by snow geese (*Anser caerulescens*) and nutria (*Myocaster coypus*) in North American marshes, whereas a variety of animals, including invertebrates as well as alligators (*Alligator*), muskrats (*Ondatra*), beavers (*Castor*), seals (species of Pinnipedia), bison (*Bison*), and elephants (*Elephas* and *Loxodonta*), create patches by grubbing, burrowing, nest building, and trampling (McKee and Baldwin, Chapter 13).

Succession and competition

Succession and disturbance are intertwined concepts; a study of one must inevitably consider the other. Disturbance initiates succession, influences its subsequent trajectory, and can determine its rate, endpoint, and duration through subsequent intervention. Although succession is not inevitable, it is likely to occur following most disturbances, and disturbance effects often are measured by their influence on succession. The manipulation of succession (i.e., management) can reduce the severity of disturbance and contribute to restoration.

Most chapters in this volume address succession (Fig. 33.1), suggesting its importance in understanding disturbance; this is particularly true for restoration following human activities. Moreover, ten chapters address competition as it is influenced by disturbance. The interactions of competition with disturbance and succession will be summarized briefly, more extensive

coverage of competition being found in the contributions by McKee and Baldwin (Chapter 13) and Wilson (Chapter 26).

Each disturbance type puts a unique imprint on the landscape, which initiates a particular successional sequence. Attempts at generalization about both disturbance effects and subsequent successional trajectories are difficult but useful exercises. Generalizations are useful because patterns emerge at broad spatial and temporal scales (Walker, Chapter 25). Succession generally is considered to be reset by disturbance (McKee, Chapter 13). However, disturbance also can accelerate succession by enhancing the dispersal of propagules, reducing competitive intensity (Wilson, Chapter 26), creating safe sites, or providing protection from grazers (Matthews, Chapter 2). On the other hand, disturbance can keep succession at a particular stage (Matthews, Chapter 2).

The intensity of a disturbance, and the shape of the patch that it creates, determine which species survive the initial impact, what propagules remain viable in the soil or on plants to colonize the disturbed site, and how far exogenous propagules must travel to reach the site of disturbance (Whigham et al., Chapter 8). Substrate characteristics affect the initial supply of nutrients, water, seeds, and spores. Microbes are not only central to the success of plant colonization through mycorrhizae and nutrient mobilization, but also undergo successional sequences of their own (Allen et al., Chapter 22). The pre-disturbance biota often influences the pattern of the disturbance (cf. Whigham et al., Chapter 8). Patchiness (Pickett et al., Chapter 31), and spatial and temporal heterogeneity, have a pivotal impact on all interactions between disturbance and succession (e.g., dispersal, colonization, nutrient supply, microbial activity, and susceptibility to subsequent disturbance).

Animals interact with plants in the post-disturbance environment in numerous ways and often undergo successional changes as well (Walker, Chapter 25; Willig and McGinley, Chapter 27). Animals affect plant pollination, fecundity, dispersal, productivity, health, competitive balances, and, ultimately, plant species composition (Crawley, 1997). Animals (including insect herbivores) can retard succession or accelerate it (Matthews, Chapter 2; Engelmark, Chapter 6; Schowalter and Lowman, Chapter 9) through their preferences for mid- or early-successional plant species, respectively.

Plant–plant interactions (e.g., Cooke, Chapter 14;

Wilson, Chapter 26) may be categorized as negative (competition) or positive (facilitation), even though they actually represent a continuum of possible interactions along a competition–facilitation gradient (Callaway and Walker, 1997). Competition is capable of altering the rate of succession, whereas facilitation can alter its rate or trajectory. Disturbance subsequent to an initial disturbance (termed an “influx variable” by Matthews, Chapter 2) can determine the relative importance of competitive and facultative interactions through its potential determination of both proportions and densities of plant species (e.g., tall trees may be preferentially damaged during a windstorm).

The ultimate convergence of vegetational composition following spatially separated or floristically unique seres may be guided by non-disruptive, but ubiquitous, disturbances (Matthews, Chapter 2). Alternatively, disruptive disturbances, stochastic dispersal processes, or differential species colonization in early succession may promote divergence (Matthews, Chapter 2; del Moral and Grishin, Chapter 5; Webb, Chapter 7).

Recovery times for various pre-disturbance conditions differ widely. Soil nitrogen can take more than 1000 years to recover following some primary successions (Walker, Chapter 25). In contrast, population- or community-level characteristics of soil faunas (Allen et al., Chapter 22), some soil nutrient pools (Johnson and Schultz, Chapter 23), and plant canopies (Whigham et al., Chapter 8) under favorable conditions of secondary succession may take less than five years to recover. Forest species composition (Binkley, Chapter 18), fine root biomass (Silver et al., 1996), and woody litter-fall typically recover within 50–100 years (Zimmerman et al., 1996). Only multidisciplinary and long-term studies of disturbance can provide the necessary understanding of the mode and tempo of responses by biotic and abiotic characteristics during secondary succession (see fig. 1 in Zimmerman et al., 1996).

The study of succession has been more formalized than the study of disturbance during the past 100 years, despite the initial linkage of the two concepts by Clements (1916) and other early ecologists. Disturbance theory is developing rapidly, particularly as the roles of humans (landscape ecology) and spatial heterogeneity (patch dynamics; Pickett et al., Chapter 31) are examined. Generalizations about disturbance must incorporate successional concepts and *vice versa*. As demonstrated by the geoeological model of Matthews

(1992), disturbance mediates ecological processes, initially as well as throughout the successional process.

Nutrient cycling and primary productivity

Disturbance is a major factor controlling nutrient cycling and primary productivity (Lodge et al., 1991, 1994; see also D’Antonio et al., Chapter 17). These ecosystem attributes, discussed in several chapters of this volume (Fig. 33.1), not only are affected strongly by disturbance, but have considerable influence on disturbance regimes themselves. Specific effects of and responses to disturbance depend on the timing and nature of the disturbance, as well as the particular aspect of nutrient cycling or primary productivity of interest. Despite this complexity, some generalizations are possible. To the extent that disturbances remove plant biomass, they generally initiate a typical pattern of responses: an immediate increase in available nutrients, decomposition, and light, as well as a decrease in intra- and inter-specific competition. These increases can be offset by subsequent decreases in soil organic matter, leachable and volatile nutrients, and density or diversity of soil organisms. Recovery times to pre-disturbance levels of nutrient supply and primary productivity differ widely, from years to centuries, depending on the climate, the nature of the disturbance, and the target biota. Effects of disturbance on secondary productivity (i.e., rate of production of heterotrophic biomass) have not been well studied (Majer, 1989; Schowalter and Lowman, Chapter 9; Willig and McGinley, Chapter 27), although limited descriptive data are available for some systems (see Garrison and Willig, 1996; McMahan, 1996; Pfeiffer, 1996; Reagan, 1996; Stewart and Woolbright, 1996; Waide, 1996; Willig and Gannon, 1996).

Disturbance impacts and ecosystem responses

It is important to distinguish between the intensity (e.g., wind speed) and severity (damage caused) of a disturbance, and to delineate carefully the immediate, short-, mid-, and long-term responses of the abiotic and biotic aspects of the system of interest (Willig and McGinley, Chapter 27). Disturbance can continue to affect ecosystem processes long after the initial event (e.g., Matthews, Chapter 2). Similarly, the post-disturbance ecosystem interacts with and may itself alter aspects of the system. Characterization of responses to disturbance should include explicit spatial and temporal scales (Pickett et al., Chapter 31). Hereafter,

we summarize the initial impacts of disturbance on nutrient cycling and primary productivity, as well as the immediate, short-term, and mid-term responses to disturbance. Subsequently, we discuss long-term responses and ecosystem recovery.

Impacts, and short- to mid-term responses:

Terrestrial disturbances generally involve some type of soil degradation (Barrow, 1991; see also Sojka, Chapter 21) including compaction, burning, loss of organic matter, acidification or alkalization, flooding, salinization, and addition of toxins, herbicides, or agrochemicals. In the most severe disturbances, soils are entirely lost through burial (e.g., under lava, ice, pavement), removal (blasting, mining), or burning.

Erosion is a pervasive source of reduced productivity through decreased water storage (increased runoff) and associated losses of nutrients and organic matter. Pimentel and Harvey (Chapter 4) note that, during the last 40 years, 30% of the world's arable land has become unproductive because of erosion. Wind erosion, with or without human influence, also can substantially reduce the capacity of soils to support plant growth. However, nutrient deposition from wind-borne particles also is a significant input to many ecosystems (Goodall and Perry, 1981; Burrows, 1990; Walker, 1993; Perry, 1994; see also Sukopp and Starfinger, Chapter 16).

Direct wind damage alters primary productivity and nutrient cycling in many ecosystems, but particularly in temperate, tropical, and high-elevation forests. The immediate consequences include loss of plant biomass, increases in light penetration to the forest floor, and increases in leaf litter and woody debris. Often, leaves have a higher content of nutrients than after natural leaf-fall, because no retranslocation has occurred (Lodge et al., 1991; see also McKee and Baldwin, Chapter 13). Such litter inputs generally increase the availability of nutrients (particularly nitrogen) as a result of enhanced leaching and decomposition (Whigham et al., Chapter 8). Microbial processes (including denitrification and soil respiration) are altered as well, with above- and below-ground spatial heterogeneity increased through the formation of canopy gaps and the uprooting of trees (Webb, Chapter 7). The likelihood of wind damage is difficult to predict, and the distribution of particular ecosystem responses is difficult to generalize – they depend on the species composition of the forest (Webb, Chapter 7). In many ecosystems, humans have

altered species composition, but even forest harvesting has the same general impact on nutrient cycling and productivity: nutrient availability increases from reduced plant uptake and increased decomposition of soil organic matter (Binkley, Chapter 18). The general pattern of increased resource availability in forests following wind disturbance is not universal (e.g., litter may not decompose) and repeated disturbances often lead to overall decreases in nutrient availability and primary productivity.

Fire can be a natural or anthropogenic disturbance. It affects most vegetation types, especially grasslands, shrublands, and forests. Initial impacts of a fire include destruction of plant biomass, volatilization of nutrients, and deposition of nutrient-rich, but nitrogen-poor, ash on the surface of the ground. Abiotic responses that follow include erosion, leaching, and cation adsorption. Biotic responses include decomposition of soil organic matter and initial increases in primary productivity associated with increased nutrient uptake or fixation by plants (Bradbury, Chapter 24). Loss of soil organic matter from the ecosystem can inhibit or stimulate productivity, relative to pre-disturbance conditions (Engelmark, Chapter 6).

Grazing is another disturbance of both natural and anthropogenic origin, which can decrease nutrient availability (through changes in soil pH, increased leaching, changes in litter quantity and quality), and primary productivity (through foliage removal, alteration of life forms, mortality; Schowalter and Lowman, Chapter 9). However, nutrient availability also can increase following grazing (e.g., less litter to inhibit nitrogen-fixing organisms, or immobilize nutrients; McKee and Baldwin, Chapter 13), and compensatory growth can lead to net increases in primary production in fertile environments (Schowalter, Chapter 9; Oesterheld et al., Chapter 11). Insect outbreaks are a special case of herbivory which can dramatically reduce plant biomass, and alter nutrient cycling and microclimatic conditions over large areas. Grazing and other agricultural practices can make trees more susceptible to herbivore outbreaks (Schowalter and Lowman, Chapter 9). The interactions of grazing, fire, and precipitation are modeled by Oesterheld et al. (Chapter 11). They suggest that primary productivity, essentially driven by precipitation, is most affected by fire at high levels of precipitation (more current-year standing litter that is of low quality for herbivores). Further, the effects of grazing on primary productivity presumably remain constant (positive or negative)

for all levels of precipitation, because as primary productivity increases with precipitation, the proportion of plant biomass eaten by grazers increases also. The net effects of grazing on nutrient cycling and productivity are therefore dependent on numerous interacting variables, including the intensity of the grazing itself.

Flooding can have the same general effects as wind, fire, and grazing (increased nutrient availability; increased decomposition and detritivore populations; decreased plant biomass and plant uptake of nutrients, followed by re-establishment of plants; and decreased nutrient availability). However, much depends on the duration and timing of inundation (McKee and Baldwin, Chapter 13). Disturbances typical of wetlands include wave action, ice formation, saltwater intrusion, flooding, burial by wrack, dredging, fishing, boating, and water-borne pollutants.

Animal activities (e.g., trampling, mound-building, defecation) constitute a suite of disturbances that tend to be widespread but not severe (Willig and McGinley, Chapter 27). Losses in productivity, and increases in nutrient cycling and decomposition, may be small but cumulative. Animal activities generally remove plant biomass, thereby opening space and redistributing resources for use by colonizing organisms. Earthworm invasions can decrease or increase soil turnover and nutrient availability, depending on the type of earthworm and pre-invasion conditions (D'Antonio et al., Chapter 17). This again indicates an essential requirement in assessing any disturbance effect or response: a careful definition of what specific pre- and post-disturbance ecosystems are being compared. Animals are especially important in increasing local spatial heterogeneity of nutrient supply and associated primary productivity.

Urbanization represents an extreme type of disturbance, with a unique impact on nutrient cycles and primary productivity (Sukopp and Starfinger, Chapter 16). Nutrient availability, microbial activity, and primary productivity can be reduced through leaching in acidic soils, soil compaction, and toxins or heavy metals in land-fill soils. Nutrient levels and productivity can increase as a consequence of aeration from the addition of rubble soils or the addition of nutrients in dust or fertilizers. Unlike most disturbances, where increases in detritivore populations result in increased decomposition, the severity of urban disturbances (similar to severe fires or primary succession) may severely reduce microbial biomass or

diversity, resulting in reduced decomposition and litter accumulation.

Long-term responses and restoration: Clearly, each disturbance elicits a characteristic suite of ecological responses within a particular community type, depending on the nature of the disturbance (intensity, frequency, extent) and the community (land-use history, as well as physiological and life-history attributes of species; Bradbury, Chapter 24). Zimmerman et al. (1996) evaluated several responses of the biota of a tropical rainforest in Puerto Rico to hurricane damage, and found at least six different response curves by various components of the biota over a five-year period. Some responses involved post-hurricane increases (stream concentrations of nitrate, forest-floor biomass, primary productivity) followed by decreases back to pre-hurricane levels over a period of one to five years. The other responses (including aboveground potassium pools, tree biomass, litter-fall, and root biomass) involved initial decreases followed by various rates of return to pre-hurricane levels. This illustrates the difficulty in generalizing about responses to disturbance, and long-term responses in particular. Obviously, long-term responses for the microbiota may not represent the extended time periods that are applicable to long-lived trees; temporal scales must be relative to the taxon of interest (Willig and McGinley, Chapter 27; Pickett et al., Chapter 31). Nonetheless, generalizations about long-term responses include a gradual decrease in nutrient availability coupled with increased decomposition and plant growth. Primary productivity peaks and then declines as longer-lived plants sequester nutrients. Changes in species composition affect the disturbance regime, and plants affect soil development through stabilization, break-up of the substrate, transfer of nutrients from the subsoil, rhizosphere exudates, litter addition, and as hosts for mycorrhizae and nitrogen-fixing organisms (Walker, Chapter 25). Spatial heterogeneity in nutrient availability and primary productivity generally increases with disturbance (e.g., formation of canopy gaps, unburned patches), but some disturbances (e.g., plowing) can decrease spatial heterogeneity.

Stability and resilience

Ecosystem stability can be defined as the constancy of a parameter that characterizes community- or ecosystem-level attributes through time (e.g., species composition,

nitrogen mineralization). As such, it includes resistance to disturbance, as well as the ability to recover from a disturbance. Resilience is specifically the likelihood that parameters of a community or ecosystem will recover following disturbance. Ecosystems can be easy to disturb (unstable) or not (resistant), and may easily recover (be resilient) or not (Barrow, Chapter 28). Stability is thus the antithesis of disturbance, and resiliency characterizes the process of recovery from disturbance. Both concepts evolved from a steady-state view of ecosystems (Odum, 1971; see also Giampietro, Chapter 32), wherein disturbances were aberrations from which ecosystems recovered, to resemble eventually a pre-disturbance condition. Despite the fact that disturbance is an integral part of ecosystem dynamics (Cooper, 1926; Sousa, 1984b), both terms are still useful – stability as a contrast to disturbance, and resiliency as an indication of the potential for recovery that can guide restoration (Hobbs, Chapter 29). A further evolution of the concept of stability is embodied in meta-stability, the condition in which patches of a landscape may change, but all types of patches (or species, or processes) are still represented in the larger spatial and temporal context of the landscape. This shifting mosaic suggests that an ecosystem does not either resist or become totally altered by a disturbance, but is partially modified by it at various scales (Pickett et al., Chapter 31). Other chapters of this book also address the concept of stability or resilience (Table 1.2, p. 14).

Disturbance does not necessarily prevent stability. Disturbance can maintain populations of disturbance-adapted or colonizing species. Disturbance also can maintain later successional stages, as in old-growth forests in southeastern Alaska (U.S.A.) by recycling nutrients through wind-throws (Matthews, Chapter 2) or through a wave-like regeneration pattern of fir forests in New England (U.S.A.) or Japan (Engelmark, Chapter 6). Later successional stages often are considered to be more stable than are early ones, in part, perhaps, because stress-tolerant species are more common in later stages. Ghera and León (Chapter 20) note the difficulty of eradicating stress-tolerant weeds in agricultural systems. In this case, annual disturbance by grazers or cropping promotes stability of species composition. Resilience also can be influenced by past or current land-use and disturbance history (Komárková and Wielgolaski, Chapter 3; Hobbs, Chapter 29).

Eckert and Carroll (Chapter 30) define resilience as the range of variation that ecosystem processes

and patterns can undergo before the system changes into a new system. Thus, patterns of fluctuations and extreme conditions in a disturbance regime become critical. Because most management practices involve manipulation of the disturbance status of an ecosystem (Pickett et al., Chapter 31), land-use policies should prevent human exploitation from exceeding the limits of resiliency of an ecosystem (Eckert and Carroll, Chapter 30). Similarly, Barrow (Chapter 28) suggests that local and regional management of ecosystems gives the best chance of recovery and sustainability of ecosystem functions, because there is maximal overlap between patches of the regional mosaic to ensure survival of some if others are destroyed. Yet, increasingly, disturbances are global in nature, and international cooperation is essential for arriving at effective scientific and societal solutions (Barrow, Chapter 28).

Predictability

Disturbance at most temporal and spatial scales is unpredictable (consider, for example, human attempts at weather prediction). This large stochastic component may please theoretical ecologists, but makes management of disturbance effects difficult. Humans approach this dilemma in two ways: through evaluation of historical disturbances to find patterns or explanations, and through extrapolations of models or short-term patterns into the future. Some of these approaches have been addressed elsewhere in this volume.

Historical reconstruction of disturbances ranges in scale from looking for meteorite impacts to explain Permian extinctions, through paleontological examination of pollen records, to evaluation of windstorm impacts during the last century. Catastrophic disturbances often leave a legacy, such as carbon residues from major fires. Windstorm impacts can be analyzed by examining historical land surveys of blow-downs, residual effects of mounds on soil profiles, tree rings, presence of shade-tolerant or shade-intolerant tree species, meteorological models, and aerial photographs (Webb, Chapter 7). Historical records of agricultural practices can indicate changes in plant species composition (Ghera and León, Chapter 20).

Predicting the future disturbance regime is especially difficult (Lugo and Scatena, 1996; see also Whigham et al., Chapter 8), even if one has determined historical frequencies and return intervals of a disturbance, and has distinguished that disturbance type (e.g., hurricane)

from the background disturbance regime including all other causes of mortality (e.g., tree-falls from senescence or disease). Successional pathways often are predicted in advance, and some general patterns (e.g., increasing biomass, decreasing allogenic influences) appear to be robust. However, closer examination of specific seres often indicates little congruence between reality and prediction. The rate of change often is predicted more easily than is the specific trajectory of species change. This could be due to variability in the potential suite of colonizers at a given site and the random success of those colonizers. Also, similar habitats can support different species (del Moral and Grishin, Chapter 5).

Disturbance may have a non-directional or directional influence on succession. Matthews (Chapter 2) suggests that disturbance alters the direction of succession under several distinct conditions. First, he proposes that disturbance early in succession can cause sites of similar age to diverge (e.g., in species composition) as a consequence of differential response to a variable disturbance regime. These sites may later converge to a similar species composition as a consequence of biotic factors. Alternatively, Matthews (Chapter 2) suggests that a low-level, homogeneous, and widespread disturbance that does not alter species composition can cause convergence of sites of similar age. The ultimate test of ability to predict the consequences of disturbance involves estimating human impacts on the biosphere (Giampietro, Chapter 32). Human economies, lifestyles, indeed survival, depend on proper forecasting, balancing trade-offs, and effective national and international leadership.

Thresholds

Biological thresholds can be defined as the minimum level of stimulus needed to elicit a response. In this sense, disturbance needs to reach a given intensity or frequency to alter some ecosystem parameters. The alteration can come abruptly or gradually (Pickett et al., Chapter 31). Given the relative absence of simple linear responses in ecology and the prevalence of complex interacting factors and indirect responses (Barrow, Chapter 28; Hobbs, Chapter 29; Eckert and Carroll, Chapter 30), ecological thresholds are more likely to be gradual than abrupt. The importance of thresholds in the processes of disturbance and response is reflected in the chapters of this book addressing this concept (Fig. 33.1).

Thresholds along a precipitation gradient determine the relative importance of three variables for above-ground net primary production in Argentina. Climate predominates where annual precipitation ranges between 200 and 450 mm; grazing and fire balance each other where annual precipitation ranges between 450 and 700 mm; and fire predominates where annual precipitation exceeds 700 mm (Oesterheld et al., Chapter 11). A threshold of irreversibility is a condition from which an ecosystem is no longer capable of recovery without intervention and restoration. This threshold is illustrated as the amplitude or range of a system parameter. Hartshorn and Whitmore (Chapter 19) suggest that isolated forest remnants reach a threshold for loss of biodiversity or ecosystem function beyond which they are both susceptible to invasion and difficult to restore. Finally, Schowalter and Lowman (Chapter 9), use the concept of threshold differently. They suggest that, at some undefined level of intensity or frequency of disturbance, insect outbreaks go from being background trophic interactions to become a disturbance (see also Willig and McGinley, Chapter 27).

Biodiversity and functional redundancy

Biological communities exhibit emergent properties, distinct from those at the level of populations or individuals. Among such emergent attributes is biodiversity. Biodiversity comprises three interrelated components: genetic diversity, taxonomic diversity, and functional diversity (Solbrig, 1991), and considerable controversy surrounds the contrast between functionally redundant species and those taxa which perform keystone services in maintaining ecosystem integrity (Jones and Lawton, 1995). Nonetheless, most disturbance studies addressing issues of biodiversity have been restricted to considerations of species diversity (for an exception, see Willig et al., 1996, who consider changes in functional diversity as a consequence of natural and anthropogenic disturbance). Although species diversity is an index which integrates information concerning the number of species (richness component), as well as their proportional abundances (evenness component), discussion of community-level issues in disturbance ecology most frequently is restricted to species richness. In part, this occurs because species richness is a conveniently calculated index of community organization which may be affected by various attributes of a disturbance regime. Indeed, both spatial variation in the compartmentalization of

diversity (landscape heterogeneity and patch dynamics) and temporal variation in diversity (ecological succession) are consequences of disturbance. On the other hand, biodiversity is thought by some to enhance ecosystem stability and resilience, and thus moderate the effects of disturbance on various properties of ecological systems. A consideration of differences in species composition may also reflect functional aspects of biodiversity. Themes related to biodiversity figure prominently in a number of the chapters in this compendium, whereas consideration of functional redundancy is infrequent and cursory (Fig. 33.1).

The effects of disturbance on species richness are variable and driven by complex and context-dependent mechanisms. Some disturbances (e.g., erosion and volcanism) consistently reduce diversity, whereas other types of disturbance may enhance diversity, depending on spatial scale and intensity (Willig and McGinley, Chapter 27).

Soil erosion consistently reduces biodiversity in both terrestrial and aquatic systems (Pimentel and Harvey, Chapter 4). This is especially true of agricultural systems, where the loss of soil organic matter and reduction in soil quality directly reduce productivity, and indirectly reduce diversity of soil animals and microbes. Because agriculture dominates nearly half of the earth's terrestrial systems (United States Department of Agriculture, 1993), the effects of erosion on diversity are quite severe. Nonetheless, a variety of amendments (additions of organic matter or straw mulch) may restore (at least temporarily) an appreciable proportion of the soil diversity previously lost to agricultural development. The effects of erosion are not limited to the terrestrial system in which the disturbance occurs. The soil particles transported by wind and water as a result of erosional processes are frequently deposited in aquatic systems, leading to eutrophication and reductions in species diversity. Applications of biocides (herbicides, fungicides, rodenticides, insecticides) to agricultural crops as a means of enhancing yield have effects on non-target taxa as well. When such non-target taxa provide essential ecosystem functions, such as nitrogen-fixation, pollination, or seed dispersal (Allen et al., Chapter 22; Johnson and Schultz, Chapter 23; Willig and McGinley, Chapter 27), the consequences can be far-reaching. For example, bee populations may be declining or extirpated in some agricultural areas, reducing the reproductive success of plant species dependent upon them for pollination and altering their genetic structure.

Similarly, volcanoes consistently reduce biodiversity by decimating plant, animal, and microbial populations through production of lava, lahars, pyroclastic flows, and debris flows (del Moral and Grishin, Chapter 5). Plant communities that develop subsequently on volcanoes are non-equilibrium and support fewer species than do areas unaffected by volcanic eruptions. In addition, the plant communities associated with volcanoes are in disharmony, supporting eclectic combinations of taxa as a response to aleatory features of colonization dynamics.

Wind-generated disturbances (e.g., hurricanes, tornadoes) can increase or decrease diversity, or have no effect at all (Webb, Chapter 7). A similar variety of disturbance effects was found in a survey of ecological research in North American wetlands by McKee and Baldwin (Chapter 13). At the level of the patch, the specific impact of a disturbance depends on the size and boundary characteristics of the patches that it creates, the degree to which it reconfigures the distribution of essential resources, and the pattern of mortality that it causes (e.g., differential mortality of shade-tolerant versus shade-intolerant species). At the level of the landscape, the creation of patches of different sizes and qualities, and the attendant secondary succession that follows disturbance, may enhance diversity regardless of within-patch effects.

Many systems attain highest diversity at intermediate levels of disturbance (Connell, 1978). Shrublands and woodlands under Mediterranean climates attain highest taxonomic and structural diversity if subjected to moderate grazing such that open habitats are maintained with regular disturbance (Rundel, Chapter 10). This is true of both plant and animal communities. Similarly, vegetation attains highest species richness in coastal marshes with intermediate intensities of disturbance by grazing by mammals, deposits of wrack, or scouring (McKee and Baldwin, Chapter 13). Demarais et al. (Chapter 15) intimate that intermediate levels of disturbance from military training activities enhance plant species richness by re-setting successional stages to pre-climax seres.

Among the most important ways whereby a disturbance regime affects biodiversity is through evolutionary mechanisms. That is, particular disturbance regimes act as selective agents with respect to life-history characteristics of microbes, plants, and animals. Indeed, disturbance may have a significant impact on the ecological attributes of species that persist as part of regional species pools. Differences in species

composition among areas differing in disturbance history are frequently a consequence of the adaptive nature of life-history characteristics of potential colonists. This is clear in areas subject to volcanic disturbances (del Moral and Grishin, Chapter 5), where hemicryptophytes and geophytes are favored in areas subjected to blast effects; tephra is particularly harmful to mosses, lichens, low herbs, and taxa incapable of rhizomatous growth. In tropical forests, the successful germination and persistence of many plants (e.g., *Cecropia*, *Heliconia*, *Macaranga*, *Ochroma*, and *Trema*) depend on the continual production of gaps where microclimatic conditions (light regime, temperature, and moisture) differ from those of the otherwise undisturbed forest matrix (Hartshorn and Whitmore, Chapter 19). In some cases, gaps are the prime regeneration sites for up to half of the species of native trees (Hartshorn, 1978). The pervasive distribution of naturally produced gaps in time and space may result in some tropical species of trees being "pre-adapted" to survive anthropogenic disturbances such as those produced by modest selective logging. For example, 3–8 years after the cessation of logging in a tropical forest of Borneo, population densities of most bird species and avian guild structure returned to pre-disturbance conditions (Lambert, 1992). Organisms that could flee from the initial impact of logging practices, or that could easily recolonize once logging ceased, showed few long-term changes as a consequence of disturbance. Similarly, life-history characteristics of many species of plants, animals, and microbes in the boreal forests of the New and Old Worlds are fire adaptations (Engelmark, Chapter 6).

Anthropogenic disturbance is perhaps the greatest threat to world-wide biodiversity. Lands directly modified for agricultural development (croplands, grazing lands, managed forests) and urbanization clearly experience severe *in situ* reductions in species richness (Pimentel and Harvey, Chapter 4; Cooke, Chapter 14; Sukopp and Starfinger, Chapter 16; Hartshorn and Whitmore, Chapter 19). Moreover, anthropogenic disturbance has a cosmopolitan distribution (see the back endpaper of this volume), and, because of the rate of increase of human populations, will likely continue to expand well into the next century (Barrow, Chapter 28; Giampietro, Chapter 32). Ironically, some areas dedicated to human uses may act as refuges for important components of the biota. Military lands, although subjected to training exercises, may be considerably less developed or modified than adjacent areas used

for agriculture, industry, or cities (Demarais et al., Chapter 15). As a consequence, such lands may harbor relatively unmodified natural communities as well as endangered species of plants and animals. Similarly, land-fills located in areas of high urbanization (Sukopp and Starfinger, Chapter 16) can be rich in species, and include populations of taxa that are otherwise endangered or threatened by other aspects of human encroachment. Nonetheless, improved protection of biological diversity will require concerted efforts to preserve ecological systems rather than the protection of single species or endangered taxa (Eckert and Carroll, Chapter 30).

Invasive species

Because disturbance removes biomass and opens space, colonization by neighboring or newly introduced species is inevitable, except in the harshest conditions. The process of colonization is dependent on many variables including climate, microsite availability, dispersal distances and capabilities, substrate conditions, residual soil or organisms, secondary disturbances, and stochastic events (del Moral and Grishin, Chapter 5).

In this section, we focus on the interaction of a particular subset of colonizers, the invasive (non-indigenous, alien, or exotic) species, and summarize conclusions from chapters of this book addressing the interaction between invasive species and disturbance (Fig. 33.1). Recent books that provide an overview of the topic include those of Cronk and Fuller (1995), Pyšek et al. (1995), Luken and Thieret (1997) and Shigesada and Kawasaki (1997).

Although invasive species of plants are found in areas where natural disturbances have reduced plant cover, they are particularly associated with anthropogenic disturbances. In both cases, their introduction is usually from human activities. For example, alien grasses, herbs, shrubs, and trees dominate volcanic disturbances in New Zealand, Hawaii, and Japan, and these invasive species are often the product of purposeful human introductions (e.g., to control erosion; del Moral and Grishin, Chapter 5). Invasive species in a disturbed area are often from similar but distant environments. Most grasses that are prevalent as invaders of habitats in Mediterranean climates around the world originated in Europe (Rundel, Chapter 10). Such habitats may be particularly susceptible to invasion because of low vegetative cover during summer droughts, and a long history of species adaptation to human

intervention in Europe (fire, grazing, deforestation: Rundel, Chapter 10). Interestingly, native grasses still dominate on low-nutrient serpentine soils in California (Rundel, Chapter 10), and are reinvading old, nutrient-poor agricultural systems in Argentina (Ghersa and León, Chapter 20), suggesting that habitats of high productivity favor invasion. Urban environments also are dominated by weeds, in part because cities are centers of transportation and provide warmer microsites for weeds from more southerly climates (Sukopp and Starfinger, Chapter 16).

Disturbance generally promotes invasion of non-native species, particularly when the disturbance is severe or persistent (D'Antonio et al., Chapter 17). Good invaders tend to be ruderals with high fecundity, well-dispersed seeds, rapid growth, low root/shoot ratios, large seed banks, and flexible life histories (Rundel, Chapter 10). However, invasions also occur without disturbance, and invasive species often colonize undisturbed areas surrounding a disturbance (D'Antonio et al., Chapter 17).

The impacts of invaders are complex. They can outcompete native vegetation, alter successional pathways, influence ecosystem parameters, and change disturbance regimes. For example, Argentine ants (*Solenopsis* and related genera) hinder dispersal of native seeds by indigenous ants in South Africa, exotic fungal pathogens kill plants in the family Proteaceae in Australia, and invasive grasses promote fire in the arid southwestern United States (Rundel, Chapter 10). In many cases, humans intentionally introduce non-native plants to restore ecosystem function to a badly damaged site rapidly, because the non-natives grow more quickly. However, the risk is that introduced species may inhibit establishment of native vegetation (Hartshorn and Whitmore, Chapter 19; Hobbs, Chapter 29). Widespread human disturbances have promoted a global mixing of species and sometimes a reduction in species diversity. Understanding the dynamics of invasions will aid humans to incorporate exotics properly into management and restoration plans.

Restoration and management

Restoration and management are human attempts to alleviate negative impacts of disturbance. As such, they represent the optimistic view that human intervention can restore damaged ecosystems faster than the ecosystems are being destroyed. Earlier in human history, relocation was an option (Barrow, Chapter 28), but the

effects of human impact are too severe and extensive to avoid any longer. Many chapters address the issues of restoration, management, and the related topic of risk assessment (Fig. 33.1). We use the term "restoration" in the broad sense for all efforts to repair ecosystems, not in the narrow sense of return to the original system (Cooke, Chapter 14; Hobbs, Chapter 29).

The best management option is to avoid degradation or to prevent it from crossing irreversible thresholds, after which restoration efforts are needed (Hobbs, Chapter 29). For example, Demarais et al. (Chapter 15) document ways in which military training activities may be modified to reduce environmental damage, and Hartshorn and Whitmore (Chapter 19) note that strip-cutting is better than clear-cutting for regeneration of tropical forests. With respect of endangered species, stopping habitat destruction is essential before the species is lost (Bowles and Whelan, 1994). Risk assessment attempts to predict where early intervention can reduce site degradation. Predicting which trees are at risk from wind-throw can help foresters to design planting densities and thinning schedules so as to minimize the loss of mature trees (Webb, Chapter 7). Certain types of hazard, both natural (frosts and avalanches) and anthropogenic (military training), are readily predictable, others (effects of global climate change) are not (Barrow, Chapter 28). Humans can attempt to minimize damage from predictable events (e.g., make fire breaks or build according to earthquake codes), but too often governments require proof that a disturbance is real before action is taken (Barrow, Chapter 28). Such delays frequently make mitigation efforts more costly. Similar problems exist on a personal level if perception and probability of risk are not strongly coupled. People are much more worried about the (rare) earthquake or nuclear accident than the (very common) car accident. Environmental impact assessments are now commonly used to predict the effects of human activities (e.g., on wetlands, or the fate of endangered species). Evaluations of the success of such predictions are critical for both individuals and governments to prevent the negative impacts of disturbance, or to ameliorate conditions in post-disturbance scenarios.

Restoration is deemed necessary for a wide variety of reasons, including the management of catchments or air quality, the preservation of species or ecosystem functions, acceleration of natural successional processes, growth of crops, removal of pollutants, and even the re-establishment of realistic conditions for military

maneuvers (Demarais et al., Chapter 15). When the explicit goals of a restoration effort are stated clearly, the success of the project can be evaluated in an unambiguous fashion. In many cases, a return to a pre-disturbance condition or to a nearby, relatively undisturbed condition is desired, but this approach is challenging because so-called "natural" habitats are spatially heterogeneous and may also vary through time (Hobbs, Chapter 29). Increasingly, the re-establishment of certain vital ecosystem attributes (Aronson and Le Floch, 1996) is a criterion for success.

Restoration techniques are of necessity site-specific, and vary from complete reconstruction of an ecosystem to minor manipulations of ecosystem attributes. Techniques include identification and removal of stressors, and replacement of key ecosystem components lost in the disturbance (Hobbs, Chapter 29). Recovery of severely disturbed habitats, such as mine wastes, is impeded by soil acidity and presence of toxins (Cooke, Chapter 14). In the United States, rushing the process, for instance to meet certain regulations, ironically has resulted in delayed succession. For example, laws mandating a return to 90% of original site productivity within five years resulted in the planting of grasses and legumes or pine trees (*Pinus strobus*) which inhibited subsequent forest succession. This result is generalizable: without a good understanding of natural regenerative processes, human interference can slow rather than accelerate recovery. A less comprehensive restoration technique might simply be the scarification of the surface of mine wastes to increase soil moisture (Allen et al., Chapter 22). Disturbance itself is used to adjust successional trajectories toward a desired endpoint, as when competition from early-successional species is reduced so that later-successional trees can establish.

Successful restoration depends on clear identification of ecological endpoints with regard to system structure and function, as well as an understanding of natural succession and the successional dynamics at the disturbed site. Restoration also depends on the ability of management procedures to mimic, replace, or compensate for the multiple effects of a disturbance regime (Pickett et al., Chapter 31). Such understanding is rarely complete, so that trial and error will likely characterize restoration efforts. The strongly site-specific nature of restoration does not preclude some generalizations about the best procedures to utilize. The reassembly of a functioning ecosystem, whether it mimics the pre-disturbed system or not,

is an acid test for ecologists (Jordan et al., 1987), and reliable guidelines are emerging (see Hobbs, Chapter 29, for references). However, the link between biological realities and environmental policy is still too tenuous (Wali, 1992). Past environmental policies have had both favorable consequences (establishment of national parks) and unfavorable ones (laws allowing uncontrolled mining or ranching or forest removal). One may hope for a future in which management of ecosystems emphasizes the necessity for land managers to recognize the value of natural components of ecosystems, as well as the importance of participation by those who will be affected by management decisions (Eckert and Carroll, Chapter 30).

SYNTHESIS AND FUTURE DIRECTIONS

As a first step toward synthesis, we develop a conceptual model that explicitly links disturbance regime, successional dynamics, and spatial heterogeneity into a common framework. Any particular point on the earth's surface occupies a portion of geographic space represented by its latitude, longitude, and elevation. In addition, that point occupies a position in ecological space (E) defined by its location on any of a number of gradients representing environmental characteristics. Environmental characteristics may be biotic (e.g., the number of individuals of each of a set of species, species richness, functional diversity) or abiotic (e.g., light level, soil moisture, pH, temperature).

Succession

Disturbance (e.g., a hurricane) affects a region of geographic space by altering abiotic or biotic portions of ecological space (Fig. 33.3). For example, high winds generated by a hurricane can uproot and kill trees, thereby creating gaps in the canopy, with an attendant increase in light and temperature at the ground. The direct effects of the hurricane (D) cause a shift (E) in the ecological conditions of the point at which the tree fell. Such direct effects initiate a cascade of subsequent responses by the biotic (B) and abiotic (A) environments, which constitute secondary succession. For example, previously dormant seeds of light-tolerant species in the soil may germinate in the newly formed gap, changing the species composition of the site. As seedlings grow, they shade the litter (decrease soil temperature) and attract a suite of insect

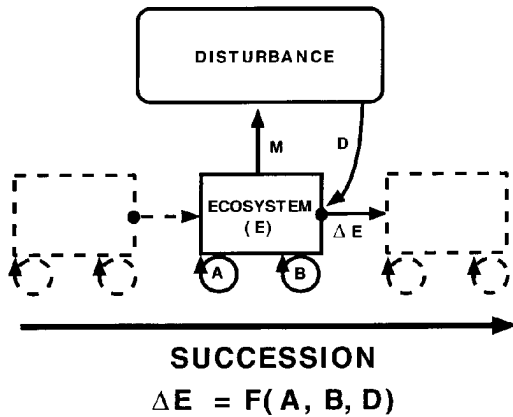


Fig. 33.3. Generalized conceptual model representing the manner in which a disturbance (D) affects a geographically explicit portion of a landscape (E), causing a change (ΔE) in its ecological characteristics (see text for details). A and B represent feedbacks from the current environment based on abiotic and biotic characteristics, respectively, that affect successional trajectories. Both A and B embody the legacy of previous disturbances. The current state of the ecosystem has feedbacks to the disturbance regime (M) through alteration of the frequency, extent, or intensity of each disturbance element in the disturbance regime (Fig. 33.2). Arrows represent inputs or flows; squares represent state spaces. Dashed arrows represent changes in ecological space wrought by previous disturbances (D_{i-1} , A_{i-1} , B_{i-1}), whereas dashed squares represent past (left, E_{i-1}) or future (right, E_{i+1}) ecological space, which has characterized or will characterize the site as a result of succession.

herbivores, changing the faunal composition of the site. Hence, the site will follow a path in ecological space initiated by the disturbance and modulated by the surrounding environment (e.g., seed bank, species pool of insect herbivores).

Of course, the occurrence of a disturbance at a site in the past does not necessarily mean that the site is immune to future disturbances. For example, two weeks after the fall of a tree, a six-week drought may occur which dries the litter and causes enhanced mortality of the snail fauna occupying the site. This second disturbance directly alters successional trajectories, and brings with it a suite of attendant indirect effects as well. Together, the legacy of changes initiated by the hurricane combine with those of the drought to produce a new trajectory of change in the biotic and abiotic characteristics of the site (Fig. 33.4).

Finally, the occurrence of a disturbance can affect the likelihood and characteristics of future disturbances. The tree that fell during the hurricane may have

damaged another tree on the perimeter of the gap (Fig. 33.2). This may sufficiently weaken the tree at the perimeter so that it responds to the added wind turbulence at the gap's edge during a subsequent tropical storm by the trunk snapping, producing a tree-fall and increasing the size of the gap.

In summary, at any point in time, trajectories of succession depend upon (1) direct effects associated with current disturbances (D); (2) factors associated with previous disturbances, both abiotic (A) and biotic (B); and (3) the environment in which a site occurs (e.g., the pool of colonist species¹). The change in ecological characteristics of a site can be quantified by the relationship:

$$E = F(D, A, B | E),$$

where $|E$ incorporates the effects of D , A , and B that are conditional on the current ecological state of the site (E).

Any particular site is subject to a regime representing

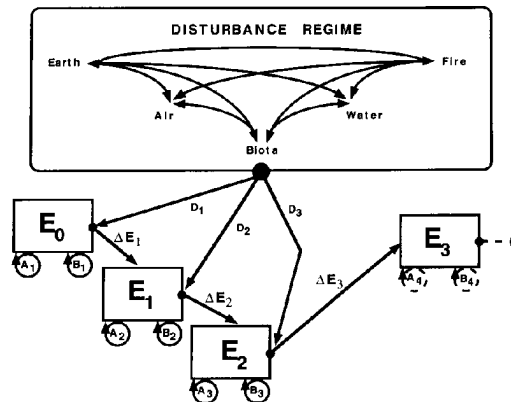


Fig. 33.4. Ecological succession may be considered to be a consequence of the trajectory of changes (ΔE_i) that a site experiences over time as a result of the cumulative impact of the disturbance regime (see Fig. 33.2). Elements of the disturbance regime derived from earth, air, water, fire, and the biota (Walker and Willig, Chapter 1) interact with each other, often in a complex fashion, and synergistically constitute a forcing function at any point in time. The likelihood of any of these elements of the disturbance regime impinging on a site, as well as their defining characteristics, may have been affected by previous disturbances. Hence, trajectories of response at a site may be complex and difficult to predict because of the multifaceted way in which past and current disturbances interact with each other in the context of the current environment to elicit changes in the biotic characteristics of a site.

¹ This aspect is often referred to in the literature as a "mass effect" or "rescue effect".

all of the possible disturbances to which it could be subjected (Fig. 33.4). Hence,

$$E = F(D_1, D_2, \dots, D_n, A, B | E),$$

where the subscripts of D represent each of the possible disturbance elements that constitute the disturbance regime of the area. Each of the possible disturbances (D_i), whether they are associated with earth (tectonic), air, water, fire, or the biota, has associated with it a likelihood of occurrence (P , proportional to the frequency of occurrence and extent) and a probable intensity (I , based on a distribution of possible intensities). Hence,

$$D_i = P_i I_i.$$

Clearly, quantitative prediction of trajectories of response to disturbance is difficult because of the inherent complexity of the system. This sentiment echoes similar statements that characterize most of the preceding chapters of this book. The complexity likely is a consequence of the structure of the system (Figs. 33.3, 33.4), as well as the non-deterministic and non-linear dynamics characterizing many of the cause and effect relationships (Kolasa and Pickett, 1991; Jones and Lawton, 1995; Haefner, 1996). Nonetheless, modeling approaches based on Markovian and semi-Markovian perspectives hold promise, especially when they incorporate higher-order dynamics and history in predicting ecological trajectories (Henderson and Wilkins, 1975; Horn, 1975; Cohen, 1976; Usher, 1981, 1987; Caswell, 1989; Tanner et al., 1994, 1996)

Patch dynamics

Any site or patch occupies a geographically defined position in a heterogeneous landscape, with various patches interacting with each other (Forman and Gordon, 1981; Forman, 1997). Just as a particular site can be represented by its position in ecological space, a suite of sites can be visualized in the same ecological space (Fig. 33.5). The proximity of such sites in ecological space represents their similarity in biotic or abiotic characteristics, but because of disturbance their relationships may differ over time, some moving in parallel, others converging, and still others diverging. General patterns of succession may be visualized in such a scenario (Fig. 33.5A) and provide insight to questions concerning the spatial organization of the ecological variability of a landscape subject to a disturbance regime.

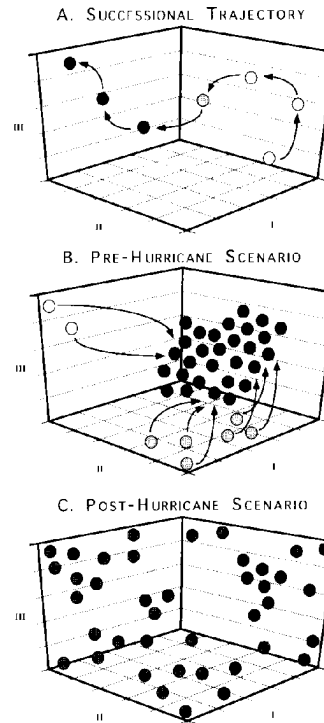


Fig. 33.5. Disturbance-initiated succession involves a sequence of changes in abiotic attributes (e.g., temperature, soil moisture, solar irradiation) and biotic attributes (e.g., species composition, species richness, species evenness, N mineralization rates). Any point in geographical space can be represented by a suite of ecological characteristics. Nonetheless, visualization in multidimensional space is difficult. Consequently, data reduction techniques are used to produce a few important axes of variation (e.g., axes I, II and III), which are orthogonal combinations of the suite of ecological characteristics. (A) A disturbed point (open circle) undergoes succession whereby its ecological characteristics (position on axes I, II, and III) change over time, as represented by the color changes in the circles from open, through shades of gray, to black. Sequences of states over time representing trajectories of response to disturbance may be depicted by circles connected by arrows. (B) The tabonuco forest of Puerto Rico prior to Hurricane Hugo was visualized as an extensive forest matrix (solid circles) interrupted by a number of sites subjected to tree-falls (dark gray circles) and a few sites subjected to landslides (light gray circles). Each of the disturbed sites was believed to undergo secondary successional changes which eventually return sites to the general condition of the matrix (i.e., recovery). (C) The direct effects of Hurricane Hugo were to cause considerable damage to the forest, killing and damaging many trees and opening extensive portions of the canopy (gray circles). Only a few stands occupying protected sites based on topography and slope were unaffected by the hurricane (solid circles), reconfiguring the forest so that it was a heterogeneous mélange of disturbed sites interspersed with a few undisturbed sites.

For example, the tabonuco forest of Puerto Rico was considered to be a mosaic of patches prior to the impact of Hurricane Hugo, with differences among sites related to the effects of disturbances such as tree-falls and landslides (Fig. 33.5B). The general perception was that most sites were relatively “undisturbed” and considered part of the forest matrix. Nonetheless, variation among sites in the matrix may be a consequence of a variety of attributes including slope, aspect, elevation, and stochastic events. In addition, some patches were recently subjected to tree-falls and considered to be moderately disturbed, whereas a few sites were recently subjected to landslides and considered to be severely disturbed. As a result, the “Swiss cheese” image of a forest based on geographic considerations (i.e., an extensive forest matrix interrupted by occasional small and larger gaps, tree-falls and landslides) can be visualized in ecological space as a core of numerous sites (matrix) surrounded by near (tree-fall) and distant (landslide) outliers (Fig. 33.5B).

This same approach can be used to visualize the ecological variability of the tabonuco forest after the impact of a severe disturbance such as Hurricane Hugo (Walker et al., 1991, 1996). The direction and intensity of the hurricane, in conjunction with topographic features of the Luquillo Mountains, resulted in severe damage to most areas of the forest, although some sites were relatively undisturbed (Fig. 33.5C). As a result, most sites in the forest were highly, though variably, dispersed in ecological space, and only a few sites retained characteristics of the former matrix. In geographic space, the Swiss cheese was mostly holes.

Agents of control during succession

Temporal trajectories in ecological space followed by disturbed sites as a consequence of secondary succession (Fig. 33.5) can be examined within the framework of a conceptual model such as that outlined above (Fig. 33.6). For heuristic purposes, we consider the ecological trajectories associated with three of the possible control agents: stochastic events (Fig. 33.6A), current ecological characteristics (Fig. 33.6B), and physical characteristics (Fig. 33.6C). If physical characteristics of the site primarily guide succession, then sites with similar slope, aspect, or elevation should converge, regardless of current ecological characteristics (Fig. 33.6C). This same pattern of response would characterize controls associated with previous landuse history. In contrast, if ecological characteristics

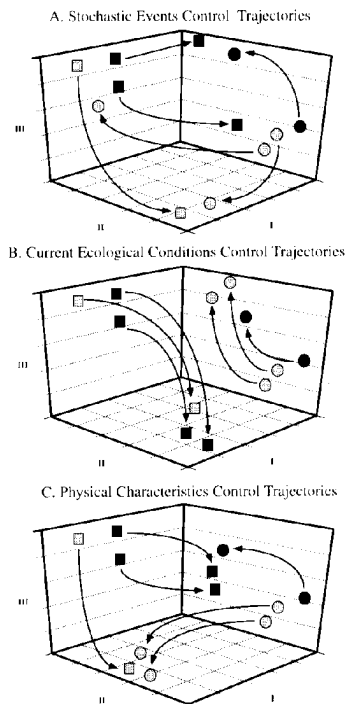


Fig. 33.6. Sites within a landscape can be represented by their position in ecological space, as defined by biotic or abiotic gradients. Trajectories of secondary succession may be controlled by a number of factors, including current ecological characteristics (represented by shape of points; squares versus circles), previous land use (shading of points; black versus gray), or stochastic processes. (A) If stochastic processes affect successional pathways, then neither previous landuse (e.g., shading of points) nor current ecological characteristics (shape of points) of sites should produce patterns in the trajectories of response to a disturbance. (B) If current ecological conditions (shape of points) primarily determine the path of succession, then sites sharing current ecological space should follow parallel trajectories of recovery. (C) If physical characteristics or previous land-use (shading of points) has the dominant role in affecting succession, then sites should converge in ecological space based on conditions related to previous land-use history.

of the immediate post-disturbance environment play the dominant role in channeling succession, then disturbed sites occupying similar positions in ecological space should follow parallel trajectories (Fig. 33.6B). Finally, if stochastic events or factors unknown to the investigator direct secondary succession, then trajectories should not follow either pattern (Fig. 33.6A).

Of course, ecological systems are notoriously complex, and the challenge for the future is to determine the biological circumstances which may favor one sort

of control agent over another (*sensu* the evolution or ontogeny of theory: Pickett et al., 1994). At least four tasks are inherent in that challenge. First, to determine if some types of disturbance are more associated with one type of control mechanism than another. Second, to evaluate if the relative importance of control mechanisms varies over time (e.g., stochastic control early in secondary succession, followed by physical controls later in secondary succession). Third, to discover if some organismal groups (e.g., herbs versus hardwood trees, bats versus rodents, micro-organisms versus macro-organisms) or processes (e.g., N mineralization, P cycling, rates of herbivory) are more often regulated by one control mechanism than another. And fourth, to evaluate if considerations of ecological scale affect the detection of types of control mechanisms.

Accomplishments

Disturbance as a theory unites concepts in succession and landscape ecology. Like all theories, it has exhibited an ontogeny since its popular formalization (Bormann and Likens, 1979; Sousa 1984a,b; Pickett and White, 1985). Nonetheless, the theory is not yet mature and might best be characterized at a stage between the consolidating and empirical-interactive phases of development described by Pickett et al. (1994).

In many ways, the chapters in this book substantially contribute to the maturation of disturbance theory. Almost all of them provide *facts* (conformable records of phenomena), *definitions* (conventions and prescriptions necessary to communicate clearly), or *concepts* (regularities in phenomena). Some (e.g., Schowalter and Lowman, Chapter 9; Willig and McGinley, Chapter 27; Pickett et al., Chapter 31) have clarified the *domain* of the theory (the scope of the phenomena in space and time). Others have contributed new *models* (conceptual constructs that represent or simplify nature) or tested extant *hypotheses* (statements representing components of theory) related to disturbance (e.g., Rundel, Chapter 10; Oesterheld et al., Chapter 11; MacMahon, Chapter 12; Ghersa and León, Chapter 19; Allen et al., Chapter 22; Walker, Chapter 25; Wilson, Chapter 26; Willig and McGinley, Chapter 27; Hobbs, Chapter 29; Eckert and Carroll, Chapter 30). The earlier part of this chapter has presented the many confirmed *generalizations* (condensations and abstractions from

a body of facts that have been tested) that appear throughout the volume.

Future directions

Regardless of location, the study of disturbance requires a long-term perspective (Magnuson, 1995), and is best conducted by multidisciplinary teams of scientists who simultaneously examine patterns and processes at a variety of spatial and temporal scales (Levin, 1995). Many of the chapters in this book conclude with a suite of recommendations for future research. Rather than repeat these recommendations here, we focus on overarching issues that are not biome-, taxon-, or process-specific.

- (1) The broad generalizations that currently characterize disturbance theory need to engender falsifiable hypotheses. The theory of disturbance needs to become more predictive, and the predictions need to be more quantitative. This is particularly critical in restoration and management scenarios.
- (2) Models such as those that appear in this chapter (Figs. 33.3, 33.4), as well as those that appear elsewhere in this volume, need to be incorporated into synthetic landscape models. More specifically, the interacting cells of the landscape model should represent the geographic space of an ecosystem, with explicit flows occurring between adjacent cells in the landscape.
- (3) For any particular disturbance type, research should be designed to distinguish the effects of frequency, extent, and intensity on a suite of biotic and abiotic attributes. The recent work on the effects of the extent and pattern of fires on secondary succession (Turner et al., 1997) serves as a worthy model.
- (4) The study of disturbed ground needs to become more comparative. This is particularly critical, given the importance of historical legacies and contingencies (Berlow, 1997). Site-specific response to disturbance must be distinguished from more pervasive or general results; replication is necessary to achieve this goal. Indeed, many of the insights presented in this volume derive from observations at multiple sites. Moreover, identification of important environmental gradients along which to stratify field observations or experiments may provide the best basis for comparative study.
- (5) Future research should assess the degree to which disturbance-mediated changes in above-ground structure and function correspond to those which occur

below ground. The degree to which above-ground trajectories of recovery reflect or fail to reflect below-ground trajectories has not been sufficiently addressed in the contemporary literature.

- (6) The disciplines of land and resource management, range and wildlife management, risk assessment, and urban planning need to become more familiar with the theory of disturbance. Effective utilization, conservation, and protection of the earth's resources require the development of intervention strategies that are harmonized with the natural disturbance regimes of target ecosystems and landscapes.
- (7) Theoreticians and field biologists studying the ecology of disturbed ground need to consider more fully the application of their work to practical questions of management, conservation, and remediation. Indeed, all scientists have a responsibility to consider the needs of society and to contribute actively to public discourse on matters about which a scientific perspective is critical.

The study of disturbed terrestrial ecosystems has provided a wealth of knowledge concerning ecological relationships. Understanding the dynamics of such ecosystems contributes to wise stewardship and may be critical to the future of the biosphere. Indeed, if scientists and managers are to provide effective guidance to decision-makers and politicians, then theories must become more robust and the empirical evidence on which they are constructed must be more broadly based. For both practical and theoretical reasons, the scientific community should marshal considerable effort in the future to advance the study of disturbance in terrestrial ecosystems.

EPILOGUE

Studying disturbance is difficult. Understanding its consequences is even more challenging. To the scientist and environmental manager, historical legacies, scale-dependence, multiple causation, inter-correlation, temporal variation, and spatial heterogeneity conspire to make patterns complex and detection of underlying mechanisms elusive. We are reminded of an observation by Plato in *The Republic*, Book VII: "Picture men in an underground cave, with a long entrance reaching up towards the light along the whole width of the cave . . . such men would see nothing of themselves or of each other except the shadows thrown by the fire on

the wall of the cave . . . The only truth that such men would conceive would be the shadows."

Although we are limited by the data that we have collected and by the theories that we have developed, we are encouraged that, even at this early stage of understanding disturbance, the shadows reveal the substance of the phenomena to which this book is dedicated. Indeed, we are inspired by the content of this book, and hope that others will be similarly motivated to redouble efforts to study the ecology of disturbed ground and seek the light at the end of the tunnel.

ACKNOWLEDGMENTS

The ideas presented in this chapter were inspired by the various contributions to this book. In addition, our graduate students and faculty at our home institutions, as well as our colleagues in the Luquillo Long-term Ecological Research program, have contributed in numerous ways to the development of the chapter. Charles V. Cogbill, Mark M. McGinley, Daryl L. Moorhead, and Jess K. Zimmerman provided helpful comments on earlier versions of the manuscript.

In part, this research was performed under grant BSR-8811902 from the National Science Foundation to the Institute for Tropical Ecosystem Studies, University of Puerto Rico and the International Institute for Tropical Forestry, as part of the long-term ecological research program in the Luquillo Experimental Forest. Additional support was provided by the Forest Service (U.S. Department of Agriculture), the University of Puerto Rico, Texas Tech University, and the University of Nevada.

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