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4 Dynamic forest mosaics

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A stand of forest trees is quite tangible to us; however, many of the processes that shape the biological diversity of that stand are invisible because they relate to events that have happened during some distant past or because they occur in the landscape beyond the area of forest we can see. Some scientists have called this phenomena 'the invisible present' and the 'invisible place' (Magnuson 1990, Swanson and Sparks 1990) meaning that the wrong temporal and spatial perspectives can produce erroneous conclusions. Humans and their management systems have typically perceived ecosystems at short distances and over short time frames. However, processes such as dispersal, disturbance, and succession, which control the state and dynamics of ecosystems and biological diversity, operate across a much wider range of spatial and temporal scales. This chapter is about seeing these large-scale temporal and spatial phenomena and understanding how they relate to the conservation of biological diversity.

Understanding the dynamics and heterogeneity of natural forest landscapes has become very important as management objectives for forests increasingly include the maintenance of biological diversity. Using natural or semi-natural ecosystems as a template for management is quite challenging, requiring understanding not only the patterns of forest change, but also the processes that underlie them. Recent advances in theory and empirical studies of vegetation ecology and landscape ecology indicate that if goals of maintaining biological diversity across landscapes are to be achieved in the long run, then management and conservation need to broaden their focus to include variability, scale, pattern, disturbance, and biotic processes. This is a daunting task that requires both a conceptual framework to organize and simplify ecosystem complexity and knowledge of the details of particular systems.

Our overall objective in this chapter is to synthesize some of the more recent findings about the temporal and spatial variability in forests and examine their implications for maintaining biological diversity. Our specific objectives are: (a) to review recent advances in the concepts and

understanding of vegetation dynamics and spatial patterns at stand and landscape scales; (b) identify the major physical and biotic processes that are responsible for vegetation dynamics and pattern; (c) briefly review some of the major ecological consequences of forest dynamics and heterogeneity; (d) review ways in which temporal and spatial ecosystem complexity can be simplified for management and conservation purposes; and (e) examine three case studies that illustrate different natural systems and different management problems.

Forest dynamics: a complex of causes and patterns across time and space

SPATIAL AND TEMPORAL SCALES OF CHANGE

Forest structure, composition, and ecological processes change over a vast range of spatial and temporal scales. For example, at fine spatial scales sunflecks beneath a forest canopy create variation in carbon fixation and microclimate, at the scale of leaves or small gaps, which changes in a matter of seconds or minutes. At the very coarse scales, forests have changed over thousands or millions of years over entire continents as a result of climate change, evolution, and continental drift. A positive relationship exists between the spatial scale or extent of physical and biological processes and the temporal variability of those processes – small events and processes occur more frequently than large ones (Figure 4.1) (Delcourt and Delcourt 1987, Johnson 1996). Biotic processes such as establishment and competition occur frequently at microscales, whereas succession and dispersal occur over larger spatial scales. Although relatively infrequent, long-distance dispersal events can have important consequences to population viability and community dynamics. Disturbances occur across a wide range of microscales to mesoscales and frequently set the spatial and temporal context for biotic processes which are nested within the disturbances.

Forest management activities and policies operate within a limited range of mesoscales (Figure 4.1). Human activities typically range from the scale of individual trees to entire landscapes or regions and the time frames range from years to decades to centuries. The temporal scale is frequently set by political and planning cycles (2–10 years), economic timber rotations (30–80 years), and span of professional careers (40–50 years), and not by natural disturbances intervals (1–1000 years) and life spans of
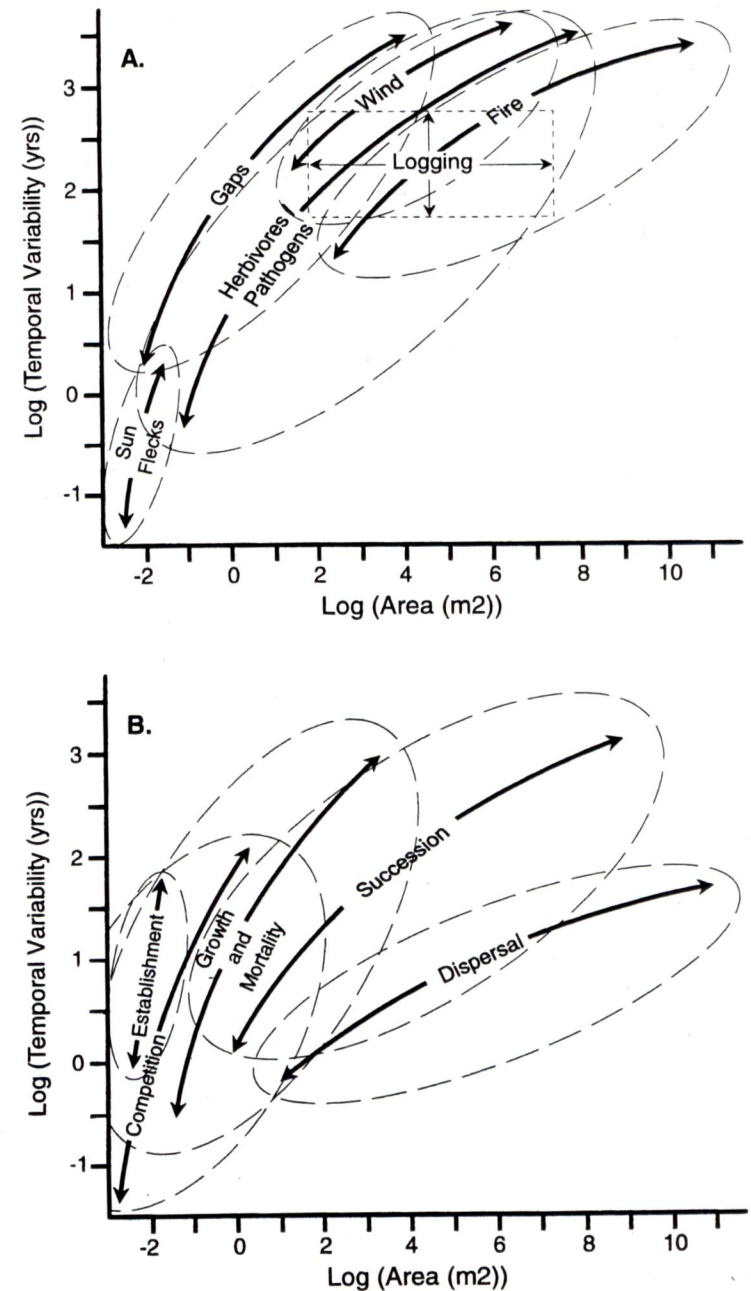

Fig. 4.1. Relation between spatial scale and temporal variability for micro to meso scale forest disturbance (A) and biotic development (B).

dominant tree species (100 to 1000 years). Similarly, economic feasibility typically determines the size of human forest disturbances, which can range from single trees in selection systems to hundreds or thousands of hectares for large clearcutting operations. In general, forest management disturbance events do not occur at large spatial scales and low frequencies relative to the domain of natural disturbances (Figure 4.1). While individual forest harvesting events occur over relatively small areas they may, however, accumulate over large areas defined by ownership boundaries and large planning and jurisdictional units.

DRIVERS OF FOREST DYNAMICS

The condition of the vegetation in a stand, landscape, or region is a product of the interplay of forces of disturbance and biotic development on a stage set by patterns and dynamics of climate, soil, and landforms. Understanding and managing forest dynamics is a major challenge that requires knowledge of complex interactions among these process at multiple scales.

Disturbance

Disturbances are a major driver of vegetation change and not necessarily rare events that are 'outside' the system (Pickett and White 1985, Pickett et al. 1989). The sudden destruction or death of plants and/or animals can result in a cascade of biotic and physical changes in ecosystems that can play out over centuries and large landscapes. Episodic disturbances appear to control tree regeneration in most forest types (Crawley 1990). However, definitions of disturbance vary and these differences can lead to confusion with regard to understanding and managing vegetation dynamics. For example, disturbance can be defined in terms of changes in physical environment, effects on biota, mechanisms or type, and uniqueness or rarity in system history. Some authors have described disturbance as changes that are not normal or are outside of some natural range of variation (Rykiel 1985). While this concept may be useful for some purposes it creates a problem by requiring detailed knowledge of history of disturbances which is lacking for most ecosystems or landscapes. We use the definition of Pickett and White (1985, p. 7) who define disturbance as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.' This broad definition includes both destructive events and severe or prolonged environmental

fluctuations that result in disruptions to ecosystems and it avoids interpretation of whether the disturbance is 'endogenous' or 'exogenous' or within the range of natural variability. Such interpretations can still be made and can still be useful in the context of a particular ecosystem or species. Disturbance definitions that emphasize physical changes in ecosystem components such as light, moisture, nutrients, substrates, and biotic effects on community and population structure, can be readily linked to the biotic processes that drive change following the disturbance. Of course, this definitional approach still requires subjective decisions about the degree of disruption that constitutes 'disturbance'.

Physical attributes of disturbances include type, magnitude, and intensity, timing and spatial distribution (Heinselman 1981, Pickett and White 1985). Because of the high variability of disturbances in space and time a single disturbance event at a specific site has limited value as a predictor of future disturbances and as a model for conservation. Consequently, disturbances are described in terms of a disturbance regime which is the aggregate behavior of disturbance over long time frames and large areas. Aggregating disturbance behavior over large scales reduces variability in disturbance, making it more feasible to compare and predict ecosystem dynamics. Disturbance regimes can explain differences in biological diversity among landscapes and regions. For example, Bunnell (1995) found that regions in western Canada with higher natural fire frequencies have a larger proportion of species that breed in early successional conditions than regions with lower fire frequencies.

Disturbance type is one of the most important characteristics of a disturbance regime. The effects of disturbance from fire, wind, logging, and landslides can be quite different. For example, fire can kill all vegetation over very large areas but the effects of wind and pathogens can be very specific to particular canopy layers or species in the forest (White 1979). The most severe disturbances are those such as landslides and agriculture that destroy vegetation and alter soil and landform characteristics. Since forests are highly layered ecosystems, disturbances can affect one layer and leave other layers relatively intact. For example, surface fires may kill only the shrub and herb layer but not the tree layer, whereas crown fires will kill all the trees in a stand but may allow root systems of shrubs and herbs to survive, enabling these species to dominate in the early stages of vegetative regrowth (Stickney 1986). Wind damage that uproots trees and churns the mineral soil has a different effect on ecosystems than wind breakage which only disturbs the above-ground portions of ecosystems. In some cases different types of disturbance can have similar effects. For

example, dense understories of shade-tolerant conifers on dry sites in the western United States can be selectively killed either by low intensity fire or by insects and disease (Campbell and Liegel 1996). In many cases, interactions occur between disturbances (Veblen *et al.* 1994). For example, following fire, forests in the Pacific Northwest are frequently susceptible to bark beetle outbreaks that result from the accumulation of large amounts of dead trees (Agee 1993) and landslides that result from loss of root strength on steep slopes (Swanson 1981). Because variability within types of disturbances is high the evaluation and prediction of disturbance effects is more dependent on the actual characteristics of the disturbance (e.g., frequency and severity) than the general classification of its type (e.g., fire, wind, human vs. natural) (Bazzaz 1983).

The relative importance of different disturbance regimes varies across biomes and regions. Fire has been a major large-scale disturbance in almost every major biome including tropical forests (Spurr and Barnes 1980, White 1979, Heinselman 1981, Attiwill 1994b) and has affected the evolution of many life history characteristics of the component species. Fire occurrence within biomes is typically quite variable – most frequent in flammable vegetation types and dry regions, landscapes, and topographic positions and least frequent or essentially absent where vegetation is resistant to fire and conditions are moist (Zackrisson 1977, Mueller-Dombois 1981, Whitney 1994, Syrjänen *et al.* 1994). In regions such as the northeastern United States, Pacific coastal forests of Canada and southeastern Alaska, the British Isles, boreal spruce forests of northeastern Europe, and tropical rainforests, wind is the a dominant disturbance (Webb 1958, Bormann and Likens 1979, Ruth and Harris 1979, Peterkin 1996, Syrjänen *et al.* 1994, Attiwill 1994a).

The magnitude of the disturbance is usually expressed as either intensity, or physical force, or as severity, the amount of live organic matter killed or removed. Severity is more easily related to biological responses than the force (amount of energy per unit area per unit time) of the disturbance event which may be hard to measure and relate to physical characteristics. Fire severity can range from little or no death of forest trees to almost complete destruction of all above and below-ground vegetative parts (Agee 1993). Hurricane disturbances vary in severity according to elevation, topography, and forest composition. For example, the highest severity windthrow from Hurricane Hugo in Puerto Rico occurred at lower elevations on northwest and north aspects in tall broadleaf forest types (Foster and Boose 1995). While attention is often focused on the death and destruction caused by disturbances, the recovery of ecosystems following

disturbance is strongly controlled by the organisms and structures that survive disturbances. This 'legacy' of disturbance can determine the speed and direction of vegetation succession following disturbance. The effects of biological legacies have been documented in many ecosystems (Perry 1994). The eruption of Mt St Helens and destruction of thousands of hectares of forest vegetation provided many good examples of how legacies of surviving plants and structures formed the basis of recovery patterns in this severe disturbance (Franklin *et al.* 1985).

The timing of disturbances can have profound effects on ecosystem composition and structure. Timing can be viewed in three primary ways: seasonality (time during the year) duration, and frequency which is usually expressed as return interval, or rotation time (time required to disturb an area equivalent to the area of study). The timing of disturbance during the year is important in ecosystem response. For example, flooding during a dormant season will have very different effects on trees than floods during the growing season (Oliver and Larson 1990), and fire during moist springs may damage developing plant parts, such as buds and fine roots, more than in the fall (Agee 1993). Many disturbances such as fire and windthrow are short-lived events; however, others such as drought, flooding, and insect outbreaks can persists for months or years, and the severity of their effects, of course, increases with duration. Prolonged drought can lower chemical defenses in tree foliage leading to widespread insect outbreaks (Perry 1994). Dry years and multi-year droughts related to global weather cycles may account for most of the large fires and periods of frequent fires in boreal and temperate forest ecosystems (Bonan and Shugart 1989, Swetnam and Betancourt 1990, Swetnam 1993). The disturbance characteristic with the most profound influence on vegetation may be frequency. As intervals between fires, wind, or defoliation decrease, species composition and life history characteristics can shift toward dominance by shade-intolerant, rapidly colonizing species with early ages of sexual maturity (Agee 1993), or species with abilities to sprout and recover following destruction of above-ground parts. Where high winds are frequent, such as at high elevations and coastal areas, wind can kill or damage some species, shifting the competitive balance toward lower-stature, wind-resistant vegetation (Oliver and Larson 1990). High frequencies of fire can shift vegetation from trees to shrubs or grasses in many areas of the world, including Australia, Africa and North America (Pyne 1992, Belsky 1995, Whitney 1994).

The spatial distribution, extent, and shape of disturbances is also an important feature of disturbance regimes. Disturbances often occur more

frequently in some parts of landscapes than others: e.g., floods in riparian areas and fires on dry sites and exposed topographic positions (Swanson *et al.* 1988). In Labrador, for example, fire and topography jointly influenced patterns of forest vegetation with nearly all patches of birch (*Betula*) forest occurring on steep slopes or ridges with high moisture (Foster and King 1986). Lightning would ignite fires on ridge tops covered by spruce–fir (*Picea–Abies*) forest, sweep down the ridges, and stop at existing birch stands or wetter areas in the valley bottoms. The newly burned areas along the slopes would then provide opportunities for birch to colonize. However, when fire intensity becomes extreme, topography may not influence fire distribution (Turner and Romme 1994). Wind and fire disturbances can have characteristic patch size distributions depending on the landscape and disturbance regime (Figure 4.1) (Forman 1995). Disturbances resulting from lower intensity wind events create gaps in the range of 50 to 500 m² for tropical forests, and fires in boreal ecosystems are typically large, ranging from a few thousand hectares to over 200 000 ha in Alaska (Dyrness *et al.* 1986, Attiwill 1994a, Essen *et al.* 1997). The ecological effects of disturbance size are largely a function of biological and physical edge effects between disturbed patches and the surrounding undisturbed forest. Large disturbance patches have lower edge to interior area ratios and will have lower densities of seed rain from the surrounding forest (Oliver and Larson 1990) and more extremes of microclimate (Geiger 1965). Absolute disturbance patch size may be less important to microclimate than the ratio of the diameter of the disturbance patch to the height of the surrounding vegetation (Geiger 1965).

Natural vs. anthropogenic disturbances

The direct and indirect effects of human disturbances on biological diversity and ecosystems are subjects of considerable debate and interest. It is no wonder that there is concern over the role of human disturbance, given the intensity and extent of direct human disturbances including: clearcutting; road building; flood control; drainage of wetlands; fire control; hunting; thinning and salvage logging; recreation; forest clearing for agriculture and development; application of chemical for fertilizer and pest and pathogen control; and indirect effects of non-forest activities on climate and atmosphere. While much of the concern derives from directly observed effects of specific forest management activities on biological diversity (FEMAT 1993) additional worries come from the more general issue of whether humans are part of nature or not. This is ultimately a philosophical debate (Hunter 1996) for several reasons including the evidence

that humans are part of the same evolutionary process that produced the 'nature' we value. Furthermore, it is difficult to find a forest or landscape where humans have not had some direct or indirect influence and the concept of 'natural' may be more realistically thought of as a continuum of 'naturalness' (Peterken 1996). We try to avoid this debate by focusing not on the source of the disturbance, human or nature, but on the characteristics of the disturbance regime as described above. Bazzaz (1983) argues that 'the distinctions between natural and man-made disturbances are less important and what matters is not what caused the disturbance but what are the nature and consequences of disturbance and how do species and populations respond to them over ecological and evolutionary times.'

Using a framework of disturbance ecology, it is possible to evaluate how well disturbances that derive from direct and indirect human sources match disturbance regimes of the past which have shaped many ecosystems and to which many species are adapted. In many cases anthropogenic disturbances do not match well with natural disturbance regimes, especially in terms of frequency, size (Figure 4.1) and severity. Given our increasing awareness of the important role of disturbance in ecosystems it is possible to design management plans on the basis of natural disturbance regimes (Spies *et al.* 1991, Hansen *et al.* 1991, McComb *et al.* 1993, Attiwill 1994a). This approach has limitations, however, because we lack detailed knowledge of past disturbance regimes and ecological effects of current ones. This lack of understanding should be a caution against applying an ecological engineering approach everywhere in the landscape. However, in landscapes where human activity is a reality and threats to biological diversity are high, using natural disturbance regimes as a model for management may be the best way of maintaining biodiversity while meeting other human needs (Attiwill 1994a).

Biotic processes

Just as landscape-scale phenomena may not be apparent at the stand scale, the fine-scale biotic processes that gradually change vegetation following disturbance may also be invisible at the landscape scale. Early research on forest succession focused on endpoints, such as climax, and classifications of stages or pathways; recent research has emphasized successional mechanisms and the biotic drivers of successional change. This has been valuable in that it has helped to demystify the process of succession, taking it out of the realm of some sort of organismic community into the realm of population dynamics and interactions of individual species.

Many models of the mechanisms or causes of succession have been put

forth (Glenn-Lewin et al. 1992). We will briefly mention a few here. In the classical model of Clements (1916) succession was a temporal sequence of plant communities, each of which changed the local environment and facilitated invasion by the next community. The processes that drove this model included disturbance, migration, ecesis or establishment, biotic reaction or environmental change, and competition. The endpoint of these processes was a stable climax vegetation that was the same for nearly all sites in a climatic region. Ecologists challenged this classical model almost from the beginning with alternative ideas including: (a) plants respond individualistically rather than as a community (Gleason 1917); (b) the sequence of succession is not fixed or predictable but was often determined by the first species ('intial floristics') to occupy a site following disturbance (Egler 1954); and (c) several different alternative mechanisms of vegetation change occur including facilitation (Clement's biotic reaction), tolerance (new species take over a site by tolerating the environment created by other species and growing through them) and inhibition (new species take over a site only after the inhibition of existing species has been broken by small canopy gap disturbances) (Connell and Slayter 1977). 'Vital attributes' or differences in life history traits among species, such as growth rates, longevity, age at reproduction, and response to disturbance have also proved valuable in explaining the process of successional change (Noble and Slayter 1980). The combination of life history characteristics and disturbance leads to successions that follow multiple pathways. Pickett et al. (1987) have proposed a hierarchical framework for vegetation dynamics that includes disturbance and biotic processes (Figure 4.2). Particularly important biotic processes are colonization, competition, and growth rate and longevity/mortality. We describe these processes in more detail below.

The most limiting stage of plant succession occurs at the beginning. Succession begins with colonization, which consists of dispersal and establishment, and is a function of seed source patterns, site availability and environmental patterns. For colonization to occur, seeds or propagules (including vegetative parts) must be present on a site (stored in soil or canopy) or disperse in from source areas. Succession may be most closely linked to environmental patterns during the early stages when plants are small and highly sensitive to the environment. The spatial and temporal variation of forest composition is strongly linked to dispersal and establishment in many ecosystems (Hobbs 1994, Masaki et al. 1994, Clark and Ji 1995, Pacala et al. 1996). The absence of a plant species from a site may not be a result of lack of suitable environment but simply of the
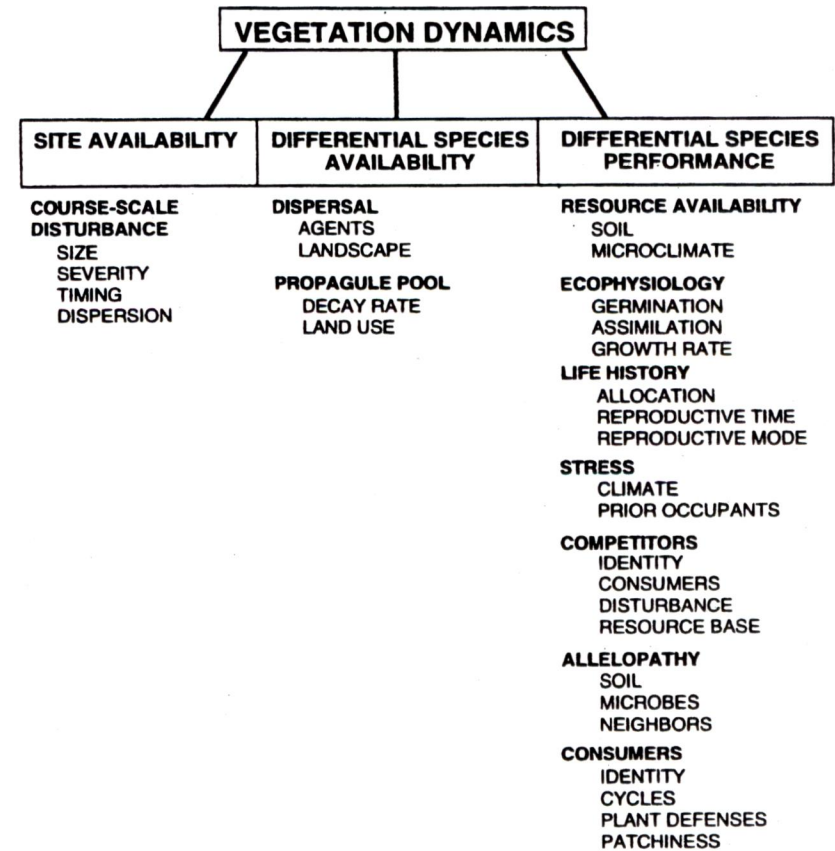
Fig. 4.2. Hierarchical framework of vegetation dynamics phenomena and processes. (From Pickett et al. 1987.)

fact that not enough time has elapsed since a disturbance or loss of the species for new propagules to reach the site and become established (Busing et al. 1995, Poage and Spies 1996, Sillett 1994, Duffy and Meier 1992, Halpern and Spies 1995). Conversely, the presence of plants on a site, which may otherwise not be optimal habitat, may be a result of 'mass effects' of an abundant local seed source (Cody 1989, Tilman 1988).

Once plants have established on a site, competitive interactions among forest plants become the primary drivers of forest succession and stand development in many environments (Oliver and Larson 1990, Glenn-Lewin et al. 1992). However, other biotic interactions such as herbivory and mutualism can also play important roles (Crawley 1990, Oliver and Larson 1990). Where mixes of species initiate succession following disturbance,

changes in forest structure over time can be accounted for simply by differences in growth rates (Oliver 1978). Differences in shade tolerance also play an important role. Early successional plants are typically less competitive for light resources and put more of their energy into fecundity, early seed production, rapid growth, and 'escaping' succession to find new sites than late successional species (Harper 1977). Stands formed by early successional species are often subject to invasion by shade-tolerant trees that are more competitive than shade-intolerant species for scarce light and nutrient resources. Traits that allow a tree to persist and regenerate repeatedly in the absence of large disturbances include shade tolerance, longevity, clonal growth, and internal cycling of nutrients. What late successional species gain in competitive traits they apparently lose in fecundity, early sexual maturity, growth rates, and sometimes in seed size and dispersal capability (Harper 1977, Tilman 1988). While early successional species are not well adapted to persisting through succession (in the absence of large disturbances), it is not true that late successional species are absent from early successional environments. Shade-tolerant species can colonize early successional environments if seed sources are nearby, suitable germination sites are present, and climatic conditions are suitable (Oliver and Larson 1990).

By combining a diversity of species, life history traits with environmental heterogeneity we can see how succession can be resistant to explanation by simple models. Tilman (1988) argues that differences in multiple resources such as soil nutrients, moisture, and light control long-term successional dynamics. In his model, competitive abilities of different species shift across resource gradients, making the distinction between early and late successional species dependent on environmental context. This can help us understand why it can be very difficult to predict the spatial patterns and rates of succession across a landscape: spatial heterogeneity of resources can alter competitive abilities of species and patterns of seed rain can result in species persisting on sites where they are not very competitive or being absent from sites on which they are competitive. Add disturbance to the system and vegetation dynamics become wonderfully complex!

PATTERNS AND PATHWAYS OF VEGETATION CHANGE AT LANDSCAPE SCALES

The diversity of processes involved in succession can produce an incredible variety of patterns and pathways of vegetation over time and

landscapes. The classical model of succession had great appeal because of its simplicity. More recent models that emphasize processes, unpredictability, and complexity, are more realistic but may be less appealing from a management perspective, where simplicity and efficiency are valued. Landscape ecologists typically view landscapes as populations of patches of different types (Forman 1995). Biotic processes operating at the scale of individual plants or interplant interactions may be too fine scale for coarse-scale spatial models of landscapes (Johnson 1996). Is there some way to reduce the complexity of the current models for applied purposes? Are there general patterns that help us understand, communicate, and manage these dynamics at landscape scales? We think the answer is yes. Instead of viewing succession from only an ontological perspective (i.e., emphasis on process and causal mechanisms), a phenomenological perspective (i.e., a description of patterns, pathways, and probabilities), can be useful in management and landscape-scale applications. Repeating patterns of change emerge at landscape scales and some order can be found through descriptions of successional pathways, patch mosaics, and seral stages that facilitates the understanding and management of vegetation at landscape scales. The challenge and art is to simplify without losing important attributes and to work with simplifications without losing sight of the underlying complexity.

Successional pathways and climax

As mentioned above, Clements (1916) classical model of successional processes did not match the reality that ecologists were observing. The same is true of his description of successional patterns and pathways across landscapes. Whittaker (1953, 1973) pointed out that within a climatic region, instead of one climax vegetation type, many are possible depending on soil and local climate variations. His classic study (Whittaker 1956) in the Great Smoky Mountains demonstrated the intricate relationships between the mosaic of forest communities and gradients of elevation and moisture. Cove forests that include beech (*Fagus gradifolia*), tulip tree (*Liriodendron tulipifera*), basswood (*Tilia americana*), sugar maple (*Acer saccharum*) and hemlock (*Tsuga* spp.) develop in sheltered areas at lower elevations; dry exposed sites tend to be occupied by pines and oaks. Thus, the idea that vegetation converges on the same equilibrium endpoint across landscapes is inadequate for understanding and managing vegetation dynamics (Glenn-Lewin et al. 1992). The concept of climax as a stable end point is also misleading. It is uncommon for vegetation or ecosystems to reach an equilibrium point or condition of no net

change, which requires a perfect balance between opposing forces of disturbance and biotic development (Pickett and McDonnell 1989). The failure of equilibrium models to represent adequately the reality of vegetation dynamics has led to alternative theoretical formulations based on multiple pathways, non-equilibrium theory, and chaos theory (Cattelino *et al.* 1979, Wu and Loucks 1995, Stone and Ezrati 1996). These new formulations focus more on dynamics and variability than single endpoints. Rather than equilibrium it is more realistic to think in terms of 'quasi-equilibrium', 'dynamic equilibrium', or slowly changing systems, and to recognize that the rate and direction of change in vegetation is dependent on spatial and temporal scale.

Classifications of successional patterns can help us visualize how landscape composition and diversity will change over time. If we can assign probabilities to different patterns or pathways then we can project potential outcomes of different management actions using simple models. At least five different, phenomenological classifications of successional pathways have been identified. They include convergence (different sites become more similar), divergence (similar sites become more different), cyclical (repeating and alternating vegetation types), and multiple pathways (Frelich and Reich 1995). While these may sometimes appear to be mutually exclusive hypotheses, they may be viewed as variations of a generalized, multiple pathways model in which vegetation can follow different pattern types depending on the diversity of species in a landscape, their life history characteristics, the disturbance regime, and the environment. To some degree the differences between these characterizations of vegetation change are a function of spatial and temporal scale. For example, succession in hardwood forests in the northeastern United States has been described as cyclical (Forcier 1975) (yellow birch to sugar maple to beech and back to yellow birch again following gap disturbances) but early succession following stand replacement disturbances in these forests follows multiple pathways based on the presence or absence of pin cherry which, in turn, depends on bird dispersal and time since last disturbance (Marks 1974).

The term 'climax' no longer has value to many plant ecologists because it is associated with the Clementsian climax of superorganism and stable end points. However, 'climax' does not have to be a Clementsian term if it is put in the context of contemporary views of multiple dynamic equilibria (climaxes) within a particular spatial and temporal scale. Some ecologists still find it useful to use 'climax' or the potential natural vegetation(s) in a less formal way with the caveats that disturbance will intervene, and that

communities based on too precise a listing of species may be nothing but random, ephemeral assemblages (Shrader-Frechette and McCoy 1993). Most applied ecologists who deal with real pieces of ground still need to use some way of classifying and mapping the potential vegetation assemblages that could occur over time on a site (Peterken 1996).

Vegetation as a dynamic mosaic

Another useful way of understanding vegetation dynamics is to characterize it as a shifting mosaic of patches of different ages and developmental stages (Watt 1947, Bormann and Likens 1979). This concept is a particularly useful abstraction at landscape levels (Remmert 1991) where the units are patches of vegetation that change like a kaleidoscope. The power of the shifting mosaic idea lies in three areas. First, it helps to illustrate one of the paradoxes of vegetation dynamics – the fact that vegetation can be both highly dynamic and yet appear to be slowly changing or even unchanging if the overall pattern stays the same but the spatial distribution of individual patches changes. This, of course, results from the fact that individual plants or patches of plants can change quite dramatically over time and space but when viewed over a large enough area, such as a large stand or landscape, these patches can be sufficiently out of synchrony that the net effect is a shifting mosaic of patches whose aggregate characteristics (e.g., biomass, species diversity, patch type and size distribution) may change very slowly (Figure 4.3). Second, the emphasis on population dynamics of patches and the disturbances that destroy and create them provide a framework for nesting process studies of population ecology of plants within more phenomenological approaches (i.e., description of patches, pathways and transition probabilities) (Forman 1995). For example, the population dynamics of patches of even-aged plants can be used to estimate rates of canopy gap formation (Clark 1991, 1992). Third, the spatial aspect of this concept provides a framework for how spatial characteristics such as patch sizes or juxtaposition of patches can affect overall system behavior. For example, systems with fine-grained patch structure may favor shade-tolerant species whereas systems with coarse-scale disturbances may favor shade-intolerant species (Spies and Franklin 1996). The spatial nature of this concept also allows it to be represented in maps which help humans to understand and manage natural systems.

The shifting mosaic concept has typically been applied to relatively small canopy gaps in forests, although there is no theoretical reason why it must be restricted to this size of patch. The importance of canopy gap
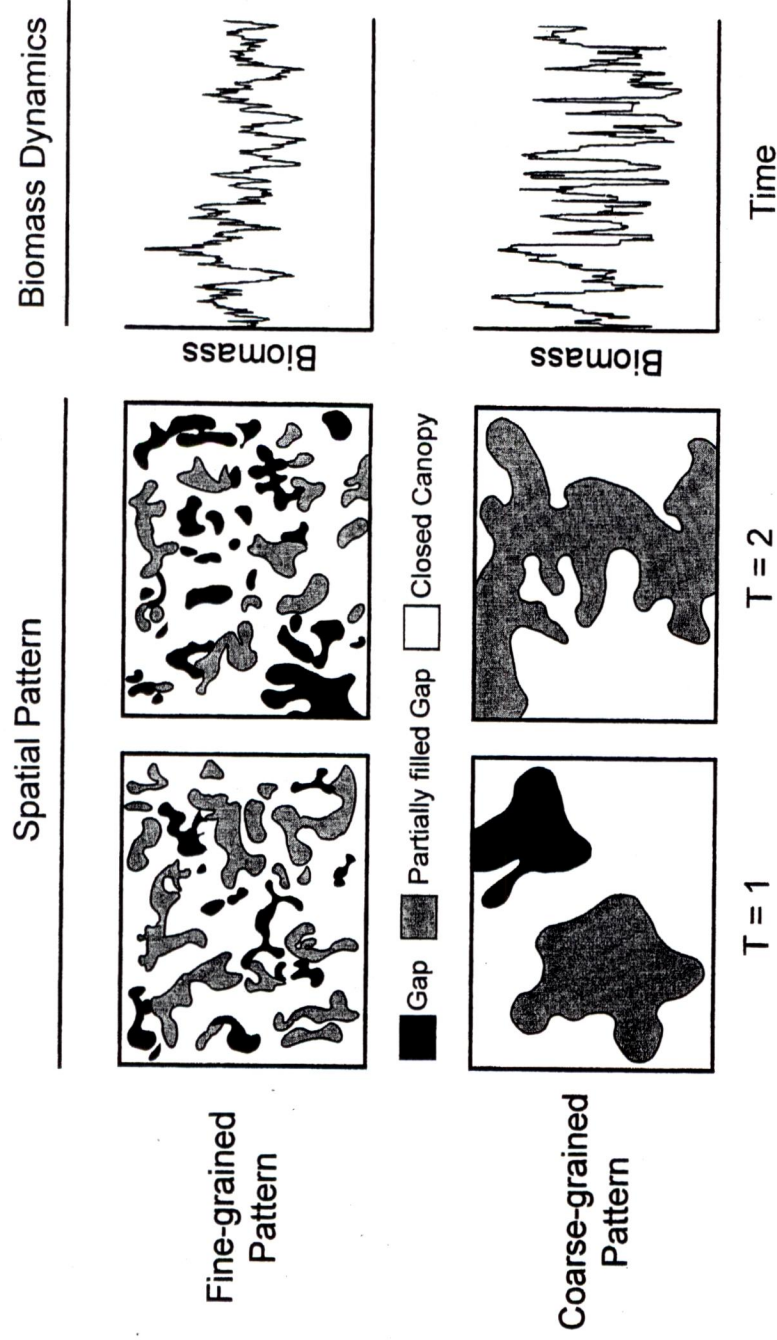
Fig. 4.3. Shifting mosaic over space and time illustrating attenuation of temporal variability in biomass at different spatial grains or scales.

dynamics to forest dynamics has been identified in many forests, especially in temperate forests in eastern North America and the New World tropics (Shugart 1984, Runkle 1985, Platt and Strong 1989, Attiwill 1994a). However, the importance of gap dynamics has been recognized in other regions including temperate Asia (Yamamoto 1992) and boreal Scandanavia (Leemans 1991). Most canopy gaps are small, ranging from single trees covering a few tens of square meters to small groups of trees covering hundreds of square meters (Attiwill 1994a). Gap creation rates range between 0.2% to 2.0% of a stand each year, which is equivalent to a rotation period of 50 to 500 years (Runkle 1985, Spies *et al.* 1990). Although canopy gaps may be relatively small they may cover 5% to 30% of a forest, and influence more than 50% of a forest, if canopies bordering the gaps ('expanded gap', Runkle 1982, 1992) are taken into account (Lertzman *et al.* 1996). Canopy gaps do not have the same effect on resources or vegetative response in all forests. For example, Canham *et al.* (1990) found that single-tree gaps do not produce the same amount or pattern of resources in forests with different canopy heights and from different latitudes. At low latitudes single-tree canopy gaps can provide significant levels of light resources; at high latitudes, single-tree gaps in tall forests transmit very little direct radiation to the forest floor.

Many forest mosaics are driven by large patches created by fire or large windstorms (Attiwill 1994a). Coarse-scale disturbances can create patches of 50 to 1000 ha in the case of windstorms (Canham and Loucks 1984) and over 200 000 ha in the case of fire in boreal systems (Dyrness *et al.* 1986). Where these coarse-scale disturbances occur more frequently than the life spans of the trees, canopy-gap dynamics may be relatively unimportant in explaining forest dynamics and biological diversity (Denslow 1987, Yamamoto 1992). In other landscapes fine-scale disturbances can be superimposed on patches originating from coarse-scale disturbances that occur with similar or lower frequencies (Spies and Franklin 1989, Clark 1991).

Vegetation states in time

Emphasis on process, quasi-equilibria, and multiple pathways may appear to argue against the development of classification schemes for succession. These classifications will invariably be subjective and the results of analyses and models based on these schemes will be more or less a function of the classification definitions (Usher 1992). However, for practical applications in which relatively simple questions are being addressed, the development and use of seral stage or developmental phase classifications
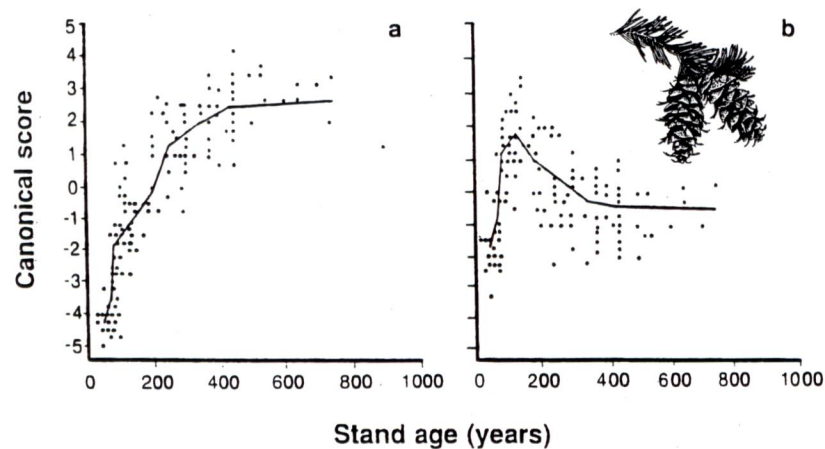
Fig. 4.4. Relationship of canonical variates of stand structure to age in a 1000-year chrono-sequence of Douglas-fir stands. (From Spies and Franklin 1991.)

can be quite appropriate. A classification approach is especially needed where spatial analysis is done and successional stages must be mapped as patch, stand or cover types.

Most classifications of forest successional stages recognize four to six major types and potentially many more if these are stratified by different environments, or potential natural vegetation types (e.g., based on climate or soil). The primary stages are: (a) stand initiation or establishment; (b) stem exclusion or thinning; (c) understory reinitiation; (d) transition or transition old-growth; and (e) shifting mosaic ('true old-growth') (Bormann and Likens 1979, Oliver 1981, Oliver and Larson 1990, Peet and Christensen 1987). Additional classes have been sometimes added to the early and late stages (Thomas 1979, Spies 1997). These stages can be distinguished based on either population processes (the origin and status of different tree population cohorts) (Oliver and Larson 1990) or on structural differences in live and dead forest vegetation that are expressions of the population and disturbance processes (Spies 1997). Changes in structure and composition tend to be rapid during the first stages and then gradually decline in later stages (Figure 4.4) (Spies and Franklin 1991, Spies and Franklin 1996, Peterken 1996). However, slow changes in old growth resulting from successional and disturbance processes may continue for centuries if the species are long lived and if shade-tolerant species are slow to colonize and grow into the canopy.

Ecological characteristics of late-successional and old-growth stages

Few issues have been more controversial in forest management and conservation circles than those surrounding late succession and old growth. Old growth is probably the only stage of forest development to have been the subject of congressional hearings in the United States (House of Representatives, 1990). Yet, it may be the least-studied stage of succession (Oliver and Larson 1990). The lack of scientific understanding of old growth is probably a result of emphasis of forestry research on earlier stages of forest development associated with economic rotations, and the lack of late-successional stands in most landscapes. In addition, the relatively rapid compositional changes that occur in early succession make younger stages more suitable for study during the course of a research grant than older more slowly changing stages.

Old-growth forests have been defined from a variety of ecological and social perspectives (Oliver 1981, Hunter 1990, Spies 1997, Davis 1996, Peterken 1996). Old growth is frequently associated with absence of evidence of human activity (Leverett 1996); however, this meaning is more accurately described by the term 'virgin' forest which is a commonly used term in Europe and elsewhere (Peterken 1996). The term 'primary forest' is also used to describe the original forests of an area prior to cutting for agriculture or settlement and seems to be favored by ecologists working in tropical regions as well as Europe. Old-growth definitions based on absence of human influence are problematic for several reasons, including the fact that many forests have been influenced by indigenous or pre-modern humans at least indirectly (Foster *et al.* 1996). Defining old growth based on the structure of current old-growth stands may also present problems if those definitions are used to set goals for old-growth restoration. It may not be possible to grow future old growth that is similar to current old growth because many present-day old-growth stands can comprise anomalous or unique assemblages in comparison with their predecessors (Foster *et al.* 1996) or are relics of past climates and disturbance regimes (Spies and Franklin 1988).

Ecological definitions of old growth have typically been based on age, live and dead stand structure, or population processes. A common denominator in many of these definitions is the presence of a population of old trees and their associated structures (e.g., dead trees, tree canopy gaps). The age at which this occurs and the associated structures that would develop would depend on the life history characteristics of the tree species and the disturbance regimes that create and maintain old growth (Spies and Franklin 1996). In the broadest sense all tree species or forest

types can develop an old-growth stage as populations of trees age, develop large crowns, become damaged, deformed, diseased, die, create gaps for new establishment or release of regeneration, and produce relatively large (for the species) standing dead and fallen trees. In this sense, a short-lived species like aspen (Populus spp.), with a potential life span of around 100 years, will develop an old-growth stage as well as long-lived species like giant sequoia (Sequoia gigantea) which has a potential life span of over 2000 years. It is, however, the old-growth types from long-lived species (those trees whose expected life spans exceed 200 years) that are least common in forest landscapes.

Although net rates of change in old-growth forest attributes may be small at stand and landscape scales, these forests are far from static. The degree of change in old-growth stands is a function of the attributes which are measured, the particular ecosystem studied, and the spatial scale of investigation. Mortality rates within old-growth stands can range between 0.3 and 1.1% per year (Peterken 1996). Overall biomass may remain steady despite relatively high levels of mortality (Franklin and DeBell 1988). At landscape scales, pollen diagrams from temperate forests often reveal relatively stable forest composition over hundreds of years (Foster and Zebryk 1993, Worona and Whitlock 1995). Pollen studies generally show less stability at stand scales than landscape scales (Peterken 1996) but some old-growth stands have been relatively stable in composition for thousands of years at relatively fine spatial scales (Davis et al. 1994). Unfortunately while pollen studies can characterize long-term compositional changes fairly well, they are not able to detect long-term structural changes in age and stand structure which may be more distinctive in old growth than are compositional changes (Spies and Franklin 1991).

The relative frequency, severity, and size of disturbance determines the amount and kind of old growth in a landscape (Spies and Franklin 1996, Johnson et al. 1995). Old-growth forests in which the canopy trees can regenerate in small canopy-gap disturbances will frequently develop a fine-grained patch structure and will theoretically develop a 'reverse-J' age-class distribution or become multi-cohort over long time periods. However, few old-growth stands actually show this; they are more typically characterized by irregularities in age distributions as a result of intermediate-scale or moderate-severity disturbances (Peterken 1996). Old growth in landscapes characterized by large disturbances such as fire will have a coarse-grained mosaic of age classes, which will eventually require large disturbances to maintain the landscape age-class pattern and distribution. In old-growth systems with large trees that survive low

to moderate severity fires, such as pine (Pinus spp.) and Douglas-fir (Psuedotsuga menziesii), fire, instead of wind, may create gaps and heterogeneity.

Landscape dynamics and age/seral class distributions

The proportion of different age classes or seral stages across a landscape and over time is one of the fundamental characteristics of the vegetation mosaic. Under natural disturbance regimes these proportions will vary over time and across landscapes depending on the frequency, intensity, and pattern of disturbances and the rates of development of different seral stages. The age-class distributions of large landscapes under natural or semi-natural disturbance regimes are generally not well known (Hemstrom and Franklin 1982, Johnson et al. 1995). In many cases the amounts of different age classes over time do not appear to be constant but fluctuate over time. A steady-state condition of relatively constant proportions of different age classes appears to be uncommon, even for large landscapes (Hemstrom and Franklin 1982, Baker 1989, Turner et al. 1993). Quasi-equilibrium conditions seem to be most common where small-scale wind and treefall disturbances dominate the regime and fire is rare, such as in parts of New England (Bormann and Likens 1979), and the north central United States (Frelich and Lorimer 1991). Rather than search for the elusive equilibrium it is more realistic to evaluate the relative variability of different landscapes. Turner et al. (1993) evaluated disturbance regimes from several different types of landscapes based on four factors: (a) interval between disturbances; (b) rate of recovery of a seral stage; (c) spatial extent of the disturbance; and (d) spatial extent of the landscape. They found that variability increased as the ratio of the disturbance interval to the recovery interval decreased and as the ratio of the disturbance extent to the landscape extent increased (Figure 4.5). In other words, where disturbances were frequent and landscapes were relatively small, variability in older age classes was high. Shugart (1984) also observed that when the disturbance size approached the size of the landscape, amounts of different patch types became quite variable over time. This general finding is, of course, one reason (but not the only one) why nature reserve design puts a premium on large areas (Chapter 16). Large habitat areas are more stable than small ones. However, it must be remembered that few landscapes, even under 'natural' conditions, were ever constant in the amount of different age/seral classes over time.

The rarity of constancy in natural landscapes does not necessarily argue for the view that whatever humans do will produce the same ecological
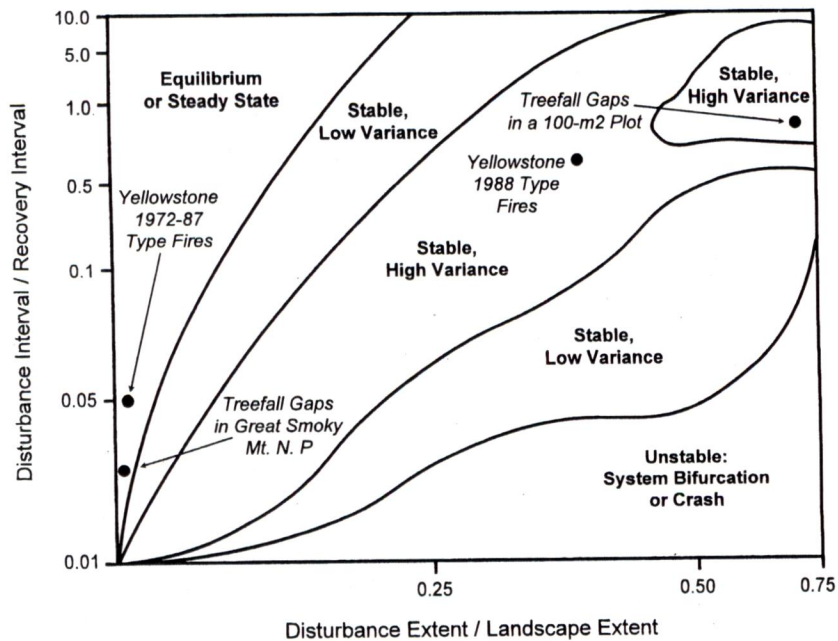
Fig. 4.5. State-space diagram of the temporal and spatial characteristics of disturbances and landscapes illustrating different types of landscape dynamics. (From Turner *et al.* 1993.)

outcomes (Sprugel 1991). One of the distinctive features of natural landscape age-class distributions, regardless of how variable they may be, is the presence of a 'tail' in the forest age-class distribution that extends into older ages. The tail results from the fact that natural disturbances, such as fire, insect outbreaks and large windstorms do not always remove the oldest age classes in a landscape – they typically disturb young stands as well. In fact, in some cases young stands with green fuels close to the ground may be more likely to burn than older stands with higher canopies (Agee and Huff 1987). In addition, lakes and soil and topographic variability create areas where stands may escape fire and wind disturbances for long periods (Bergeron 1991, Syrjänen *et al.* 1994, Foster and Boose 1995). The fact that natural disturbances do not remove all stands and do not necessarily only destroy older stands leads to landscapes in which some older stands survive. It is possible to estimate what the age-class distributions of landscapes would look like under these natural disturbance regimes using a well-accepted fire-frequency model (Van Wagner 1978, Johnson and Gutsell 1994). The cumulative survivorship distribution is determined from the following equation:

$$A(t) = \exp - (t/b)$$

where t is the time since last disturbance and A(t) is the survivorship distribution, and b is the disturbance cycle (time required to disturb an area equal to the study area), the inverse of which is the disturbance frequency at any given point in the landscape. Applying this model, which assumes equal probability of disturbance among the age classes, produces the expected distribution shown in Figure 4.6 for different fire frequencies and ages of old growth.

The age-class distributions of forest landscapes almost never fit this model distribution exactly and may deviate from it considerably (Van Wagner 1978, Johnson *et al.* 1995) Forest landscapes may deviate from expected model age-class distributions as a result of either changes in disturbance frequencies over time or the lack of validity of the assumption of uniform flammability with age. The model can be modified using a Weibull formula to estimate the distribution where disturbance probabilities are not uniform across the age classes (Johnson and Gutsell 1994). This model can then be used to estimate the amount of landscape that occurred in an old-growth condition if old growth can be defined in terms of age since the last major disturbance. For example, if old-growth forests develop in around 150 years, and the average stand replacement disturbance frequency is 300 years, then the expected long-term amount of old growth will be about 61% (Figure 4.6).

Compositional responses to forest dynamics

The ecological changes resulting from disturbances and vegetation development vary by species and ecological process. Disturbances themselves kill both animals and plants; however, we confine our focus on the direct effects on vegetation and the indirect effects on animal habitat and ecosystem functions.

The differences in vegetation structure and species composition between early successional forest conditions and later stages when tree canopies close and increase in height have been documented in many studies (Gashwiler 1970, Helle 1985, Haila *et al.* 1994). Of course, the structural and compositional changes that occur when forests change to meadows, prairies, fields, and recent clearcuts, or vice versa, are greater than changes that occur with transitions among various stages of closed-canopy forest development. Early stages of forest succession are characterized by species with high colonization abilities and later stages by species better adapted to slowly changing habitats or, in the case of plants, by shade-tolerant species that can compete well for light resources but
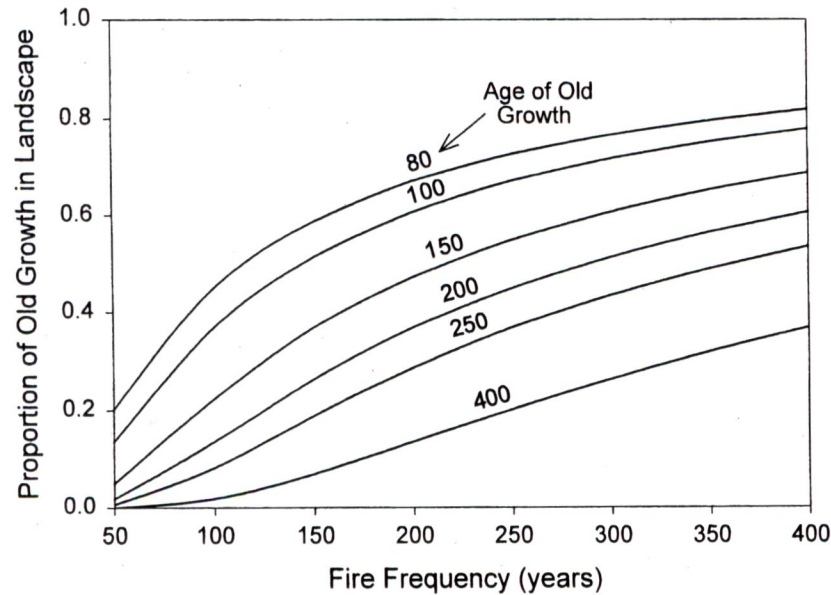
Fig. 4.6. Theoretical proportions old growth forests in landscapes in relation to disturbance frequency and age at which old growth develops.

may have poor dispersal abilities (Tilman *et al.* 1994). Landscapes in which early and late successional habitat are intermixed may provide conditions suitable for species such as various deer species which require both foraging and cover habitat (Thomas 1979). Conversely, the quality of habitat of the remaining forest patches may decline through fragmentation effects, such as microclimate changes (Chen *et al.* 1995) herbivory, predation at edges (Alverson *et al.* 1988), higher rates of mortality in dispersing juveniles, and increased rates of disturbance (Franklin and Forman 1987) (Chapters 6 and 7).

Although changes from late to early stages of forest development are most drastic and may account for the greatest alterations of biological diversity, changes in the quality and diversity of mid to late successional forests through management for wood production can also alter biological diversity and threaten the viability of species and ecosystems (Heliövaara and Väisänen 1984, FEMAT 1993, Essen *et al.* 1992). Forest management for wood production typically decreases the interval between disturbances, alters landscape age-class distributions, decreases the diversity of forest structure and composition at stand and landscape scales, and results in forest fragmentation. These changes may not result

in much change in forest cover in a landscape; however, they may alter forest quality and affect species and processes that are sensitive to it.

Few studies have documented the differences in the fauna and flora of managed and unmanaged forests. However, a comprehensive study of differences in natural forests of mid to late seral stages has been made in the Pacific Northwest (Ruggiero *et al.* 1991). The plant and animal communities of closed canopy forests in over 200 stands ranging in age from 40 years to over 900 years were studied across the entire region. The stands in this chronosequence range in development from stem-exclusion stage through old-growth stages. Forest structure varied dramatically (Spies *et al.* 1988, Spies and Franklin 1991) (Figure 4.4). Diversity of plant and animal species tended to be higher in old growth than in earlier closed canopy stages, although differences in diversity were small. Community overlap, the proportion of species not showing statistical differences among forest age classes, typically ranged from 56% for trees and amphibians to 91% for shrubs and herbs (Hansen *et al.* 1991). Sensitivity of bird species abundance to age class differences was highest in the Coast Range subregion (Huff and Raley 1991) where disturbance history created a greater difference in forest structure among the age classes than in other subregions (Spies *et al.* 1988). No species of plant or vertebrate occurred exclusively in the old-growth forests, although many occurred more frequently there than in younger forests. Plant species showing the greatest abundance in older forests were small shade-tolerant forest herbs, canopy lichens (*Lobaria* spp.) and Pacific yew (*Taxus brevifolia*), all of which may be less abundant in younger stands because of slow rates of colonization (Halpern and Spies 1995, Sillett 1994). Vertebrate species with greater abundances in older forests included the northern spotted owl (*Strix occidentalis caurina*), which appears to prefer multi-layer canopies for foraging and large trees for nesting, bats (*Myotis* spp.) which use snags and large damaged or diseased trees for roosting. Brown creepers (*Certhia americana*), a bark-gleaning bird, and shrew-moles (*Neurotrichus gibbsii*), which apparently prefer sites with deep accumulations of fine and coarse litter, were also more abundant in the old-growth stage (Aubry *et al.* 1991). Although these studies in the Pacific Northwest have provided much valuable information about changes in species composition during succession, it must be remembered that the results do not necessarily apply to managed stands in heavily managed landscapes.

Spatial heterogeneity

As we mentioned at the beginning of this chapter forest dynamics and spatial heterogeneity are closely linked (Figure 4.1). In many ways forest dynamics and spatial patterns are just two sides of the same coin. They are often generated by the same forces, are highly variable both spatially and temporally, are systematically described to help us understand, communicate, and manage them, and they both can have strong effects on the abundance and distribution of organisms and functions of ecosystems. In this section we focus specifically on the causes, characterizations and effects of spatial pattern. We are just beginning to understand spatial patterns in forests. The recent development of high-speed computing, GIS (geographical information systems), remote sensing, and spatial statistics now gives tools to help us see patterns that we could not see before and evaluate their ecological effects.

CAUSES OF SPATIAL PATTERNING

The forces that cause forest dynamics also result in spatial patterning. However, spatial pattern will occur even in the absence of disturbance and successional processes. Spatial variation in environmental factors such as elevation, slope, aspect, and soil type creates complex abiotic templates upon which forest communities develop (Chapter 5). Many studies have described these types of relationships in a variety of landscapes (e.g., Whittaker 1956, Reiners and Lang 1979, Spies and Barnes 1985).

We have already given some examples of how biotic interactions can influence forest succession. Another interaction that may strongly influence dynamics and spatial pattern is herbivory by dominant organisms. Beavers (*Castor canadensis*) create openings and impose a strong spatial pattern on the distribution of forest and non-forest communities across a landscape (e.g., Johnston and Naiman 1990). Selective foraging by moose (*Alces alces*) in boreal forests creates distinct patterns in the distribution of deciduous and coniferous species (e.g., Pastor *et al.* 1988, McInnes *et al.* 1992). Herbivory by ungulates such as elk (*Cervus elaphus*) on aspen (*Populus tremuloides*) in the northern Rockies may be one of many factors influencing the spatial distribution of aspen (e.g., Romme *et al.* 1995). Pests and pathogens also generate spatial patterns in the distribution of species and of age classes of trees (e.g., Sprugel 1976, Sato and Iwasa 1993, Castello *et al.* 1995).

Human activities create strong spatial patterns in many forests. Patterns of land use and forest harvest are two conspicuous human influences on spatial pattern, although there are many others. The dispersed cutting patterns implemented in forests of the Pacific northwestern United States has resulted in a sharp decline in the average patch size and connectivity of older forests and a dramatic increase in edge habitat (Franklin and Forman 1987, Li *et al.* 1993, Spies *et al.* 1994, Wallin *et al.* 1994). Similar results have been observed in Swedish boreal forests (Edenius and Elmberg 1996). In general, disturbance suppression, the use of small prescribed disturbances, and fragmentation from clearcutting all tend to produce landscapes with smaller more numerous patches that are closer together; restoration of a natural disturbance regime following fragmentation or disturbance suppression tends to produce the opposite trends (Baker 1995). Because forests take a long time to develop, the patterns created by human activities may be very persistent, even after the activity ceases (e.g., forest harvest patterns, Wallin *et al.* 1994). Simulation studies have suggested that landscapes require one-half to two rotations of a new disturbance regime for their structure to adjust to that new regime, regardless of how the disturbance regime has been altered (Baker 1995).

Patterns of human settlement have profoundly influenced forest structure and heterogeneity for millennia (e.g., Ellenberg 1988, Burgess and Sharpe 1981, Turner *et al.* in press, Essen *et al.* 1997). For example, forest covered about half of the conterminous U.S. at the time of European settlement. Although the forests had been influenced for centuries by Native American land-use practices, forest clearing for fuel, timber and other wood products, and cropland lasted through the 1920s and led to profound changes in abundance and spatial distribution of forest communities (e.g., Whitney 1994, Meyer 1995). Old-growth eastern hemlock and mature hardwoods dominated northern Wisconsin in the 1800s. By 1931, following extensive cutting and burning of slash, young forests covered more than 50% of the landscape, and by 1989 a mixture of second-growth hardwood and conifer communities dominated (White and Mladenoff 1994). Although the total area covered by forest has increased since 1900 (following cropland abandonment) across much of the eastern United States, the composition of these forests is often quite different from those in the 1700s (Turner *et al.* in press).

Thus, forest landscape patterns result from the interplay of abiotic constraints, biotic interactions, and disturbances. The pattern is not simply a constraint imposed on the ecological system by topography and soils.

Instead, there is an intimate tie between pattern and process that forms an important core to the understanding of forest landscapes (Urban *et al.* 1987).

CHARACTERIZING SPATIAL HETEROGENEITY

Quantitative methods are required to describe spatial patterns: (a) to relate patterns to ecological processes; (b) to monitor changes through time; (c) to compare different forests, and (d) to evaluate the effects of alternative forest management options within a spatial context. Overviews of the various metrics for quantifying spatial pattern are readily available elsewhere (e.g., O'Neill *et al.* 1988; Turner 1989, 1990; Baker and Cai 1992; Turner and Gardner 1991; McGarigal and Marks 1995), and we will not review these here. Rather, we will briefly discuss some of the important factors that must be considered in performing or interpreting such analyses.

A landscape is typically represented as a grid of cells, and this grid then provides the basis for quantitative analysis. (Data may also be represented in vector format, but the gridded form is more common and is consistent with remotely sensed imagery.) The spatial scale of these data strongly influences the numerical results of any pattern analysis (Turner *et al.* 1989). Spatial scale encompasses both the *grain*, or resolution of the data – e.g., the size of the grid cells or the minimum mapping unit – as well as the *extent*, or size of the area to be analyzed. Recent analyses suggest that the grain of the data used for spatial analyses should be two to five times smaller than the spatial features of interest (O'Neill *et al.* 1996). In addition, the spatial extent should be two to five times larger than landscape patches to avoid bias in calculating landscape metrics (O'Neill *et al.* 1996).

The choice of what categories to include in a spatial analysis is critical, as the classification strongly influences the numerical results. For example, when describing a forested landscape, one might classify the forest based on dominant species or by successional stage. The patches identified by these two schemes would usually be very different, and the metrics describing them would also be dissimilar. The classes must be selected for the particular question or objective. For example, general categories (e.g., deciduous vs. coniferous forest) might be appropriate to study landscape patterns in the eastern United States, but various forest community classes would be needed to study patterns within a particular landscape such as the Great Smoky Mountains National Park.

There is no single metric that is, by itself, sufficient for quantifying spatial pattern. The choice of which metrics are 'best' must be based upon

the question at hand. Many metrics of spatial pattern are strongly correlated with one another, containing much redundant information. Riiters *et al.* (1995) examined the correlations among 55 different landscape metrics by means of a factor analysis and identified only five independent factors. Thus, many typical landscape metrics are not measuring different qualities of spatial pattern, and the set of metrics to be used in concert should be carefully selected.

ECOLOGICAL CONSEQUENCES OF SPATIAL PATTERN

Spatial pattern can exert a strong influence on population dynamics and ecosystem processes, and many effects have been described (e.g., Forman 1995, Chen *et al.* 1995). Indeed, understanding spatial ecological dynamics has been labeled 'the final frontier' for ecology (Kareiva 1994). Despite the recent interest and progress, it remains challenging to determine for various processes or organisms the conditions under which spatial heterogeneity is and is not important. We highlight here several of the well-described ecological consequences of spatial pattern, focusing on the importance of habitat connectivity for species, the influence of landscape context on local processes, land–water interactions, and the spread of disturbance.

Habitat connectivity has important effects on the persistence and abundance of species (Chapter 7). It is clear that the actual spatial arrangement – not simply the variance – of habitat and barriers affects the location, movement patterns, foraging dynamics, and persistence of organisms. To understand connectivity (or its inverse, fragmentation), one must characterize suitable habitat from the perspective of the particular species of interest (Wiens 1976). 'Perspective' here refers to describing the physical and biological environment at an appropriate spatial scale (Wiens 1989, Pearson *et al.* 1996); simply identifying what is connected or fragmented from a human perspective may not be relevant to another species. In forested landscapes, stand age often interacts with community composition to define suitable habitat. For example, in the southeastern coastal plain of the United States, suitable habitat for Bachman's sparrow includes both early- and late-successional forest, but not the middle seral stages (Pulliam *et al.* 1992). This leads to rather complex interactions between habitat connectivity for this species and forest management (Liu 1993). Habitat connectivity for species requiring old-growth forest has received considerable attention (e.g., FEMAT 1993) and is clearly an important consideration for forest mosaics.

Local ecological processes may respond not only to local conditions but also to the landscape context (Turner *et al.* 1995), and this is another consequence of spatial patterning. For example, some species respond more to the pattern of forest and non-forest communities in the surrounding landscape than to the local habitat structure. In his study of wintering birds, Pearson (1993) found that the occupancy of a habitat patch may depend on other surrounding patches, and occupancy may be enhanced if the patch is surrounded by additional suitable habitat. Thus, the landscape context must be considered along with site-specific attributes when considering species abundance and biodiversity (Franklin 1993).

Land–water interactions are strongly influenced by the spatial patterns of vegetation, especially the presence and integrity of riparian communities (Chapter 8). Riparian forests along streams can filter undesirable excess nutrients in landscapes in which forests are mixed with agricultural or urban land uses. In a Maryland watershed, dramatic reductions in water-borne nutrient loads (C, N and P) occurred within riparian forest (Peterjohn and Correll 1984). Riparian buffers can reduce nitrate-N concentrations by up to 90% in shallow groundwater (Osborne and Kovacic 1993). The coupling of natural and managed forests within a watershed has important implications for water quality. For example, shading of streams by trees can help maintain cool temperatures required by salmonids (Chamberlin *et al.* 1991). Landslides originating in steep forested headwall areas can deliver large wood and sediment to streams that may have positive or negative effects, depending on the kind and size of trees and size and amount of the sediment delivered to the stream. Thus, riparian forests are important not only for the functions they provide as live intact vegetation, but also for the large organic matter they deliver when disturbance occurs near streams.

Spatial patterning may also influence the spread of disturbances and the patterns of succession. Various spatial locations across a landscape may be differentially susceptible to disturbances, though this is by no means uniform. In forests of central New England, for example, slope position and aspect strongly influence probability of disturbance (Foster 1988a, 1988b). Exposed hilltops and southeastern slopes tend to be more susceptible to storm-related hurricane damage. However, disturbance in forests in the upper Midwest showed no significant response to topographic features (Frelich and Lorimer 1991). Beyond the influence of landscape position, connectivity of forest habitat may influence the spread of pests or pathogens. In northern Ontario, Canada, the best predictor of the duration of outbreaks of forest tent caterpillars was the amount of forest

edge per km² of forest (Roland 1993). As succession proceeds following a disturbance, the spatial patterning of the disturbed and undisturbed areas within a forested landscape can influence community structure by influencing local site conditions (e.g., temperature, light availability) and seed sources. The effect of disturbance size and spatial configuration is probably most important when the biotic residuals (e.g., in situ propagules or surviving plants) are low and when disturbance size is large (Turner *et al.* in prep).

Implications for management

GENERAL PRINCIPLES

The 'new ecology' or new paradigm of ecology that has emerged in recent years (Botkin 1990, Zimmerer 1994, Pickett and Ostfeld 1995, Christensen 1997) has replaced 'balance of nature' with 'ecosystem dynamics' or 'flux of nature' as the dominant metaphor of ecology. According to Pickett and Ostfeld (1995) the classical paradigm leads to many false assumptions that undermine many, but not all, of the principles that management systems have been based on. These are: (a) systems are closed to outside influences and therefore management can ignore changes outside management boundaries; (b) systems are self-regulating, will remain relatively stable in the face of environmental change, and therefore management can rely on benign neglect; (c) systems possess a single end point at which they are at equilibrium and therefore a management strategy of benign neglect will allow systems to maintain stability or return to the same compositional and functional state they were at in the past; (d) succession always proceeds through the same pathway so temporal changes are predictable and will take care of themselves; (e) disturbance is something that is outside the system so management can ignore it or try to stop it if it occurs; and (f) humans are not components of ecosystems so, for example, past impacts of Native Americans on current ecosystem conditions can be ignored.

The new paradigm is based on the assumptions that: (a) ecosystems and landscapes are dynamic, (b) disturbance is a critical component of systems; (c) ecosystems are controlled by biotic and physical processes that occur at different spatial scales and levels of the biological hierarchy; (d) succession does not necessarily follow the same path and end at the same equilibrium point; (e) spatial pattern is important to biological

diversity; (f) pattern–process interactions are organism specific; and (g) human activities of the recent and distant past have had strong influences on many ecosystems that we may perceive as 'natural' today (Pickett and Ostfelt 1995, Turner et al. 1995). The new metaphors of ecology may help us to sustain biological diversity but they probably make management more complex and difficult. Incorporation of these new principles into management must be based on understanding of the ecological limits or domains where successional and evolutionary processes can sustain biological diversity. In addition managers must have some idea of how these limits are distributed across landscapes and spatial scales and how they can vary over time.

DISTURBANCE

One of the foundations for conservation of biological diversity in forest landscapes is understanding and managing the disturbance regimes of a landscape under past natural or semi-natural conditions. The alteration of landscape disturbance regimes by humans has had four major effects: (a) exclusion of fire from fire-dependent ecosystems; (b) reduction in structural and compositional diversity through intensive forest management; (c) conversion of forests to other land-cover types such as agriculture and development; and (d) alteration of hydrological processes and disturbance regimes. Ultimately, the effects of human activities on climate and atmospheric conditions may produce the most pervasive changes of all.

Human alteration of fire regimes has had profound effects on the structure, composition, and function of many forest ecosystems. In some cases, human activity has increased fire frequency and intensity causing losses in species diversity and ecosystem productivity. For example, fire frequency and severity increased during the period of European settlement and logging of virgin forests in many areas of the world including Australia (Attiwill 1994a) and eastern North America, where pine and hemlock populations were depleted from many landscapes in the Great Lakes region. Losses of organic matter and nitrogen from soils have also resulted from hot and frequent slash fires associated with logging and land clearing (Whitney 1994) and slash and burn agriculture in tropical areas (Ramakrishnan et al. 1981, Mueller-Dombois 1981). On the other hand, suppression of fire by humans has drastically changed successional pathways, forest composition and structure, and increased the incidence of disease and insect outbreaks in many forest ecosystems including boreal forests

(Heinselman 1981), temperate coniferous forests in western North America (Kilgore 1981), oak forests in eastern North America (Abrams 1992), Mediterranean vegetation types (Naveh 1974) and fire-adapted eucalypt forests in Australia (Attiwill 1994b). The implications to managers are clear: if you change the fire regime you change the ecosystems and the landscape.

Intensive forest management for timber and wood fiber production has altered disturbance regimes by increasing the frequency and severity of disturbances in many landscapes relative to natural and semi-natural disturbance regimes (Spies and Cline 1988, Franklin and Forman 1987, Hansen et al. 1991, McComb et al. 1993, Swanson et al. 1993, Essen et al. 1992, Hunter 1990). In addition, the size and pattern of cutting units typically results in dissection from roads and perforation and fragmentation of remaining forest patches, thereby increasing edge effects (Chen et al. 1995) and decreasing the ability of some organisms to move around the landscape (Forman 1995, Spies et al. 1994, Hunter 1997). Increased frequency and severity of management disturbance has resulted in losses of old-growth forests and threats to species associated with old growth in the Pacific Northwest (FEMAT 1993) and reduction in structural (e.g., large trees, snags, decayed fallen trees) and compositional (deciduous trees in coniferous plantations) diversity and associated plant and animal species in intensively managed boreal forests (Essen et al. 1992, Angelstam 1997). Some foresters have stated that clearcutting imitates severe wildfire. While this may be true in some landscapes for some disturbance regime attributes (e.g., opening size and frequency), the degree of similarity with wildfire is typically low because of the high level of biomass removal from traditional clearcuts, the uniformity of structure within clearcuts, the low diversity of patch sizes, and the high cutting frequency (in landscapes where natural fire return intervals exceed 100 years). In landscapes with low to moderate severity fire regimes, logging practices can be made more similar to the natural disturbance regime by leaving live and dead trees as individuals and in groups (Franklin 1989, Attiwill 1994a) and altering cutting unit sizes and patterns (Franklin and Forman 1987). In landscapes with high severity fires, variation in severity probably left patches of relatively unburned forest especially near wetlands, rock outcrops or other fire breaks and in moist topographic positions. In this type of landscape logging frequency and severity can be varied across the landscape to imitate potential natural variation in fire frequency associated with different landscape units (Angestam 1997).

Conversion of forests to agriculture and development has had enormous impacts on the loss of forest biodiversity throughout history

(Williams 1989). The conversion from forest management to intensive agriculture results in drastic semi-permanent changes at stand and landscape scales. Much of the losses of virgin forest in the eastern United States can be attributed to clearing of forest for agriculture (Whitney 1994). Landscape effects of conversion to agriculture include rapid and severe forest fragmentation (Curtis 1959). Some forest landscapes such as New England have been able to recover to some degree from conversion to agriculture (Foster 1995). Many forest animals such as bear (*Ursus euartos*), cougar (*Felis concolor*), and moose (*Alces alces*) have begun to repopulate these former agricultural landscapes as forest cover has reached high levels. However, subtle changes in soil and species composition still remain over 150 years following abandonment of farming in this region. The message to management is that restoration of forests from loss and severe disturbances in agricultural landscapes is possible even where forests have been removed and soils altered, but it will be a slow process and will probably not return to the same structure and composition that occurred before the disturbance.

Human effects on the hydrology of rivers and wetlands is another example where humans have altered the frequency and severity of disturbance regimes causing declines in some species and changes in community structure (Johnson et al. 1976, Nilsson et al. 1991). In the case of rivers, logging operations which used rivers as transportation corridors frequently produced log jams and splash dams which when broken caused severe floods that removed riparian vegetation and aquatic habitat (Whitney 1994, Sedell et al. 1991). Conversely, channelization and damming of rivers has often resulted in fewer floods and narrower, less complex river channels and floodplains (Chamberlin et al. 1991). The effects of altered flow and meandering rate can reduce the abundance of early successional species (*Populus* spp. and *Salix* spp.) reducing species diversity and habitat complexity (Johnson et al. 1976). The message to management is that floods are critical disturbances in maintaining the diversity and function of riparian forests.

VEGETATIVE PROCESSES

Management of landscape dynamics must not only be based on disturbance regimes, but also vegetation processes that underlie the ecosystem response to disturbances. Following disturbance, vegetation composition and structure may not change in desirable ways or at desirable or expected rates because of biotic interactions. The existence of alter-

native stable states of vegetation (where some alternatives do not meet biodiversity goals) has been linked not only to disturbance regimes but also to regeneration and establishment stages, and competitive ability and longevity of vegetation (Hobbs 1994). The absence of plants in many landscapes may be a result of loss of propagule sources rather than absence of suitable habitat (Duffy and Meier 1992, Sillett 1994). Understanding potential bottlenecks in vegetation processes that lead to particular vegetation states is an important part of managing landscape dynamics. For example, loss of inputs of large dead conifer trees into streams as a result of logging along streams has been associated with declines in the quality of salmonid habitat in the Pacific Northwest (FEMAT 1993). Consequently, one goal of management for biodiversity in this region is to increase the supply of large conifer trees along streams. This goal may not be achieved by simply setting up riparian reserves. Many existing riparian areas lack conifer regeneration today probably because of lack of seed sources for some shade-tolerant conifer species and because of competition from aggressive deciduous shrubs and trees in moist streamside environments (Minore and Weatherly 1994, Pabst and Spies 1998). As a result, achieving aquatic conservation goals in this region is dependent on finding ways to establish conifers in the face of biotic constraints. Management practices that may be required to deal with vegetation processes include planting of desirable species, elimination of undesirable species, and manipulating stand density. The vegetation process that is probably most sensitive to landscape-scale alterations by humans is dispersal. Managers can actively disperse propagules (e.g., through planting or seeding) but to provide for the entire suite of species that may have mobility problems it may be more cost effective to retain source areas for natural dispersal within landscapes. Source areas can take the form of individual retention trees with complements of epiphytes, small patches of trees with both epiphytes and protected forest floors, or riparian zones and larger patches that contain species with low capacities for dispersal.

SOME RECOMMENDATIONS FOR MAINTAINING TEMPORAL AND SPATIAL HETEROGENEITY OF LANDSCAPES

Maintain the tails of age class and patch size distributions

Under typical forest management plans which are based on the concept of a 'fully regulated' forest the tails of age-class distributions are cut off, beyond the rotation age. Very young stages may be cut off as well if

silvicultural practices accelerate canopy closure. Consequently, conserva-
tion of biological diversity in forest landscapes would be promoted by
maintaining a broad range of age classes including a significant portion of
old stands and old structures. The exact amount would depend on the dis-
turbance regime and other factors.

As with old stands, very large patches are typically lost from managed
landscapes (Spies *et al.* 1994). A variety of authors (e.g., Wright 1974,
Pickett and Thompson 1978) have suggested that natural areas should be
sufficiently large to include a mosaic of all normal stages in community
development, and that natural processes of perturbation and recovery
should be allowed to occur without intervention. The argument for large
patches is not restricted to strict forest reserves, but applies to more
actively managed areas. In landscape lacking reserves, harvest scheduling
and road building can be modified to create large blocks of forest that may
slowly change across the landscape. The size and number of large forest
blocks, whether actively managed or reserves, will be a function of distur-
bance regime, biodiversity goals, and practical considerations. By
knowing the frequency and extent of disturbances within a landscape, the
spatial extent necessary to incorporate this disturbance could be deter-
mined. Obviously, landscapes characterized by very large scale patterns of
disturbance and recovery would necessitate a much larger natural area
than might be required under systems in which perturbations are small
and frequent. The importance of infrequent disturbances, especially if
they are large in size, is noteworthy (Turner and Dale in prep). If the rare
disturbances which affect a large portion of a system are neglected, our
understanding of landscape dynamics as well as species persistence, ener-
getics, soil, and nutrient relations will be impeded (Franklin and
Hemstrom 1981). Management strategies that retain large forest blocks
are a common element of many forest landscape management designs
(Harris 1984, FEMAT 1993, Crow *et al.* 1994). Less common are conserva-
tion designs that allow large-scale disturbances to occur (Hunter 1993).

Develop goals for spatial pattern

Landscapes managed with uniform cutting unit sizes and spatial
distributions can develop into relatively homogeneous mosaics despite
apparent diversity in forest conditions. In other words, pattern diversity
can be low which could result in loss of some species and processes.
Elements of spatial pattern include amount, proportion, size, interpatch
distance, variation in patch size and interpatch distances, and landscape
connectivity (Harrison and Fahrig 1995). Strictly speaking, absolute or rel-

ative amount of a forest type is not spatial because it does not require
knowledge of the distribution of habitat across space. Many of these char-
acteristics are dependent on each other; for example interpatch distance is
related to amount of a particular forest type in the landscape. The amount
of a forest type may be the single most important attribute; however,
spatial patterning that affects edge density and connectivity can also be
important to species and processes that depend on flows between land-
scape elements and through landscapes (Franklin and Forman 1987).
Maintenance of some large patches in landscape will reduce edge density.
Connectivity can be provided through corridor-like features, 'stepping
stones', or reduced contrast between the habitat type of interest and its
surrounding matrix. Since organisms perceive landscapes differently, no
one design will be best for all (Hunter 1990). However, in general, spatial
designs that provide for the most specialized species with the largest
home ranges or large area needs should provide for the spatial needs of
organisms with more general habitat needs or small area needs.

Altering spatial pattern of cutting may compensate for 'high' rates of cutting for some components of biological diversity

The effects of cutting pattern on species and landscape pattern and
process are generally dependent on disturbance rate and amount of suit-
able habitat (Spies *et al.* 1994, Harrison and Fahrig 1995). At high rates of
cutting amounts of interior forest habitat are low no matter what the
spatial pattern of cutting and at low rates of cutting, varying spatial pattern
has little effect on amount of edge or interior forest. At intermediate rates
of cutting, different patterns of cutting can result in very different propor-
tions of edge and interior forest conditions. Some cutting patterns pre-
serve interior conditions and connectivity more than others (Franklin and
Forman 1987) so that for a constant rate of disturbance (or commodity
outputs) different levels of edge or interior habitat may be achieved
through different disturbance patterns. Managers may be able to take
advantage of this compensation to meet goals of interior or edge condi-
tion while maintaining the same rate of cutting on an area basis. However,
there is a limit to which changing cutting pattern can compensate for rela-
tively high rates of cutting. The effects of spatial pattern are also dependent
on the proportion of habitat in a landscape (Andrén 1994, McGarigal and
McComb 1995). Where habitat is very abundant or very low, spatial pattern
may not be as important. However, where habitat is moderately low in a
landscape the condition of the landscape matrix may become even more
important (Franklin 1993). This may be especially true in intensively

managed landscapes where only a few isolated older forest islands exist. In this situation, retention of elements of natural forest (e.g., large trees, snags, fallen trees, hardwoods) in the managed matrix may provide important refugia or dispersal habitat.

Landscape locations are important and processes vary across environmental gradients within landscapes

Landscapes are fundamentally structured by the physical template of the earth's surface (Swanson *et al.* 1988, Rowe and Barnes 1994). The physiographic template should serve as the basis of managing landscapes for biological diversity (Barnes *et al.* 1982, Lapin and Barnes 1995). Elements of location that are important include: position along topo-climatic and topo-edaphic gradients, watersheds, riparian areas, wetlands, cliffs, talus and caves and special soils and geological formations (Chapter 5). One important implication to management is that allocation of reserves, and other management practices across landscapes should correspond to the physical template as much as possible so that management is working with nature and not against it. For example, Angelstam (1997) has proposed a landscape conservation scheme for boreal forests in which reserves and management intensity are tailored to site types with different frequencies of fire based on their topographic and soil conditions.

Three case studies

While general concepts and theories provide a framework for understanding and managing forest mosaics, the knowledge required to understand the dynamics of a particular landscape and to achieve particular conservation goals must also come from a solid empirical knowledge of the environmental patterns, disturbance regimes and vegetation processes of specific places. In the following section we present three case studies to illustrate the diversity and complexity of landscape dynamics and to show how information about disturbance and succession can form the basis of conservation plans and practices for different management goals.

MIXED HARDWOOD–CONIFER REGION OF NORTHERN LAKE STATES

The landscapes of the northern lake states region of the United States are a mosaic of hemlock–hardwood forests, white and red pine forests, and boreal spruce–birch–fir forests (Frelich and Reich 1996).

Although topographic relief in this area is low, there are strong physiographic controls over vegetation patterns as a result of differences in soil drainage and texture (Pregitzer and Barnes 1984, Spies and Barnes 1985). Both wind and fire are major natural disturbances in the region but the two disturbance types differ in their dominance across the region and within landscapes. Fire frequencies increase from east to west. Heinselman (1973, 1981) estimates that natural fire rotations ranged from 50 to 100 years in the 'near boreal' pine, spruce and fir forests of the western and northern parts of the region, to 150 years in white/red pine forests, and from 350 to over 1400 years for the northern hardwood–hemlock forests on mesic soils (Stearns 1949, Whitney 1986, Frelich and Lorimer 1991). Where fire is infrequent, wind becomes an important disturbance agent. Frelich and Lorimer (1991) estimate that rotation periods range from 69 years for low severity disturbance (<10% canopy removal) to almost 2000 years for high severity disturbances (>60% canopy removal) at the scale of their sample plots (0.5 ha). Many of these larger disturbances were apparently associated with thunderstorm downbursts which produce patches ranging from a few meters to over 1 km in widths (Canham and Loucks 1984). The relatively fine scale of the disturbance regime of the northern hardwood forests creates forests with uneven-age distributions in contrast to the more even-aged distributions found in jack pine and red pine forests which are typically of fire origin. Consequently, the hemlock–hardwood forests of this region are characterized as 'quasi-equilibrium' landscapes (Frelich and Lorimer 1991), whereas the fire-prone boreal forest types of the region with high frequencies of large fires are not equilibrium landscapes (Baker 1989). Successional pathways within these forests can be relatively simple in the case of hemlock–hardwood forests which may cycle between dominance by different hardwood species in small gap disturbances to complex in the case of white pine dominated forests which can move between at least three different types depending on the disturbance frequency and intensity (Frelich and Reich 1996).

The juxtaposition of wetlands, mesic moraines, and dry outwash plains, results in a relatively fine-grained mixture of boreal, pine and northern hardwood forests (Barnes *et al.* 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985). The particular pattern of ecosystem types may influence disturbance and vegetation dynamics in these mosaic landscapes. Fire-resistant hardwood forest types may experience more fires if they are adjacent to dry fire-prone pine forests. Wetlands and lakes may act as fire breaks and islands may be isolated from large fires but more exposed to lightning strikes and smaller fires (Bergeron 1991). Mass

effects (Cody 1989) of local seed sources may also play a role in maintaining species on sites where they are not most competitive. For example, drier deciduous forests adjacent to hemlock-dominated wetlands may be more susceptible to invasion by hemlock than when they are further away from hemlock seed sources (Spies 1983, Frelich *et al.* 1993). Spatial pattern development does not necessarily require variability in disturbance and environment. A shifting mosaic of hemlock patches and sugar maple patches may arise simply as a result of competitive interactions of the species and operate within the coarser scale patterns set up by disturbances (Frelich *et al.* 1993).

Logging and logging related fires in the 1800s and early 1900s removed almost all of the original forest cover. Areas that have escaped human disturbance in the last 150 years exist in one large wilderness area (Boundary Waters Canoe Area) and several smaller wilderness areas and small set asides. Today, areas are dominated by forests less than 150 years old. Given the long return intervals between severe disturbances in hemlock–hardwood forests, almost any forest management regime that uses clearcuts larger than a few hectares and rotations under 200 years is probably larger, much more severe, and more frequent than the natural disturbance regime dominated by wind and small gap disturbances. Under natural disturbance regimes more than 90% of the hemlock–hardwood landscape type was probably in an old-growth state (>120 years) (Frelich and Reich 1996). Under timber management (40 to 120 year rotations), very little of the hardwood landscape would be in an old-growth condition. In contrast, in boreal landscapes of wilderness areas where fire rotations were 50 years, human fire suppression has decreased disturbance frequency relative to presettlement disturbance regimes. This change of disturbance regime is changing successional pathways toward shade-tolerant species and the role of small canopy gap disturbances in succession is becoming more important than it was in presettlement times (Frelich and Reich 1995). Jack pine, a fire-dependent species, may be lost from these landscapes. Even if fire occurs in the future, seed sources of jack pine may not be available to colonize burns and composition may shift more to aspen.

Human disturbances can either increase or decrease landscape heterogeneity in these landscapes depending on the focus and scale (Baker 1992, Mladenoff *et al.* 1993). A clear signature of forest cutting on landscape patterns was observed in the upper Midwestern United States (Mladenoff *et al.* 1993): the disturbed forest landscape had significantly more small forest patches and fewer large, matrix patches than the intact landscape, and forest patches in the disturbed landscape were simpler in shape (Figure
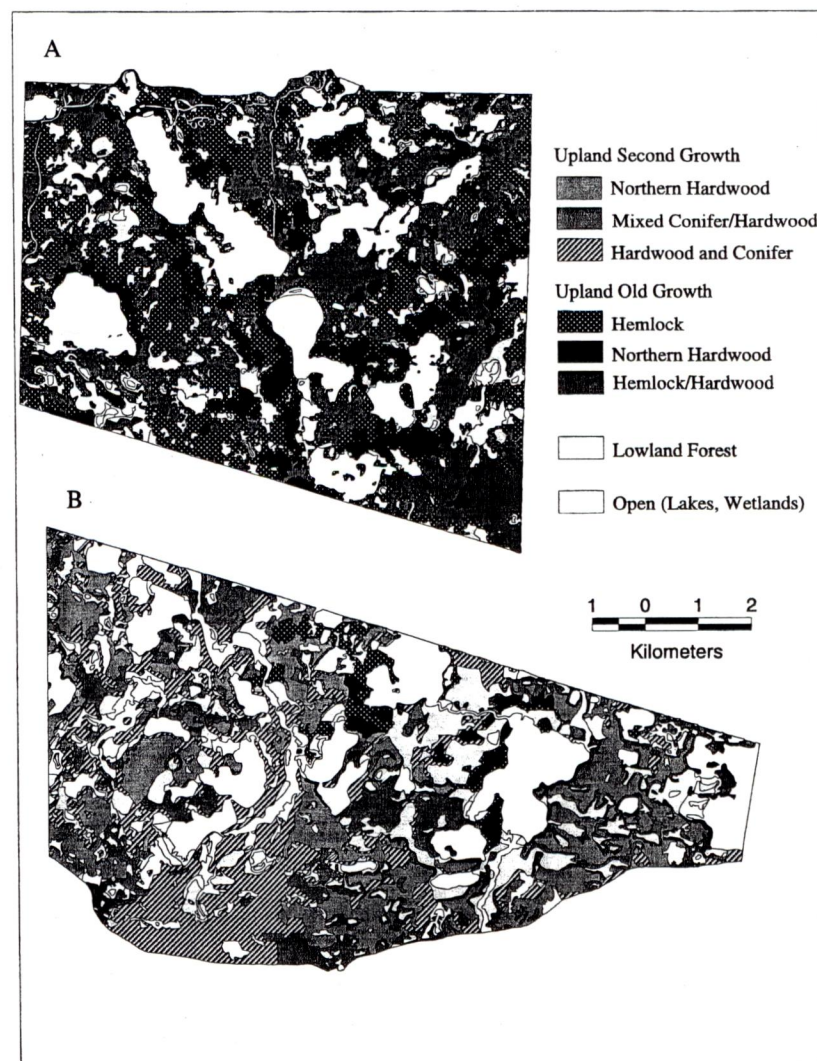
Upland Second Growth
- Northern Hardwood
- Mixed Conifer/Hardwood
- Hardwood and Conifer

Upland Old Growth
- Hemlock
- Northern Hardwood
- Hemlock/Hardwood

- Lowland Forest
- Open (Lakes, Wetlands)

Fig. 4.7. Spatial pattern of forest communities in northern Michigan, USA: (A) Sylvania Wilderness Area, an intact forested landscape, and (B) Border Lakes, a similar region which has been subjected to forest harvesting. (From Mladenoff *et al.* 1993, p. 297.)

4.7). In addition, certain types of juxtapositions between different forest community types (e.g., hemlock–lowland conifers) were present in the intact landscape but absent in the disturbed landscape.

The implications to management in this region are that: (a) human alterations of disturbance regimes relative to natural and semi-natural

systems have produced different landscape dynamics leading to losses of biological diversity at landscape scales; (b) the diversity of ecosystems and forest dynamics along climatic and species gradients makes it impossible to apply the same practices to maintain biological diversity across the region; (c) landscape management designs for conservation goals will need to be based on restoring disturbance processes such as fire, and recreating or maintaining the important older age classes, larger patch sizes, and connectivity (Crow *et al.* 1994).

FIRE-DOMINATED LANDSCAPES OF THE NORTHERN ROCKIES: YELLOWSTONE NATIONAL PARK

Yellowstone National Park (YNP) offers a good case study of a fire-dominated landscape and the problems of managing fire in a landscape where commodity extraction does not exist and ecological goals are paramount. The park encompasses 9000 km² in the northwest corner of Wyoming and is primarily a high, forested plateau. Approximately 80% of the park is covered with coniferous forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*). Fire has long been an important component of this landscape, and, as in most other parts of the Rocky Mountains, fire has profoundly influenced the fauna, flora, and ecological processes of the Yellowstone area (e.g., Houston 1973, Loope and Gruell 1973, Taylor 1973, Arno 1980, Romme 1982, Romme and Despain 1989, Despain 1991). Reconstructions of fire history demonstrated that extensive fires had occurred in the early 1700s and that the landscape was a non-equilibrium mosaic of forest stands in differing successional stages (Romme 1982). With the initiation of a natural fire program in Yellowstone, 235 lightning-caused fires were permitted to burn without interference. Most of these fires went out by themselves before burning more than a hectare, and the largest fire burned about 3100 ha in 1981. However, fires in 1988 affected more than 250 000 ha in YNP and surrounding lands as a consequence of unusually prolonged drought and high winds (Renkin and Despain 1992, Bessie and Johnson 1995). The enormous extent and severity of the 1988 fires surprised many managers and researchers, and such large fires may represent a major disturbance event that occurs at 100 to 300 year intervals in this landscape (Romme and Despain 1989) (Figure 4.8).

Fires in Yellowstone have created a mosaic of burn severities across the landscape as a result of variations in wind, topography, vegetation, and time of burning (Rowe and Scotter 1973, Wright and Heinselman 1973, Van Wagner 1983). The 1988 fires provide an ideal opportunity to study the

ecological effects of fire size and pattern (Christensen *et al.* 1989, Turner *et al.* 1994). Some areas of Yellowstone experienced stand-replacing crown fires, other areas experienced stand-replacing severe-surface burns, and still other areas received light-surface burns in which trees were scorched but not killed. Understanding the effect of fire on landscape heterogeneity is important because the kinds, amounts, and spatial distribution of burned and unburned areas may influence the re-establishment of plant species on burned sites. Although the fires were quite large, the majority of severely burned areas were within close proximity (50 to 200 m) to unburned or lightly burned areas, suggesting that few burned sites are very far from potential sources of propagules for plant re-establishment (Turner *et al.* 1994).

How has the fire-created mosaic influenced the developing forest community? Burn severity and patch size both had significant effects on initial postfire succession (Turner *et al.* 1997). Severely burned areas had higher cover and density of lodgepole pine seedlings, greater abundance of opportunistic species, and lower richness of vascular plant species than less severely burned areas. Larger burned patches had higher cover of tree seedlings and shrubs, greater densities of lodgepole pine seedlings and opportunistic species, and lower species richness than smaller patches. Surprisingly, dispersal into the burned areas from the surround-

Fig. 4.8. View across the landscape of Yellowstone National Park, Wyoming, following the 1988 fires that affected about 45% of the park. (Monica Turner photo, October 1988).

ing unburned forest has not been an important mechanism for re-establishment of forest species thus far. Most plant cover in burned areas consisted of resprouting survivors during the first three years after the fires, and the seed from these residuals effectively filled in much of the burned area.

The patterns of initial postfire succession were surprisingly more variable in space and time than current theory would have suggested (Turner *et al.* 1997). Although succession across much of YNP appears to be moving toward plant communities similar to those that burned in 1988, primarily because of extensive biotic residuals even within large burned areas, there are some profound differences in plant re-establishment. For example, forest re-establishment is questionable in large burned areas that were old (>400 years) forests with low pre-fire serotiny (Turner *et al.*, unpublished data). Even where forests are regenerating, there is tremendous spatial variation in succession across the landscape – ranging from dense 'doghair' stands of lodgepole pine to sparse lodgepole pine stands. Thus, the 1988 fires may have initiated multiple successional pathways related to differential fire severity, fire size, pre-fire community structure. These alternative pathways include development of non-forest communities in some areas previously characterized by coniferous forest.

Unanticipated recruitment of seedling aspen in areas of Yellowstone previously dominated by lodgepole pine also followed the 1988 fires (Romme *et al.* 1997). Tree-sized aspen have not regenerated since park establishment in 1872 (Kay 1993, Romme *et al.* 1997) and aspen occupied only about 1% of YNP prior to the 1988 fires (Despain 1991), occurring almost exclusively on the low-elevation sagebrush–grasslands in northern YNP. However, abundant aspen seedlings were observed in 1989 across widely distributed burned areas of the Yellowstone Plateau, and these seedlings, though browsed by ungulates, were still persisting eight years after the fire. The flush of post-fire aspen seedling establishment may enhance the long-term ability of this species to persist in YNP by providing sources of seedling and vegetative reproduction. The increased genetic diversity in the seedling populations (Tuskan *et al.* 1996) may enhance the ability of aspen to withstand current climate conditions, levels of interspecific competition, and ungulate browsing (Jelinski 1993).

Future forest conditions in the regions with very low tree seedling densities are least predictable in Yellowstone. Continued measurement will be necessary to determine whether succession there is simply proceeding at a much slower rate toward a coniferous forest or whether a non-forest com-

munity will persist. Little is known about how long-term dynamics will influence indicators of ecosystem function at landscape scales.

Given the persistent spatial variation in post-fire stand densities and herbaceous cover across the YNP landscape, implications for long-term ecosystem function are substantial. If fire management policies do not allow a full range of patch sizes and severities the structure and composition of the Yellowstone landscape will change and with uncertain effects on species populations that may cascade across several trophic levels. The essential debate in management at Yellowstone is whether a more active prescribed fire management scheme is needed than the current policy allows. Under the current policy lightning-caused fires are permitted to burn, prescribed fires are used to a limited extent to reduce fuel levels around human settlements, and non-intentional human-caused fires are suppressed (Knight 1991). Some scientists argue that more prescribed burning is necessary to counteract the effects of fire suppression prior to the 1970s which may have created abnormally high fuel loads that now threaten to create much larger and more intense fires than have occurred in the past (Bonnicksen 1989). The fact that fires that start outside the park are typically suppressed probably means that fire frequency has decreased within the park. On the other hand, the presence of humans within the park may produce higher frequencies of ignition of fire. The 2.5 million hectare area of the National Park and adjacent National Forest Wilderness areas may be large enough to maintain a more passive approach to fire management. However, without a better understanding of the fire regimes of the past, it will be difficult to determine just how well either more passive or more active management strategies will achieve park goals.

PACIFIC NORTHWEST CONIFER FOREST LANDSCAPES

The coastal (west of the crest of the Cascade Mountain Range) forests of the Pacific Northwest are dominated by Douglas-fir and western hemlock and are characterized by variable fire-dominated natural disturbance regimes. Wind can be an important disturbance in immediate coastal areas in sitka spruce (*Picea sitchensis*)/western hemlock forests which experience episodic, catastrophic windstorms (Ruth and Harris 1979). However, fire still occurs in near-coast areas of Washington, Oregon and northern California. Fire frequencies in this region range from 90 years on dry sites or drier parts of the region to over 900 years in the moist coastal and northerly parts. Fire occurrences are irregular and

difficult to predict (Agee 1993). Fires can be very large – over 200 000 ha – and severe, killing all trees in very large patches (Agee 1993). Moderate sized landscapes (100 000 ha) such as Mt Rainier National Park do not appear to be in a quasi-equilibrium (Hemstrom and Franklin 1982). Given the large size of many fires, it appears that quasi-equilibrium conditions would not occur in areas of less than a million hectares and perhaps much larger. However, in the long term average amount of old-growth forests (>200 years) is estimated to range from about 40% to 80% (Spies and Franklin 1988, Booth 1991, Fahnestock and Agee 1983, Ripple 1994). Fire severity increases and frequency and patchiness appear to decrease with increasing moisture, which promotes fuel accumulation. Fire can set up large (10^3 to 10^4 ha) patches of similar-aged forest in the landscape and subsequent small gap disturbances and patchy low to moderate severity fires diversify and propel these cohorts into old-growth stages of development. In the drier interior parts of the region, where mixed forests of ponderosa pine (*Pinus ponderosa*), Douglas-fir and white fir (*Abies concolor*) and other conifers occur, high natural fire frequencies (<20 years) maintained many forests in ponderosa pine with relatively open understories and low fuel accumulations. With fire suppression many of these stands have developed dense understories of shade-tolerant Douglas-fir and white fir and higher fuel accumulations, changing the fire regimes from low-severity surface fires to high-severity crown fires (Seidel and Cochran 1981, Agee 1993).

Successional development in the coastal region is relatively slow and long – a function of long establishment periods and long-lived seral dominants (>750 years). Structural differentiation can require over 400 years to level off (Spies and Franklin 1991) (Figure 4.4). Successional pathways are relatively simple, converging on a variety of shade-tolerant conifer forests depending on elevation and climatic gradients (Franklin and Dyrness 1973, Franklin and Hemstrom 1981, Ohmann and Spies 1998). Small canopy-gap disturbances from wind and disease, which occur every 100 to 200 years and average 300 m² in size, play an important role in the development of old-growth forest structure (Spies et al. 1990). In wetter parts of the region, particularly in moist riparian zones where deciduous trees and shrubs are competitive, hydrological and logging disturbances can result in the development of relatively stable patches of deciduous shrubs that resist invasion by conifer seedlings (Minore and Weatherly 1994). This state is potentially undesirable from an aquatic habitat perspective, especially in watersheds lacking large conifers that were removed by extensive logging. Large conifer wood helps to create stream

habitat complexity and lack of large conifers in watersheds reduces the inputs to streams from individual treefalls and landslides.

The disturbance regime imposed by humans in this region is typically based on intensive forest management with relatively short rotations (40 to 80 years), clearcut logging and preference for conifers, especially Douglas-fir. On public forest lands, which occupy about half of the forest area, the rate of cutting has been substantially reduced since the early 1990s (FEMAT 1993). Despite these recent changes, 30–40% of public forest landscapes contain a legacy of a patchwork of forest plantations that were established in the 1950s through the 1980s. Relative to natural disturbance regimes, logging disturbances have typically been more frequent, more severe, left fewer biological legacies (i.e., structures and species that survive disturbances) and created more edge and fragmented landscapes (Spies and Cline 1988, Hansen et al. 1991, McComb et al. 1993, Franklin and Forman 1987, Chen et al. 1995, Spies et al. 1994). Interestingly, the typical patch size clearcuts (10–20 ha) may be similar to that of wildfires in the southern part of the region, where fires tend to be patchy (Morrison and Swanson 1990, Spies et al. 1994). However, the range of clearcut sizes is much narrower than the range of wildfire sizes. The high frequency of clearcutting on private lands (40–50 years) and the relatively high rate on public lands (80 years) until the early 1990s results in larger patches (100s to 1000s of ha) of young plantations as clearcut units coalesce over 10 to 20 year periods.

Recent changes in forest management policies on public lands have reduced rates of cutting and, where logging is still allowed, have increased the amount of live and dead trees that are left on the site (FEMAT 1993). On private lands, intensive forestry is still practiced, although state forest policies require retention of some trees in riparian and upslope stands. It is unlikely that wildfire regimes will be allowed to spread except in some wilderness areas. The area of old-growth forest has declined by over 50% in the last 50 years (Bolsinger and Wadell 1993). The only remaining old forest is on public lands and concern over species viability and historical losses of old-growth forests means that further losses of old forest, even from natural events such as wildfire, are not desirable.

The Northwest Forest Plan (FEMAT 1993) is one of the most comprehensive regional forest conservation plans that relies on application of conservation biology, landscape ecology and ecosystem management. The plan, whose goals are the protection of terrestrial and aquatic species associated with late successional and old-growth forests and conservation of old-growth ecosystems and watersheds, relies on a set of strategies

including species-based conservation, reserve-based ecosystem conservation, and active management and restoration. Under this plan 80% of a 10 million hectare federal landbase (out of a total of 57 million ha of public and private land) in western Washington, Oregon, and northern California is in some form of high-level protection including national parks and wilderness areas (29%), late successional reserves (29%), riparian reserves (9%), special management areas (e.g., scenic areas, natural areas and adaptive management areas [13%] where no existing old-growth can be cut [FEMAT 1993, p. II-26]). The remaining 20% of the landscape forms the 'matrix' where most of the scheduled timber harvesting will occur (Figure 4.9).

The land allocations within this plan are based on many principles of forest ecology, landscape ecology and conservation biology. For example, the protection of many existing old-growth stands in late successional reserves is based on the understanding that these older age classes were relatively common in these landscapes under natural fire regimes and that land clearing and intensive forest management have reduced the abundance of these ecosystems across all ownerships. Thus, the federal landbase is the only area where this type of ecosystem occurs and is allowed to develop. In addition to providing for the tails of the age-class distributions, the federal lands also now provide for some of the largest patches (10^4 to 10^5 ha) of continuous forest in the region. The design of the Northwest Forest Plan also took spatial pattern of forest practices into account through consideration of spacing of reserves to facilitate dispersal of the northern spotted owl and use of riparian reserves to provide for land–water interactions (e.g., inputs of large conifer wood) and contribute to connectivity of forest cover across the landscape. Where management is more intense in the matrix lands, patchy fires are simulated in logging operations by leaving at least 15% of the logging unit in small patches (0.2 to 1.0 ha) of large live trees and existing standing dead trees and retaining existing large wood on the forest floor. These retention guidelines are intended to provide for disturbance-sensitive elements of biological diversity that can use old-forest structures through cutting cycles. Finally, the importance of vegetative processes is recognized in the plan for managing existing plantations within the late successional reserves. The development of trees in these relatively dense stands does not follow the same pathway as old-growth stands which developed under lower densities and through a series of partial disturbances (Tappeiner et al. 1997). As a result, it may be that trees in these stands will develop old-growth characteristics (e.g., large limbs and epi-
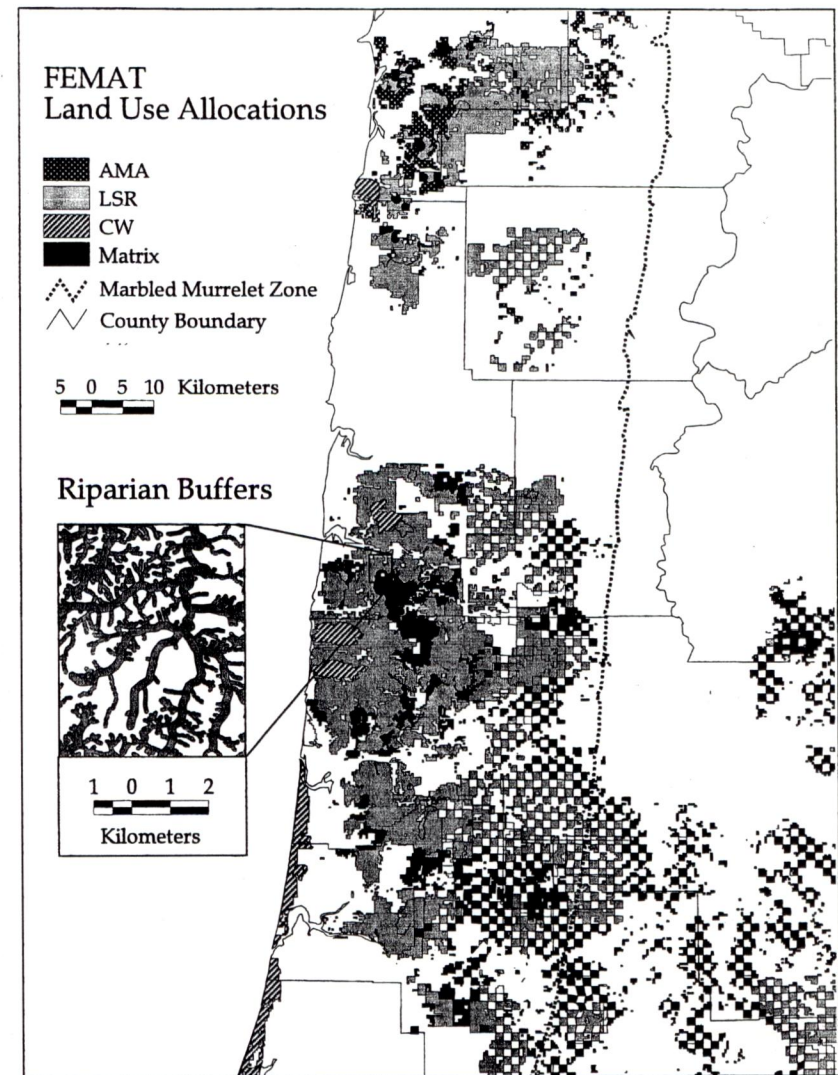
Fig. 4.9. Spatial distribution of late-successional (old-growth) reserves (light gray), key watersheds (stripped) and matrix lands (dark gray) in western Oregon on Federal lands and examples of riparian reserve strategy. (Adapted from FEMAT 1993.)

cormic branch fans) more slowly than under natural conditions. Consequently, thinning may be needed in young plantations (<80 years old) to facilitate their development into late-successional and old-growth forest structure.

Summary

Forests are dynamic mosaics driven by disturbance and biotic processes. The patterns and rates of temporal and spatial change vary with scale of observation and may differ across forest types and regions. The regime of a disturbance can be used to evaluate its potential ecological effects and evaluate how changes in management practices might affect forest dynamics and biological diversity. Scientific perspectives on disturbance and forest succession have changed in recent decades from emphasis on equilibrium and end points to emphasis on process, pathway and heterogeneity. Although forest dynamics is a complex process, it can be divided into several stages that are useful in management and mapping of forest mosaics. Because of past land-use and forest management practices the later stages of succession, especially old-growth forests, are lacking in many landscapes. The absence of old age classes and associated habitats has resulted in loss of biological diversity in many regions.

Forest landscapes are rich in spatial heterogeneity from a variety of causes, including environment, biotic interactions and disturbance and succession. Spatial patterns can have strong influences on population dynamics and ecosystem processes including the spread of disturbance. Human activities have had a profound effect on forest structure and pattern. In managed forest landscapes, cutting patterns often result in reduction in patch sizes and increases in edge densities. Spatial heterogeneity can be described using a variety of metrics. No single metric alone is sufficient for quantifying spatial pattern and the choice of metrics will depend on the question and process at hand.

Maintenance of temporal and spatial heterogeneity in landscapes can help to conserve biological diversity. Specific recommendations include: (a) maintain tails of age class and patch size distributions; (b) develop goals for spatial pattern; (c) take advantage of tradeoffs between rates of cutting and spatial pattern; (d) incorporate important locations on the physical template of the landscape into planning and management. Three case studies are presented which illustrate the diversity of landscape dynamics, the importance of disturbance, succession, and spatial pattern in biological diversity and challenges and solutions to managing dynamic forest mosaics.

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5   Abiotic factors

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The western edge of Yellowstone National Park (YNP) is one of North America's most striking borders between a natural landscape and a human-altered one. Within YNP, vast stands of centuries-old coniferous forest are broken only by paths of recent wildfires. Outside the park, numerous clearcuts fragment what forest remains. Yellowstone's old-growth forests and wildfire patches are rich in structural complexity, with many canopy layers, tree sizes, and/or abundant snags. West of the park, structural complexity has been greatly reduced by clearcutting and fire suppression. Most modern ecologists would predict that the structural complexity in YNP supports a diverse community of animals and plants, while fewer native species are expected to occur in the human-impacted lands outside of the park. Science, however, is full of surprises.

When we sampled the bird community in this area, we found as expected that individual bird species differed in abundance among natural old-growth forests, wildfire patches, and clearcuts. However, bird species richness and total bird abundance did not differ among these stand types (Hansen and Harting, in prep). Moreover, bird density was low in all three stand types; only about 25% of what we had found in similar stands in western Oregon. Why is bird richness not strongly related to structural complexity in this landscape and bird abundance low compared with other biomes?

Nineteenth-century ecologists would likely not have been surprised at our observations in Yellowstone. They might have suggested that abiotic factors like topography, climate, and soil can exert a stronger influence on species than structural complexity. While many modern ecologists have focused on the important relationships between natural disturbance, structural complexity, and species diversity (Chapter 4), classical ecologists looked more towards the role of abiotic factors in controlling communities. Early biogeographers like Merriam (1894) were struck by how well the distributions of broad vegetation classes correlated with altitude, and referred to elevational bands as 'life zones'. Clements (1936) and

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