

# LANDSCAPE DISTURBANCE DYNAMICS

**D**isturbances are integral to ecological systems and affect landscapes across a wide range of scales. The causes of disturbance, the patterns and dynamics they produce, and their ecological consequences are major research topics in landscape ecology. Interest stemmed initially from recognition that disturbance was a conspicuous agent of pattern formation; they create complex landscape mosaics that we readily see. At the same time, disturbances were recognized as a natural agent of change within ecological communities, which contributed to the shift from an equilibrial to nonequilibrial view of the natural world that occurred in the late twentieth century (Wu and Loucks 1995; Perry 2002). Disturbances are key drivers of spatial and temporal heterogeneity because they alter the state and dynamics of a system. In landscape ecology, disturbances are ideal subjects for studies of pattern-process interactions because they both respond to and create landscape pattern.

*Disturbance* has been defined in numerous ways, and we follow the general definition offered by White and Pickett (1985): “any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability of the physical environment.” Natural disturbances include

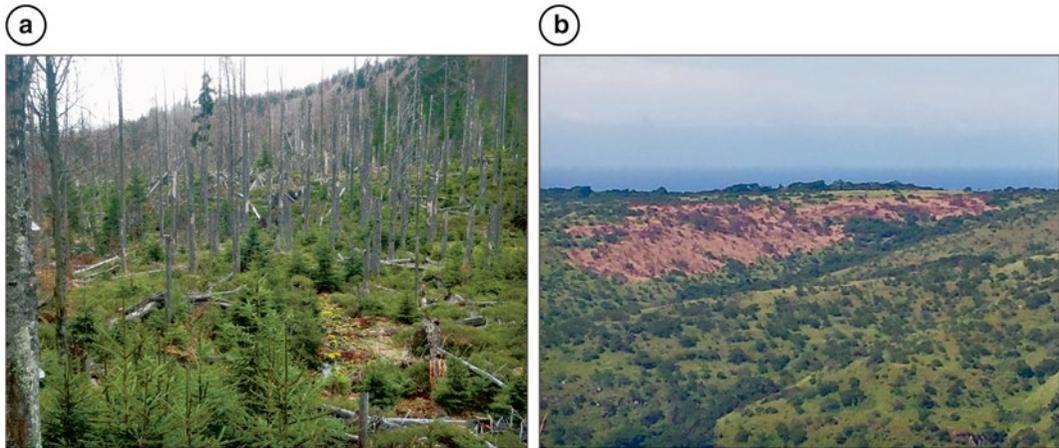


FIGURE 6.1.

Illustration of two disturbances. (a) Standing dead spruce trees in the Bavarian Forest National Park, Germany, were killed by a high-severity bark beetle outbreak; note abundant natural regeneration.

Photo by M. G. Turner. (b) Fire scar in South Africa in landscape where woody vegetation is expanding. Photo by E. A. H. Smithwick

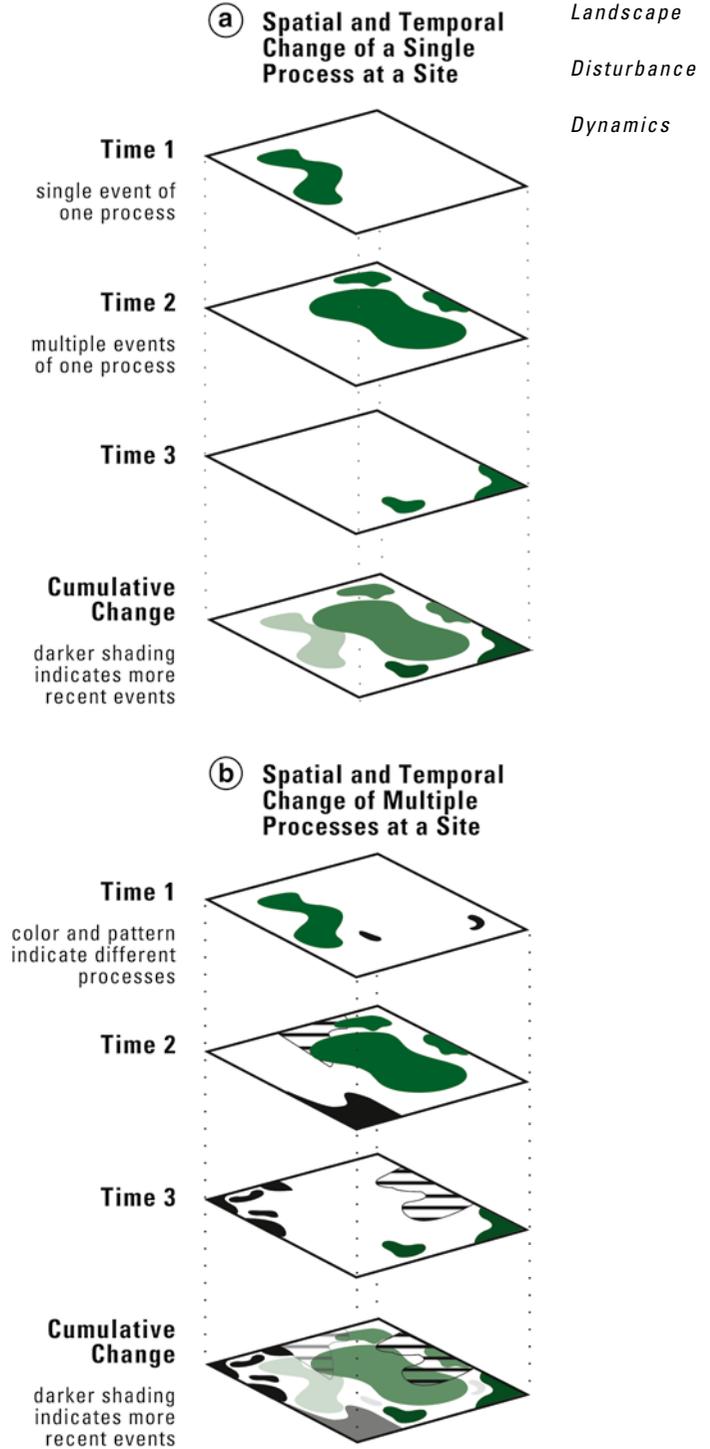
familiar events such as wildfires, floods, hurricanes, windstorms (e.g., tornadoes, blowdowns), and avalanches (Fig. 6.1). Some ecological systems even require disturbances for maintenance of community structure and ecosystem function (White 1979; Collins et al. 1998). For example, hurricanes contribute to the maintenance of species diversity in many tropical forests, and regular fires may maintain species composition and age mosaics in some landscapes, like prairies and boreal forests. There has been considerable interest in determining whether human activities can be managed to mimic the patterns and effects of natural disturbances and thereby reduce undesirable deleterious effects (e.g., Hunter 1993; Attiwill 1994; Delong and Tanner 1996).

Disturbances produce mosaics of seral stages (Fig. 6.2) that ecologists have long recognized as essential drivers of landscape pattern (e.g., Cooper 1913; Leopold 1933; Watt 1947; Reiners and Lang 1979; White 1979). The literature on *patch dynamics* (Watt 1947; Levin and Paine 1974b; Whittaker and Levin 1977; Pickett and Thompson 1978; Pickett and White 1985; Levin et al. 1993), in which ecological systems were conceptualized as mosaics of patches generated by disturbances, was an important precursor to the more explicit treatment of disturbance in landscape ecology; a concise overview of patch dynamics can be found in Wu and Levin (1994). Patch dynamics implied a relatively distinct spatial pattern but did not establish constraints on patch size, persistence, composition, or geographic location, which may shift through time (Levin and Paine 1974b). In addition, spatial and temporal relationships among patches and with the surrounding matrix were implied. Finally, and perhaps foremost, patch dynamics emphasized change (Fig. 6.2).

FIGURE 6.2.

Diagrams illustrating patch dynamics. (a) Representation of a process that varies in space and time in a hypothetical landscape. Layers represent the site at different points in time, with the patches representing a disturbance impacting different parts of the landscape at each time interval, and the cumulative pattern of the disturbance. Each patch may differ in age, depending on the time it was last disturbed. (b) Representation of multiple processes acting on the same landscape through time and cumulatively. When viewed through time, the landscape looks like a changing patchwork in which patches result from disturbances that differ in frequency, intensity, size, and shape.

ADAPTED FROM PARKER AND PICKETT (1998)



Interest in disturbance dynamics has intensified in the twenty-first century (Jentsch 2007; Turner 2010; Peters et al. 2011). Disturbance is a “hot topic” in land and resource management because many disturbance regimes (defined below) seem to be changing due to human activities—especially climate warming. For example, the risk of large fires is increasing in many areas of the world (Westerling et al. 2006; Chapin et al. 2008; Bowman et al. 2009; Girardin et al. 2009), including even the tundra on the North Slope of Alaska (Qui 2009). The Millennium Ecosystem Assessment (2005) reported an increase in the frequency of wildfires as well as floods during the twentieth century in Europe, Asia, Africa, the Americas, and Oceania. Because disturbances can threaten human life and property, often with catastrophic effects on the built environment (e.g., Hurricanes Katrina, which hit New Orleans in 2005, and Sandy, which hit New York in 2012), the consequences of disturbance for human economies and wellbeing are of substantial concern. The potential for disturbances to catalyze major shifts in ecosystems and landscapes, and feedback to global cycles (e.g., carbon cycling), also contributes to the heightened sense of urgency.

In this chapter, we introduce disturbance terminology and concepts then focus on how disturbances interact reciprocally with landscape pattern. We first review how landscape pattern influences disturbance, including work in the emerging field of landscape epidemiology, and then how disturbances create a spatial mosaic in the landscape. We next cover key concepts that require disturbance and succession to be considered jointly and conclude by highlighting disturbance-related questions in contemporary landscape ecology.

## DISTURBANCE AND DISTURBANCE REGIMES

Disturbance events happen over relatively short intervals of time: hurricanes or windstorms occur over hours to days, fires occur over hours to months, and volcanoes erupt over periods of days or weeks. In origin, disturbances may be abiotic (e.g., hurricanes, tornadoes, or volcanic eruptions), biotic (e.g., the spread of an exotic pest or pathogen), or some combination of the two (e.g., fires require conditions suitable for ignition and burning, which are abiotic, as well as sources of adequate fuel, which are biotic). Disturbances usually result in “open space,” such as gaps in otherwise continuous vegetation, and they alter levels of resources such as light and nutrients. By producing these open spaces, disturbances create patchiness in a landscape and initiate secondary succession in the disturbed patches. In landscapes subject to large, infrequent disturbances, the spatial pattern imposed by a disturbance event can structure the landscape until the next disturbance occurs. The eruption of Mount St. Helens in 1980 and the Yellowstone fires of 1988 are examples where the large disturbance established the template for species and ecosystem processes in a landscape for decades or centuries to come.

Consequences of disturbance for the biota depend not only on features of the disturbance but also on the state of the system before it was disturbed. For example, tree height influences the extent of uprooting and stem snapping that occurs in forests affected by catastrophic wind. The successional stage of a community when it is disturbed may control the availability of propagules that, in part, shape the composition of the post-disturbance community. The context of the surrounding landscape may also play an important role in post-disturbance succession. Disturbance dynamics and succession are intertwined in their effects on landscape patterns and change, and the successional changes that follow disturbance are main components of our understanding of disturbance in a landscape context.

Ecologists distinguish between a particular disturbance event—like an individual storm or fire—and the *disturbance regime* that characterizes a landscape (e.g., White and Jentsch 2001). The disturbance regime refers to the spatial and temporal dynamics over a longer time period and is described by characteristics such as the spatial distribution of disturbances; disturbance frequency, return interval, and rotation period; and disturbance size, intensity, and severity (Table 6.1). It is important to recognize that definitions of disturbance and disturbance regimes are

*Landscape*  
*Disturbance*  
*Dynamics*

TABLE 6.1.

DEFINITIONS OF COMPONENTS OF A DISTURBANCE REGIME, ADAPTED FROM WHITE AND PICKETT (1985) AND TURNER ET AL. (1998b).

Term	Definition
Frequency	Mean or median number of events occurring at an average point per time period, or decimal fraction of events per year; often used for probability of disturbance when expressed as the decimal fraction of events per year
Return interval	Mean or median time between disturbances; the inverse of frequency; variance may also be important, as this influences predictability
Rotation period	Mean time needed to disturb an area equivalent to some study area, which must be explicitly defined
Size	Area disturbed, which can be expressed as mean area per event, area per time period, or percent of some study area per time period
Intensity	Physical energy of the event per area per time (e.g., heat released per area per time period for fire, or wind speed for storms); characteristic of the disturbance rather than the ecological effect
Severity	Effect of the disturbance event on the organism, community, or ecosystem; closely related to intensity, because more intense disturbances generally are more severe
Residuals	Organisms or propagules that survive a disturbance event; also referred to as biotic legacies. Residuals are measure of severity, and thus (at least within one disturbance) an index of intensity

inherently scale dependent (Allen and Starr 1982; Pickett et al. 1989; Turner et al. 1993; Wu and Loucks 1995; White and Jentsch 2001). A particular disturbance may be a disruptive force at fine scales but a stabilizing force at broad scales, where average values over large areas may show minimal change. Thus, as with seemingly all aspects of landscape ecology, one must be cognizant of the scales of the phenomena under consideration.

Comparisons among different disturbances and ecosystems are challenging because so many features, such as the assemblage of species and nature of the disturbance, vary so widely. Developing generality in disturbance ecology requires finding patterns amidst such diversity (White and Jentsch 2001). To support such comparisons, Peters et al. (2011) proposed a new conceptual framework that disaggregates a disturbance event into three measurable components: (1) environmental drivers and their associated characteristics, which interact with (2) initial properties and spatial structure of a given ecological system to determine (3) physical and biological mechanisms that result in a change in system properties (Fig. 6.3). This framework augments a tradition of disturbance research in ecology by focusing explicitly on underpinning mechanisms, disturbance legacies, and influences on future system state (Fig. 6.4, Peters et al. 2011). This disaggregated approach is valuable for landscape studies because it facilitates a more explicit consideration of the multiple contingencies (see Chap. 2) that cause landscapes to respond in different ways.

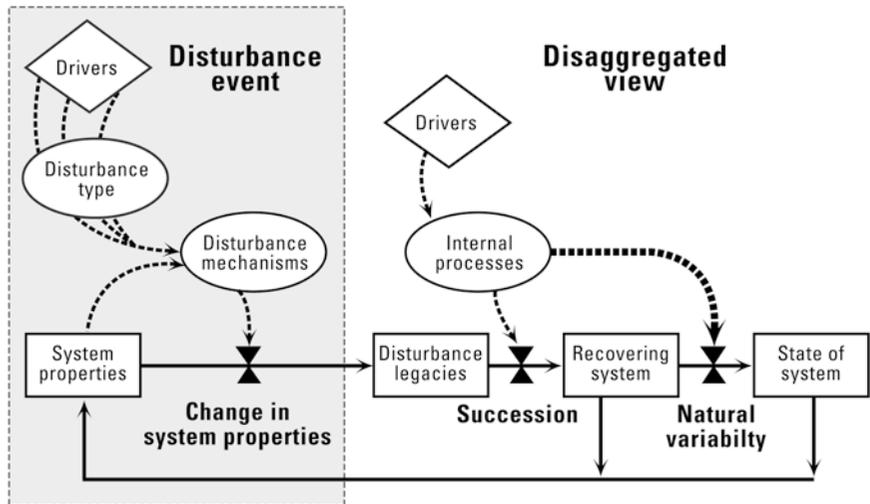


FIGURE 6.3.

Disaggregated view of disturbance. The disturbance event consists of environmental drivers, initial system properties, and physical and biological mechanisms of effect. These result in a disturbed state with legacies that interact with subsequent drivers to influence system response.

ADAPTED FROM PETERS ET AL. (2011)

a

Components of a Disturbance Event		
<b>Drivers</b>	<b>Mechanisms</b>	<b>Initial system properties</b>
<i>Climatic and atmospheric</i>	Abrasion	Height
Wind	Combustion	Physiology
Precipitation	Biomass removal	Grazing tolerance
Temperature	Harvesting	Drought tolerance
Nitrogen deposition	Herbivory	Biomass
CO <sub>2</sub>	Defoliation	Flammability
<i>Physical</i>	Soil compaction	Density
Ocean and surface water movement	Erosion/deposition	Patch size, spatial arrangement
Tectonic activity	Water logging	Soil properties
<i>Biotic</i>	Resource change	Topography
Invasive species		Phenological state
Pests, pathogens		
<i>Anthropogenic</i>		
People, economics, culture		

b

Driver	Disturbance Mechanism								
	Abra	Comb	Harv	Herb	Defo	Comp	Ero/Dep	Water logging	Resource change
Wind	X	X			X		X		X
PPT		X					X	X	X
Temp		X		X	X				
N-dep				X	X				X
CO <sub>2</sub>									X
Physical						X	X	X	X
Biota				X	X				X
People	X	X		X	X	X	X	X	X

Abra: abrasion

Comb: combustion

Harv: harvest

Herb: herbivory

Defo: defoliation

Ero/Dep: erosion/deposition

Comp: compaction

PPT: precipitation

Temp: temperature

N-dep: nitrogen deposition

FIGURE 6.4.

Components of a disturbance event (a) and the mechanisms that underpin the effects of different disturbance drivers (b).

ADAPTED FROM PETERS ET AL. (2011)



## EFFECT OF LANDSCAPE HETEROGENEITY ON DISTURBANCE

Landscape pattern can influence disturbance dynamics in two general ways. First, the position of different locations in a landscape can affect susceptibility to a particular disturbance. Second, the configuration of habitats that are and are not susceptible to a particular disturbance can affect how the disturbance spreads through the landscape. We discuss both modes of influence, then consider the emerging area of landscape epidemiology, which bridges these modes and focuses on the role of landscape pattern for disease.

### *Landscape Position and Vulnerability to Disturbance*

Are various spatial locations in the landscape differentially susceptible to disturbance? If so, can we predict which areas are more or less susceptible to particular types of disturbance? *Landscape position* typically refers to the topographic position of a site or group of sites, including relative elevation, landform, slope, and aspect (see Chap. 2). Susceptibility to disturbance at particular landscape positions can be evaluated by comparing the probability or frequency of occurrence of a particular disturbance at many places in a landscape. A variety of field studies have addressed these questions in different types of ecosystem.

Runkle (1985) studied the disturbance regime in cove forests of the Southern Appalachian Mountains and found it was determined by regional and local topographic position. Cove forests occur in sheltered areas at middle elevations and are dominated by mesophytic species (e.g., sugar maple, *Acer saccharum*; yellow buckeye, *Aesculus sylvatica*; yellow birch, *Betula lutea*; American beech, *Fagus grandifolia*; white basswood, *Tilia heterophylla*; and eastern hemlock, *Tsuga canadensis*). Wind-related disturbances were dominated by small disturbance events, resulting in the deaths of one or a few canopy trees (a *forest gap*) at any given location. Interestingly, the rate of repeat disturbance was high. Having initially sampled vegetation in 273 gaps, Runkle revisited these gaps 6–7 years later. New gaps often were forming close to the old gaps such that the changed environmental conditions (e.g., greater sunlight) were maintained, and the process of gap closure was slowed. Thus, landscape position influenced the disturbance regime, and new gap disturbances were more likely to occur in the vicinity of old gaps. Among forest types in the southern Appalachians, cove forests are also those most influenced by human land-use change (Turner et al. 2003a), indicating another interesting influence of landscape position on gap dynamics.

Subsequent research on disturbance in the Appalachian Mountains considered the interaction between landscape position and fire. Using mapped perimeters of fires that burned between 1930 and 2003 in two national parks (Great Smoky Mountains and Shenandoah), Flately et al. (2011) found that effects of topography on fire varied with climate. Fire was more frequent on dry south-facing aspects, on

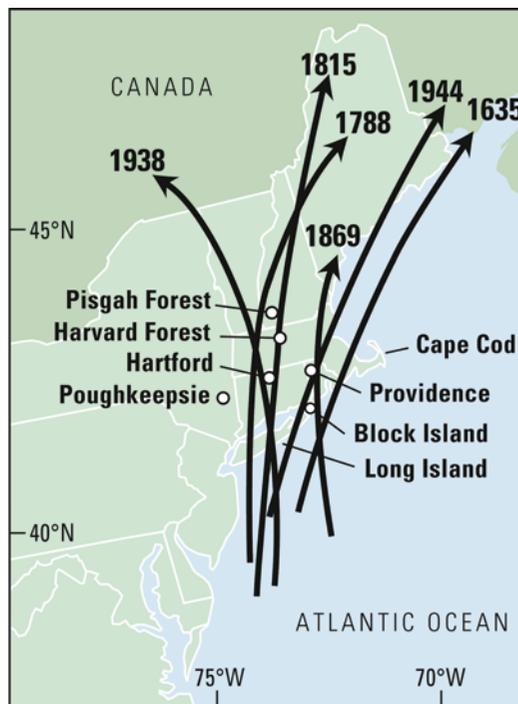
ridges and at lower elevations. However, this influence of landscape position on fire was weaker during dry years and in Shenandoah, the drier of the two parks. This study illustrates how broad-scale spatial variation in climate, which imposes regional-scale pattern on fire occurrence, can influence the fine-scale interactions of landscape position and fire. Such hierarchical interactions among drivers have long been recognized in disturbance ecology, but interest has resurged in the context of cross-scale interactions driving regional dynamics (discussed below).

Studies in old-growth forests of New England also demonstrated that disturbance acts selectively within a landscape, and sites can be arranged along exposure gradients. Foster (1988a, b) examined a natural disturbance regime characterized by frequent, local events, such as windstorms, pathogens, and lightning strikes, and occasional broad-scale damage by hurricanes and winds. Slope position and aspect controlled the susceptibility of a site to disturbance. For example, hurricane winds that affect the region typically come from the southwest and move eastward, and site susceptibility to hurricane damage was controlled by the degree of exposure to those winds (Fig. 6.5). Following a major hurricane in 1938, exposed southeastern slopes and northwest lakeshores had the greatest damage, and exposed hilltops were also strongly affected. Further work combined analysis of remotely sensed, historical and field data with a meteorological model and a topographic exposure model (Foster and Boose 1992; Boose et al. 1994). Results of these integrated studies demonstrated that forest damage due to hurricanes resulted from characteristics of the storm (e.g., wind directions and maximum gusts), exposure, and the height and composition of the vegetation.

FIGURE 6.5.

Tracks of six severe hurricanes that caused significant forest damage in New England.

ADAPTED FROM BOOSE ET AL. (1994)



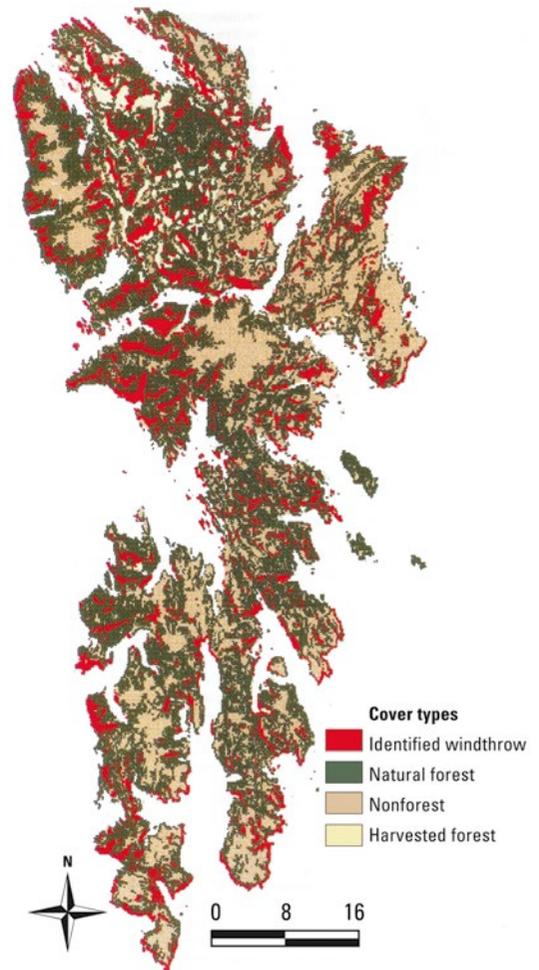
Disturbance effects related to exposure have now been reported for many different landscapes. Levels of hurricane damage in Hawaii varied substantially along an elevational gradient (Harrington et al. 1997), and forest stands of similar composition in Minnesota suffered different amounts of windstorm damage based on their location (Dyer and Baird 1997). In coastal temperate rainforest in complex terrain on Kuiu Island, Alaska, long-term spatial patterns of windthrow (Fig. 6.6) were predictable based on slope, elevation, soil stability, and exposure to prevailing winds (Kramer et al. 2001). Twenty percent of the forests of Kuiu Island were affected by catastrophic windthrow (rather than by small gap disturbances), largely concentrated along ridges and valleys that run parallel to prevailing storm winds (Kramer et al. 2001). And in southwest Tasmania, Australia, fires were most likely to burn on flats, ridges, and steep north-facing slopes, and least likely to burn in valleys and on steep south-facing slopes (Wood et al. 2011). Landscape positions that were protected from fire (i.e., topographic fire refugia) were the locations preferentially occupied by rainforest.

FIGURE 6.6.

Spatial pattern of windthrow on Kuiu Island, Alaska, along with nonforest area and timber harvest. Patterns were used to determine how slope, elevation, soil, and exposure controlled vulnerability of forests to windthrow.

FROM KRAMER ET AL. (2001);

REPRODUCED WITH PERMISSION



In landscapes subject to fire, landscape position may affect probability of ignition (e.g., Burgan and Hartford 1988; Chou et al. 1993.) In Glacier National Park, Montana (USA), lightning ignitions are greatest on ridgelines and south-facing slopes (Habeck and Mutch 1973). Human influences in the landscape may also affect vulnerability to fire. In the upper midwestern US, Cardille et al. (2001) investigated the relationship between wildfire origin locations and environmental and social factors for >18,000 fires between 1985 and 1995. Fires were more likely to occur in areas of higher human population density and road density. Fire occurrence was also related to size and nearness to roads in boreal forests of Alaska, USA (Calef et al. 2008), but with an interesting twist. Probability of fire was greater near roads because ignitions increased, but fire size was lower within 30–40 km of villages and roads because of fire suppression. Such effects can be surprisingly widespread; Calef et al. (2008) suggested that these human influences on fire pattern affected 31 % of interior Alaska!

Proximity to habitat edges is another way in which landscape position can influence vulnerability to disturbance. In tropical forests of Australasia and Amazonia, Laurance and Curran (2008) observed that fragmented forests were especially vulnerable to wind disturbance along the forest edges. Small forest fragments, with their high perimeter-to-area ratios, were more susceptible, although edge orientation relative to prevailing winds was also important. Land–water margins, another kind of edge, may also influence susceptibility to disturbance. Following a 1998 ice storm in the Adirondack Mountains of north-central New York (USA), Millward et al. (2010) studied damage to forests at the terrestrial–aquatic interface. Ice-storm effects depend on the amount and duration of ice accumulation, wind, and characteristics of the trees and stand. Using field observations and vegetation indices from satellite imagery, Millward et al. (2010) found that forests in riparian zones along large streams (fourth and fifth order) or within 25 m of lake shorelines had significantly more ice-storm damage than did interior forest positions. Furthermore, canopy disturbance declined (by as much as 3.5 times) with movement inland from the land–water margin (Millward et al. 2010). An interesting implication of these findings was that landscape position affected the inputs of wood from the terrestrial to aquatic ecosystem because it influenced susceptibility to ice-storm damage.

Although landscape position effects on disturbance have been reported for many landscapes, there are exceptions; some studies report a weak influence of exposure or find no evidence of significant effects of landscape position on disturbance. In Upper Michigan (USA), Frelich and Lorimer (1991) studied three tracts of old-growth forest in which the disturbance regime included effects of fire, wind, drought, insects, disease, ice storms, and lightning strikes. They tested for differences in the disturbance regime between: upland and lowland sites; aspect classes; slope classes; and the hemlock zone along Lake Superior and the interior forests dominated by sugar maple. Extensive field sampling was conducted, but no signifi-

*Landscape*  
*Disturbance*  
*Dynamics*

cant effects of these factors were observed. The upper Midwest has relatively little topographic relief, and Frelich and Lorimer (1991) suggested that the lack of topographical influence on the disturbance regime in this landscape may reflect the types of windstorms that occur in the Upper Great Lakes Region as compared to those that occur in the Eastern United States. The windstorms that do the greatest damage in the Upper Great Lakes have strong downward components, compared to the horizontal winds of hurricanes; even the Southern Appalachians, where Runkle conducted his work, are influenced by hurricanes, albeit infrequently. In coastal forests in southern Mississippi (USA) where topographic relief is also minimal, stand age rather than landscape position was the best predictor of forest damage following Hurricane Katrina, which made landfall on the central Gulf Coast in 2005 (Kupfer et al. 2008). Uplands in the region are broad and gently sloping, and in that setting, aspect was of modest importance and only in older stands (Kupfer et al. 2008). Studies of the spatial pattern of tornadoes have also demonstrated an absence of physiographic control (Peterson and Pickett 1995). Downbursts (strong downdrafts of air from a thunderstorm or large cumulus cloud that generate an outflow of wind that travels away from the point where it hits the ground) and tornadoes can hit any position in the landscape, resulting in little differentiation among topographic positions.

The extensive 1988 fires in Yellowstone National Park provide another example in which topographic position exerted little influence on susceptibility to disturbance. Topography can influence fire spread, as flames burn more readily uphill than downhill because of the tendency for hot air to move upward. Therefore, leeward slopes often burn with less intensity than windward slopes (Heinselman 1996). However, the burning conditions that occurred in Yellowstone during 1988 were so extreme that slope position, fuel, and even natural firebreaks (e.g., streams, rivers, and even the Grand Canyon of the Yellowstone River) did not impede the fire. Landscape position had little influence on susceptibility to fire because the extreme drought and wind that occurred in Yellowstone during the summer of 1988 overrode fine-scale variation in fuel burning conditions (Turner and Romme 1994).

#### SYNTHESIS

Can general conclusions be drawn regarding how landscape position influences disturbance? Landscape position influences susceptibility to disturbance when the disturbance itself has a distinct directionality (e.g., hurricane tracks or prevailing winds) such that some locations are usually more exposed than others. In addition, landscape position may influence susceptibility if the disturbance is of moderate intensity, such that its severity is influenced by subtle differences in the landscape. However, if the disturbance itself has no spatial directionality (e.g., downbursts), or it is so intense that its severity is unaffected by differences in the landscape (e.g., high-intensity crown fire), then landscape position does not influence susceptibility to the disturbance.

*Effect of Landscape Heterogeneity on the Spread  
of Disturbance*

*Landscape  
Disturbance  
Dynamics*

Understanding effects of landscape heterogeneity on the spread of disturbance was identified by Risser et al. (1984) as a fundamental question in landscape ecology, and this was the theme of the first US landscape ecology symposium, held in 1986 (Turner 1987b). Risser et al. (1984) noted that spatial homogeneity often enhances the spread of a disturbance; consider the spread of pests through agroecosystems, the perpetuation of wildfire or epidemics such as Dutch elm disease. They also noted that other disturbances may be enhanced by landscape heterogeneity; for example, fragmented forests harbor larger populations of deer that disturb surrounding crops or overbrowse native forest species. Landscape heterogeneity also enhances recovery rates by providing refuges for organisms that recolonize disturbed areas. Many studies suggest an interaction between landscape heterogeneity and the spread of disturbance, whether it enhances or retards spread differs among disturbance types (Turner and Bratton 1987; Castello et al. 1995). We'll consider several examples that illustrate aspects of this important interaction.

THEORETICAL DEVELOPMENT

An influential conceptual study by Franklin and Forman (1987) examined the probability of disturbance, e.g., wildfire, windthrow, and pests, as a function of spatial patterns imposed on a forested landscape by clearcutting. Franklin and Forman (1987) explored consequences along a gradient of forest conditions from "primeval" to a completely clearcut landscape. They used simple geometric models (Fig. 6.7) to evaluate how patch size, number of patches, and lengths of edge changed under different cutting patterns; temporal dynamics (e.g., succession) were not considered. Next, implications of these alternative arrangements of forest and cutover lands for disturbances were evaluated. Windthrow susceptibility was assumed to increase with the amount of edge, the isolation of forest in small patches, and with increasing wind fetch. Results of the model demonstrated that windthrow potential would increase initially with forest cutting and continue to increase as forest patches became isolated on all sides (Fig. 6.8a). Wind fetches progressively increased with cutting; after 80 % of the original forest was cleared, windthrow risk to all remaining patches peaked. Susceptibility to both fire ignition and spread, along with risk of particular pest and pathogen outbreaks, were also considered (Fig. 6.8b, c). These simple and insightful models suggested a striking influence of landscape heterogeneity on disturbances, although specific effects varied by disturbance type.

Another conceptual framework for studying effects of landscape heterogeneity on disturbance was developed by Turner et al. (1989a) based on the neutral landscape model approach (see Chap. 3). The landscape was represented as a grid of 10,000 cells containing habitat that either was or was not susceptible to a

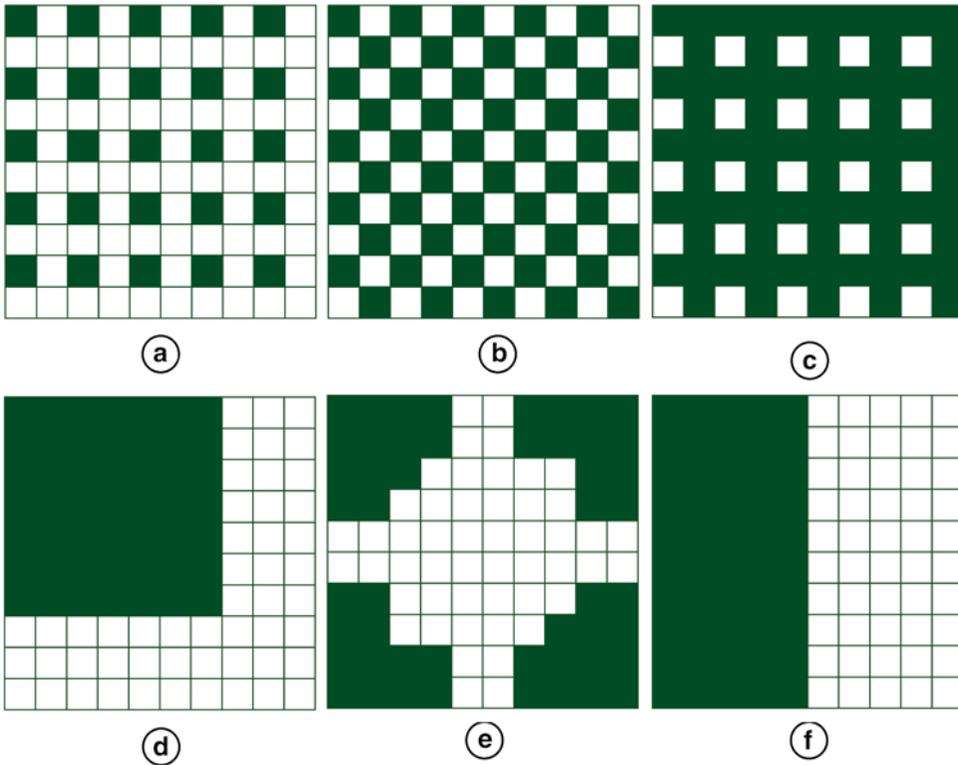


FIGURE 6.7.

Patterns of clearcutting developed under various models by Franklin and Forman (1987). In (a–c), a dispersed cut pattern is used in which the amount of cutover area (*black*) varies but there is a regular distribution across the landscape. In (d–f), the cutover area is 50 % but it is arranged as a single nucleus, four-nucleus, or progressive parallel cutting system.

ADAPTED FROM FRANKLIN AND FORMAN (1987)

given disturbance. Susceptible habitat was distributed at random and occupied different proportions,  $p$ , of the landscape ranging from 0.1 to 0.9. Disturbance was then simulated by two simple parameters:  $f$ , the probability of initiation of a new disturbance in a susceptible site, and  $i$ , the probability that the disturbance, once initiated, would spread to adjacent sites of the same habitat. Numerous simulations were conducted in which  $p$ ,  $i$ , and  $f$  were varied, and the disturbance was allowed to progress until it was extinguished or could not spread any further. Final disturbance extent and landscape patterns were then analyzed. Simulation results demonstrated a qualitative shift in the influence of the landscape on disturbance spread with changes in  $p$  (Fig. 6.9). When  $p$  for susceptible habitat was less than the critical threshold of connectivity, the percent of available habitat that was disturbed was affected most by  $f$ , the probability of new disturbances being initiated, and  $i$  had little effect. That is, the fragmentation of susceptible habitat into

FIGURE 6.8.

Predicted susceptibility of forests in the Douglas-fir region to various types of disturbance as a function of the percent of the landscape that is clear cut, as shown by the checkerboard model (see Fig. 6.7b).

- (a) Potential for windthrow in residual forest patches.
- (b) Potential for wildfire ignition and spread.
- (c) Susceptibility to insect and fungus pests.

ADAPTED FROM FRANKLIN AND FORMAN (1987)

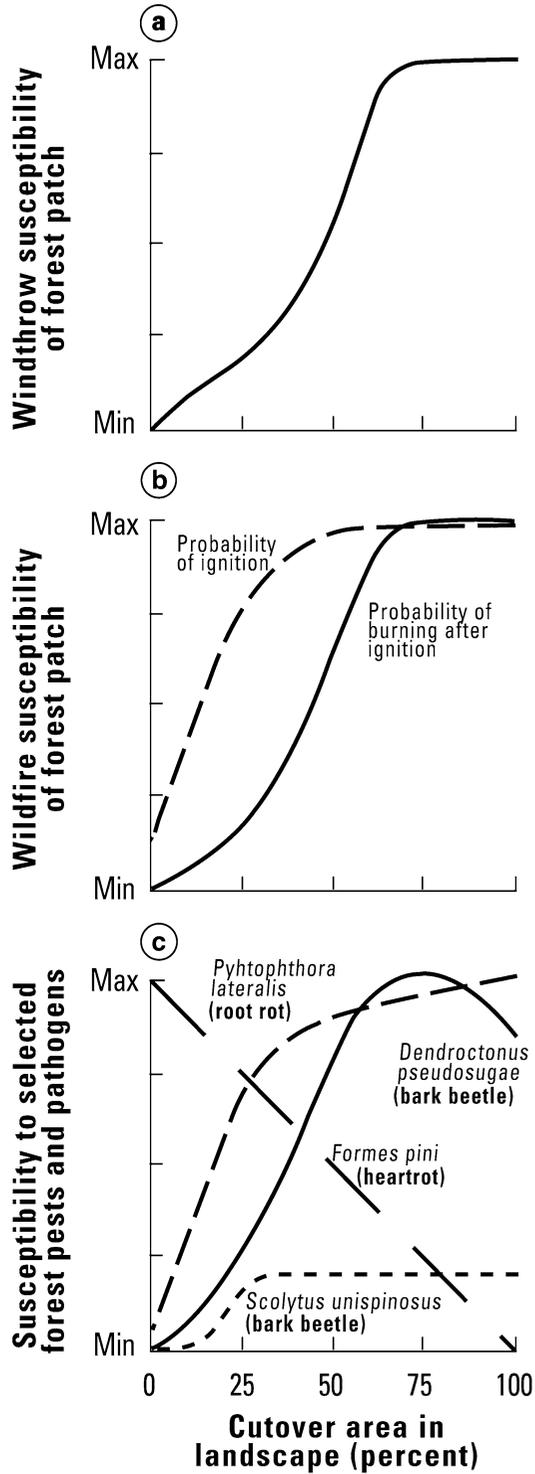
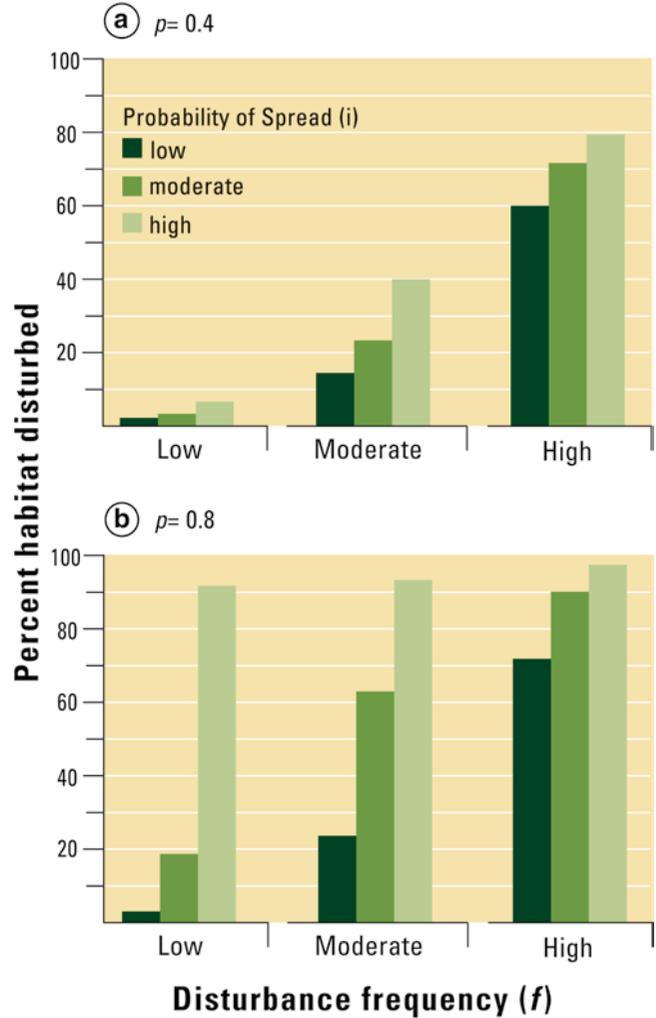


FIGURE 6.9. Simulated percent of susceptible habitat disturbed as a function of the  $f$ , the probability of disturbance initiation, and  $i$ , the probability of the disturbance spreading to adjacent susceptible sites. (a) Initial proportion,  $p$ , of the landscape occupied by susceptible habitat is 0.4, below the threshold of connectivity. (b) Initial proportion,  $p$ , of the landscape occupied by susceptible habitat is 0.8, above the threshold of connectivity.

ADAPTED FROM TURNER  
ET AL. (1989A)



small, isolated patches prevented disturbance spread across the landscape; the only means for affecting a large proportion of the habitat was to initiate disturbance in many patches. In contrast, once  $p$  for susceptible habitat was greater than the critical threshold of connectivity, the probability of spread,  $i$ , controlled the percent of habitat that was disturbed. Under these landscape conditions, susceptible habitat formed large, continuous patches, and even a single disturbance could potentially spread across the entire landscape.

Several additional theoretical frameworks consider the role of spatial pattern in disturbance spread. Under the umbrella of cross-scale interactions, Peters et al. (2004b) proposed a conceptual framework for understanding when a series of interactions and feedbacks among fine- and broad-scale processes lead to unexpected “catastrophic” events. This framework emphasizes conditions under which fine-scale processes propagate nonlinearly to have broad-scale impacts, as well as when broad-scale drivers simply overwhelm fine-scale processes. The model links the initiation of

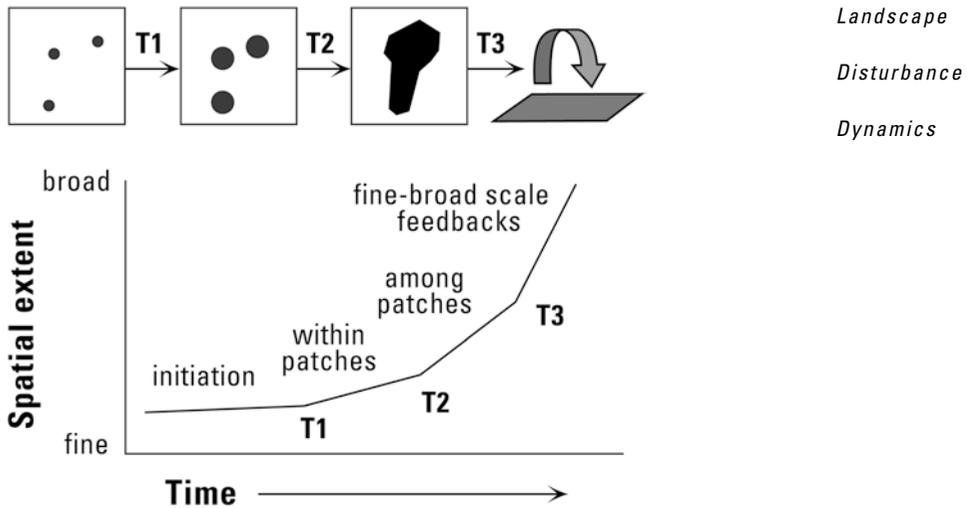


FIGURE 6.10.

Conceptual framework proposed by Peters et al. (2004b) illustrating a series of spatial nonlinearities and thresholds that may lead to “surprises,” or unexpected and even catastrophic events. Event initiation ( $T1$ ) represents the initiation of a disturbance event, which is often stochastic because occurrence, timing and location are difficult to predict. Within-patch expansion of the disturbance ( $T2$ ) depends is contingent on the state of the system and external drivers. Spatial spread of the disturbance ( $T3$ ) is influenced by landscape composition and configuration, and by external drivers

a disturbance event, its within-patch expansion, and its spatial spread among patches (Fig. 6.10). The rate of disturbance spread depends on spatial configuration, connectivity, and flows within and among landscape elements.

The cross-scale interactions framework was used to evaluate dieback of piñon pine (*Pinus edulis*) in northern New Mexico, USA, in part because the dieback could not be attributed to a single cause (Allen 2007). Feedbacks between pattern and process were identified within three different spatial scale domains and included numerous nonlinear, synergistic interactions. Cross-scale interactions were also invoked by Raffa et al. (2008) to explain the series of thresholds that must be surpassed, at multiple scales, for populations of native bark beetles to transition from the endemic to outbreak phase. Another theoretical framework for disturbance that incorporates spatial heterogeneity focuses on self-organized patchiness and catastrophic shifts in ecosystems (e.g., Rietkerk et al. 2004). Regional disturbance regimes play a part in broader considerations of regime shifts, as they may be sensitive indicators of tipping elements (sensu Lenton et al. 2008) that exhibit threshold-like behavior. *Tipping elements* refer to subsystems that can be switched into different states by small perturbations (Lenton et al. 2008). The *tipping point* is the corresponding critical point—in

a forcing driver—beyond which the system is altered. As emphasized in hierarchy theory (Allen and Starr 1982; O'Neill et al. 1986) and neutral landscape models (Turner et al. 1989a), these theoretical disturbance frameworks emphasize scale, threshold phenomena, and nonlinear dynamics as key determinants of landscape dynamics. Further, the theoretical frameworks underscore the importance of spatial heterogeneity for understanding the rates and patterns of disturbance.

#### EMPIRICAL STUDIES

Many studies have focused on the spatial spread of natural disturbances, with pest or pathogen dynamics and fire receiving most attention. There is a rich and varied literature on the subject, and examples discussed here are illustrative and by no means comprehensive.

**Insect outbreaks.** Landscape heterogeneity due to forest fragmentation enhanced outbreaks of the forest tent caterpillar (*Malacosoma disstria*) in northern Ontario, Canada (Roland 1993). Outbreaks in boreal mixedwood forests were of longer duration in areas that had higher landscape heterogeneity resulting from forest clearing and fragmentation. This caterpillar exhibits cyclic population outbreaks and declines with a period of about 10 years, and outbreaks occur in forests that have at least some aspen (*Populus tremuloides*). Following an outbreak, the decline from peak density is associated with high mortality caused by a virus and a parasitic fly. However, the duration of the high-density outbreak phase can vary between 2 and 9 years among regions. Using aerial survey data on the spatial extent of three complete caterpillar outbreak cycles over an area of 26,623 km<sup>2</sup>, Roland (1993) calculated mean outbreak duration in 261 townships in eight forest districts and compared this to measures of forest and landscape structure. Results demonstrated a strong effect of forest fragmentation as measured by edge density (km forest edge per km<sup>2</sup>). Within townships, each 1 km/km<sup>2</sup> increase in edge density increased duration of the outbreak by 0.92 years. Outbreaks in townships with continuous forest cover lasted only 1–2 years, whereas townships with 2.0–2.5 km/km<sup>2</sup> of edge lasted 4–6 years (Fig. 6.11). Among districts also, the outbreaks were longer in those districts that had high average fragmentation (Fig. 6.11). At both levels, the amount or proportion of

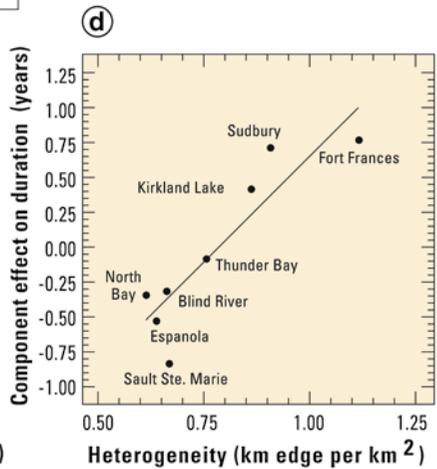
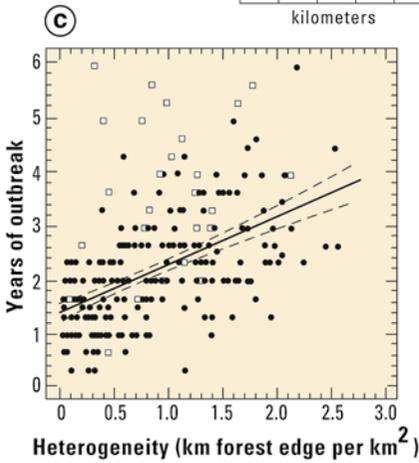
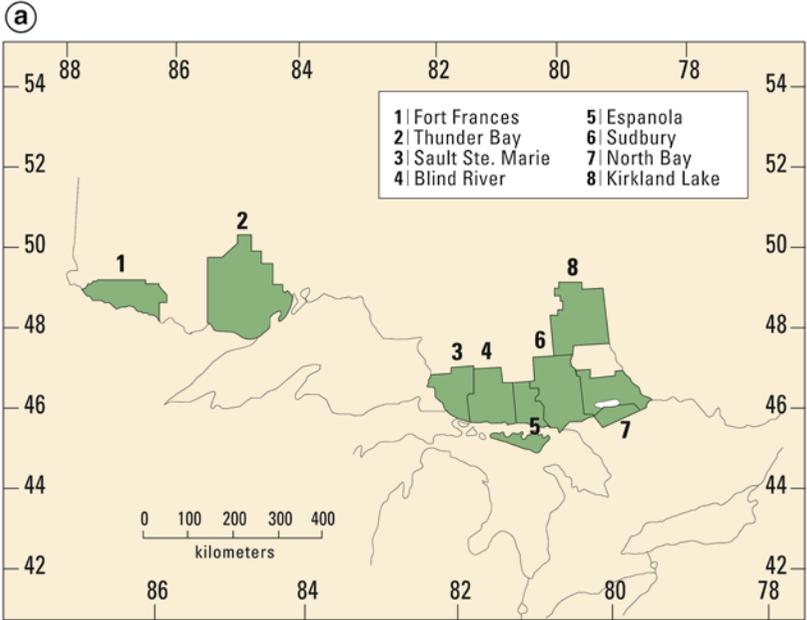
---

FIGURE 6.11.

(a) Areas of Ontario, Canada in which duration of forest tent caterpillar outbreaks were related to forest and landscape structure. (b) Example from one township (MacPherson Township, North Bay District) showing the distribution of forest (*green*) and nonforested (*white*) land. (c) Mean duration of forest tent caterpillar outbreak for 261 townships as a function of edge density for all townships. (d) Effect of mean habitat heterogeneity on outbreak duration within the eight forest districts.

REDRAWN FROM ROLAND (1993)

*Landscape*  
*Disturbance*  
*Dynamics*



aspen was not significant. Roland (1993) suggested several explanations for these results. Broad-scale fragmentation of the forest may affect the interaction between the natural predators on the caterpillar, in that dispersal of the pathogens may be limited by forest fragmentation. In addition, many species of Lepidoptera lay more eggs along the edges of host-plant patches than within the interior, so the forest tent caterpillar abundances may also be greater initially along the forest edges. Warmer microclimatic conditions along the patch edges may also lead to more rapid development of the insect.

In contrast, reconstructions of regional outbreaks of western spruce budworm (*Choristoneura occidentalis*) in the western USA during the past three centuries suggested that landscape heterogeneity decreases the spread of this pest. Swetnam and Lynch (1993) found that the twentieth century had the longest intervals of reduced budworm activity, and an outbreak that occurred through the 1970s and 1980s was unusually severe. Also, budworm infestations and epidemic periods appeared to be most synchronous during the twentieth century, meaning that they were likely to occur simultaneously in many different geographic locations. Budworm infestations develop and spread under conditions of high tree density and connectivity among forest stands, and this was pointed out by interesting variation in the chronologies. For example, a widespread outbreak that occurred during the 1900s–1920s was missing from the Colorado Front Range and the Sangre de Cristo Mountains. Swetnam and Lynch (1993) attributed this absence to the rapid changes that had occurred in the Southern Rocky Mountain mixed conifer forests during this period. Extensive logging and previous fires had reduced conifer densities substantially, and the resulting landscape heterogeneity, in which forests were sparser and less connected, retarded spread of the budworm. Subsequent fire suppression, reduced sheep grazing, and favorable climatic conditions allowed host-tree seedlings to become established, setting the stage for a dramatic future increase in tree density and forest connectivity. During the first part of the century (including the period of the widespread outbreak), these developing forests were less susceptible to budworm outbreaks because they contained few mature trees, and the open stand structure limited dispersal of the budworm. By the 1940s, however, these mixed conifer forests had greater canopy closure, the mature host trees became an important component of stand composition, and the forests were more spatially continuous across the landscape than they had been in presettlement times. Budworm outbreaks subsequently became more widespread and more severe than in earlier periods. Thus, decreased landscape heterogeneity, induced by human activities, resulted in increased spread and synchrony of spruce budworm outbreaks. Regional patterns of budworm outbreak, observed as synchrony among widely dispersed stands, were related to climate control on budworm dynamics—primarily through spring rainfall. However, differences in local patterns resulted especially from land-use history in which stand density, stand

age, and landscape pattern could override effects of the broad-scale climatic influences (Swetnam and Lynch 1993).

Landscape heterogeneity also plays a role in bark beetle outbreaks in forest landscapes. During the first decade of the twenty-first century, the frequency, extent, and severity of outbreaks of native bark beetles (Dendroctonae) in western North America have exceeded those documented over the past 125 years (Fig. 6.12). Nearly every coniferous forest type was affected between 1997 and 2010 (Raffa et al. 2008; Meddens et al. 2012). Eruptions of individual species have been larger than previously reported, and temporal synchrony among species appears to be greater. A complex set of controls and feedbacks operate across multiple scales to control bark beetle population dynamics, and numerous thresholds must be exceeded for an outbreak to develop. Included among these is the landscape pattern of forest stands vulnerable to beetle attack. Abundant and well-connected stands of trees that are homogenous in species, age, and genetic structure can enhance the expansion of an outbreak, whereas more heterogeneous forest patterns can impede spread (Raffa et al. 2008). In western Canada, management practices resulted in forests in which nearly 70 % of the lodgepole pine (*Pinus contorta*) was >80 years old and in size classes vulnerable to mountain pine beetle (*Dendroctonus ponderosae*). This host abundance was three times the amount of susceptible pine observed in the previous century (Taylor and Carroll 2004). Along with environmental conditions (e.g., warmer climate increasing overwinter beetle survival and shortening the life cycle) that have become more favorable to bark beetles, the structure and connectivity of the forests increased the likelihood of beetle outbreaks spreading across the landscape.

**Fire.** The role of landscape heterogeneity in controlling fire spread has been explored in a variety of systems. In some coniferous forests, landscape heterogeneity in forest age classes can affect fire spread (e.g., Givnish 1981; Foster 1983; Foster and King 1986). If flammability is related to stand age (e.g., by affecting fuels), the spatial distribution of old and young stands may enhance or constrain fire spread. In California, fires in chaparral burned well in old stands, but diminished in patches of younger vegetation (Minnich 1983). There may be critical thresholds in environmental constraints that determine whether or not landscape heterogeneity will influence the spread of crown fire (Turner and Romme 1994; Renkin and Despain 1992). Landscape pattern may have little influence on crown-fire behavior when burning conditions are extreme (Turner and Romme 1994; Fig. 6.13). Under conditions of extreme drought and high winds, all fuels across the landscape become highly susceptible to burning and may render the occurrence of large stand-replacing fires inevitable (Fryer and Johnson 1988; Johnson 1992; Bessie and Johnson 1995).

For fire, the degree to which landscape factors affect fire spread or severity depends on the relative importance of *top-down* versus *bottom-up* factors (Littell et al. 2009). Top-down forces include the strong influence of regional climate and

*Landscape*

*Disturbance*

*Dynamics*

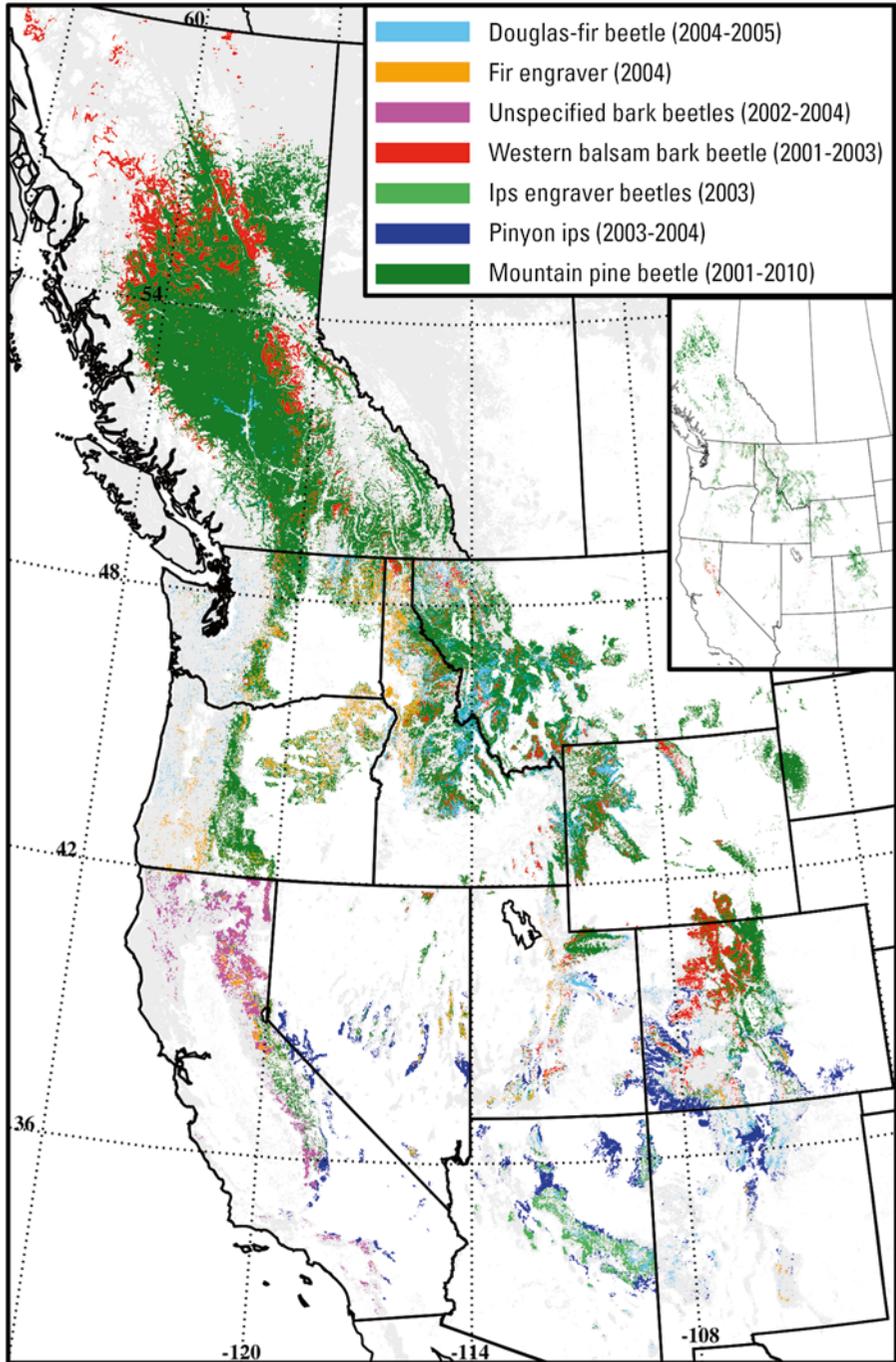


FIGURE 6.12.

Major bark beetle outbreaks in the western United States and British Columbia, Canada between 2001 and 2010. Light shading depicts all forested areas.

REPRINTED WITH PERMISSION FROM MEDDENS ET AL. (2012)

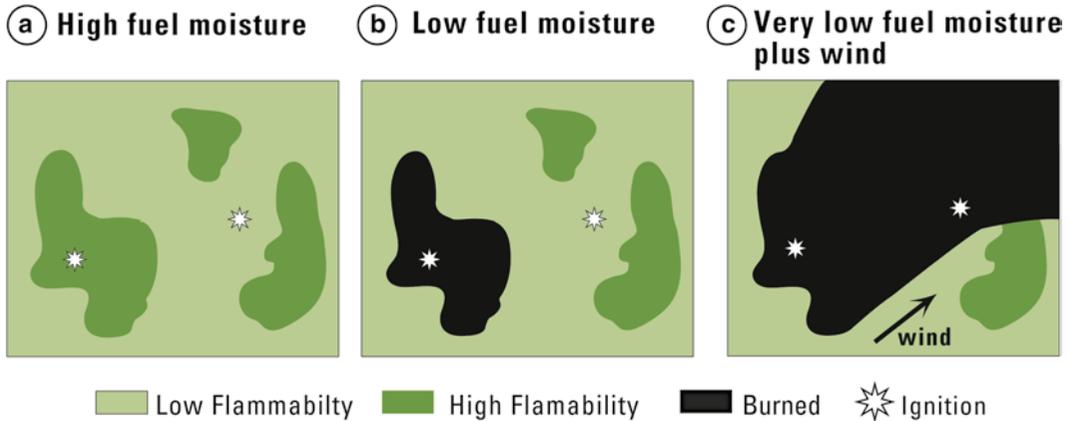


FIGURE 6.13.

Interaction between hypothesized thresholds in both meteorological conditions and landscape pattern that interact to produce large crown fires. (a) If fuel moisture is high, lightning strikes (*stars*) are unlikely to initiate a fire, even if the strike occurs in highly flammable forest (*dark green*). Landscape pattern does not control fire spread. (b) If fuel moisture is low, but burning conditions are not extreme, then crown fires (*black*) are likely to be constrained by the spatial distribution of highly flammable patches in the landscape. (c) If fuel moisture is extremely low and there are strong winds, crown fires (*black*) are likely to burn through a variety of fuel types. Under these conditions, the patterning of more flammable stands does not constrain fire spread.

ADAPTED FROM TURNER AND ROMME (1994)

regional geomorphology, which affect large areas and influence fire frequency, size, and severity. Bottom-up forces include local factors, such as stand and landscape structure and topography, which are more spatially variable. In general, bottom-up factors relate to the amount and connectivity of fuel in the landscape. Evaluating top-down and bottom-up controls on fire regimes has received much recent attention (e.g., Heyerdahl et al. 2001; Mermoz et al. 2005; Meyn et al. 2007; Morgan et al. 2008; Parisien et al. 2011; Parks et al. 2012). All fire regimes are influenced by both, but regimes characterized historically by infrequent, high-severity fire typically have strong top-down forcing and may show little influence of bottom-up factors (e.g., the 1988 Yellowstone Fires; Turner et al. 1994b). In contrast, regimes characterized by frequent, low-severity fire typically have strong bottom-up forcing and are more responsive to landscape pattern. For example, drier low-elevation and mid-montane forests in western North America historically experienced frequent fires that maintained an open forest structure. Such fires are very responsive to local fuel availability, and antecedent weather conditions that produce lush herbaceous growth are often associated with big fires. For example, large fires at lower elevations in southeastern Arizona, USA, occurred when antecedent conditions remained

wet until just before the fire season (Crimmins and Comrie 2004). In forests adapted to a low-severity fire regime, changes in forest structure, such as increased tree density from fire-exclusion, can increase wildfire spread and severity (Schoennagel et al. 2004; Miller et al. 2009). Some landscapes are characterized by mixed-severity fire regimes that contain areas of both high- and low-severity fire and are governed by a delicate balance between top-down and bottom-up controls (Perry et al. 2011). Indeed, the importance of mixed-severity fire is being recognized in more and more landscapes. The degree to which fire-prone landscapes can be managed to achieve desired management goals remains a hot topic in landscape ecology and natural resource management (Stephens et al. 2013; Moritz et al. 2014).

**Synthesis.** Given the wide range of studies on the subject, can we generalize about whether landscape heterogeneity does or does not enhance the spread of disturbance? The answer depends on whether the disturbance spreads *within* the same cover type, such as the spread of a species-specific parasite through a forest, or whether it crosses boundaries and spreads *between* different cover types (Turner et al. 1989a). If the disturbance spreads within the same cover type, then greater landscape heterogeneity should retard the spread of disturbance. This was observed in the spruce budworm and bark beetle examples (Swetnam and Lynch 1993; Raffa et al. 2008), and the spread of fires under moderate burning conditions (Turner and Romme 1994). If the disturbance spreads between cover types or is otherwise enhanced by edge effects, then increased landscape heterogeneity should enhance the spread of the disturbance. This was observed in the forest tent caterpillar (Roland 1993) and windthrow (Franklin and Forman 1987) examples. Other studies suggest circumstances in which landscape heterogeneity does not influence disturbance spread because the broad-scale abiotic controls override the local landscape controls; large infrequent crown fires (Turner and Romme 1994) and tornadoes (Peterson and Pickett 1995; Frelich and Lorimer 1991) provide examples. In sum, there are important controls at multiple scales, and the role of landscape heterogeneity in enhancing or retarding disturbance spread strongly depends on whether other thresholds have been exceeded (e.g., Peters et al. 2004a, b; Allen 2007; Raffa et al. 2008). Clearly, landscape heterogeneity and disturbance remains an active and vibrant area of landscape ecological research, both in theory development and empirical study.

#### LANDSCAPE EPIDEMIOLOGY

Landscape epidemiology is an emerging interdisciplinary related to disturbance spread. *Epidemiology* deals with the spread of a disease from individual to individual through a population and predicts outcomes, such as rate of spread and the proportion of the population affected by the disease. *Spatial epidemiology* is the study of spatial variation in disease risk or incidence, and while many studies focus on the spatial dynamics of disease, the role of landscape structure has only recently received study (Ostfeld et al. 2005). *Landscape epidemiology* aims to identify the

factors that influence the spatial spread of diseases among subpopulations of human, animal, or plant hosts (Plantegenest et al. 2007; Reisen 2010; Meentemeyer et al. 2012). Because research in landscape epidemiology comes from studies on a wide range of host taxa, relevant studies are also found under other names (e.g., *landscape pathology*, which focuses on tree diseases, is the intersection of forest pathology and landscape ecology; Holdenrieder et al. 2004).

How might landscape heterogeneity affect disease? Landscape structure (and thus land-use change) may affect disease dynamics through influences on abiotic conditions (such as changing edge conditions or environmental gradients) and on species interactions that contribute to disease prevalence or spread (Ostfeld et al. 2005). Landscape structure becomes important for disease risk or incidence if it influences disease vectors, reservoirs, or pathogens.

Parallels between the spread of natural disturbances and diseases have been apparent for some time. For example, O'Neill et al. (1992) developed a model derived from epidemiology theory and applied it to the spread of disturbance in a landscape. Results demonstrated that the spatial pattern of susceptible sites, particularly as related to their connectivity, could determine the total extent of a single disturbance event. Spatial models of disease spread proved useful for understanding and predicting the spread of pests, pathogens, and disease (e.g., Hohn et al. 1993; Liebold et al. 1993; Castello et al. 1995; Nicholson and Mather 1996). Since then, a growing number of empirical studies have elucidated ways in which landscape heterogeneity affects disease incidence and spread. These studies seek to relate the spatial patterns of disease dynamics to attributes of the landscape, much as ecologists relate spatial patterns of natural disturbance to landscape structure. Studies in landscape epidemiology often consider both the influence of landscape position (i.e., related to host landscape pattern) on disease incidence and the influence of landscape structure (i.e., connectivity) on disease spread.

Landscape epidemiology studies have revealed effects of landscape structure on the incidence of many different pests and diseases, especially if pattern affects pathogen dispersal vectors. Landscape position is important for passive transport of pathogens by wind or water, and landscape elements may be barriers or conduits for spread. For example, windbreaks surrounding vegetable gardens in Provence, southeastern France, acted as barriers that slowed the dispersal of vectors of cucumber mosaic virus (Marrou et al. 1979). In contrast, road and creek corridors were conduits that increased the dispersal of spores of *Phytophthora lateralis*, a nonnative root pathogen that causes "root rot" in Port Orford cedar (*Chamaecyparis lawsoniana*) in the Pacific Northwest (USA) (Jules et al. 2002). Spores were unintentionally transported in mud on vehicles traveling the road network, from which they dispersed along the stream network. Because the spores disperse by gravity, landscape position also played a role: uninfected trees also were more vulnerable when located downslope of infected trees, rather than upslope.

*Landscape*  
*Disturbance*  
*Dynamics*

The recent dieback of oaks (*Quercus* spp.) known as sudden oak death (SOD) provides another example of landscape influence on disease. Oak trees have died along hundreds of kilometers of the California coast, and a non-native pathogen, *Phytophthora ramorum*, was identified as the cause. The pathogen causes rapid development of cankers that girdle the tree and cause its death. Analyses of the spatial pattern of oak mortality revealed that proximity to forest edge was most important, and this effect was explained by the abundance of understory hosts in edge environment (Kelly and Meentemeyer 2002). Increased diversity of other host species that are less competent appears to dilute transmission of the disease by competent hosts; disease risk was lower in sites with higher species diversity (Haas et al. 2011). However, landscape connectivity also plays a role. Ellis et al. (2010a) tested the importance of connectivity relative to other environmental variables in determining the spatial distribution of SOD. Among several measures evaluated, a connectivity term calculated with effective distances (Euclidean distance modified to account for how landscape structure can influence spread) performed best. Environmental variables were relatively more important, but connectivity still mattered (Ellis et al. 2010a, b).

In agricultural landscapes, crop damage due to pests and pathogens may depend on composition and configuration of the surrounding landscape. For example, an increase in landscape complexity in 1.5-km diameter landscapes around canola fields was associated with decreased damage by the canola pollen beetle (*Meligethes aeneus*) and increased parasitism of the pest by parasitoids (Thies et al. 2003). Patterns in the surrounding landscape also influenced the abundance of *Delphacodes kuscheli*, an insect known to transmit Maize Rough Dwarf Virus to maize fields in Argentina (Grilli 2010). The composition, configuration, and stability of patches in the surrounding landscape can influence potential pathogen reservoirs and the abundance of alternative hosts, which can affect damage levels on a focal species.

Landscape patterns related to habitat fragmentation and edges also play a role in the epidemiology of human diseases. Globally, the trend of emerging infectious diseases appears to be associated with ecotones, especially edges that are created or modified by humans (Despommier et al. 2007). Among emerging diseases, Lyme disease has been studied most thoroughly, and landscape structure has emerged as a particularly strong driver. Lyme disease is the most frequently reported vector-borne disease in the United States and Europe (Killilea et al. 2008, and references therein). In North America, Lyme disease is caused by *Borrelia burgdorferi*, a spirochete bacterium, which is vectored by ticks of the genus *Ixodes*. Many birds and small mammals are potential reservoir hosts, but the dominant hosts are rodents (e.g., white-footed mice, *Peromyscus leucopus*). Humans become infected when bitten by a tick that was infected previously when feeding on an infected host (Killilea et al. 2008). Incidence of Lyme disease requires reservoir hosts, ticks, and humans to occur in close proximity, and thus the factors that influence tick presence and abundance, the mammalian and avian community, and the presence of humans may all influence disease prevalence.

Landscape patterns influence the prevalence of Lyme disease in the tick populations, with fragmented forest landscapes (i.e., many small forest fragments and a lot of forest-edge habitat) having higher entomological risk (Allan et al. 2003; Brownstein et al. 2005). Tick density and infection prevalence were both higher in forest fragments that were smaller and more isolated. The elevated level of tick infection was linked, in turn, to changes in composition of the vertebrate community. The vertebrate community becomes less diverse as forests become fragmented, with many species disappearing in small forest patches. The species-poor communities have abundant white-footed mice, which is the most competent host for the disease-causing bacterium (LoGiudice et al. 2003). As new host species are added to a depauperate community, the tick infection rate declines (LoGiudice et al. 2003) because the nonmouse hosts are much less competent. Thus, the higher species diversity in the community of hosts dilutes the effects of the white-footed mice. Surprisingly, while the patterns of the host reservoir and tick infection rates are linked clearly to landscape structure, the patterns of Lyme disease incidence in humans remain to be explained (Brownstein et al. 2005; Killilea et al. 2008). However, the strong influence of total forest and forest edge on tick infection rates suggests that landscape designs that reduce the amount of forest edge could help mitigate Lyme disease risk (Jackson et al. 2006).

A landscape connection has been suggested for the spillover of bat viruses to human populations, including the 2014 outbreak of Ebola in West Africa. Much like the example discussed above for the series of thresholds that must be passed for endemic bark beetle populations to irrupt, a hierarchy of conditions is required for people to become infected by viruses that originate in bats (Plowright et al. 2015). At the landscape level, land-use changes that increase interaction between species, leading to more contact between human and bat populations, are associated with increased likelihood of transmission to humans. In areas of central and northwest Bangladesh with recurring outbreaks of Nipah virus, which is transmitted by fruit bats (*Pteropus giganteus*, also called flying foxes), landscape composition and structure influences disease incidence (Hahn et al. 2014a). Villages in the “Nipah Belt” have forests that are more fragmented than forest surrounding other comparable villages that had no reported outbreaks of Nipah virus. Detailed studies of habitat selection of the fruit bats, along with characteristics of the villages and landscape, are helping to develop land management strategies that can protect fruit bats while minimizing risks to public health (Hahn et al. 2014a, b).

The conceptual framework of landscape ecology promises to complement understanding of disease emergence and spatial dynamics in ways that may help to reduce the incidence of troubling diseases (Plantegenest et al. 2007). A landscape perspective on disease management also can contribute to sustainable land-use patterns (Holdenrieder et al. 2004). Ongoing studies in landscape epidemiology will reveal which site factors and landscape patterns affect susceptibility to a wide range of diseases in plants, animals, and people.

*Landscape*  
*Disturbance*  
*Dynamics*



## EFFECTS OF DISTURBANCE ON LANDSCAPE HETEROGENEITY

Studies of how disturbances respond to landscape patterns have produced a rich understanding of one side of the reciprocal pattern-process relationship. We now turn to the other side this relationship: the role of disturbances in generating landscape patterns.

### *The Disturbance-Generated Mosaic*

When a disturbance occurs, it does not act uniformly throughout a landscape. Rather, disturbances create very complex patterns across the landscape in which the disturbance may affect some areas but not others, and severity of the disturbance often varies considerably within the affected area. When we talk about the *disturbance mosaic*, or the spatial pattern created by disturbance, we refer to the spatial distribution of disturbance severities across the landscape. For example, the 1988 fires in Yellowstone National Park created a complex pattern of burned and unburned areas across the landscape (Fig. 6.14), and the burned areas themselves



FIGURE 6.14.

The landscape mosaic created by the 1988 Yellowstone fires as observed from the air in October 1988, shortly after the fires had been naturally extinguished

(PHOTO BY M. G. TURNER)

had widely variable severities within them (Christensen et al. 1989; Turner et al. 1994a). Even very large crown fires rarely consume an entire forest because variations in wind, topography, vegetation, and time of burning result in a mosaic of burn severities (effects of fire on the ecosystem) and islands of unburned vegetation across the landscape. Complex mosaic patterns of disturbance have been described in many systems, including even benthic communities in the Antarctic for which ice scouring is the key disturbance (Teixido et al. 2007).

Many studies have made excellent use of landscape metrics to describe disturbance-created landscape patterns. In such studies, the proportion of the landscape that is disturbed or in different disturbance-severity categories is determined, and landscape composition and configuration metrics are computed. For example, the number, size and shape complexity of forest patches were used to describe changes in forest fragmentation following a mountain pine beetle epidemic in British Columbia, Canada (Coops et al. 2010). Understanding disturbance-driven changes in variability per se also can be insightful (Fraterrigo and Rusak 2008). Variability can be quantified using either absolute measures (e.g., standard deviation), which tend to increase with the mean; or relative measures (e.g., coefficient of variation), which are normalized and more comparable among different properties. Measures of variability can be highly sensitive and independent of the mean, thereby capturing effects that may be obscured by averaging. For example, spatial variability in forest stand structure (measured by the coefficient of variation in stand density among stands of similar age) *increased* following fire in the Yellowstone landscape, then slowly declined for the next 175–200 years (Kashian et al. 2005b). In contrast, variability in a range of physical, chemical, and biological properties (also measured by the coefficient of variation) *decreased* with flooding in a river–floodplain landscape (Thomaz et al. 2007). Thus, disturbances can both amplify and dampen variability, and not surprisingly, effects of disturbance on variability can differ with scale (Fraterrigo and Rusak 2008). Increased variability has been suggested as a leading indicator of qualitative changes arising from disturbance (e.g., van Nes and Scheffer 2005; Brock and Carpenter 2006). Quantifying and tracking changes in disturbance-induced variability through time may lead to new ecological insights about pattern-process dynamics as well as improved methods for anticipating big changes.

Considerable interest in large, infrequent disturbances (Turner et al. 1997a; Turner and Dale 1998) emerged following a number of natural disturbances that received considerable attention from the ecological research community and the general public (e.g., the eruption of Mount St. Helens in 1980, the 1988 Yellowstone fires, the 1993 floods in the Midwestern US, and Hurricanes Hugo in 1989 and Andrew in 1992). Foster et al. (1998) compared landscape patterns produced by different large, infrequent forest disturbances (Fig. 6.15). Here, we draw upon the synthesis by Foster et al. (1998) and more recent empirical studies to illustrate the variety of landscape patterns generated by wind, floods, and fires.

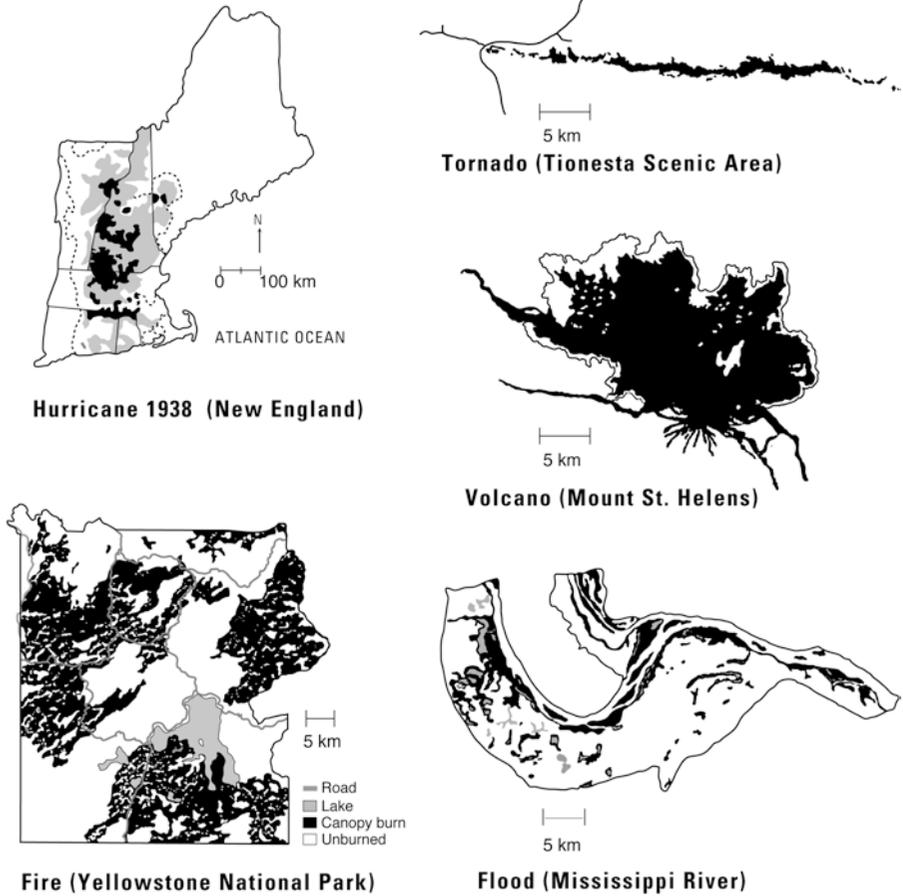


FIGURE 6.15. Landscape and regional-scale patterns of forest disturbance resulting from five contrasting large infrequent disturbances: the 1938 hurricane in New England, the Yellowstone fires of 1988, the eruption of Mount St. Helens in 1980, the tornado at the Tionesta Scenic Area in Pennsylvania, and floods in the Mississippi River in 1993. The areas of greatest disturbance are shown in *black*. Lesser disturbance severity is shown in *gray*.

FROM FOSTER ET AL. (1998)

Hurricanes produce a patchwork of forest age and height structure, uproot mounds and downed boles, standing broken snags, and leaning and damaged trees (Fig. 6.15; Foster 1988a; Foster et al. 1998). Severe windstorms, such as the extensive windstorm that affected 150,000 ha in the Boundary Waters Canoe Area (BWCA) in northern Minnesota, USA, in 1999 have similar effects (Lain et al. 2008). In addition, increased accumulations of fine woody debris and leaves may increase the likelihood of fire occurring in the same area (Patterson and Foster

1990; Paine et al. 1998; Woodall and Nagel 2007). In contrast to hurricanes, tornadoes are relatively small and short-lived, although they are violent and unpredictable. A grouping of tornadoes that affected Pennsylvania, Ohio, New York and Ontario in 1985 illustrates the landscape pattern of severe tornadoes (Peterson and Pickett 1995). Tracks of the tornadoes were oriented eastward and northeastward, resulting in more than 800 km of tornado damage. Path widths averaged 500 m and ranged from <200 to >2750 m. The damage patterns of tornadoes are remarkable for the sharpness of the edges between intact forest and completely windthrown areas (Peterson and Pickett 1995). Hurricanes, blowdowns, and tornadoes are extremes in the gradient of size and severity of wind damage; however, all storm types have a gradient of intensities and severities and vary in the spatial extent of damage (Foster et al. 1998).

Seasonal flooding is a natural process in many river systems, and the suppression of floods is actually a major disturbance to most river–floodplain ecosystems. However, exceptional floods may create extensive and heterogeneous disturbance patterns in the riverine landscape. A case study of extreme flooding in the Sabie River, Kruger National Park (South Africa) provides an example (Parsons et al. 2005). High-resolution aerial photographs were used to quantify patch mosaics in different geomorphological channel types before and after flooding, and to determine whether flooding changed the extent of patches, generated new patch types, removed existing patch type, or altered patch shape or aggregation. The flood left a heterogeneous imprint of biotic and abiotic patches in the river landscape, and the effects on the mosaic different among channel types (Fig. 6.16; Parsons et al. 2005). In turn, these patterns influenced the riparian vegetation response. In large river–floodplain landscapes, flood duration varies spatially across the floodplain with land elevation and is a critical influence on survival of biotic populations (Sparks et al. 1998).

Many studies have quantified spatial patterns of fire throughout the world, and interest in understanding fire patterns has grown as the annual area burned continues to increase. An excellent synthesis of patterns and scales of heterogeneity created by large fires in US landscapes is provided by Keane et al. (2008). Large fires usually occur during moderate to extreme drought, often with high winds (i.e., strong top-down forcing). In northern and montane forest landscapes, large infrequent fires account for <3 % of all fires but more than 95 % of the land area burned (Johnson 1992). Large fires create a mosaic of patches that vary in size, shape, and severity, as illustrated by 1988 Yellowstone fires (Christensen et al. 1989; Turner et al. 1994a). Large fires may contain more high-severity fire within their perimeter as compared to small fires, but the extent of high-severity fire is often less than people expect. For example, consider burn severity and patch metrics for 25 small (<3000 ha) and 11 large (>10,000 ha) fires in the northern Rocky Mountains (Keane et al. 2008). There were few statistically significant differences in proportions of burned area for small and large fires, and even the large fires averaged only 25 % of the area in high-severity fire. However, spatial patterns differed (Keane et al. 2008).



FIGURE 6.16.

Pre- (a) and post-flood (b) views of the Sabie River landscape. The riparian forest can colonize substrate across the entire width of the channel, as shown in the upper pre-flood photo.

FROM PARSONS ET AL. (2005)

In large fires, patches were fewer and larger, had less edge, and were more regular in shape than in small fires (Table 6.2). Landscapes of mixed-severity regimes have a wider range of spatial and temporal variability in the disturbance mosaic, but they typically include many small and few large high-severity patches (Perry et al. 2011). The complexity of the burn mosaic means that even areas of high-severity fire may

TABLE 6.2.  
SELECTED LANDSCAPE METRICS DESCRIBING THE POSTFIRE LANDSCAPE MOSAIC  
OF BURN SEVERITIES FOR 25 SMALL (<3300 HA) AND 11 LARGE (>10,000 HA)  
FIRES IN THE NORTHERN ROCKY MOUNTAINS.

Attribute	Small fires	Large fires	P value
<i>Proportion (p) of fire by burn-severity class</i>			
Unburned	0.21	0.15	0.105
Low	0.25	0.21	0.273
Moderate-low	0.18	0.18	0.273
Moderate-high	0.19	0.20	0.702
High	0.16	0.25	0.052
<i>Patch metrics</i>			
Patch density (patches 100 ha <sup>-1</sup> )	91	67	0.003
Landscape shape index (unitless)	23	103	0.0001
Edge density (m ha <sup>-1</sup> )	306	247	0.0005

DATA WERE DERIVED FROM LANDSAT TM (THEMATIC MAPPER) IMAGERY, FIRE SEVERITY WAS CHARACTERIZED USING THE DIFFERENCED NORMALIZED BURN RATIO, AND LANDSCAPE METRICS WERE COMPUTED IN FRAGSTATS.

Source: KEANE ET AL. (2008)

contain a substantial amount of internal edge and be surprisingly close to unburned or less severely burned areas (e.g., Turner et al. 1994a; Donato et al. 2009).

Analyses of disturbance patterns can provide insight into the processes controlling disturbance, and they may also be sensitive indicators of changing disturbance regimes. Increased access to remotely sensed imagery and algorithms for fire-severity mapping has facilitated such studies. For example, Collins et al. (2007) used satellite data and the differenced Normalized Burn Ratio (dNBR) to describe landscape patterns of fire severity in two fires Sierra Nevada wilderness areas (USA). The dNBR index is calculated by comparing pre-fire and post-fire remotely sensed imagery (Key and Benson 2006) then categorizing values by burn-severity class. They then used FRAGSTATS to compute the area-weighted mean patch size for each burn-severity category. The two fires had similar proportions of burned and unburned, but the two fires produced very different disturbance mosaics. One fire had larger patch sizes of high-severity fire, whereas the other fire had larger patch sizes of low-severity fire within the fire perimeter (Collins et al. 2007). Weather was more important in explaining patterns in the higher-severity fire, and vegetation more important for the lower severity fire (Collins et al. 2007). In a southern African savanna, fire patterns were compared in areas that differed in

dominant land-use, and landscape metrics were computed from annual maps (1971–2001) that included burned areas (Hudak et al. 2004). In the savanna, more burning increased patch size, size variability, shape complexity, suggesting that fire promoted landscape heterogeneity (Hudak et al. 2004).

Landscape patterns generated by human activities have also been well studied, especially patterns resulting from forest harvest strategies (e.g., Franklin and Forman 1987; Li et al. 1993; Gustafson and Crow 1996). Detecting differences in landscape mosaics resulting from forest harvesting vs. natural disturbances have been a primary research focus. Delong and Tanner (1996) compared the spatial characteristics of landscapes in British Columbia subjected to regularly dispersed 60–100 ha clearcuts with the historic patterns generated by wildfire. Wildfires created a more complex landscape mosaic that included a greater range of patch sizes and more complex disturbance boundaries. In addition, individual wildfires were often >500 ha in size, but unburned forest patches remained within the perimeters of the fire (DeLong and Tanner 1996). Harvesting created more fragmented habitat than fire in western Canada (Wang and Cumming 2010) and Greater Yellowstone, USA (Tinker et al. 2003). In the Yellowstone region, timber harvesting on the Targhee National Forest produced landscape patterns in which the number of patches was three times greater and patch sizes were 70 % smaller than patterns produced from wildfires (Tinker et al. 2003). However, contrasting results were observed for forests in northwestern Ontario, Canada, where Gluck and Rempel (1996) observed that patches in clearcut landscapes were larger in size and more irregular in shape than patches in a wildfire landscape.

There has been much discussion in the literature about developing management strategies that mimic natural disturbances in a particular landscape (Hunter 1993; Attiwill 1994), with the implicit assumption that ecological processes will be better maintained in this way. Runkle (1991) suggested that temperate deciduous forest should be harvested in a pattern that mimics small treefall gaps, whereas Hunter (1993) recognized that boreal forests would require very large clearcuts if they were to imitate the size and arrangement of boreal fires. Improved understanding is needed of the nature and dynamics of disturbance mosaics in a wide variety of landscapes and how these differ from those generated by human disturbances. We re-visit this topic later in this chapter when discussing the historic range of variability.

#### SYNTHESIS

The key take-home message regarding disturbance-created landscape patterns is that they are remarkably diverse and complex. This general conclusion comes from studies of many different disturbances in a wide range of landscapes. Disturbance is the key driver of spatial pattern in many landscapes, producing a mosaic of undisturbed and disturbed patches that vary in size, severity, shape, and arrangement. In turn, succession makes this mosaic pattern dynamic.

*Disturbance and Spatial Patterns of Succession*

*Landscape*

*Disturbance*

*Dynamics*

Disturbance and succession are inextricably linked when we consider landscape dynamics. Ecologists have been trying to understand and predict vegetation change since the very beginnings of the discipline, and excellent treatments of the development of successional concepts can be found in Glenn-Lewin et al. (1992) and Walker and del Moral (2003), along with a wonderful synthesis and historical perspective by Christensen (2014). Recovery following disturbance can be very sensitive to spatial pattern created by disturbance and is strongly influenced by the spatial pattern of biotic residuals that are left behind.

The legacies and residuals that remain after the disturbance play a big role in post-disturbance succession (Turner and Dale 1998; Swanson et al. 2011; Donato et al. 2012). Ecological legacies of disturbance have both biological and physical components. *Biotic legacies*, or *residuals*, refer to the types, quantities, and patterns of organisms and biotic structures that persist from the pre-disturbance ecosystem. For example, residuals may include surviving individuals, standing dead trees, vegetative tissue that can regenerate, seed banks, litter, carcasses, and microbial and fungal soil organisms. These organic structures create habitat for surviving and colonizing organisms following disturbances (Swanson et al. 2011). *Abiotic legacies* are physical modifications of the environment that may result from the disturbance, such as mudslides or slope failures, lava flows, or movements of rocks or boulders in streams. Understanding the nature of the disturbance mosaic and the factors controlling these landscape patterns is essential for predicting ecosystem dynamics and vegetation development in disturbance-prone landscapes (Swanson et al. 2011; Donato et al. 2012).

A thorough understanding of succession must include understanding of how successional processes vary with respect to disturbance intensity, size, and frequency (van der Maarl 1993; Turner et al. 1998a; White and Jentsch 2001). Investigations into mechanisms of plant succession following fire and other disturbances often emphasized the autecology and life history attributes of individual plants and species (e.g., Connell and Slatyer 1977; Noble and Slatyer 1980; Peet and Christensen 1980; Pickett et al. 1987a, b; Halpern 1988, 1989). These studies also demonstrated that species responses may vary with different kinds and severities of disturbance and with the larger spatial and temporal context of the disturbance (also see Pickett 1976; Finegan 1984; Glenn and Collins 1992). Patch size, heterogeneity, and distance from undisturbed sites can affect species in a manner dependent on their life history characteristics (Denslow 1980a, b; Hartshorn 1980; Miller 1982; Malanson 1984; Green 1989; Peterson and Carson 1996).

Life history traits related to the ability of the pre-disturbance populations to resist or tolerate a particular type of disturbance interact with disturbance intensity to influence the species composition of residuals. For example, mobility and degree of adaptation to flooding were critical in determining the effects of the 1993 Mississippi River floods on taxonomic and functional groups of organisms in the

midwestern USA (Sparks et al. 1998). Virtually all individuals of tree species that could not tolerate the anoxic conditions that developed under extended soil saturation during the growing season died (Sparks et al. 1998). In contrast, some species of aquatic plants survived by growing upward into the lighted zone as the flood rose, and a rare species of false aster (*Boltonia decurrens*) that requires fresh mudflats for seed germination increased dramatically (Smith et al. 1998).

Residual plants that reestablish vegetatively following disturbance often achieve large sizes more quickly than those that start from seed, and species with abundant or larger residual seeds have a head start on those that must disperse into the disturbed area from the surroundings. One example comes from the regeneration of a large forest windthrow. In 1985, a powerful tornado created a 400-ha area of windthrow in the old-growth hemlock-northern hardwoods forest of the Tionesta Scenic Area in northwest Pennsylvania. During initial revegetation following the windthrow event, thickets of surviving advance regeneration of *Fagus grandifolia* and *Acer pensylvanicum* had a substantial size advantage over individuals that germinated after the disturbance, and that size advantage has been maintained (Peterson and Pickett 1995). These thickets of advance regeneration severely inhibited local colonization by *Betula alleghaniensis*, which is abundant in other areas of the blowdown with fewer residuals (Peterson and Pickett 1995). The relationship between disturbance severity and species-regeneration mechanisms (e.g., vegetative reproduction or seed dispersal and establishment) was nicely presented by Roberts (2004; Fig. 6.17). This framework emphasizes herbaceous vegetation, but it explicitly considers the relative abundance of biotic legacies and their role in post-disturbance succession.

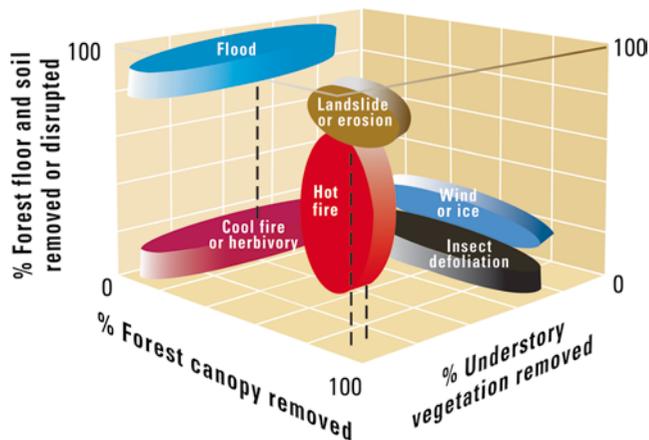


FIGURE 6.17.

Conceptual model of disturbance severity with each of three major vertical layers in the forest ecosystem on a separate axis. Labeled polygons relate the ranges in condition on these three axes to common natural disturbances in North American forests.

ADAPTED FROM ROBERTS (2004)