7 Disturbance Ecology and Habitat Dynamics

Stuff happens: fires, hurricanes, volcanoes, floods, and earthquakes. On average, approximately 450,000 ha are burned in the United States annually, over 1 million ha are affected by hurricanes and over 20 million ha are affected by insects and pathogens (Dale et al. 2001). The economic cost to society is over 1 billion dollars/year in the United States (Dale et al. 2001). To most people, these events are catastrophes. They can kill people, destroy property, and they can be catastrophic for other organisms too. Wind uproots trees, fires burn dead wood, and floods erode streambanks. They can also be events that renew habitat for other species. Indeed biodiversity conservation depends on disturbance. Wind adds dead wood to a forest, fires open the tree canopy and initiate a new forest, and floods create a new seedbed for willows and cottonwoods. Disturbances to forests have occurred for as long as there have been forests. Animals living in forests have adapted to many of these disturbances and some species rely on disturbances to provide food, cover, and water for survival. Understanding characteristics of disturbances and how disturbances influence habitat elements in stands and over forests can provide information that forest managers can use to provide habitat for selected species or to aid in conserving biodiversity. Knowledge of natural disturbances can help when developing silvicultural systems that might meet the needs of forest-associated wildlife (Franklin et al. 2002).

There are several characteristics of disturbances that can be used to understand potential effects on forest development, forest function and the sizes, numbers and distribution of habitat elements: type of disturbance, size and pattern, frequency, and severity. Disturbance type is also important, with changes in habitat elements being quite different depending on the cause of the disturbance (e.g., fire vs. wind). Estimating these characteristics of natural disturbances can facilitate prediction of forest recovery and the subsequent development of vegetation structure.

DISTURBANCE SIZE AND PATTERN

Disturbances come in many shapes and sizes. The size of a disturbance can influence animal species that either remain in or recolonize after a disturbance (Rosenberg and Raphael 1986). Nearly 3 million ha of forest burned in the United States in 2002, a particularly bad fire-year. Some such as the Biscuit fire in southern Oregon were 200,000 ha in size. Most however were much smaller. In fact, there are usually many more small fires than large fires (Figure 7.1). Similar negative exponential distributions of disturbance size have been reported for wind disturbances (Foster and Boose 1992) and tree-fall gaps (Foster and Reiners 1986). Generally, there are many more small nonhuman disturbances than large disturbances across most forested landscapes.

Species that benefit from a disturbance seem to be associated with disturbances of different sizes. Black-backed woodpeckers, elk, and bison colonize forests following large severe fires as millions of dead trees and millions of kilograms of forage become available (Figure 7.2). On the other extreme, white-footed mice (Figure 4.1) are favorably affected by openings of 0.1 ha in size, and decrease in abundance in larger openings (Buckner and Shure 1985). A similar species, deer mice, was not found in these small openings but increased in abundance in larger openings (Buckner and Shure 1985). Disturbances also can increase the probability that certain invasive species might become established (Hobbs and Huenneke 1992) and how long they may persist (Blair et al. 2010).

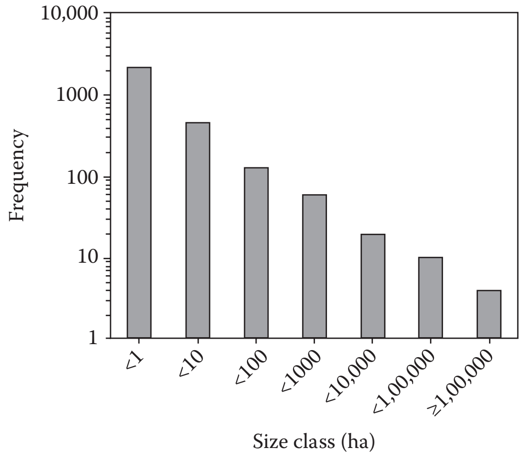

FIGURE 7.1 Histogram of the fire-size distribution for 2898 lightning fires during 1980–1993. Data are shown as counts on a logarithmic scale, in logarithmic bin-widths. (From Cumming, S.G. 2001. *Canadian Journal of Forest Research* 31:1297–1303. With permission.)

For species adversely influenced by a disturbance, the likelihood that they would be displaced by severe disturbances increases as the disturbance approaches and surpasses the size of the species home range (Gosse et al. 2005). But they may not be displaced if the disturbance is sufficiently small relative to the home range size (Hayward et al. 1999, Leonard et al. 2008). Some species that inhabit forests have been able to persist by including fine-scale disturbances within their home ranges, or by recolonizing stands of sufficient size that regrow to the point where necessary habitat elements become available.

Related to the disturbance size is the shape of the area created by a disturbance. We will cover edge effects in Chapter 16, but the function of an opening can be quite influenced by its departure from a circle because circles have the least edge per unit area of any regular shape. Consequently, two disturbances, both of 100 ha in size, may function quite differently for some species if one is circular and the other is shaped like an amoeba. More complex shapes can provide better opportunities

FIGURE 7.2 Bison (shown here), elk, and other herbivores benefited from the large and severe fires in Yellowstone National Park.

for cover adjacent to food for some herbivores (Clark and Gilbert 1982) and can exacerbate the likelihood of colonization by invasive species (Cumming 2001).

Disturbance pattern is the spatial arrangement of the disturbance patches. Pattern is related to the size of a disturbance but, in addition to the areal extent of a stand or landscape affected by a disturbance, the pattern created by disturbance can influence the distribution of resources within and among potential home ranges for a species. Clumped distributions of fine-scale disturbances (e.g., clusters of root-rot pockets that kill trees) may result in a cumulative decrease in habitat availability within an individual's home range. A more random or uniform distribution of disturbances (e.g., lightening strikes) may allow that individual to tolerate the same disturbance density because only a small portion of any one individual's home range in the stand would be affected.

DISTURBANCE SEVERITY

Crown fires and volcanoes are severe disturbances. A tree falling in a forest is not a severe disturbance. The severity of a disturbance reflects the impact on the stand or forest. Is the stand completely replaced or are only a few trees removed providing more growing space to the remaining trees? The severity of a disturbance influences the amount of organic material destroyed and redistributed by the disturbance and hence the amount and form (living or dead) of material that remains after the disturbance. Mount St. Helens was a severe disturbance, but even after its eruption, many pieces of the previous forest persisted. Trees were buried in ash, but so were seeds, fungi, and many species of animals that survived below ground. These biological legacies and the chance occurrence of them in places where they could grow and recolonize give rise to a landscape that is now on a trajectory to establish a new forest (Nash 2010). It is these same legacies that remain following a disturbance that may directly or indirectly provide the habitat elements needed for various species. Tree-fall gaps in later stages of forest development produce snags and logs, and sites where regeneration can become established in the openings allowing vertical complexity to increase. Similarly, following a hurricane or a fire, we see abundant dead wood and the establishment of a new cohort of plants and animals. The residual structures following severe disturbances such as these may persist into the next stand and provide the large trees and snags used by some species as the new stand grows (McComb and Lindenmeyer 1999; Figure 7.3). The diverse early successional conditions represented by disturbances leaving a diverse suite of biological legacies are rare in many landscapes as natural disturbances are partially replaced by uniform approaches to forest management (Swanson et al. 2011).

FIGURE 7.3 Legacy trees, snags, and logs retained following a timber harvest in the Blue River Ranger District, Willamette National Forest, Oregon. (Photo by Bruce McCune. With permission.)

The legacy from the previous stand can be represented in the amount of dead wood, number of live trees remaining, depth of the leaf litter, and the vertical and horizontal complexity in the stand (Spies 1998, Franklin et al. 2002). The residual organic material that remains after disturbance can influence the direction of succession and the rate of subsequent development following the disturbance (Franklin and Halpern 1989). Biological legacies such as these can also provide a seed source for the new stand and ensure sources of mycorrhizal fungi are available to reinnoculate the disturbed site (Dahlberg 2001). Legacies can also be particularly important to species later in the development of forests. Northern spotted owls, for instance, are associated with biological legacies such as remnant large old trees that provide nest sites in many northwestern U.S. forests (North et al. 1996).

DISTURBANCE FREQUENCY

The frequency with which a disturbance occurs in a forest will influence the tree species composition and the amount of living and dead organic material present on the site over time. Hurricane frequency, for instance, can influence the proportion of large areas in early vs. late stages of forest development (Figure 7.4). Frequent intense disturbances can delay the onset of forest development, or may preclude it. Infrequent low severity disturbances may lead to development of vertical structure in a stand. Frequency can be characterized in several ways: disturbance rate, percent of a stand disturbed on an annual basis, or the return interval (time between disturbances). The return interval for disturbances of certain types and intensities varies considerably among forest types. Fire return intervals may be as frequent as once every 2–5 years in some savannah systems (Harrell et al. 2001), and as long as once every 300–400 years in northwestern coniferous forests (Wimberly et al. 2000). Return intervals between management events in managed forests also vary, and when the return interval for a managed forest departs significantly from the return interval that has occurred naturally for thousands of years, then the risk of losing habitat elements and associated species can increase (Hansen et al. 1991).

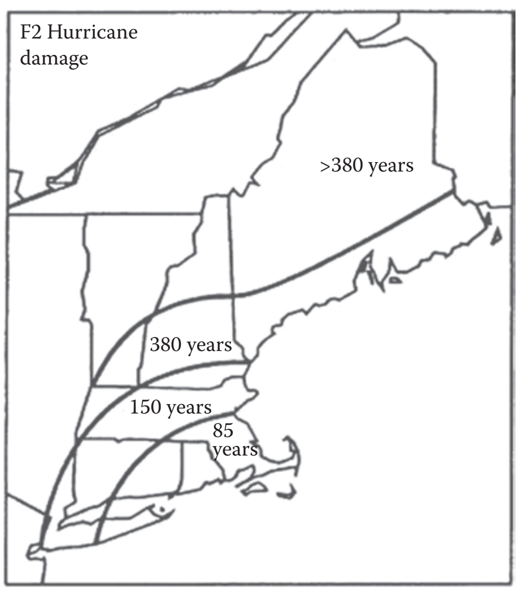

FIGURE 7.4 Zones of hurricane frequency in New England showing mean recurrence intervals between consecutive hurricanes of sufficient force to blow down forests. (From Boose, E.R., K.E. Chamberlin, and D.R. Foster. 2001. *Ecological Monograph* 71:27–48. With permission of the Ecological Society of America.)

DISTURBANCE FREQUENCY, SIZE, SEVERITY RELATIONSHIPS

Imagine a forest of 1000 ha in size and uniformly old and unmanaged. Then consider the frequency with which tree-fall gaps occur in that forest. Big trees die and fall, creating an opening in the forest probably many times each year. Disturbance sizes are small, severity is low (little biomass removed) and frequency is high. Now consider the frequency with which a stand-replacement fire or hurricane might occur in that forest. On average perhaps once every 100 years? 200 years? Longer? When it does occur it may affect the entire 1000 ha and be quite intense. Although a generalization, frequent small-scale disturbances are often of low severity. In general, large severe disturbances are infrequent. In situations where we may prevent a disturbance from occurring as frequently as it might ordinarily occur, then the severity can be unusually high when it does occur. For instance, by controlling and preventing fire in many western U.S. forests, trees become more susceptible to insect defoliation and the accumulation of large fuels. So when a fire does occur, then it is unusually large and intense. Indeed, balancing disturbance frequency, severity, and size through natural disturbances and silviculture is a key to providing habitat elements, water, timber, and other ecosystem services from these forests.

STAND DYNAMICS

A fire burns a forest, a hurricane blows over half of the trees in a stand, or an ice storm causes damage to a northern hardwood stand, reducing timber quality and value. How do stands respond to these disturbances? Early ecological perceptions of vegetation change following a disturbance provided the basis for the concept of ecological succession (Palmer et al. 1997), which presumed that there is a somewhat predictable change in the structure and composition of a stand following a stand-replacement disturbance. Although subsequent ecological research confirms that the recovery process in forests is not so deterministic (Palmer et al. 1997), simple concepts of ecological succession are a place to start to understand how forests change following a disturbance. Forest development is a continuum that we often break into arbitrary classes to help us simplify the complexity of forest change. After disturbances, forests develop through four general physiognomic stages: “stand initiation,” “stem exclusion,” “understory reinitiation,” and “old growth” (Oliver 1981, Oliver and Larson 1990) (Figure 7.5). Disturbance severity and frequency determine which species will dominate the forest during each of these stages. It is important to keep in mind, however, that these stages are merely convenient ways of understanding a sere, which is a set of forest communities that develop during stand regrowth following a disturbance.

Stand Initiation

A disturbance usually kills or damages trees and consequently creates both growing space for the remaining trees or sites for germination and growth of new trees. Forests often contain large amounts of dead wood and live plants following most natural disturbances, and the disturbance often creates a suitable site for regeneration by seedlings (regeneration from seed) or sprouts (vegetative regeneration). This stage of stand development is called stand initiation. In many forests, regeneration occurs naturally through *advance regeneration* present in the stand prior to the disturbance or natural regeneration that occurs from seedling establishment or sprouting following the disturbance. Forest managers may choose to control the species and number of regenerating trees by artificial regeneration, which involves planting seedlings at a particular spacing. The early growth and survival of regeneration can be controlled, ensuring that the future stand will be composed of the trees species and trees sizes desired by the land manager. Plantations of black spruce in Canada, Douglas-fir in the Pacific Northwest, and loblolly pine in the Gulf Coast are examples of artificial stand initiation. We will discuss this process in more detail in Chapter 8. In many forests, planting trees is unnecessary because it is expensive and there is an abundant natural regeneration. Following an intense

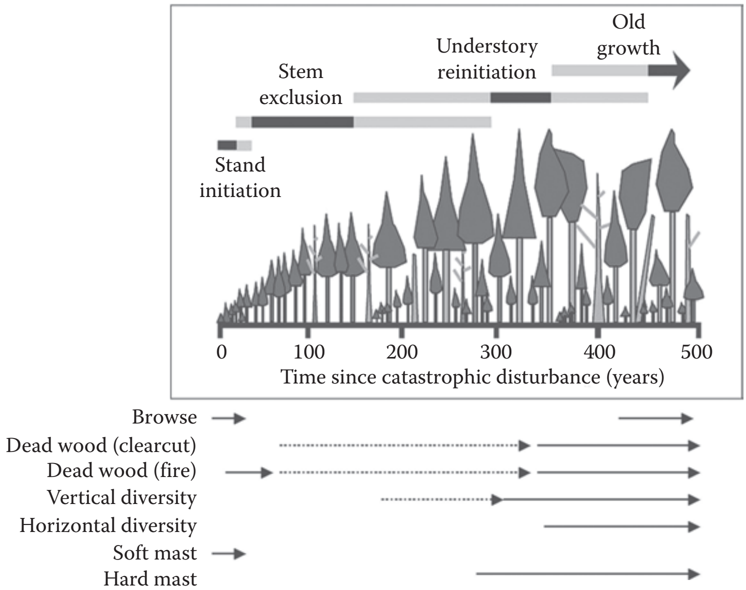

FIGURE 7.5 A conceptual timeline portraying developmental stages for temperate rain forests of southeast Alaska. Shaded bars represent temporal overlap among developmental stages. (From Norwacki, G.J., and M.G. Kramer. 1998. *The Effects of Wind Disturbance on Temperate Rain Forest Structure and Dynamics of Southeast Alaska*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-421.)

disturbance in central and northern hardwood forests of the eastern United States, it is common to expect 8000–100,000 woody stems/ha (including trees and shrubs) within a few years following a disturbance (Annand and Thompson 1997, Schuler and Robison 2002). Unoccupied growing space for plants following a disturbance will become occupied if water, light, and nutrients are sufficient. From the standpoint of providing habitat elements, this early stage of stand development tends to be a grazing-based system, with much of the net primary production available to herbivores through forage. Foraging also occurs below ground with species such as pocket gophers feeding on root systems of the newly established plants. However, if the disturbance killed but did not remove trees from the previous stand as might occur in a low severity fire or a wind storm, then much of the energy available in the dead wood is also available to other organisms through wood decomposition.

Trees remaining after a disturbance, or on the edges of disturbances, if not too severely damaged by the disturbance are suddenly free from competition by other trees and can respond by expanding their crowns and/or root systems and growing rapidly (Chen et al. 1992). In low severity disturbances, which tend to be more frequent, this "thinning effect" in forests allows remaining trees to continue to grow, rather than succumb to competition. In so doing, large trees develop in these stands and when they die, larger snags and logs are produced than would likely be produced at the same time in the absence of disturbance.

As plants begin to regenerate a site following a disturbance, eventually all the growing space in the site will be occupied. Foresters often use *basal area* as an index to the area of the stand occupied by trees. Basal area is the cross-sectional area of all trees on an acre or hectare. So imagine a hectare of forest (an area of 10,000 m^2 or a square 100 m on each side; 2.47 acres). If you cut all of the woody stems off at 1.4 m (4.5 ft) above ground and measured the area of all the cut surfaces and summed these areas, then you would have an estimate of basal area in hectare. The maximum basal area that a site can support will depend on moisture, growing season length, tree species, and nutrients, among other things. Through stand development, basal area will increase rapidly at first and then slow and finally reach a point where it fluctuates around a certain upper level. Two very similar sites can support the same basal area but have very different tree densities. One site can have high basal area in a few large trees and the other site can have the same basal area represented in many small trees. Once *stocking*, or the degree to which a site is occupied by trees of various sizes, reaches a certain combination of tree density and basal area, then competition between the trees begins to greatly influence the structure and dynamics of the stand.

Stem Exclusion

Once all of the growing space is occupied and plants begin to compete for light, soil moisture, or nutrients, then competition for those sparse resources begins to occur. Due to species characteristics such as growth rates, shade tolerance, and moisture tolerance, some plants are better able to use the resources of the environment than others. The plants that are not as fit in this competitive environment begin to grow more slowly and eventually die. The trees that remain during this process begin to stratify into crown classes that represent the various abilities of the trees in the stand to cope with competition (Figure 7.6). *Dominant* trees are the most fit in this environment and they form the uppermost canopy. They typically receive sunlight from above and the sides and have deep crowns and hence high leaf area (the area on the ground covered by leaves in the trees overhead) so they can photosynthesize well and grow rapidly. *Codominant* trees receive sunlight from above and so grow well and form most of the primary canopy layer. Codominant trees may have somewhat smaller crowns and may not grow as fast as the dominant trees, but they still contribute significantly to stand structure. *Intermediate* trees have smaller crowns, grow more slowly, and may contribute little to the upper canopy. *Suppressed* trees grow very slowly and have small crowns; they often die due to lack of light or moisture. *Wolf trees* are those legacy trees from the previous stand that may have very deep crowns because they were open-grown during the stand initiation phase.

The stand eventually develops a uniform canopy, further limiting the light available to plants beneath the canopy. During this stage, we see vertical structure become simplified into one dominant canopy layer and forage resources decline markedly. In hardwood forests of the eastern United States, it is common to see 90%–99% of woody stems die during these early stages of stand development. Although there can be instances where insect herbivory in these dense stands can be high (e.g., spruce budworm irruptions), most of the energy available for animals is through decomposition and the forest is now a detrital-based system. However, because most of the trees that die are smaller than the dominant and codominant trees, pieces of dead wood produced during this phase are small and decay rapidly.

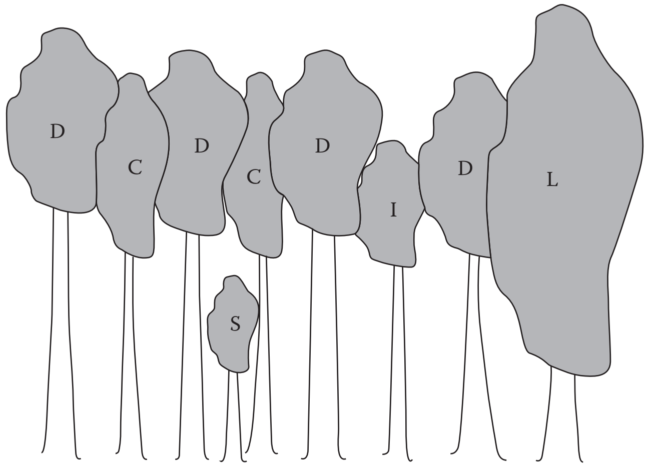

FIGURE 7.6 Crown class differentiation during development of an even-aged stand.

Understory Reinitiation

As the trees in a stand begin to continue to differentiate into crown classes, and some of the larger trees begin to die, the openings created by the dead trees create gaps in the canopy, allowing sunlight to enter to the forest floor. As sunlight enters, shade-tolerant understory plants can begin to establish and we begin to see a somewhat more complex forest structure. In many cases, seedlings will become established on the forest floor without a noticeable gap and survive until a gap is formed nearby, giving them a boost of growth. The gap may close and the shade-tolerant tree may have to wait for one or more additional gap events to reach the canopy. Less commonly, establishment may come from seeding into a tree-fall gap from the surrounding trees or may be the result of seeds stored in the soil in a *seedbank* waiting for the correct light and moisture conditions to allow germination. Forage resources begin to return to the stand, though they are often low in quantity and quality. Any dead wood remaining from the disturbance that created this new stand has largely decayed by this time. Consequently, dead wood abundance is quite low at this stage, though a few large snags and logs are starting to form in the stand both through competition and from insects, disease, wind, and other small-scale disturbances.

Old-Growth

As regeneration in the tree gaps grows and eventually replaces the dominant and codominant trees that have died in the stand, a new stand structure develops. Old growth or a *shifting gap phase* allows a structurally more complex stand to grow. This structure is created as trees age and die or are killed by diseases, insects, and other factors that lead to individual tree death in the stand, allowing regeneration to form in gaps throughout the stand. The stands begin to accumulate large pieces of dead wood, have trees of a variety of sizes and species, are vertically more complex, and increase in horizontal patchiness. Although the primary energy pathway in these stands is still through decomposition, small patches of forage develop. These forage patches in old forests can be quite variable in quality depending on the species and growth rates of the plants that fill the gaps. Frequent low-intensity fires, for instance, can create "gapiness" in forests and maintain a high level of forage availability (Figure 7.7). In some situations, tree seedlings

FIGURE 7.7 Repeated low severity fires in some forests can increase forest gapiness, renewing forage availability for species such as this white-tailed deer.

growing in partial shade have higher levels of defensive chemicals in their foliage than seedlings in direct sunlight (Tucker et al. 1976). Happe et al. (1990) found higher levels of defensive compounds in plants in clearcuts than in old-growth forests however. Clearly, these plant defensive strategies vary among forest types.

SUCCESSION AS A CONTINUUM OF HABITAT ELEMENTS

Stages are convenient ways of understanding stand dynamics. These stages are idealized and may occur at various spatial scales within and among stands. A continuous process of disturbance and regrowth occurs at various times and over various areas so a continuum is the appropriate context in which to place these stages. Habitat elements and other aspects of forest structure and composition also change over this continuum (Figure 7.5). Following a stand replacement disturbance such as a fire or hurricane, forage and soft mast production are typically highest in the earliest stages of development and decline markedly as crowns close. Once gaps begin to form as large trees die, then a modest recovery of these elements can be expected. Large pieces of dead wood also are most abundant following a disturbance, but they decay and are absent in the middle stages of succession. Abundant dead wood is added once again as large trees begin to die late in stand development. Hard mast production starts to occur once mast-bearing tree species reach maturity and develop large crowns during mid- to late stages of development. Spies (1998) provided two generalized curves to understand some of these changes in forest structure and composition over time following a stand replacement disturbance in Douglas-fir forests (Figure 7.8). Similar trends can be expected in other forest types, although the time scale would likely be different for other forests. Elements of forest structure that follow curve 1 (U-shaped) include the amount of dead wood, horizontal complexity, plant and animal species diversity, and susceptibility to fire. For instance, after a disturbance, we may expect to find large amounts of dead wood, diverse plant communities, and edges between disturbed and undisturbed sites. As tree crowns close and shade out many plant species and as dead wood decomposes, we reach a low point in both factors. Then as trees age and die and gaps form, we see greater diversity and more dead wood in the stand. Factors that follow trend line 2 (sigmoidal) include the diversity of tree sizes, vertical complexity, average tree size, incidence of tree damage and hollow trees, leaf litter depth, surface area of bark per tree, and live plant biomass. All of these factors increase over time as the stand moves from stand reinitation to old-growth. In some forest types, curve 2 can also represent changes in dominance by shade-tolerant species.

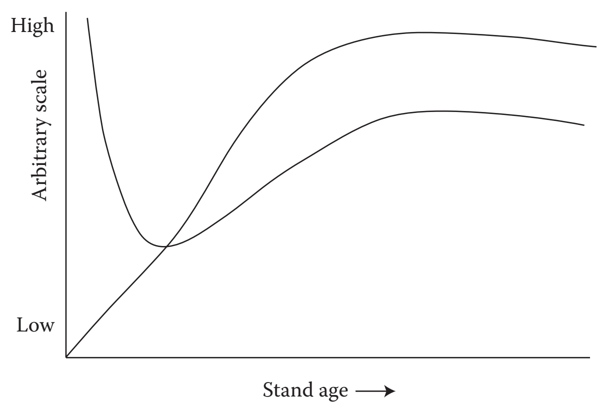

FIGURE 7.8 Generalized patterns of habitat element change over time in Douglas-fir forests. The time scale is different in other forest types. (From Spies T.A.1998. *Northwest Science* 72:34–39.)

Successional Pathways

The discussion of stand dynamics so far has assumed that there is a reasonably predictable change in structure and composition over time following a disturbance. This is consistent with the view of succession proposed by Clements (1916). But succession is not quite so deterministic. Consider the theoretical changes in biomass following a disturbance that leaves soil bare (Figure 7.9). As plants occupy the site and grow, the plant community increases in biomass. Simultaneously, the plant community composition changes over time from one dominated by shade-intolerant species to include more shade-tolerant species. An intense disturbance may set succession back to a point where there is no living biomass, but roots and seeds persist in the soil (e.g., an intense fire in a hardwood forest). If there are existing seedlings, a seedbank, or a source for sprouts, then sprouts and seedlings may allow the site to recover with dominance by more shade-tolerant species than would have been there if these features were removed in a disturbance (a volcano or landslide). Disturbances that remove less biomass also recover but tend to be dominated by more shade-tolerant species. The availability of seed species in the soil seedbank, changing climate, soil pH, nutrient availability, and other factors continue to shift the final condition represented following full recovery after a disturbance (Figure 7.9). Variability in vegetation structure and composition following disturbances is to be expected due to the inherent variability in the severity, frequency, and size of disturbances affecting a forest as well as continual changes in climate, soils, and hydrology (Donato et al. 2012). Consequently, we often see a set of successional pathways that vegetation on a site could follow over time as disturbances occur and vegetation responds (Cattellino et al. 1979, Lebrija-Trejos et al. 2010).

In Figure 7.10, a site in which the potential vegetation is eastern hemlock–American beech may see a number of different vegetation states resulting from disturbance and regrowth. Following an intense hurricane and a subsequent fire or other disturbance that leaves bare soil, paper and black birch usually are the first tree species to dominate the site. Over time in the absence of a hemlock seed source, the site may move to a beech–birch stand. Should hemlock seed be available then a beech–hemlock stand may develop. From this diagram it should be clear that the same site can see several relatively long-lasting forest conditions that develop following disturbances and that these conditions each provide a different suite of habitat elements.

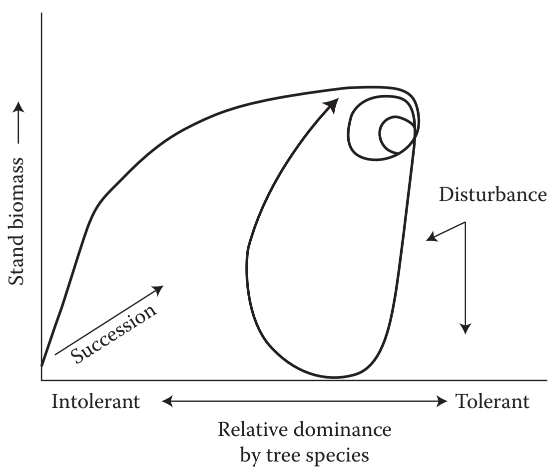

FIGURE 7.9 Theoretical changes in forest states during succession and disturbances of varying frequencies and intensities. (From Spies, T.A. 1997. *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*. Pages 11–20. Island Press, Washington, DC.)

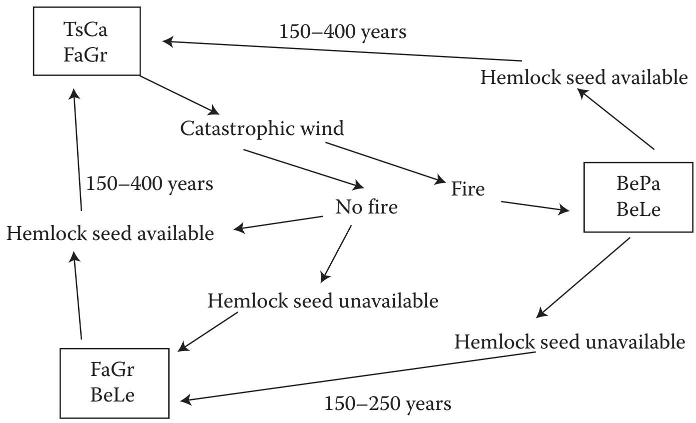

FIGURE 7.10 Successional pathways for a southern New England Forest. TsCa = eastern hemlock, FaGr = American beech, BeLe = black birch, BePa = paper birch. (Courtesy of Anthony Damato 2006.)

Management Implications from Disturbances

Management activities do not replace the natural disturbances but they can be complementary to them. Knowledge of the frequency, severity, and size of natural disturbances, and the various successional pathways that emerge from them can offer clues to management strategies that might be effective in achieving a variety of goals (Long 2009). And a departure from natural disturbances can move landscapes into new conditions that no longer reflect the conditions under which species have evolved and persisted (Cyr et al. 2009). Disturbances influence forest structure and composition, as do the myriad of physical factors (Figure 7.11). Management actions driven by the goals of society, be they economic, cultural, or spiritual, interface with the dynamic processes of disturbance and climate change (Vierikko et al. 2008). When considering the diverse suite of habitat elements that might be needed to maintain biodiversity within a forested region, it is often useful to use variability in forest structure and composition to our advantage whenever possible. Forest managers producing wood products to meet industry and societal needs want to minimize uncertainty in the production process. But from the standpoint of providing a suite of habitat elements, uncertainty and the variability that it produces is something that should be embraced and worked with and not avoided. No single stand management

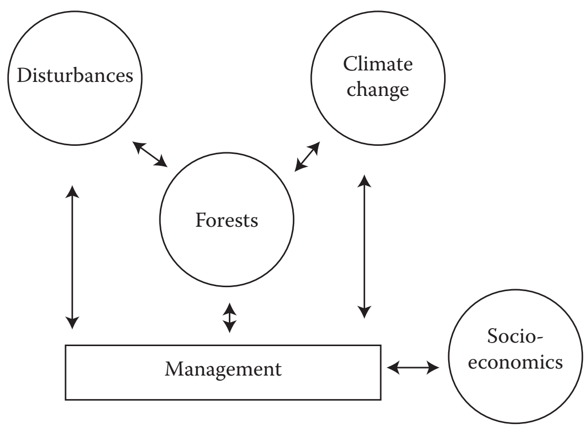

FIGURE 7.11 Interactions among forest disturbance, climate change, and management. (Dale, V.H. et al., Climate change and forest disturbances, *BioScience,* 2001, by permission of Oxford University Press.)

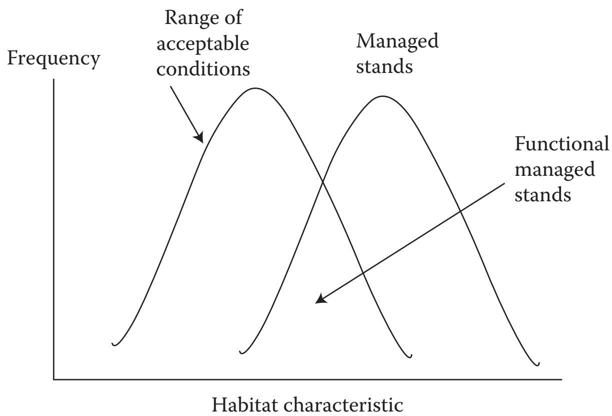

FIGURE 7.12 Hypothetical range of conditions in a habitat element that might be seen during stand development following a natural disturbance and during stand development using silvicultural practices. (From McComb, W.C. 2001. *Wildlife Habitat Relationships in Oregon and Washington*. OSU Press, Corvallis, OR.)

system will precisely match the variability inherent in natural forests that resulted from a variety of disturbance regimes. The compatibility of management and habitat goals is scale dependent both in space and time, and management often occurs over a much narrower range of space and time than scales associated with natural disturbances. Some of the variation can be incorporated into the managed forest landscapes of the region by using a variety of silvicultural systems and forest management strategies. The choice of these systems will depend on the biological, social, and economic objectives for the stand and the landscape, and they will imitate natural disturbances to varying degrees (Vierikko et al. 2008; Figure 7.12). Indeed, the basis for development of existing silvicultural systems for timber objectives was that these systems reflect the regeneration and growth strategies of the commercially important tree species in a region. Intensive timber management as currently practiced leaves less dead wood and noncommercial plant species than natural disturbances (Hansen et al. 1991) so it may not imitate natural disturbances for other forest resources as well as it does for timber. The management strategies that include goals for habitat elements for certain species or for biodiversity conservation goals require consideration of more factors than are necessary for production of commodities, but it is commodity production that can pay for the management activities needed to achieve certain habitat goals. The two goals should be complementary. In the following chapters, we will explore methods of stand and forest management than can achieve both commodity and habitat goals.

SUMMARY

On the template of the physical and cultural landscape from which vegetation arises, vegetation is further altered by disturbances. Disturbance severity, size, and frequency interact to influence the sizes, amounts, and distribution of habitat elements such as vertical complexity, forage, dead wood, horizontal complexity, and plant species composition. Vegetation regrowth following disturbance in the very simplest sense follows several stages of stand development following a stand replacement disturbance: stand initiation, stem exclusion, understory reinitiation, and shifting gap phase. These conditions occur in various scales of time and space and represent somewhat arbitrary points on the continuum of successional change. Indeed a variety of successional pathways can be seen following a disturbance depending on the severity and frequency of disturbance and the regrowth potential of the vegetation. Seed and sprout availability, shade or moisture tolerance, and time interact to determine what plant community is likely to develop and be maintained on a certain site following disturbances of varying intensities and frequencies. This knowledge of disturbance and succession can be used to craft management strategies to achieve multiple goals.

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