The Search for Generality in Studies of Disturbance and Ecosystem Dynamics

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1 Introduction

Studies of disturbance have a long tradition in vegetation ecology (Cooper 1926; Raup 1941; White 1979) and have increased dramatically during the last 30 years (Dayton 1971; Heinselman 1973; Levin and Paine 1974; Borman and Likens 1979; Sousa 1979a,b, 1984; Pickett 1980; Pickett and White 1985; Van der Maarel 1993; Bornette and Amoros 1996; Paine et al. 1998; Frelich and Reich 1999; White et al. 1999). We have learned a tremendous amount about the significance of disturbance as an ecological factor in various habitats and communities (Knapp 1974; Grubb 1977; Miles 1979; Oliver 1981; Pickett and White 1985; Goldberg 1988; Frelich and Lorimer 1991; Milton et al. 1997), about disturbance regimes (Romme 1982; Turner et al. 1993; White et al. 1999), about functional adaptations of plants (Garcia-Mora et al. 1999; Walker et al. 1999), about responses of ecosystems (Bornette and Amoros 1996; Johnson et al. 1998; Engelmark et al. 1999) and about restoring disturbance as an ecosystem process (White and Walker 1997; Covington et al. 1999). During this period, a few theories and synthetic concepts have been proposed, but we do not yet have an inclusive general paradigm for this important body of work.

In this chapter, we explore prospects for the development of generality in disturbance ecology. We discuss the need to study disturbance and to seek generality. We review disturbance definitions and concepts that derive from these definitions. We then discuss the search for generality, focusing on factors that hinder generality and approaches that allow the development of generality across diverse ecosystems and disturbances.

2 Why Study Disturbances? Why Seek Generality?

Disturbances are ubiquitous, inherent and unavoidable, affecting all levels of biological organization. Ecosystems are influenced by disturbances of various kinds, such as fires, windstorms, landslides, flooding, logging, grazing, burrowing animals and outbreaks of pathogens. Due to natural and

anthropogenic disturbances, ecosystems undergo changes that are sudden or gradual, dramatic or subtle. The presence of disturbances in all ecosystems, their occurrence at a wide range of spatial and temporal scales, and their continuity across all levels of ecological organization is the essence of their importance (Pickett and White 1985). In the following paragraphs, we further develop the rationale for the importance of understanding disturbances by discussing eight reasons that the study of disturbances is essential.

a) Patchiness and Heterogeneity

Disturbance is a primary cause of spatial heterogeneity in ecosystems (Platt 1975; Loucks et al. 1985; Collins and Glenn 1988; White et al. 2000). As a major shaping force for composition and structure in ecosystems, disturbance influences competition and environment, substrate and resource availability. Because individuals take up space and use resources, deaths and biomass destruction cause patchiness, even when this is simply a random process among individuals in the community. More often, disturbances affect many individuals at once and cause a coarse-grained patchiness. Disturbances are infrequent relative to the time between disturbances and are brief in relationship to the life span of species they affect. However, on ecosystems, they have effects that are out of proportion to their brief duration; thus, they often influence ecosystem composition and structure long after their occurrence. As a result, understanding ecosystems requires an understanding of their disturbance history.

b) Biodiversity, Adaptation and Ecosystem Response

Disturbances play a crucial role in maintaining biotic diversity (Darwin 1859; Connell 1978; Christensen et al. 1989). They have been evolutionary forces, causing adaptations in the biota exposed to them. Such functional adaptations underlie two mechanisms of ecosystem response to disturbance: complementarity and redundancy. First, species have evolved a diverse spectrum of abilities relative to disturbance. After a particular disturbance, some species increase or invade, while others decrease or retreat (Vogl 1974). Thus, ecosystem response is, in part, a result of niche complementarity. Second, when dominant species are primarily the ones affected by disturbances, other species may increase after a disturbance, even if their functional traits are similar to the previously dominant species. This has been expressed by the resilience hypothesis (Walker et al. 1999). Dominant and minor species in same functional groups are similar with respect to the contribution to ecosystem function, but they differ in their environmental requirements and tolerances and, thus, in their ability to respond to disturbances. Dominant and less dominant species switch in abundance under

changing environmental conditions allowing functional stability. Thus, functional redundancy is important in ensuring the persistence of ecosystem function under changing environmental conditions and in ensuring resilience in response to a disturbance. Moreover, apparently redundant species may operate on different spatial and temporal scales (Peterson et al. 1998), thereby reinforcing function across scales. Both complementarity and redundancy can be mechanisms that contribute to overall ecosystem stability. For example, Marks (1974) showed that fast-growing early-successional trees are able to take up dissolved nitrogen after a disturbance, thus preventing nitrogen export to groundwater and streams. Vitousek's (1984) general theory of forest nutrient dynamics suggested that early-successional species immobilize limiting nutrients quickly after a disturbance.

c) Human Effects on Natural Disturbance Regimes

Alteration, suppression and even enforcement of natural disturbance regimes by human activities are current issues in science and politics. A major way humans affect biological diversity is through direct influences on the disturbance rate and intensity. Changes in fire and hydrology, including the dynamics of flooding, are nearly universal influences caused by people. For the purpose of economic exploitation or the protection of civilization, humans often strive to eliminate natural disturbances. We thereby allow succession and lengthen the return intervals of disturbance events. However, this may result in increased magnitudes and severities of subsequent disturbances, because ecosystem susceptibility to disturbances may be enhanced. Fire control, for example, often leads to increased fire severity due to reduced landscape heterogeneity (Minnich and Chou 1997). Therefore, it is critical that we understand disturbance dynamics and build predictive models that will allow us to forecast future changes and better manage ecosystems for nature conservation and for human needs. In a broad sense, human management consists of managing disturbances and succession and includes creating, replacing or suppressing disturbances.

d) Novel Human Disturbances

Humans also introduce novel disturbances. For example, large clear cuts cannot entirely mimic the effects of wildfire on the landscape age mosaic (Hansen et al. 1991). Although some wildfires may be large in terms of the boundaries of the fire, they leave behind heterogeneous patches of mortality and survival patterns within the area burned. Tree regeneration can proceed from these areas via either seed or sprout sources (Johnson et al. 1998). Understanding how ecosystems react to natural disturbances and to what extent human disturbances resemble natural effects is a prerequisite for

evaluating how to manage the interplay between civilization and the natural environment. It is important to understand dissimilarities between natural and human disturbances in order to predict an ecosystem's ability to respond to human impact. Furthermore, in many cases of interaction and synergism, it is impossible to differentiate between human and natural causes of disturbance. Thus, information regarding disturbance characteristics and the critical limits of persistence and resilience to specific disturbances is crucial.

e)   Habitat Fragmentation

Humans affect disturbance regimes by altering the spatial pattern of ecosystems through habitat fragmentation. Habitat fragmentation can both increase and decrease the disturbance rate (Franklin and Forman 1987; Baker 1992a). For example, disturbances like fires and insect outbreaks, which spread contagiously through a landscape, are critically dependent on the nature of the ecosystems through which they spread (Turner et al. 1989). Frost (1993) has argued that habitat fragmentation has produced smaller fire compartment sizes in the longleaf pine savannas of the southeastern United States. As a result, fire frequency has decreased, because a single lightning ignition cannot burn as large an area. Bergeron and Brisson (1990) showed that the fire regime is very different on lake islands than in surrounding mainland areas in the boreal forest, simply because fire sizes could be larger in larger blocks of forest. By contrast, habitat fragmentation can also increase the disturbance rate. Increased wind disturbance on newly created forest edges is a frequent example. In addition, landslide magnitudes can be increased by patchy agricultural ecosystems in sensitive high-mountain regions, and flooding intensity increases with the increase in impervious surfaces due to urban expansion.

f)   Traditional Land Uses as Disturbance Regimes

Many landscapes were created by human-induced disturbance regimes, some of which have been in place for centuries. Burning, logging, grazing and mowing constitute major influences on cultivated landscapes. Many grasslands, fields and forests are exposed to regular, human-induced disturbances. Especially in Europe, many endangered species now persist only where traditional land-management practices continue (Grebe et al. 1999). In the southern Appalachians of North America, a similar situation occurs, with a number of rare plants occurring on mountain meadows called grassy balds, which were maintained by settlers as grazing pastures (White and Sutter 1998). Traditional human disturbances may have generally maintained early successional habitats and species in ecosystems whose natural

dynamics no longer occur or are unknown (White 1984). Among the most important influences was the frequent use of fire and grazing.

Traditional cultures with low levels of technology and relatively low human-population sizes caused great variety in species and ecosystems as a result of functional adaptation to human disturbances or the replacement of natural disturbances by human-controlled ones. Thus, the elimination of disturbances as ecological factors or the alteration of such disturbance regimes may cause dramatic successional changes in these ecosystems. The disruption of landscape-level dynamic processes and disturbance regimes, such as floods, fire or traditional land use, can be a threat to the maintenance of biotic diversity and may result in changes of the abundances of many species (Tilman 1996; Beierkuhnlein 1998). It is well known that the heterogeneity of landscapes and the diversity of species and ecological processes are lost through either succession or through land-use intensification as cultures change (Sukopp 1976; Kaule 1986; Jedicke 1994; Hagen 1996; Lux 1999). Ecologists and nature conservationists no longer consider disturbance as extraordinary and merely destructive forces; they acknowledge the generality of the occurrence of disturbances and the significance of their influence (White and Bratton 1980; Sprugel 1991). Natural and human disturbances overlay each other. We must study the impact of disturbances on both natural and cultivated landscapes and take into account the synergistic effects of both natural and human-induced disturbance regimes.

g) Climate Change

Climate change will contribute to alterations in disturbance regime, e.g. a change of fire frequency due to variations in weather conditions, or an increased flooding intensity due to altered precipitation patterns (Richter 1993). Moreover, disturbances can remove the inertia represented by existing ecosystems, thus resulting in a relatively sudden response (or adjustment) to previous climate changes. Thus, successional pathways are continuously altered in composition and velocity when exposed to varying environmental conditions.

h) Exotic-Species Invasions

Exotic invasions can occur more quickly after disturbances to ecosystems (if only because disturbances remove competitive dominants and increase the rate of establishment of new individuals, exotic or not). Exotic species can also alter the disturbance rate. For example, introduced grasses in western North America (Billings 1990) and invasive trees in the Florida Everglades have increased fire frequency and intensity (Bodle et al. 1994). Because exotic-species invasions are one of the most important global envi-

ronmental problems, these add to the rationale for studying disturbance itself.

i) Why Seek Generality?

Disturbance regimes and vegetation dynamics encompass a diverse array of cases. Disturbance can have a variety of quantitative and qualitative causes and effects. Disturbance may result in stability or change, may have purely local effects or wide-reaching influences, may be exogenous or endogenous to the ecosystem, and may be encouraged or resisted by nature conservationists and ecosystem managers. Ecosystem responses to disturbances are also diverse.

The first step towards developing generality in disturbance ecology is to find patterns in these diverse cases. Such patterns will reduce complexity and help us develop further hypotheses. It is important to identify which factors are most important under which circumstances (Sheil 1999). Thus, complexity should be structured and incorporated into hypotheses rather than avoided. Scientific progress can only occur through exploring inconsistencies regarding current hypotheses, revising old assumptions and communicating and criticizing theories (Kuhn 1962; Feyerabend 1981). In the end, the importance of scientific findings depends on their endurance (their retention through time). What endures is the identity of the pattern (Whitehead 1925). Thus, patterns on diverse scales, for diverse disturbances and in diverse ecosystems are the foci of interest in the search for generalities in disturbance ecology.

3   Disturbances and Disturbance Regimes

During the twentieth century, much attention has been focused on research concerning vegetation dynamics. Much of the attention has focused on changes after disturbances, including the development of the concepts of succession (Cowles 1899; Lüdi 1919), gap dynamics and pattern and process (Watt 1947), cyclic micro-successions (Churchill and Hanson 1958), patch dynamics (Pickett and Thompson 1978; Pickett and White 1985), mosaic cycles (Remmert 1991) and carousel dynamics (Van der Maarel 1993). Starting during the 1970s, ecologists have increasingly viewed the disturbance process itself as fundamental to understanding vegetation. The study of disturbances, their effects on ecosystems and the conditions they create for succession have become equally important to the study of succession subsequent to a disturbance (White 1979). Before we go further, we must answer the question: what is considered a disturbance?

In defining disturbance, we are immediately faced with an important choice between relative and absolute definitions. At one level, this is a se-

mantic issue, but it also raises conceptual issues in the understanding of spatial and temporal variations in ecosystems.

The relative definition of disturbance seeks to define disturbances as causing deviation from the normal dynamics of an ecosystem. Thus, destructive events like fires in grasslands or tree falls in old-growth forests, which characterize these ecosystems, are not considered disturbances. Disturbances are events that change the characteristic ecosystem processes (elimination of fire from a grassland, or introduction of fire to mesic old-growth forests that had no history of this disturbance type). White and Pickett (1985) reserved the term "perturbation" for departure from normal dynamics. Perturbations cause alteration from what is usual or expected, a relative "deviation from any nominal stage in structure or function at any level of organization" (Odum et al. 1979), including expected variance. Although the normal functioning of an ecosystem is hard to determine and depends on the scale of observation, other authors have also defined "disturbance" as an event causing departure from the normal range of conditions (Forman and Godron 1986; Van Andel and Van den Bergh 1987).

In contrast, the absolute definition of disturbance is based on physical and measurable changes in variables [changes in biomass (Grime 1979) or in the disposal of resources (Sousa 1984; Tilman 1985)], whether or not these changes are recurrent, expected or normal. Van der Maarel (1988, 1993, 1996) distinguishes between disturbance and periodicity and fluctuation, the "stochastic and patchy occurrence of environmental events, both abiotic and biotic, leading to loss in biomass" but nevertheless allowing for recovery and stability. Along with Grime (1979), he relates the term disturbance to effect (loss of biomass), while Rykiel (1985) views "disturbance" as we use "perturbation" (Jax 1999). While we adhere to an absolute definition of disturbance itself, incorporating both cause and effect, the validity of making disturbance characteristics relative in order to compare ecosystems (and thereby develop generality) is an important topic later in our essay.

a) Problems with the Relative Definition

The relative definition of disturbance is problematic for two reasons: first, the underlying assumption of normal dynamics is usually invalid or untested and, second, even when the underlying assumption is valid, the approach compares disturbances not on the grounds of effects and responses but on the grounds of statistical precedence. We explore these problems below.

The underlying assumption in the relative definition of disturbance is that we can define the normal dynamics of ecosystems. This is equivalent to the assumption that the statistical distribution of disturbance events in time and space has two key properties: stability and discontinuity. Stability ensures that the dynamic pattern continues; discontinuity ensures that the ecosystem

fluctuates within defined bounds. According to the relative definition, events within the normal domain would not be disturbances, no matter how destructive; events outside the domain would be disturbances, no matter how mild. Thus, the absence of fire in a grassland has been called a "disturbance", with fire considered normal.

We challenge statistical stability and discontinuity on several grounds. First, because climate varies, disturbances vary; we can see this in year-to-year climate differences, semi-periodic variations, such as that caused by the Southern Oscillation, and long-term climate changes (Swetnam and Betancourt 1990). This challenges the notion of dynamic stability and introduces a scale dependence; at what temporal scale do we analyze the statistical distribution? A second problem in defining the normal dynamics of ecosystems stems from variation in the intensity of a given disturbance through space. This variation, combined with the spatial variation in the ecosystem itself, produces spatial patchiness in the effects of a disturbance. Even when that patchiness is in a statistical dynamic equilibrium (White et al. 1999), the relative definition of disturbance causes problems; the normal (non-disturbance) ecosystem now contains patches of contrasting age, biomass and dynamics. As with the temporal axis, we have a scale dependence problem: at what spatial scale do we define the statistical properties of an ecosystem?

Although we reject the relative definition of disturbance, the statistical distributions of disturbance events are important. Indeed, the notion of the statistical distribution has been raised explicitly in two recent contexts. First, the idea of large, infrequent disturbances (Turner et al. 1998) is based on the common finding that the frequency and magnitude of a disturbance are inversely related (Fig. 1); small magnitude events are frequent, large ones are rare. This raises the question of whether the statistical distribution allows the clear separation of rare and non-rare events, but it is clear we can investigate this question without using the statistical distribution to define disturbance. Second, the concept of the historic range of variation is based on the idea that ecosystems are neither constant nor unbounded in their variation (Swetnam 1993; Landres et al. 1999). This implies discontinuity and stability; the bounds of variation in the last several generations of dominant plants are presumed to be definable and useful in setting nature conservation goals. Again, regardless of whether stability and discontinuity exist for particular time periods, we can investigate the historic range of variation without using the bounds of historic variation to define disturbance in a relative sense. We can use this information to ask whether current human management results in ecosystems that are within or outside the bounds of historical variation (Landres et al. 1999).
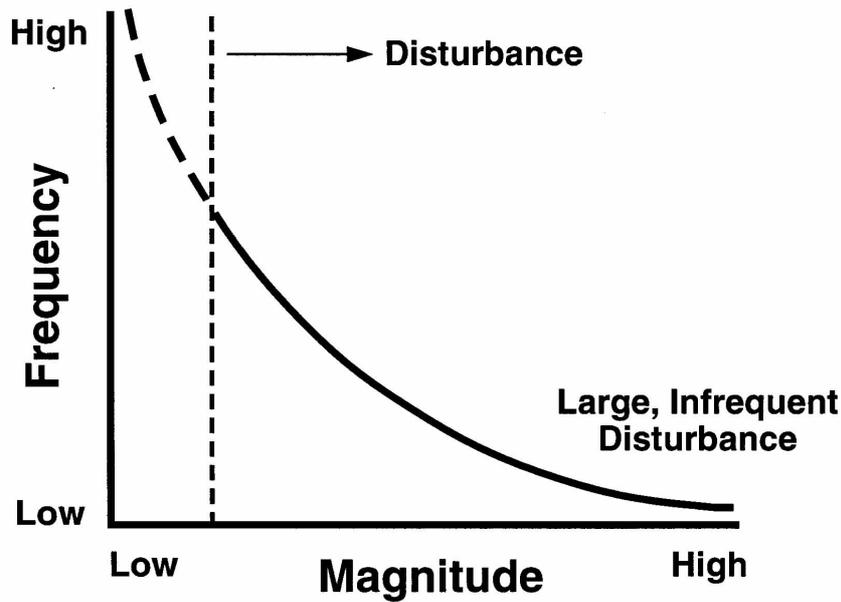
Fig. 1. Frequency and magnitude of disturbance are often inversely related. Events must meet a minimum magnitude to be considered a disturbance at a particular scale for a particular ecosystem. Large, infrequent disturbances have been discussed as a special case of disturbance. (Turner et al. 1998)

b) The Absolute Definition

The broadest absolute definition of disturbance is that published by White and Pickett (1985): disturbance is a relatively discrete event in time that disrupts the ecosystem, community or population structure and changes the resources, substrate availability or physical environment. A disturbance, in this sense, changes the state of structural and physical variables in the ecosystem, although these changes also influence ecosystem functions and processes. The White and Pickett definition is an absolute definition because it requires measurement of the disruption in structure and the changes in resources, substrates and environments, regardless of the statistical distribution of these disturbance properties. All fires in grasslands are disturbances, regardless of how recurrent or expected and regardless of how intense. The absolute definition of disturbance thus focuses our attention on the real

changes that have taken place and the mechanisms of response to those changes.

Although this definition is straightforward compared with the demands of the relative definition, it does raise several conceptual and pragmatic issues, because it poses questions regarding the relative discreteness of disturbance events, the nature and magnitude of the ecosystem property that is disrupted or changed, and the scale dependence of disturbance effects. We discuss these below.

The concept of disturbance as a relatively discrete event suggests that these events are brief and abrupt relative to the longevity, reproduction, growth rate and succession of the ecosystems in which they occur. Thus, there are two important tests in the temporal occurrence of disturbance: duration and abruptness. For example, in many ecosystems, the duration of disturbances is measured in a few weeks or less. By contrast, other changes in ecosystem properties act over longer time scales (years and longer). Disturbances must also be abrupt, rather than continuous. In this view, a continuous disruption of structure (continuous, low-level herbivory) is not a disturbance for the ecosystem as a whole. However, scale dependence occurs here; herbivory measured at small spatial scales and short temporal intervals might be defined as a disturbance to part of the ecosystem.

The absolute definition also involves specification of the nature and magnitude of the ecosystem property that is disrupted or changed. Grime (1979) proposed a simple and easily measured subset of the White and Pickett (1985) definition: disturbance as the destruction of biomass. While most of the disturbances discussed by White and Pickett (1985) involve the destruction of biomass, not all do. For example, a terrestrial fire that increases sedimentation in nearby streams would be a relatively abrupt change in substrate without, necessarily, an immediate loss or destruction of stream biomass.

Having proposed that disturbances cause changes in biomass or some other ecosystem parameter (resources, substrate), we must then address a second issue: how much change must occur in order to use the term disturbance? As White and Pickett (1985) were quick to point out, flood scour (i.e., a disturbance to a streamside moss community) is not necessarily a disturbance to the forest above. As this example suggests, the key issue is the change relative to the ecosystem studied. For example, using the Grime definition, the question is: how much biomass has been destroyed relative to pre-disturbance biomass? Like the notion of duration and abruptness, the answer to this question depends on the absolute properties of the ecosystem.

In sum, the absolute definition of disturbance suggests that the tests of disturbance are abruptness, duration and magnitude, but these are relative to the dimensions of the ecosystem studied (Fig. 2). Relativizing to the dimensions of the ecosystem studied is one path to developing generality, as we discuss below. Processes that effect function without a direct abrupt influence on ecosystem structure are stressors rather than disturbances.
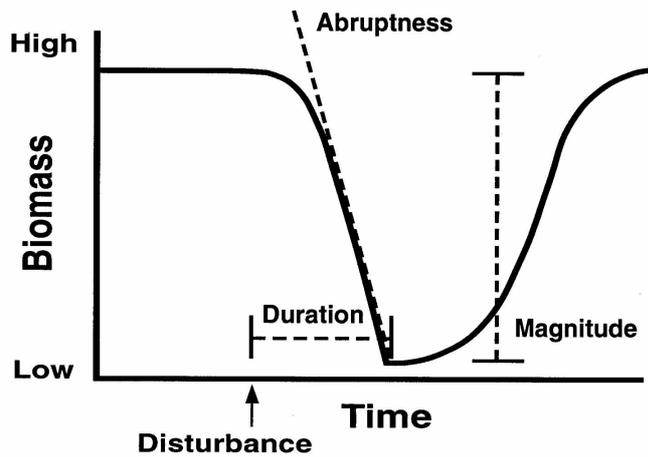
Fig. 2. Three tests of the definition of disturbance: abruptness, duration and magnitude

Processes that act over long time periods, lack abruptness and do not disrupt biomass or other physical variables are also excluded from the concept of disturbance.

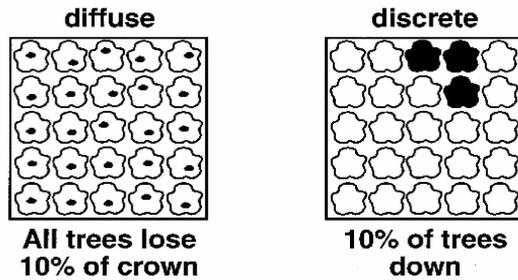c) Diffuse and Discrete Disturbances

The absolute definition of disturbance allows us to recognize that the distinction between discrete and diffuse disturbances depends on the scale of observation (Fig. 3). Diffuse disturbances are those in which relatively small patches of change are distributed over a large area; discrete disturbances are those in which the change is aggregated into large patches. However, viewed at a small spatial scale, diffuse disturbances are made of patches of discrete disturbances. Similarly, at very large spatial scales, discrete disturbances can become diffuse.

d) Site Potential and Class-I and Class-II Disturbances

Some disturbances lead to changes in site resources and in overall site potential. For example, a debris avalanche may erode soils to bedrock, thereby initiating a primary succession. Similarly, soil nutrients may become vulnerable to leaching from a site, and repeat disturbances at close intervals may lead to the sustained export of these nutrients. Also, fire may volatilize nitrogen and carbon held in organic matter; as a result, these are lost from the site. Disturbances can also increase site resources – flood and avalanche depositional zones receive the nutrients and organic matter from elsewhere in the landscape.

Diffuse vs. Discrete Disturbance
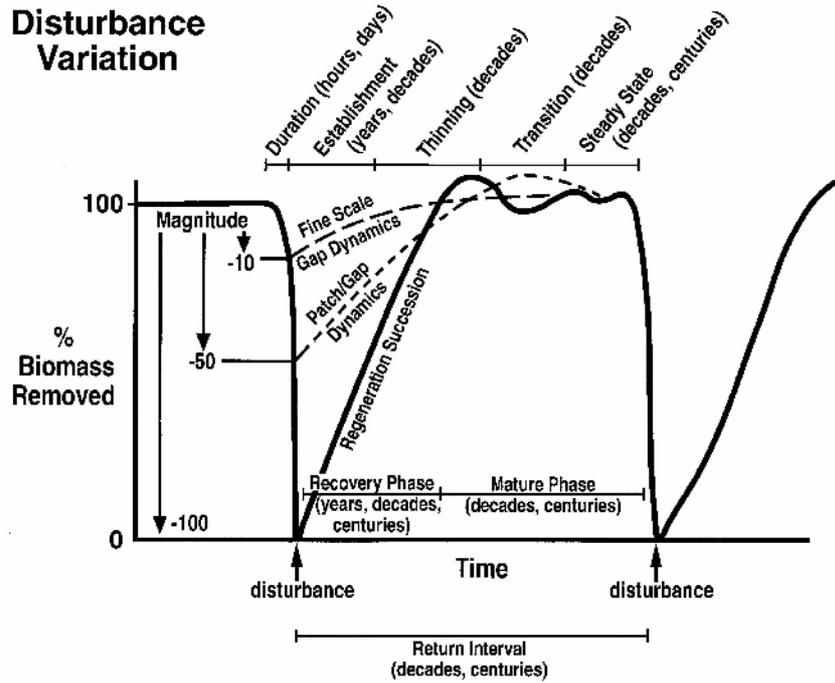
For a given average magnitude
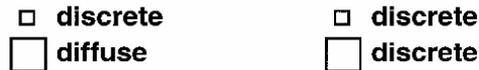
Fig. 3. Discrete and diffuse disturbances can only be defined with reference to scale. Disturbance magnitude is the same (10% of crown area) in the two cases. When this amount of damage is spread among trees (*left-hand example*), the disturbance only appears to be discrete at small scales (quadrat or grain size). When the damage is concentrated in individual trees (*right-hand example*), the disturbance effect is discrete at both scales

In contrast to these examples, many disturbances, although they may temporarily increase resources (space, light, nutrients and water), leave the overall site potential unchanged and result in straightforward secondary successions that lead back to the pre-disturbance composition, resource levels and structure (or at least back to a trajectory towards mature, late successional vegetation if the time between disturbances is not long enough for the succession to be completed). White and Pickett (1985) distinguished two cases of disturbance-induced secondary succession. Class-I disturbances are relatively fine-scale dynamics usually considered as intra-community phenomena. Classic cases are wave regeneration in fir forests (Sprugel 1976) and cyclic regeneration on small patches in shrublands (Watt 1947; Churchill and Hansen 1958; other cases are reviewed in White 1979). These small, patchwise dynamics have also been called fine-scale gap dynamics (Glenn-Lewin and Van der Maarel 1992) or simply gap dynamics (in forests and other communities where open space is created), gap-dynamics regeneration mode, micro-successions and cyclic successions (if they lead to iterative alternation among canopy dominants; Churchill and Hansen 1958; Forcier 1975). Class-II disturbances are larger-scale disturbances that initiate straightforward secondary successions in which species not dominant in the mature forest become the first generation of dominants followed by succession to mature-phase species. Class-II disturbances are usually considered to be between (rather than within) community dynamics.

Disturbance Variation

Duration (hours, days)

Establishment (years, decades)

Thinning (decades)

Transition (decades)

Steady State (decades, centuries)

Magnitude

Fine Scale Gap Dynamics

Patch/Gap Dynamics

Regeneration Succession

100

-10

-50

% Biomass Removed

-100

0

Recovery Phase (years, decades, centuries)

Mature Phase (decades, centuries)

Time

disturbance   disturbance

Return Interval (decades, centuries)

Fig. 4. Vegetation dynamics have been classified according to the magnitude of the disturbance event (here relative to 100% of pre-disturbance biomass). Fine-scale dynamics occurs after low-magnitude disturbance, patch or gap dynamics at moderate magnitudes, and regeneration succession at large magnitudes. (Van der Maarel 1996)

Class-II disturbances have also been called stand-initiating disturbances and lethal disturbances (because they cause widespread plant mortality). They are said to produce regeneration succession and catastrophic regeneration mode (Fig. 4). In both class I and class II, the disturbance leaves the original site potential unchanged, and succession re-creates the pre-disturbance composition and structure. Recognition of class-I and class-II disturbances and the separation of disturbances that do and do not alter the site potential are issues that will reappear as we discuss approaches to generality.

e)   Other Definition Issues

The absolute definition of disturbance does not require further specification of several other proposed disturbance attributes, such as the exogenous–endogenous continuum, the evolutionary or ecological precedence of disturbance, or the human/natural cause. Exogenous disturbances are those in

which the force originates outside the ecosystem; endogenous disturbances are those in which the force (often plant mortality and senescence) originates within or as a product of successional development. White (1979) and others have argued that these are the end points of a continuum. The absolute definition does not require that disturbances be defined with reference to historical precedence. For example, among disturbances, Harper (1977) defined as disasters those events that occur frequently enough to be selective agents in evolution and defined as catastrophes those events so infrequent that they do not play a role in selection. Our definition is moot regarding this distinction. The absolute definition of disturbance can also be applied to human and natural disturbances and disturbances that have both human and natural influences.

f)   Heterogeneity, Homogeneity and Scale

The absolute definition does not assume that disturbed patches in a particular ecosystem are spatially or temporally aggregated or that they have any particular distribution. Hence, the absolute definition suggests the analysis of disturbance effects within patches. As with the definition of diffuse and discrete disturbances just discussed, the observed heterogeneity or homogeneity will be a function of the scale of observation relative to the scale of these patches. As the scale of observation becomes small relative to the disturbance patches, individual patches will appear to be homogeneous, but there may be a great range of values if nearby patches experienced different disturbance magnitudes. At larger scales of observation, the variation from one patch to another may be average, producing homogeneity again.

g)   From Disturbance Event to Disturbance Regime
with Spatio-Temporal Dimensions

The sum of all disturbances affecting an ecosystem is its disturbance regime. Although the study of individual disturbance events plays a critical role, understanding the full significance of disturbances in both an evolutionary and ecological sense will require investigations of disturbance regimes. Elements of disturbance regimes are the kind of disturbance, spatial characteristics, temporal characteristics, magnitude, specificity and synergisms (Sousa 1984; White and Pickett 1985; White and Harrod 1997; White et al. 1999). Spatial characteristics include the area, shape and spatial distribution. Temporal characteristics include the duration, frequency, return interval and rotation period. Magnitude includes the intensity or physical force of the disturbance itself and the severity of impacts to the ecosystem. Specificity describes the correlation of the disturbance with the

species, size class or successional state. Synergisms include the interactions among different kinds of disturbance.

Describing a disturbance regime with these descriptors allows us to examine disturbance effects in a way that contributes to our understanding of the mechanisms of the response. However, just as the absolute definition of disturbance yields parameters that must be relativized to the ecosystem under study (biomass disturbed as a function of pre-disturbance biomass), the parameters of the disturbance regime must be relativized to the ecosystem studied to produce generality. For example, expressing the frequency of disturbance relative to the life span and growth rates of the organisms disturbed allows comparison among ecosystems and the detection of general patterns. On relativization, spatial and temporal patterns of disturbance and regeneration are similar at various scales (Fig. 5), a fact we return to in a later section of this paper.
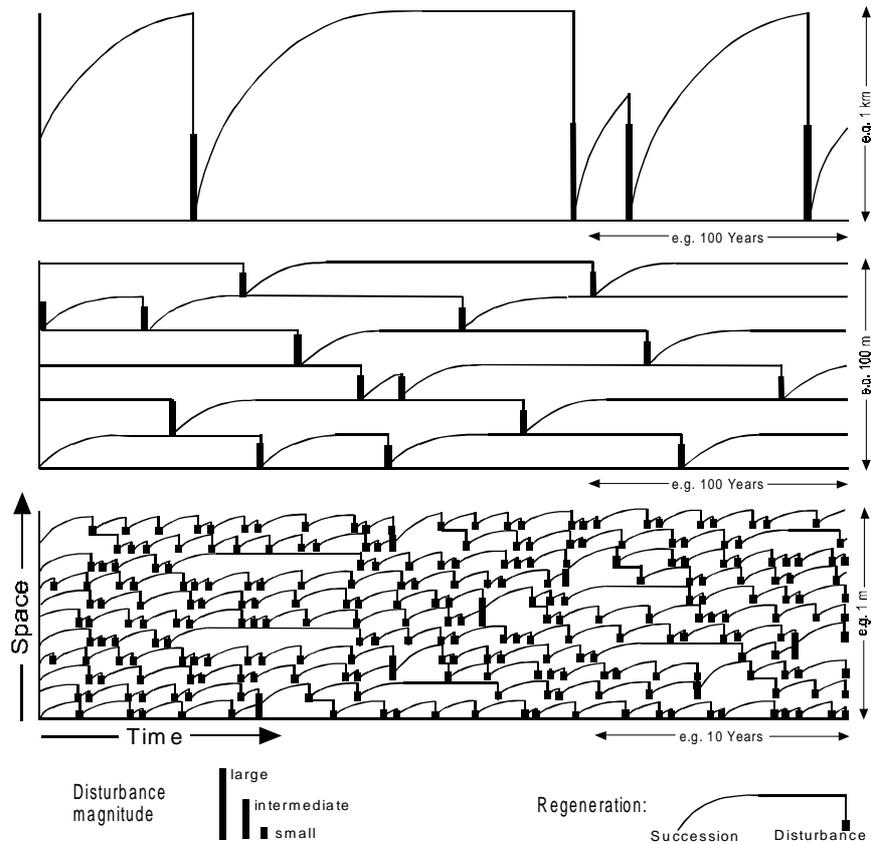
Fig. 5. Resemblance between the pattern of disturbance and regeneration at various spatial and temporal scales. (Böhmer and Richter 1997)

4   What Hinders the Development of Generality
in Disturbance Ecology?

Developing generalizations about disturbance is challenging, because these generalizations must consider diverse disturbances and ecosystems. Some disturbances affect large areas and remove all soil and biota, thereby initiating primary successions, while others merely crop the aboveground biomass without causing mortality, and initiate only the re-growth of existing individuals. Between these extremes are disturbances that cause the deaths of individuals but leave soil and biota otherwise intact, thereby initiating secondary successions. Most ecosystems are subject to more than one kind of disturbance, which varies in intensity and in the spatial patterns of its effects. These disturbances interact with other forces of vegetation change (sea level rise, climate change; White 1994).

To develop basic concepts regarding the role of disturbance in ecosystems, we must be able to organize this diversity. However, the problem is deeper than the sheer diversity of cases. In this section, in order to organize and discuss what we see as the key obstacles to the development of generality, we review major findings that have developed during the last 30 years regarding disturbance. Discussing these obstacles will allow us to describe approaches to generality in the final section of this chapter.

Below, we outline challenges in the development of generality under four headings:

1. Variation in disturbance events.
2. Variation in disturbance effects within ecosystems.
3. Variation in ecosystem response underlain by differences in the biota present and in the physical environment.
4. Influences of the scale of observation and measurement. Because disturbances are episodic in time and create patchiness in space, the scale of observation can affect findings and conclusions.

a)   Spatial and Temporal Variation in Disturbance Events

Disturbance occurrence and characteristics vary not only with ecosystem type but also with topography, climate, soil development and the history of past disturbances in the ecosystem. This variation makes disturbance regimes variable in time and space (even for one kind of ecosystem) and contributes to the difficulty of generalization.

α) Disturbances Interact with a Unique Topography Template

Regardless of ecosystem type, the surface of the earth forms a unique physical template for each natural or cultivated landscape. This template is the result of past events and generally slow-acting forces in the present. Although disturbances themselves can alter topography (avalanches, alluvial erosion and deposition, dune movement and volcanic eruptions), topography is often a "given" for scientists and conservationists – a condition that exists and that cannot be manipulated.

The outplay of disturbances will be influenced by both the force of the disturbance and the physical template over which it occurs. Topography is important, because it creates gradients, patterns of adjacency between ecosystems and island-like effects of size and isolation. Disturbance characteristics vary along environmental gradients (Harmon et al. 1983; White 1987; Veblen et al. 1994; Richter 1998). For example, slope exposure and inclination impedes or promotes fire spread and determines whether crown or ground fires occur. Topographic gradients are also correlated with productivity and rates of succession, thus altering the consequences of disturbance and the timing of a subsequent disturbance if that timing is dependent on the successional state (Romme and Knight 1981).

Landscape patterns control the adjacency and isolation of ecosystems and thus influence the disturbance regime. Some disturbances, like fire and insects, spread contagiously and affect one site as a function of the surrounding context of that site. Relatively less vulnerable ecosystems can have a higher disturbance rate, because they are surrounded by more vulnerable ecosystems or because the disturbance rate varies at ecosystem edges or ecotones, particularly when the ecotone separates ecosystems with different dominant growth forms (grasses and trees; White et al. in press). Fires affecting montane *Sequoia* forests in Sequoia–Kings Canyon National Park in California may owe their origin (in part) to fires that start in lower-elevation chaparral vegetation (McKelvey et al. 1996). Unfortunately, the national park does not protect much of the chaparral, suggesting that management ignitions may have to play a compensating role.

Conversely, sites can escape disturbance because they are surrounded by less vulnerable ecosystems. For example, natural firebreaks impede fire spreading. Human fragmentation of landscapes reduces the size of fire compartments (in longleaf pine forests in the US; Frost 1993). Bergeron and Brisson (1990) showed that the fire regimes of lake islands in the boreal forest were very different than those on the mainland. Each island required its own ignition, whereas single ignitions could burn large areas in the mainland landscape. Isolation also affects response through its influence on the distance to colonization sources.

Topography also creates island size effects. Small, isolated patches may be entirely disturbed by a single disturbance event or may entirely escape disturbance for longer than the average time for the ecosystem. Small, iso-

lated areas that are entirely disturbed in a single event may lose disturbance-sensitive species for which the nearest populations are too far away for re-colonization. Small areas that escape disturbance for long periods may lose disturbance-dependent species; the absence of these species may cause the ecosystem to respond differently to a subsequent disturbance.

β)   Disturbances Vary with Climate

A single kind of disturbance within a single ecosystem can also have variable effects at different times. For example, fire burns at a higher intensity during parts of the year that have low humidity. Recent research has also convincingly demonstrated the link between disturbance rates and year-to-year, interdecadal and longer-term climate variations (Johnson and Larsen 1991; Johnson and Wowchuck 1993). For example, fire frequency in North America has been shown to track climatic changes since the Pleistocene (Clark 1988; Swetnam 1993), to vary with the Southern Oscillation in sea-surface temperatures at roughly decadal time scales (Swetnam and Betancourt 1990) and to vary with other continental climate fluctuations (Nash and Johnson 1996).

γ)   Disturbances Vary with Soil Development

Long-term soil development can create changes within an ecosystem that influence the ecosystem response. For example, Walker and Syers (1976) showed that phosphorous becomes increasingly unavailable in succession on sand dunes. A disturbance occurring during the early part of this successional sequence will have very different effects than a disturbance late in the sequence.

δ)   Disturbances Vary with Feedback and Interactions

Disturbances vary not only with contemporary environment and the kind of ecosystem present but also with successional age, the patchiness of the pre-disturbance ecosystem and the history of disturbance. Often, the probability of disturbance increases with successional age, as when older trees of late-succession forests are more vulnerable to windfall and create larger gaps than younger trees of early-succession forests. It is frequently asserted that the probability of fire and fire intensity increases as fuels build within the ecosystem as a function of the time since the previous fire (Agee and Huff 1987). Past fire events influence the amount of fuel build-up as a historical factor (McCune 1982) and, therefore, they influence the likelihood of ignition. Situations such as these represent feedback between the community's

state and the disturbance regime, so the effect of a given physical force (wind, lightning ignition) is dependent on the community's state and, thus, the history of the ecosystem. Such feedback tends to lengthen the time between disturbances and causes them to be spaced at semi-regular intervals controlled by the time since the disturbance and the rate of succession. In general, the effects of a given disturbance at different points in time vary with the successional state and the prior history of the ecosystem.

Acting in the opposite direction, disturbance interactions can promote further disturbance. For example, wind damage can lead to insect and fungal attack; this may cause tree death, or it can simply increase the vulnerability of the trees to further windstorms. Trees on gap edges are often more vulnerable to wind, leading to gap expansion (Runkle and Yetter 1987). Some fires can create more fuels than they consume if they kill trees that then break apart and fall, increasing fuel loads after the fire and creating the conditions for a subsequent fire that is more intense than the original fire. Insect outbreaks can also cause heavy fuel loads and areas of high fire intensity. Disturbance interactions generally mean that a prior disturbance attracts a subsequent disturbance (repeat disturbances are likely), but some disturbances may decrease the probability of another disturbance (Veblen et al. 1994).

Interactions and feedback both suggest that the probability and characteristics of current disturbances can only be understood with reference to the history of disturbance. The history of disturbance is often expressed as current patchiness in the distribution of living things and organic matter. Variations in pre-disturbance vegetation influence the severity, type of damage and character of post-disturbance vegetation (Foster et al. 1998). Interactions among different kinds of disturbance add to the complexity of approaching an understanding of disturbance impacts on vegetation dynamics. The interaction of disturbances that have varying temporal rhythms and spatial extensions and are subject to varying positive or negative feedback is a major challenge. Data on many biotic and abiotic parameters and records of historical events and processes are often missing or are difficult to acquire.

b)   Spatial and Temporal Variation in the Effects
of Disturbance and Ecosystem Responses to Disturbance

Disturbance effects vary in heterogeneity, patch size, resource levels and
legacy. These post-disturbance characteristics influence the mode and speed
of ecosystem recovery towards pre-disturbance conditions or alteration
towards qualitatively different ecosystems.

α)   Disturbances Vary in the Heterogeneity They Create

While some disturbances have a narrow range of intensities throughout
large areas, thus creating relatively uniform and homogeneous conditions
throughout that area, most disturbances have patchy effects. Even when
disturbances occur with relatively uniform intensity throughout large areas,
they are likely to encounter a heterogeneous ecosystem whose characteris-
tics are determined by variable topography and patchy prior disturbances.
In some cases, however, the ecosystem itself may be relatively homogene-
ous, and the disturbance may then create relatively homogeneous effects.
For example, in relatively flat topography and in stands of homogeneous
age, a fire can sweep through a savanna, cropping the aboveground herba-
ceous biomass but otherwise leaving the ecosystem relatively intact. Such
cases are rare, however, because fire breaks, heterogeneous fuels and prior
human and natural disturbances almost always create variable conditions.
There is also a scale issue in the measurement of heterogeneity: one fire in
the savanna may cause homogeneous effects within the burned patch but,
unless the fire is as large as the savanna itself, it will cause heterogeneity at
a larger scale (the scale at which both homogeneous burned and unburned
patches exist together).
    Most disturbances cause patchy effects. Large, infrequent disturbances
like fires, hurricanes, floods or sand quarries comprise areas affected by
different disturbance intensities and leave behind heterogeneous environ-
ments. At the other end of the size spectrum, small, frequent soil distur-
bances like cryoturbation (Böhmer 1999) or ant activities (Dean et al. 1997)
generate zones of varying mechanical stress and differential reaction pat-
terns.
    These examples indicate that it is the scale of disturbance patches rela-
tive to the size of the landscape that controls the level of patchiness pro-
duced. The smaller the landscape relative to disturbance patches, the more
likely it is that it will be entirely disturbed by a single disturbance and the
more likely it is that the post-disturbance ecosystem will be relatively ho-
mogeneous. This has consequences for dynamic equilibrium because, if a
natural area is all in one age state (whether that is recently disturbed or long
undisturbed), it will lose species not competitive under those conditions

(Pickett and Thompson 1978). As a result, responses to subsequent disturbances will be altered.

β) Disturbances Vary in Patch Size

The area affected varies among disturbances. Patch size affects the environmental characteristics of the disturbed patch, such as light, humidity, soil moisture and temperature. These variables affect the decomposition of organic matter and microbial processes that affect the nutrient supply rate in the soil. However, direct measurements of the environment within patches are rarely made. The patch size may be analyzed and reported, but the significance of a given patch size for environmental conditions varies with the size of the surrounding plants (tree height) and the latitude. Canham et al. (1990) suggested that the northern, southern, eastern and western edges of a gap have different environments and that the sun angle in gaps varies with latitude (Fig. 6). The ratio of gap diameter to surrounding tree heights leads to the rule of thumb that the diameter of a patch has to be twice the height of the surrounding trees in order for the center of the gap not to be influ-
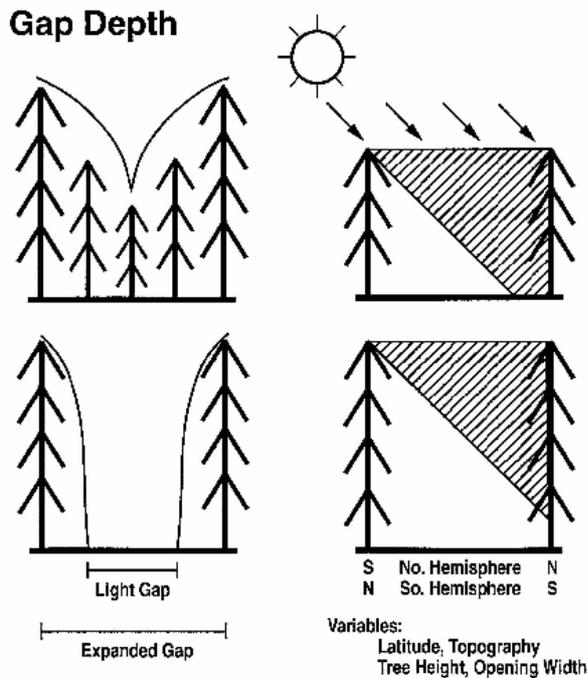

Fig. 6. The amount of light within a gap is affected by gap depth, gap width, topography, latitude and the height of the surrounding trees. (Canham et al. 1990)

enced by those trees. This is a coarse index, however, because the penetration of the influence of surrounding trees on light varies with the compass angle, latitude and slope steepness. Furthermore, the trees have other influences on the gap; for example, the influence of their root systems and leaf litter may extend to a different distance than the effect of their shade. Similarly, there is an edge effect from the gap inward to the intact forest; the penetration of the effect varies with the size of the gap and the latitude (Ryel and Beyschlag 2000). The size of the patch also affects modes of species response. For example, the patch size affects distances to seed sources and therefore affects colonization, because species have different dispersal abilities.

γ) Disturbances Differ in Intensity and Severity
and, Hence, in Ecosystem Legacy

Whether an ecosystem can respond in a particular way is also determined
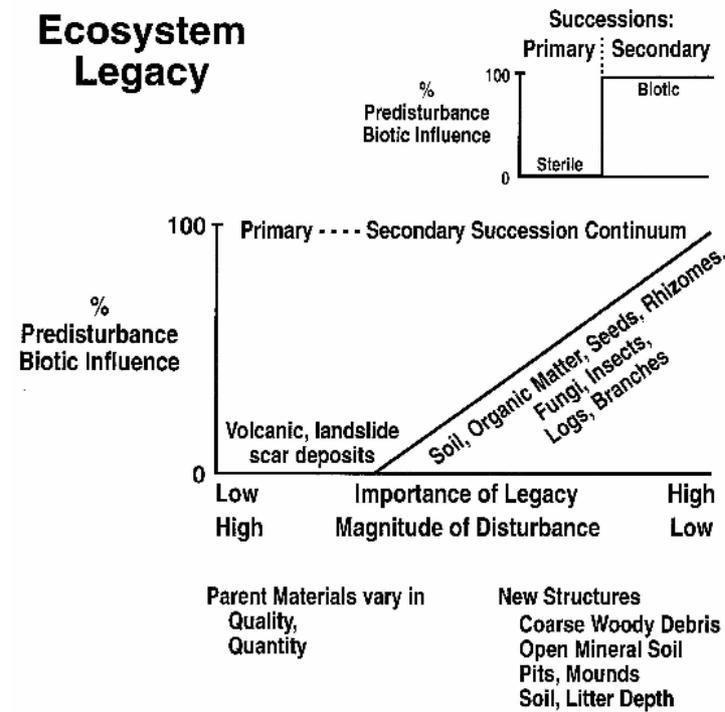
Fig. 7. The continuum from primary to secondary succession, based on ecosystem legacy and the effects of disturbance. The x-axis is a gradient of increasing ecosystem legacy and decreasing disturbance magnitude, and the y-axis represents the influence of the pre-disturbance ecosystem on recovery, from low (0%) to high (100%). The smaller diagram at the *upper right* presents the historical and overly simplified definition of primary (no influence of the pre-disturbance ecosystem) and secondary (100% influence) succession

by its history and the intensity of the disturbance. Natural and anthropogenic disturbances produce a continuum of conditions between extremes termed primary and secondary succession, which differ in the legacies that remain from the pre-disturbance ecosystem (Fig. 7). The amount and distribution of organic matter, the presence and life histories of living organisms, and soil properties all affect the recovery mode and rate (Swanson and Franklin 1992). For example, mild fires may allow perennial plant parts to survive in the soil, moderate fires may eliminate these but allow the seed bank to survive, and very intense fires may eliminate all living plants so that recovery must occur from external colonization (Schimmel and Granstrom 1994). Disturbances can also create new structures (for example, pits, mounds and woody debris in forests after a windstorm). Such structures may play a role in recovery. Pits are moist but must be colonized from nearby seed sources; mounds are relatively dry but have existing perennial plant parts and seed banks intact. Tangled branch piles may reduce the herbivory of large mammals (Peterson and Pickett 1995).

c) Rates of Response and Species Adaptations Vary among Ecosystems

Absolute values of processes that control ecosystem dynamics (such as productivity, the intensity of competition, and rates of growth, establishment, mortality and succession) vary among ecosystems because of differences in the physical environment, including differences in temperature, water availability and soil resources. This affects the speed of response to disturbance. This, in turn, may influence important ecosystem characteristics, such as the retention of nutrients through accumulation of biomass. Any gap in a tropical forest experiences canopy closure much faster than a gap of same size in a boreal forest, due to the lower growth rate in the boreal forest. The number of species or functional groups present for recovery also greatly differs.

Within these ecosystems, species vary. For example, within any forest, tropical or boreal, species differ in their growth and survival as a function of their position in a gap or intact forest patch. Thus, each ecosystem has a different range of absolute values, with individual species varying within those absolute bounds. Finally, species responses can be defined not only by their optimum conditions, but also by the breadth of their tolerance and the shape of their curves of response to a particular factor. Indeed, most species have plastic responses to the environment, and their role in post-disturbance recovery is a function not only of their optima but also of the competitive environment they encounter. For example, even shade-tolerant, slow-growing species respond to added light with accelerated growth – but at a slower rate than light-demanding species (Brokaw 1985; White et al. 1985).

The problem is more complex: the species of a particular ecosystem, and thus the range of responses to a disturbance in that ecosystem, have adapta-

tions that were shaped by past exposures to disturbances. Thus, there is a twofold historical contingency in ecosystem responses. First, in ecological time, only those species with access to the site can participate in recovery (this access can be influenced by prior disturbance) and, second, in evolutionary time, species adaptations are functions of previous evolution. Both determine the diversity of functional responses within an ecosystem. One kind of disturbance in a particular climatic setting can encounter ecosystems with different inherent diversities of species and functional responses.

Historical and evolutionary contingency makes the idea of the intermediate-disturbance hypothesis circular: intermediate frequencies maintain a range of species in an ecosystem that would not have existed in that ecosystem without prior exposure to those disturbances. Intermediacy not only maintains the species, it was responsible for their evolution. It is even possible that higher levels of diversity could evolve in the long-term absence of disturbances, thereby challenging the notion that disturbances are needed for diversity. For example, if a disturbance results in a greater niche width (or plasticity) for a species, it may limit specialization and, ultimately, diversity.

Species are also idiosyncratic in their effects on disturbance regimes. Some species are keystone species that greatly influence disturbance regimes. For example, the fuel provided by a dominant understory grass is critical to the fire regime, species diversity and pine regeneration in longleaf pine forests in the southeastern United States (Christensen 1981). That individual species can affect a disturbance is also illustrated by exotic-species invasions that have altered disturbance regimes in the western grasslands and the southern Florida everglades in the United States.

An important form of species influence on disturbance regimes is the influence associated with the effects of variation in characteristic growth forms. Dominant growth forms (trees, shrubs, forbs and grasses) are associated with different environments but also influence disturbance characteristics. The combination of changes in environmental conditions and disturbance can sharpen ecotones and produce feedback on disturbance rates across the ecotone. Generalizations will have to take into account the influence of species and growth forms on disturbance regimes and effects.

d) Methods of Sampling and Analysis

Because disturbances are episodic in time and produce patchiness in space, the observational scale will influence our findings. In addition, the direct effect of a disturbance on resources and environment is rarely measured; we usually have to use a surrogate variable, such as patch size. Finally, the difficulty of collecting data for every factor that influences a disturbance means that potentially explainable variations among disturbances are treated as stochastic noise. The role of stochastic versus deterministic forces

in ecosystems is a fundamental issue and is central in understanding disturbances.

α)   The Scale of Observation Affects Conclusions Because Disturbances Are Episodic and Patchy

Regardless of the level of heterogeneity produced, the observational scale will be critical. Depending on the size and distribution of disturbed patches, the scale of observation will influence the findings. A plot size large relative to the patch size may average across patches and produce apparent homogeneity (i.e., spatial similarity among plots). A plot size small relative to the patch size will produce apparent heterogeneity (i.e., variability among plots, although each individual plot may be internally homogeneous).

When changing the temporal scale of reference, an assessment of system response ranges from overall stability with cyclic regeneration (the period of observation encompasses the recovery interval) to qualitative change (the period of observation is shorter than length of the recovery interval). A forest community in regeneration succession 3 years after burning certainly has species and degrees of complexity other than those of the prior community. It has qualitatively changed. In 300 years, it might undergo several regeneration cycles but may still exhibit species compositions and degrees of complexity similar to those exhibited in the pre-disturbed state.

While the scale of observation does not matter in extreme cases in which the conditions produced by disturbance are homogeneous throughout large areas, the scale of observation is critical when disturbance effects are patchy and the ecosystem is heterogeneous. For example, patches in a forest after a windstorm have between 0 and 100% of their canopy biomass removed. Viewed at a small scale, the disturbance has variable effects; at larger scales, the patch variation is averaged. In large areas, biomass and composition can be constant despite fluctuating biomass and composition in local patches; this results from disturbance and recovery. The scale of measurement becomes an issue both in recognizing whether a disturbance has occurred and in comparing the magnitude of one disturbance to another or in comparing one ecosystem to another. We return to the issue of scale and stability in the last section of this paper, because a major area in the discussion of generality has been whether disturbance produces dynamic equilibrium at large scales.

The focus of interest and the level of resolution also influence conclusions regarding the ecosystem response to disturbance. Various categories of ecosystem components, e.g., floral or structural elements, may operate at different spatial and temporal scales, and these do not need to be independent from each other (Lux and Bemmerlein-Lux 1998; Beierkuhnlein, in press). Various perspectives on the ecosystems under study may thus result

in different assessments of the disturbance effects, rates of change and overall patch dynamics with varying component selections and resolutions.

β)   Surrogate Variables Are Often the Only Ones Measured

An absolute definition of disturbance suggests that resources, the physical environment and space are affected. Other than the measurement of space, however, we rarely have direct measurements of these effects; often, characteristics like patch size are assumed to be correlated with the effects of disturbance. In addition to the simple observation that this makes our analysis indirect, it introduces several other kinds of problems. For example, even if above- and below-ground effects are correlated with the patch size, they may have their own unique patch sizes. Furthermore, although the patch size is important, given patch sizes have different significances in different ecosystems. The size of a gap, for example, affects the light environment, but this effect is itself a function of the height of the surrounding trees, slope inclination and latitude (Canham et al. 1990). Patch sizes should be relative to characteristic dimensions of a particular ecosystem. For example, it has been suggested that, when the patch diameter is twice the height of surrounding trees or greater, direct sunlight will reach the soil surface. This suggests that patch sizes be measured relative to the tree height; however, the light environment will also be affected by latitude and slope inclination. Thus, we suggest that the ideal method is to measure disturbance parameters relative to real, physiologically important physical variables. For example, one should measure forest gaps relative to the effects of these gaps on light levels rather than measuring the size of gaps relative to tree heights (though the latter is a good starting point).

γ)   Disturbances Vary Both Stochastically and Deterministically

In principle, all of the complexities of disturbance regimes and ecosystem responses discussed above could be treated as explanations in the understanding of disturbance. However, the number of variables and the problems of data collection (particularly for past disturbances; White and Walker 1997) and experimentation mean that the task is difficult. Whether all residual variation can in principle be explained is a fundamental issue; in practice, there is always variation among events and among places, even for one ecosystem type affected by one kind of disturbance. Thus, there is always variation that is treated as stochastic for a particular ecosystem.

5 Approaches to Generality in Disturbance Ecology

The many challenges to generality constitute both real and methodological sources of variation in disturbance events, effects and responses. The methods of research, including the scale of observation, are beyond the scope of this review. How shall we treat variations in events, effects and responses in pursuit of generality?

Ideally, general theories hold for all ecosystems and disturbances, for different kinds or instances of disturbance within one ecosystem, and for the varying effects created by a single disturbance within a single ecosystem. In addition to this ideal case, some generalities may be restricted to a certain set of conditions or may have to be developed separately for ecosystems dominated by different growth forms. However, the goal of all generalities is to show that diverse cases are the products of the interactions of a few fundamental variables. Generality does not seek to obscure the diversity of ecosystems or disturbances, but rather to organize and explain the similarities and differences that occur. As a consequence, the search for generality must begin with a discussion of the ways in which diverse ecosystems and disturbances can be compared.

The generalities that we seek typically focus on two scales. First, we are interested in understanding variation in disturbances and responses at the patch level. Conditions within individual patches, such as resource availability and the legacy of the pre-disturbance ecosystem, influence the mechanism, rate and outcome of the ecosystem response. However, we are also interested in scales that aggregate across all patches, disturbed and not, within a larger study area. At this scale, we are interested in understanding how disturbances affect communities and landscapes; we are also interested in disturbance regimes, the interactions between patches and the sum of disturbance effects on all patches. This multiple-patch scale is often the appropriate scale of observation for such questions as the influence of disturbances on species richness and whether disturbance mosaics exhibit dynamic equilibrium or are sustainable (White et al. 1999). The scales interact: what happens within a patch can depend on the nature of surrounding patches, and what happens in the aggregate depends on the individual patches. However, we organize our discussion into issues at the patch scale and issues at the multiple-patch scale.

Because species have evolved under the influence of disturbances, because species affect disturbance and produce recovery, and because species richness is one the foci of generalization, we present a third approach to generality: the classification of species by their adaptations and behaviors before and after disturbance. Species composition and dynamics are often the foci of our research and policy interests.

In essence, we propose that the hindrances to the development of generality can best be treated if we measure absolute and relative conditions (space, environmental conditions, resource availability) at the patch scale,

consider aggregate effects and dynamics at the multi-patch scale, and examine adaptations and responses of the biota present and the influence of species and growth forms on disturbance regimes. Our approach is essentially mechanistic. It assumes that challenges to the development of generality can be treated if we reduce the problem to variation in the physical environment (absolute and relative), variation in the interaction among patches at larger spatial scales and exploration of the physiological abilities and niche characteristics of the species present.

a)   Approaches to Generality at the Patch Scale

The goal of generality at the patch scale is investigation of the way conditions in a patch influence response. What characteristics should we measure in order to compare diverse patches within and between disturbances and ecosystems?

α)   Absolute Ecosystem Characteristics and Disturbance Effects

Ecosystems vary in resource supply – i.e., in water, nutrients and light – and hence vary in properties that affect rates of establishment, growth and survival. Disturbances often make resources more available, because they cause the mortality of dominant plants, leading to less uptake of resources and increased availability through the decomposition of organic matter or through the mixing of soil layers. However, disturbances may also result in the export of resources (such as nutrients) through drainage water or through the volatilization of nutrient elements by fire. We often index disturbance effects through surrogate variables like patch size but, ultimately, basic ecosystem processes (such as photosynthesis and decomposition), and hence the response to disturbances, are better correlated with actual resource availability.

Site productivity and resource availability control the rate of return to pre-disturbance conditions on a patch. For example, the effect of a large blowdown varies on a gradient between productive and unproductive forests. At productive sites, colonization and growth are rapid, so the leaf area is re-established and canopy closure is achieved relatively quickly compared with closure at an unproductive site. Colonization of the unproductive site may take longer, resulting in a less evenly aged stand. If it takes long enough, the stand may even avoid the high densities and self-thinning that occurs in more productive sites. Establishment in large patches may also take years, with edges colonized before patch centers; the result is that high density and self-thinning are likewise unimportant. If the age and density of the canopy on recovering gaps controls susceptibility to (and thus the timing

of) subsequent disturbances, site productivity will also influence the disturbance rate itself.

This discussion argues that we need, at a minimum, two axes to organize the diversity of disturbance cases: site productivity and disturbance frequency or magnitude. Huston (1979) produced a two-dimensional field predicting species richness from disturbance frequency (correlated with mortality rate) and site productivity (correlated with the rate of species replacement after disturbance). Huston et al. (1999) predict that intermediate disturbance rates produce maximum diversity only when the population growth rate (site resource level) is moderate. At high population-growth rates, diversity peaks at high disturbance rates and, at low population-growth rates, diversity is highest at low disturbance rates (Fig. 8). This, in turn, suggests that the development of generality should include comparative studies of similar disturbances (gaps in forests) across site gradients (gradients of moisture as a function of topography).
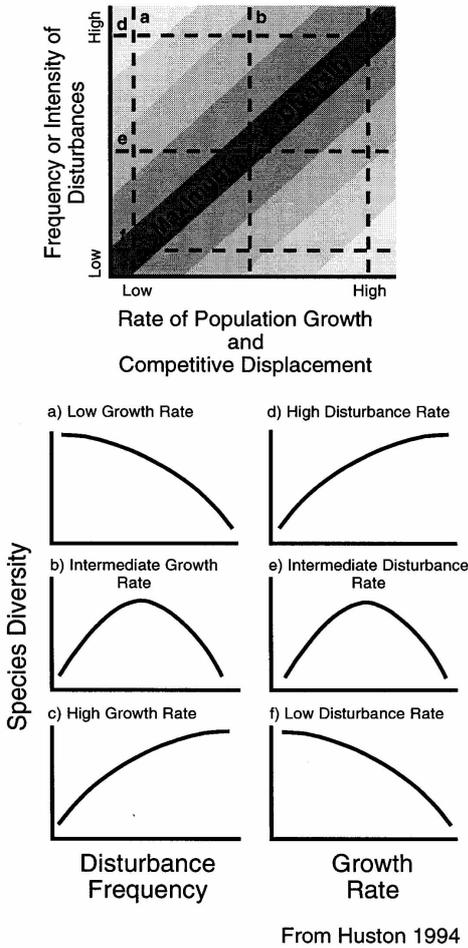
Fig. 8. The effect of the disturbance regime on species richness depends on the frequency/intensity of disturbance and the rate of population growth/ competitive displacement of the community. Intermediate disturbances maximize species richness only at intermediate population growth rates. (Huston 1994)

Not only do patches differ in size, disturbance intensity and resource availability, they may also differ in internal heterogeneity. Thus, patches could be compared not just based on average conditions but on the range of conditions present.

β) Legacies Produced by Disturbance

Patches also differ in the legacies remaining from the previous ecosystems and in the kind of structures (for example, the distribution of organic matter and debris of the plants disturbed) produced by the disturbance. These are often correlated with the disturbance intensity on the patch.

γ) Relativizing Patch Conditions to Ecosystem Characteristics

While absolute values create the overall frame of reference, ecosystems should also be compared by relativizing disturbance parameter to the characteristics of the ecosystem disturbed. For example, the frequency, size and resources of disturbed patches should be expressed relative to the life span, time for successional recovery, plant height and size, and pre-disturbance resource levels. Connell and Slayter (1977) related the frequency of disturbance to the life spans of affected organisms. The correlation between the time of the disturbance event and life-history traits has also been specified by Pavlovic (1994): "discordant disturbances" are those that interrupt life cycles, while "concordant disturbances" are less disruptive or are those to which plants are adapted.

Relative expressions are especially important for surrogate measurements of disturbance effects, such as patch size. For example, the effect of gap size on light varies with the heights of the surrounding trees, latitude and slope steepness (Canham et al. 1990). Despite the importance of the relationship of gap size to tree height, we know of only one paper that has analyzed data in this way (Qinghong and Hytteborn 1991).

δ) Comparing Disturbances with Historic Precedence

Disturbances that have historic precedence or that produce conditions that are within the historic bounds of variation for an ecosystem may produce different responses than disturbances that are novel or create conditions that are outside those bounds. The simple hypothesis is that disturbances with precedence are more likely to be responded to by an adapted biota than are novel disturbances. If the disturbance occurred before at ecological time scales (and depending on how long ago it occurred), adapted biota from that previous disturbance may remain in the landscape and, therefore, may par-

ticipate in the response to a subsequent disturbance. At evolutionary time scales, precedence would ultimately be responsible for the range of life histories present and the occurrence of species adapted to the disturbance.

Comparing disturbances to historic precedence will establish the relative novelty of conditions. However, the absolute nature of those conditions will determine both ecological and evolutionary responses. The absolute conditions may range from mild to harsh, regardless of precedence. The relationship of absolute conditions to the physiological tolerances of the species present produce the response in ecological time. The relationship of absolute conditions to genetic variation will determine whether species adapt in evolutionary time.

Related to the issue of historic precedence is whether large, infrequent disturbances produce qualitatively different responses than more frequent and smaller-scale disturbances. This question is based on the general observation that the disturbance magnitude is inversely correlated to frequency. In the extreme, "large" means that the disturbance exceeds historic variation, and "infrequent" means "without precedence". Species would not have a chance to adapt to these disturbances and, even if disturbance-dependent species were present, they would decline to extinction because of the rarity of the disturbance (Noble and Slatyer 1980). However, the concept of large, infrequent disturbances was developed for rare disturbances that are within the bounds of historic variation and have historic precedence at the 100- to 500-year time scale.

ε) Disturbance Effects on Site Quality and Ecosystem Trajectory

Some disturbances result in straightforward secondary successions that re-establish the pre-disturbance composition, structure and resources, whereas others affect site quality through long-term decreases or increases in resource levels, leading to successional trajectories that do not establish pre-disturbance conditions. Distinguishing these cases and establishing the conditions that lead to each outcome will assist the development of generality. Within disturbance types that lead to the re-establishment of pre-disturbance conditions through secondary succession, class-I and class-II disturbances simply depend on the scale of disturbance relative to the pre-disturbance structure (class-I disturbances are fine grained, class-II disturbances are coarse grained). Relating patch characteristics to the ecosystem structure will aid in the development of generality with regard to these two classes.

b)   Approaches to Generality at the Multiple-Patch Scale

The goal of generality at the multiple-patch scale is to investigate how communities and landscapes have properties that are the result of aggregation across patches or interactions between them. What characteristics should we measure in order to compare diverse ecosystems and disturbances at the community and landscape scales?

α)   Patch Dynamics and Dynamic Equilibrium

Patch dynamics studies the dynamics of individual patches and the interactions between patches within larger study areas. One of the major questions addressed at this scale is whether patches produce a dynamic equilibrium at larger scales (White et al. 1999). This question has implications for the design of nature reserves, because conservationists would like to plan for a sustainable mosaic of all age states and species (Pickett and Thompson 1978 for an early discussion of this issue; Baker 1989, 1992b for application to conservation in boreal forests).

Several ecologists have scaled disturbance effects to the spatial and temporal characteristics of ecosystems and landscapes. An early attempt was Shugart's 1:50 rule, which suggested that, when the landscape size surpasses 50 times the size of the average patch size, the biomass throughout a landscape is in dynamic equilibrium (Shugart 1984). Shugart developed this perspective from gap-simulation models; he found that the average biomass in the patches is relatively stable if there are 50 or more independent patches. This finding assumes that disturbances in patches are independent in space and are controlled by feedback between the ecosystem state and the susceptibility to disturbances within patches. Shugart made several other interesting observations: the distribution of patches in successional states is more stable and the overall habitat diversity is higher and more stable for high ratios of landscape area to patch size. Examining stability and equilibrium as functions of this ratio allows the comparison of ecosystems with diverse disturbance types and patch sizes.

A further step towards generality based on scaling to ecosystem and landscape characteristics was taken by Turner et al. (1993) with the concept of landscape equilibrium caused by various kinds of disturbance regimes (Fig. 9). They predicted both the presence and absence of equilibrium and variance in ecosystem states as functions of two ratios: the ratio of the disturbed area to the landscape area and the ratio of the disturbance frequency to the time needed for successional recovery. The smaller the patch relative to the landscape size and the lower the disturbance frequency relative to the recovery time, the greater the chance for dynamic equilibrium in all patches.

The least stringent form of dynamic equilibrium is qualitative or persistence equilibrium (White et al. 1999). In this equilibrium, there is bounded
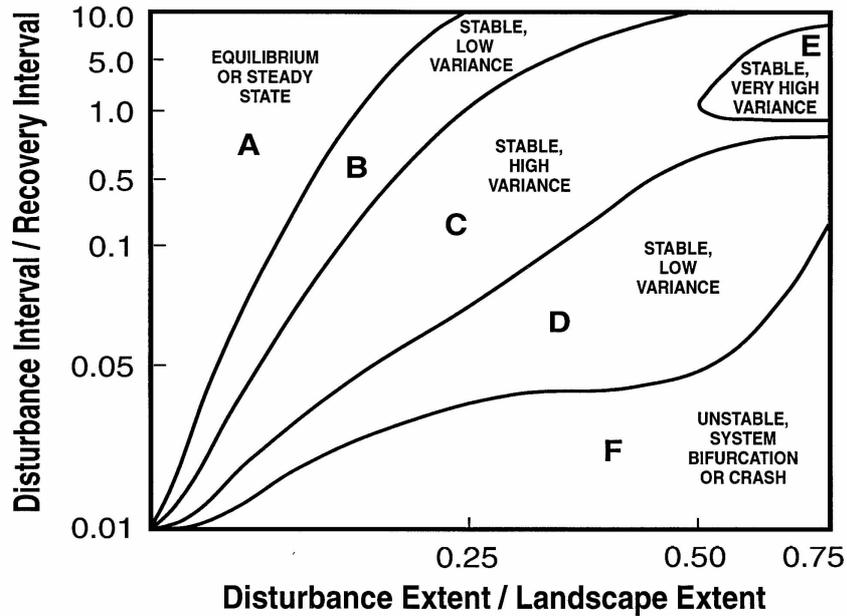
Fig. 9. Stability and variance as a function of two ratios: the relationship of disturbance patch size to landscape area (x-axis) and disturbance interval to recovery interval (y-axis; Turner et al. 1993). When the disturbance extent is small relative to the landscape area, stability is promoted. When the disturbance interval (the time between disturbances) is long relative to the recovery interval (the time needed for recovery to the pre-disturbance state), stability is promoted

variation: no species or successional states become extinct in a study landscape, but they can fluctuate in abundance. This corresponds to the Turner et al. (1993) equilibrium with variance and has been inferred for ecosystem dynamics in Yellowstone National Park (Romme and Despain 1989). Ultimately, conservation managers seek qualitative or persistence equilibrium because it suggests sustainability of species and communities but allows fluctuation compatible with that sustainability.

Steady-state equilibrium is more stringent, because variance must be small, and average values of parameters of interest must be essentially constant when measured at the appropriate scale. In the Turner et al. (1993) diagram, an equilibrium steady state is predicted when the disturbance patch size and disturbance extent are small relative to the size of the landscape or study area. As Romme et al. (1998) argued, quantitative equilibrium is rare, especially for ecosystems affected by large, infrequent disturbances.

Two other forms of equilibrium were reviewed by White et al. (1999): statistical equilibrium (in which disturbance characteristics can be described by a statistical distribution like the Weibull model; Johnson and Van Wag-

ner 1985) and stable-trajectory or stationary/dynamic equilibrium (the stable recurrence of a successional trajectory regardless of whether there is statistical or quantitative equilibrium; Loucks 1970).

Key approaches to generalization among ecosystems are the relativization of disturbance patch size to the landscape area, relativization of the disturbance interval to the recovery interval (Turner et al. 1993) and the assessment of various forms of patch-dynamic equilibrium, relative stability (in a dynamic sense) and variance.

Disturbance-caused patchiness in the ecosystem structure and age also has implications for spatial variation measured at a single point in time. Busing and White (1993) showed that the coefficient of variation for structure and composition in an old-growth temperate forest generally decreases as quadrat size increases from 0.01 to 1 ha. Coefficients of variation in total density and basal area achieve a lower boundary at quadrat sizes of approximately 0.4 ha in these big-tree forests, but coefficients of variation for individual species were high even at the 1-ha quadrat size. Busing and White hypothesized that late-successional, shade-tolerant trees would exhibit lower variation at a given quadrat size than early-successional trees, because the former would be present in all size and age classes at smaller spatial scales, whereas the latter are patchy in distribution even at the 1-ha scale because of the distribution of large disturbance patches. Busing et al. (1993) showed that spatial patchiness has consequences for estimates of biomass in these forests. Historically, ecologists have studied only the older, closed canopy patches of large trees, thereby overestimating the biomass of stands and landscapes as a whole.

A further consequence of spatial variation is the concept of the oldest patch in a landscape (Johnson et al. 1995). Under a given disturbance frequency, some patches may be disturbed more and others less than the average. If the landscape is large relative to the disturbance patches, there is a higher probability that individual patches will escape several disturbances and reach older ages than average. Thus, the larger the landscape, the older the characteristic oldest patch (Johnson et al. 1995). This has consequences for the definition of old growth and the expected structure and composition of undisturbed reference sites.

The size and isolation of patches affect their environmental characteristics, probability of disturbance, interaction with other patches, and the colonization rate and propagule sources available to them. In the extreme, patches behave like islands in the theory of island biogeography, and their constituent populations exhibit meta-population characteristics. Colonization rates may be limited on large, disturbed patches such that establishment may take a decade or more. The resulting community exhibits a greater range of ages and sizes than a smaller patch with less effect of colonization rate.

β) Disturbance Architecture

Moloney and Levin (1996) suggest that disturbance regimes be organized (McIntyre et al. 1995) according to a three-level architecture:

1. Non-spatial components: rate and intensity of disturbance
2. Spatial components: size and shape of individual disturbances
3. Spatio-temporal components of groups of disturbances: spatial and temporal auto-correlation among individual disturbances

The disturbance rate determines the immediate impact of a disturbance regime on the plant community or ecological landscape (the proportion of space changed to a different successional state), while the disturbance intensity determines how the disturbance interacts with species' life-history attributes (which defines the new successional state after disturbance). The size, shape and correlation structures among individual disturbances determine the rate at which disturbed sites can be re-colonized (depending on the species' life-history characteristics); they also eventually determine the structure of the landscape mosaic. For semi-arid shrubland, Wiegand et al. (1997) showed that the first organization level of disturbance (rate and intensity) determines most of the long-term dynamics of the plant community. The general decrease of overall plant density with increasing overall disturbance rate is an effect that involves the trade-off between disturbance-induced mortality and the ability to re-colonize new disturbance-created sites. The disturbance intensity determines the functional groups to which a disturbance provides additional establishment sites (this is also dependent on competitive ability and seed availability).

γ) Classifying Disturbance Regimes

The disturbance regime is a product of the history of disturbances and the distribution of disturbance characteristics in space. Characterization of a disturbance regime should include the means and variances associated with such parameters as the return intervals and the disturbance size, shape and intensity. We can then ask whether different kinds of disturbance regime produce different kinds of responses. For example, the inverse correlation between the disturbance frequency and magnitude has been used to ask whether large, infrequent disturbances produce qualitatively different responses than small, frequent disturbances (Romme et al. 1998; Turner et al. 1998). Three general kinds of system response to disturbances were identified: threshold responses, scale-independent responses and continuous responses.

c) Approaches to Generality Through the Classification of Species Roles

α) Successional Roles and the Intermediate-Disturbance Hypothesis

Species can be classified by successional role, tolerance to disturbance, response to disturbance and tolerance to competition. The intermediate-disturbance hypothesis (Connell 1978) proposes that species richness rises then falls along an axis of disturbance frequency, with intermediate disturbance frequencies producing the highest richness. This is because competition-intolerant species are lost if disturbance frequencies are very low, and disturbance-dependent species are the only species present if disturbance frequencies are very high. Connell's formulation did not explicitly define the measurement of frequency. Huston's (1979) formulation was based on mo del and proposed that the disturbance rate and the rate of competitive exclusion are the two axes controlling species richness.

As Hubbel et al. (1999) note, the intermediate-disturbance hypothesis suggests that niche partitioning or gap partitioning explains species coexistence. If this partitioning occurred then one might find species adapted to different parts of the gradient in gap conditions; the gradient from gap centers to edges, and from small gaps to large gaps, would show varying dominance of species with different adaptations. In contrast, if species did not partition these conditions, replacement patterns in gaps and distribution along gradients in gap conditions would be random. Based on a large survey of tropical forest gaps, Hubbel found that there is no gap-to-gap predictability of species richness in gaps or of the composition of any regeneration niche guild, including pioneers, due to strong recruitment limitations. Thus, there is no relationship between gap-disturbance regimes and tree-species richness. The topic of niche partitioning in forest gaps is an area of active research (Busing and White 1997; Brokaw and Busing 2000), with most investigators finding no evidence or weak evidence for gap partitioning in relatively small gaps. However, they find more evidence of specialization as the gap size increases and conditions within the gap contrast more with those in the forest matrix.

The lack of physical gap partitioning does not preclude variation in species adaptations to gap disturbances. For example, White et al. (1985) found that, in small gaps in old-growth *Picea abies* forests in the southern Appalachian mountains, three species competed for canopy positions in different ways. Two species were shade tolerant; therefore, at the time of gap creation, they had understory stems that were of higher density, older age and larger size than those of the shade-intolerant species, which had much higher growth rates in gaps than the shade-tolerant species. The latter did show increased growth rates in gaps than in forest understories, but those growth rates were an order of magnitude lower than those of the shade-intolerant species. The shade-intolerant species were also able to grow on fallen logs and tip-up mounds. The two shade-tolerant species dif-

fered in longevity – the one that was denser in the understory also held onto canopy positions only half as long as the other shade-tolerant species. Although the three species had different life-history strategies, they were so nearly balanced that there was no evidence of partitioning by gap size in these forests.

Marks (1974) made an interesting suggestion regarding the growth rates of trees in gap dynamics (Fig. 10). He observed that species differ in the minimum gap size required for survival (net growth Fig. 10) and that their maximum growth rates (in full sunlight) are correlated with the gap size required. Thus, shade-tolerant species that can survive in small gaps have relatively low growth rates in full sun (though they do show release compared with plants growing in the shade), whereas those that require large gaps for survival also have the highest growth rates in full sun. This is similar to the findings of Brokaw (1985) for tropical forests and White et al. (1985) for montane conifer forests, though absolute rates of growth differ among these ecosystems. Light-demanding trees need large gaps for survival but also grow faster in these gaps than shade-tolerant species.

Adapted from Marks 1974
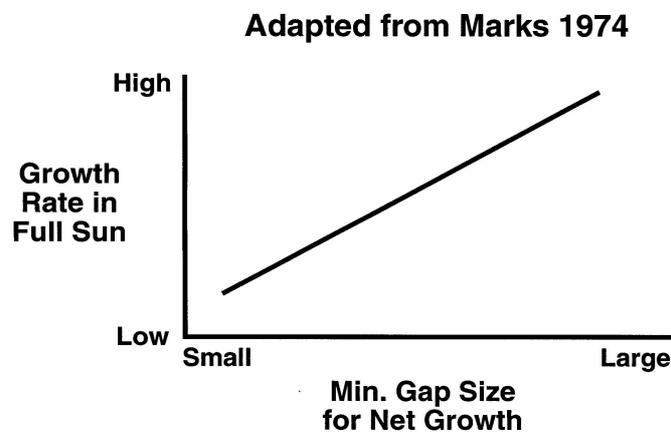
Fig. 10. The correlation between the minimum gap size needed for survival (or net growth) and the maximum growth rate in full sunlight. Shade-tolerant trees survive better in shade and small gaps (though they can grow at all gap sizes and show their highest growth rates in full sunlight). Shade-intolerant trees cannot survive long in shade and in small gaps but, in large gaps, they grow much faster than shade-tolerant species. (Marks 1974)

A. Mechanisms of Response

Crown extension →

← Height growth

Established stems →

Advanced regeneration ← New establishment
Seedling bank   Seed rain
                       Seed bank
                       Sprouting

Shade tolerance →

← Shade intolerance

Growth rate: LOW ←——————→ HIGH
Birth rate: LOW ←——————→ HIGH

B. Age Structure

Bimodal   All-aged   Even-aged except:
                                       extreme sites
                                       dispersal limitations
                                          in large patches

C. Compositional Predictability

Moderately Predictable   Stochastic   Moderately Predictable

D. Vegetation Dynamics Terminology

Fine Scale   Patch / Gap Dynamics   Regeneration Succession
Gap Dynamics

Gap Dynamics Regeneration Mode   Catastrophic Regeneration Mode
                                        Stand Initiating Disturbance
                                        Lethal Disturbance

Within Community   Between Communities

We have generalized the responses to forest wind disturbance in Fig. 11. Assuming no effects of latitude or topography, environmental factors in gaps vary with tree height, crown width and the number of trees down. Mechanisms of response, expected age structures, compositional predictability and the kinds of vegetation dynamics vary with gap size. In the middle range of disturbance sizes, we hypothesize that any strategy has a chance to be successful, and composition should be stochastic. As above, we argue that species can have different strategies even when there is no obvious gap partitioning. Different strategies may be more clearly important in the absence of disturbances (left-hand part of the gradient in Fig. 11) or in large disturbance patches (right-hand part, Fig. 11). For age structure, we note that low productivity or large patch size can slow colonization, resulting in a window of tree establishment and, thus, a broad range of ages after stand-initiating disturbances.

β) Response of Functional Groups to Disturbance

The effects of disturbance partially depend on the interaction between the disturbance type and the life-history characteristics of the component species. Functional approaches for characterizing species adaptations to disturbances were presented by Collins and Glenn (1988) in the context of life-history attributes of species and by Grime's (1979) model of the three primary plant strategies. These approaches suggest that the abundance of

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Fig. 11 A–D. Forest dynamics as a function of disturbance magnitude relative to ecosystem structure. The number of trees down (less than 1, 1, 2–10, more than 10 and more than 100), along with crown width and tree height, determine relative conditions in a gap and, therefore, the response of the seedlings and saplings in forest dynamics. The figure suggests that various aspects of forest dynamics are different in small and large disturbances. **A** Mechanisms of response: crown extension, established stems and shade tolerance are more important in small patches; height growth, the birth of new individuals and shade intolerance are more important in large patches. There is a zone of overlap where both strategies are successful. **B** Age structure: Shaded patches have old trees and suppressed seedlings; small patches allow greater survival in the understory and a greater range of ages; large patches produce even-aged stands on mesic sites, but limits to productivity and colonization can produce many years of re-establishment and a wide range of ages. **C** Compositional predictability: shaded patches are dominated by shade-tolerant species; large disturbed patches are dominated by intolerant species. Both strategies are successful in intermediate patches. **D** Vegetation-dynamics terminology: small patches have fine-scale gap dynamics that are considered to be cyclic successions and stochastic replacements within communities; large patches have regeneration succession and are considered to exist between community successions. See text for further discussion. For simplicity, it is assumed that latitude and topography do not contribute to the patterns created by gap size relative to tree height

species in functional groups not favored by disturbances will decrease with increasing disturbance rate. In the sequence of dominant species within functional groups, Wiegand et al. (1997) observed the emergence of distinct patterns with increasing disturbance rate. Such a sequence can be predicted using knowledge regarding a species' life-history attributes and the disturbance intensity. Information regarding the longevity of species is crucial in determining the effects of a disturbance on the community's structure.

γ) Resilience to Disturbance

The purpose of functional diversity and functional similarity within ecosystems has been discussed in a community-based approach by Walker et al. (1999). This paper proposed that persistence in ecosystem function under changing environmental conditions and resilience against disturbance are ensured by functional similarities among dominant and minor species. According to the resilience hypothesis, major and minor species switch in abundance during times of stress or disturbance, thus maintaining ecosystem function. Consistent with the insurance hypothesis (Main 1982; Walker 1995; Naem and Li 1997), abundant species contribute to ecosystem performance at any particular time (and are functionally dissimilar from each other). However, minor species contribute to ecosystem resilience during times of stress or disturbance (and are functionally similar to dominant species and could increase in abundance to maintain function if dominant species decline or disappear). Peterson et al. (1998) indicated that apparently redundant species operate at different scales and thus reinforce function across scales.

δ) Dominant Growth Forms

A special case of the approach to generality through the classification of species' roles is the importance of dominant growth forms. Dominance by trees, shrubs and grasses may affect the magnitude, frequency and pattern of disturbances. It is obvious that generality must be sought both within and across ecosystem types.

6 Conclusions

Despite the many obstacles that hinder the development of theory in disturbance ecology, there are ways to explore generality among disturbances and ecosystems. There is a common language used to state premises and to describe mechanisms of disturbance causes and effects. There are means of

addressing the challenge of scaling in order to synthesize the results of field studies to compare different disturbance regimes and habitats.

The first group of obstacles to generalization consists of variation in the distribution, timing and intensity of disturbance events. This variation is caused by the ecosystem type, topography, climate, soil development, history of past disturbances, feedback of successional states, and degrees of isolation and adjacency. The pursuit of generality consists of identifying these sources of variation when documenting and describing the disturbance regimes. This will allow the discovery of systematic variations in disturbance regimes; these variations can be used to organize research on the disturbance effects, recovery and recurrence.

The second group of obstacles consists of the spatial and temporal variations in disturbance effects and system response caused by variations in heterogeneity, patch size, resource levels and ecosystem legacies. These sources of variation cause differences in absolute and relative resource availability after disturbance and, through direct disturbance effects on residual biota and through spatial processes, constrain the availability of species for response to disturbances. Thus, the first task in seeking generality is to recognize that this variation exists and to seek to discover and measure the fundamental mechanisms at work. Both absolute and relative measures of disturbance effects are important. For example, the frequency, magnitude and patch size of a disturbance should be scaled to the ecosystem and landscape studied.

The third group of obstacles is related to variation in the rates of responses and species adaptations among ecosystems. These include varying productivity, growth-rates, establishment, mortality, succession, intensity of competition, history of adaptation and evolution. It is clear that an overall gradient of ecosystem productivity or site quality must be established in order to examine the effects of disturbance.

The fourth group of obstacles to generality derives from challenges in observation, sampling, and analysis, including the research focus, observational scale and use of surrogate variables. A prerequisite for the comparison of data is specification of the spatio-temporal observational scale and the level of resolution relative to the dimensions of the disturbance, components and system under study. An appropriate but difficult and expensive way to avoid problems with derived data is to measure the real environment (light levels) versus the surrogate variables (patch size). Based on this discussion, the development of generality in studies of the impact of disturbances on vegetation dynamics requires that we address a series of questions under four headings.

a)   Choosing a Focus of Interest, Level of Resolution and Degree
of Abstraction

These three specifications are necessary for comparing data and communi-
cating hypotheses, among other reasons (Pickett et al. 1989; Jax et al.
1998). Which objects (organisms, species, life forms, age structures) or
processes (burning, establishment, species turnover, persistence of function)
are studied? Under which level of resolution (individuals, categories and
their boundaries) are components (populations, successional states, func-
tional groups, structures, map units) chosen to describe the observed sys-
tem? The components chosen – and specified at any desired scale, level of
resolution and degree of abstraction – reflect the particular methods of par-
titioning and describing the observed system (Bernstein and Goldfarb 1995).
In other words, what kind of information do our observations provide re-
garding the disturbance and ecological units studied? Ecological units are
"all those units subject of ecological research, chosen by an observer in a
way that they may be characterized as new relevant objects" (Jax et al.
1998). These specifications determine criteria for what to consider "alike"
when looking for patterns or processes in other places or at other times.

b)   Establishing the Spatial and Temporal Frame of Reference

The spatial and temporal boundaries of scientific observations constitute the
frame of reference. The decision to focus on a particular time frame or spa-
tial extent is a choice regarding how to view the world and is usually based
on experience and presupposition (Wittgenstein 1953; Kuhn 1962; Sokal
1985). To compare different data sets, the frame of reference needs to be
specified in two ways:

1. Length of time (days) and amount of space (square kilometers) affected
   by disturbance
2. Length of time (years) and amount of space (square meters) investigated
   in the study

The specification of the temporal and spatial frames of reference requires
that we document how the observations are made (whether the observations
were made in discrete blocks or continuously in space and time, whether
data are reported as point samples or have been derived through the inte-
gration of observations over space or time).

c)   Describing Disturbance

We strive to compare various disturbances on the basis of common de-
scriptors. An operational method for describing disturbance qualities, their

ranges and spatio-temporal variables is provided by a limited set of disturbance descriptors. These allow a level of abstraction appropriate for application to any kind of disturbance. They characterize the kind of disturbance, intensity, duration of the discrete event, frequency in time, patch size, shape, distribution in space and selectivity to, for example, functional groups or age classes. These descriptors are suitable for generally categorizing and differentiating disturbances whether of natural or anthropogenic origin, whether observed in a historical context or introduced experimentally, whether covering intermediate or extreme ranges of temporal and spatial dimensions. Disturbance descriptors should be presented as absolute values and should be relative to the ecosystem studied. The pursuit of generality requires that one search for transferable descriptive parameters of disturbance that are individually related to the scale of the ecological system being investigated. One way to do so is to describe the dimensions of disturbance regimes relative to the spatial and temporal dimensions of the ecological units studied (Platt 1975; Paine and Levin 1981; Allen and Starr 1982; White et al. in press):

– The disturbance duration and frequency relative to the life span or recovery time of the affected organisms
– The disturbance intensity relative to the sensitivity of the successional stages
– The disturbance patch size relative to the population size or landscape extent
– The disturbance shape and distribution relative to the system heterogeneity
– The disturbance specificity relative to the species, age classes or landforms present

Fire in a forest or drought in grassland both act at the scale of whole plant communities, while gaps in the forest canopy or rabbit burrows in the grassland occur at smaller patch sizes and with higher frequency (Van der Maarel 1993). The size of individual small-scale disturbances may only affect community dynamics if it exceeds the dispersal distance of colonizer species so that re-colonization processes are involved (Wiegand et al. 1997).

Relativization can also include effects on resources like light and nutrients. In those cases, and for the spatial and temporal dimensions, ratios are the key to detecting pattern resemblances on proportionate scales. "Quantity alone does not determine pattern. It is impossible, in principle, to explain any pattern by invoking a single quantity. But a ratio between two quantities is already the beginning of pattern" (Bateson 1979). The description of disturbance must also include the historical, spatial, and biological contexts. The rate and impact of a disturbance may be contingent on the history of past disturbances in the ecosystem. The description must specify spatial patterns and processes. Disturbance responses may be contingent on the interactions of patches and the colonization of species from surrounding

places in the landscape. The available biota – including the available range of physiological traits, redundancies and complementarities – is critical to the understanding of the ecosystem effects of disturbances. The available biota are contingent on both past evolution (including exposure to disturbances) and past disturbances at ecological time scales, because this history affects what species are present when a subsequent disturbance occurs.

d)   Determining Patterns in Disturbance Regimes – Correlation of Spatial and Temporal Parameters

To phrase general hypotheses, we need means of inter-relating patterns at several different scales in order to detect similarities among disturbance regimes and ecosystems. Accordingly, we propose that an important step towards generalizations regarding disturbance regimes and ecosystem processes will emerge due to the relative scaling of their spatial and temporal patterns.

Generality seeks to establish an understanding of disturbance ecology in diverse ecosystems based on a few fundamental variables. According to our discussion, the fundamental variables required to understand disturbance effects and ecosystem responses at patch and multi-patch scales include:

– Disturbance effects on absolute resource levels
– Resource levels relative to the pre-disturbance ecosystem (including the alteration of the overall site quality, the ability to restore pre-disturbance conditions and the historic precedence of conditions created)
– The size and landscape arrangement of patches (which affects colonization rates)
– The interaction among patches as a result of the distribution of disturbance events in time and space (which controls the nature of the dynamic equilibrium, the persistence of successional states and species, the sustainability of the dynamics, and resilience)
– The overall productivity and recovery rates of ecosystems
– The influence of growth forms and species traits on disturbance characteristics

In addition to these variables, we must also characterize disturbance regimes with relativized descriptors in order to compare disturbance regimes in different ecosystems and landscapes. The final challenge is to relate fundamental variables of disturbance regimes with fundamental variables of ecosystem dynamics and disturbance effects.

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