in High Latitude Rainforests and Associated Ecosystems of the west coast of the Americas. Lawford et al 1995 Springer-Verlag

14. Implications of Patch Dynamics for Forested Ecosystems in the Pacific Northwest

G.A. Bradshaw, Frederick J. Swanson, and
Maria R. Fiorella

2249

It is not possible to discuss ecosytem processes and functions without explicit reference to the relevant scales of analysis. Although the concepts of heterogeneity and patchiness have been used for nearly twenty years (e.g., Pickett, 1991; Wiens, 1976) terms such as "pattern", "hierarchical", and "scale" appear with increasing frequency in journals from disciplines as disparate as geophysics, ecology, and oceanography (e.g., Grant, Swanson, & Wolman, 1990; Moloney, Morin, & Levin, 1991; Powell, 1989). Two current approaches to understanding patterns in the ecosystem are patch dynamics and hierarchy theory (O'Neill, DeAngelis, Wade, & Allen, 1986; Pickett and White, 1985; Steele et al., 1992; Wiens, 1976). The concepts of patch dynamics and hierarchy theory focus on relationships and phenomena across spatial and temporal scales. Hierarchy theory views the system as organized into levels by its intrinsic structure, where flux between levels is regulated by regionalized variables. On the other hand, patch dynamics has focused attention on the heterogeneous nature of the landscape, where the landscape evolves as a mosaic of patches. In ecosystems, this heterogeneity or variability is expressed as patterns in the distribution of plants, animals, and abiotic processes. More recently, these concepts have been incorporated into conservation design and forest and stream management plans (e.g., U.S.D.A., 1993; Swanson et al., 1994).

Concurrent with this conceptual shift has been the dramatic ascendence of technology used in the natural sciences. Computer accessibility and the development of accurate and innovative measurement tools have broadened the scope of field and laboratory experimentation previously hindered by feasibility constraints. For instance, satellite imagery and GIS maps provide media by which spatially explicit information from several disciplines (e.g., geomorphology, vegetation, stream hydrology, and fish population biology) can be integrated (Michener et al., 1994; Goodchild, 1993). In conjunction with these conceptual and technological advances, there has been increased concern regarding human impacts on the environment. The result has been increased conflict over natural resource management. Recognition of the cumulative effects of pollution on global climate has underscored the connectivity of local environments to events at distances and scales outside everyday perception; the range of human impact on ecosystems extends well beyond artificial borders. As a result of all three factors (i.e., conceptual, technological, and social), research and management interests have been directed to spatial and temporal aspects of natural ecosystems. The manipulation of forested landscapes, and the consequences thereof, are now consciously considered in conservation and management designs. Increasingly, management concerns are shifting to the "forest" rather than the "trees."

The temperate forests of the Pacific Northwest (PNW), U.S.A., represent a prime example of a setting in which scientific and socioeconomic concerns have converged. The Northwest landscapes form a focal point for many current political and socioeconomic debates in the U.S. environmental arena (U.S.D.A., 1993). The region has undergone a significant change in its disturbance regime due to intensive and extensive land-use practices (e.g., timber harvesting, grazing, fire suppression, and mining) (see Harris, 1984; Spies, Ripple, & Bradshaw, 1994). Before the onset of intensive timber harvesting activity, which began roughly 100 years ago and has continued intensely on public lands the past forty years, the PNW lands west of the Cascade Range crest were characterized by a fairly continuous forest cover. At present, the public and private forests of Washington, Oregon, and even Alaska are punctuated with clearcuts and managed plantations (Figure 14.1; Spies, Ripple, & Bradshaw, 1994). Widespread declines and shifts in the habitat and abundances of late successional animal species have forced a reevaluation of forest management practices regarding the effects on landscape fragmentation and population viability (Harris, 1984). Management and conservation designs developed for this region serve as a template for analogous plans in others North American regions and countries.

Ironically, land-use practices in these forests have provided landscape ecologists with a regional-scale fragmentation experiment. A strong pattern outside the natural range of variability has been superimposed on

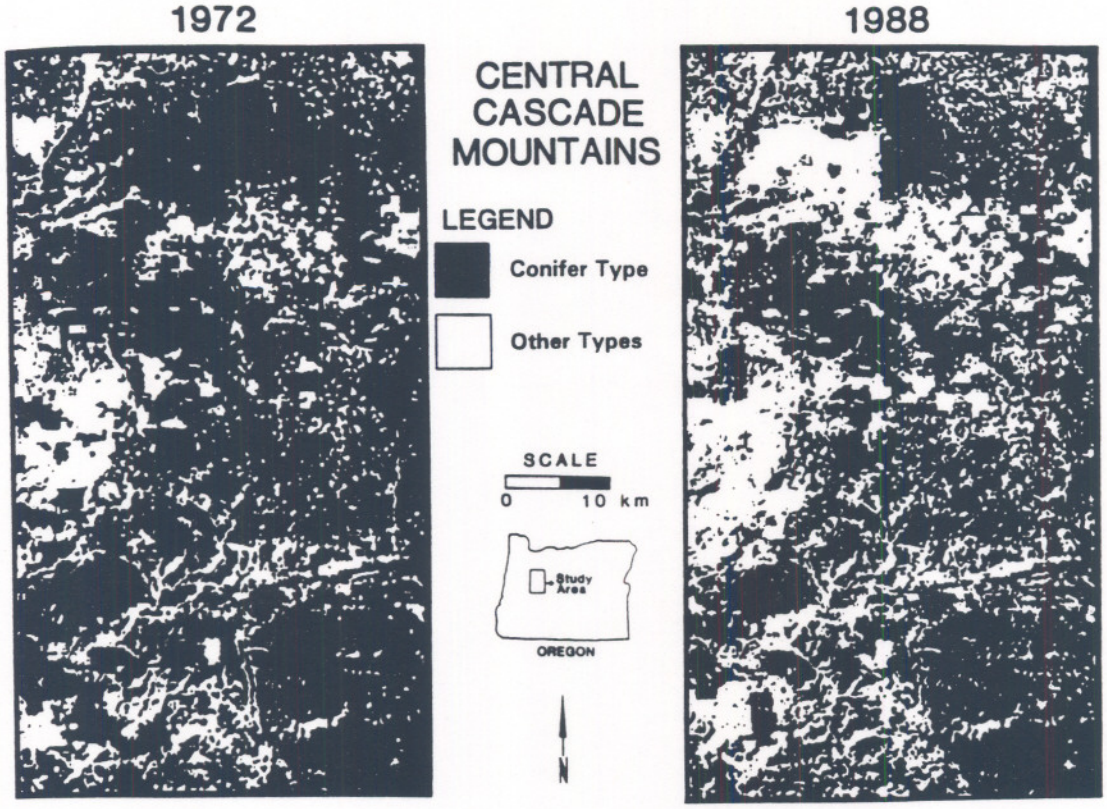


Figure 14.1. Classified satellite images depicting changes in landscape patterns that have resulted from anthopogenic disturbances created during the years between from 1972 and 1988 (Spies et al., 1994). The area covered lies west of the Cascade Range, central Oregon, U.S.A. spanning an area of 3,500 square kilometers.

the region where the same spatially and temporally varying processes are at work. We revisit the topic of landscape heterogeniety for the case of the Pacific Northwest forests with the intent of highlighting the interactions of patterns and processes across spatial and temporal scales in context of historical patterns of fragmentation. More specifically, we seek to (1) describe dominant sources and types of factors responsible for the generation of spatial structure and landscape heterogenity in PNW temperate forests; and (2) examine possible consequences of increased spatial heterogeneity of forested landscapes introduced by land conversion. It is our intent to emphasize the need to not only document the fragmentation of the landscape but understand the changing relationships between the landscape patches and matrix. Because a contol landscape at the landscape and regional scales is lacking, modeling has taken a more predominant role to elucidate large-scale processes and interactions. A simple heuristic model is employed to illustrate potential effects of local patterns (e.g., land conversion at the local scale) on the overall landscape composition over time (e.g., forested or nonforested landscape composition).

Spatial Heterogeneity

The most prominent pattern observed at the regional scale within the Pacific Northwest is the distinct longitudinal anisotropy manifested as broad north- to south-running vegetation (Figure 14.2). These vegetation patterns reflect interactions between strong west to east temperature and precipitation gradients modulated by long-term climatic variation (Franklin & Dyrness, 1973; Franklin, Swanson, Harman et al., 1991; Swanson, Franklin, & Sedell, 1990). Although precipitation generally increases as one moves northward, local variability in moisture patterns occurs as a

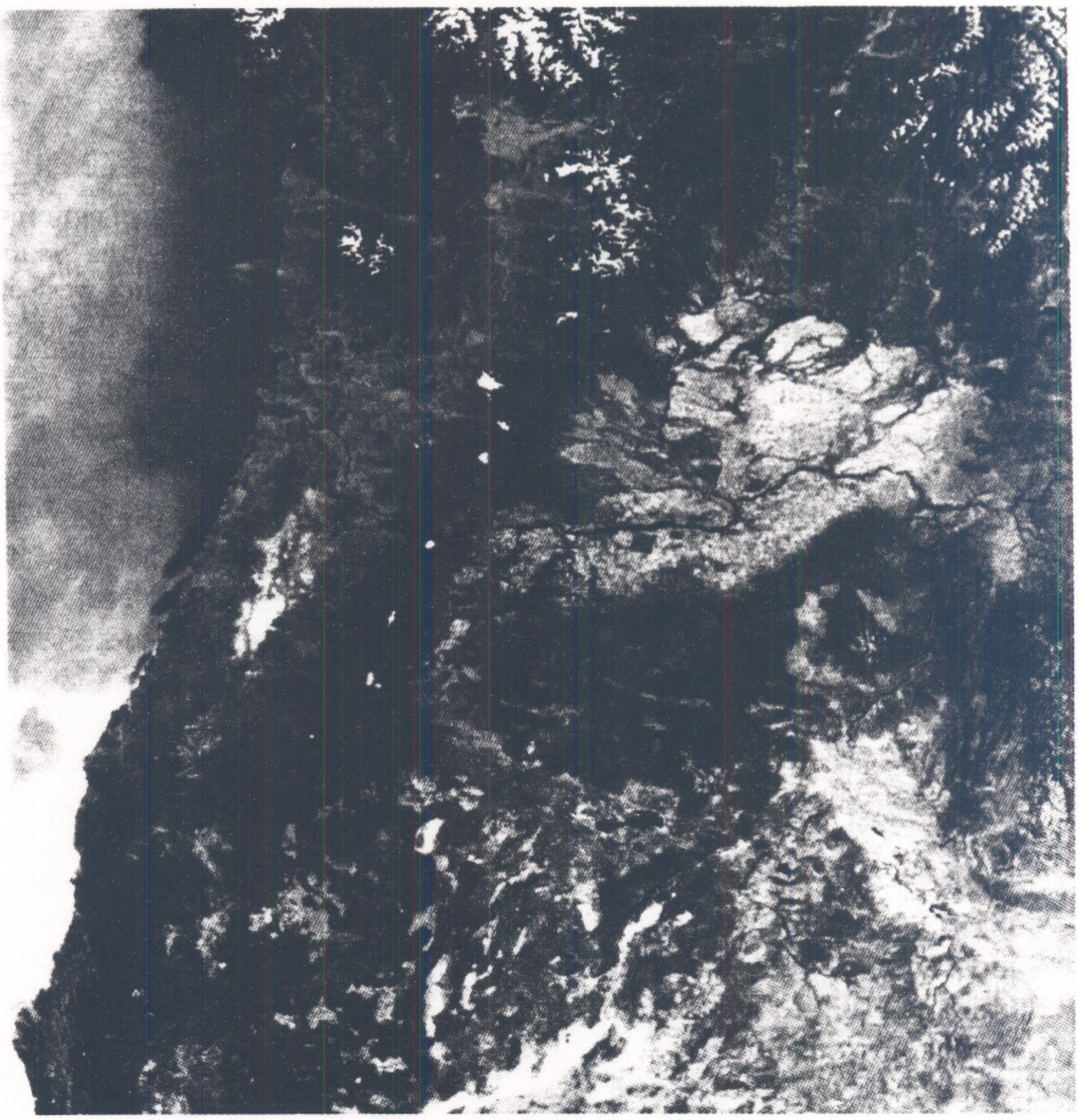


Figure 14.2. AVHRR image (resolution 1 km × 1 km) of the Pacific Northwest region covering Oregon and Washington states.

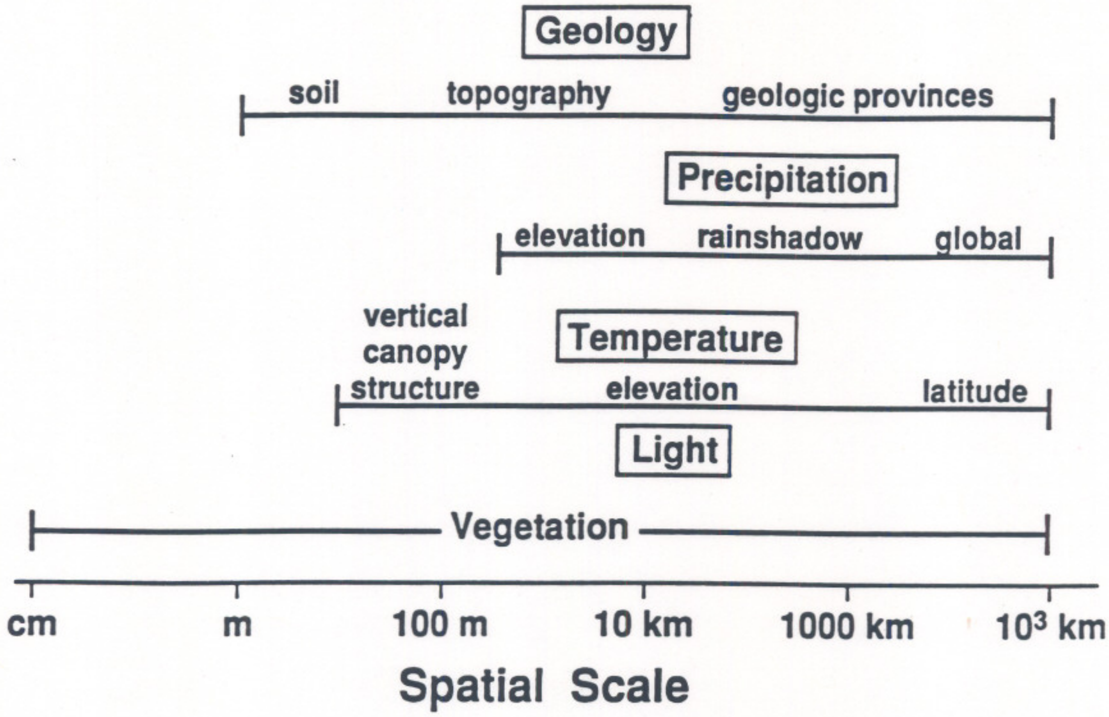


Figure 14.3. Abiotic sources of heterogeneity responsible for creating patterns in vegetation. Vegetation is viewed as a response variable to a suite of abiotic factors across scales.

result of storm patterns and local topographic contraints. A similar longitudinal temperature gradient exists, but is modulated in the coastal areas by the buffering warmer ocean current (Alaback & McClellean, 1993). However, closer examination of the broad-scale vegetation pattern reveals a less homogeneous distribution that reflects local climatic conditions coincident with topographic (i.e., aspect, slope) and structural (e.g., stand and within-gap) gradients. The interaction of abiotic and biotic processes (e.g., competition and predation) further embroider the multiscale landscape mosaic at several scales by controlling vegetation density (i.e., spatial arrangement), composition, and vertical structuring (e.g., multilayer canopies) within conifer stands (Figure 14.3). Examination of the spatial distribution of a given species can be viewed hierarchically. We illustrate this perspective by examining the spatial distribution of western hemlock.

In general, the regional distribution of many vegetation species reflect such a regional temperature and moisture "envelope" (Franklin & Dyrness, 1973). As a shade tolerant species, western hemlock (*Tsuga heterophylla*) ranges west of the Cascade crest with its northerly and southerly limits correlated with temperature and moisture extrema, respectively. Successful hemlock seedling regeneration is a function of several factors operating at various scales. Among other biotic variables, seed availability for forest regeneration is a function of seed production, species composition, seed tree proximity, and timing of release. To a certain extent, species production and timing of release are autogenically determined; however, the amount and timing of seed release are also related to regional climatic dynamics (J. Means, personal communication). Because abiotic factors (e.g., solar radiation, temperature, and moisture availability) are also modulated at several scales, the probability of seedling survivorship may depend on their values and interaction within a hierarchical framework (e.g., subgap, gap, stand, and landscape levels (Figure 14.4). Thus, heterogeneity of hemlock distribution within the region reflects the intergation of abiotic processes at several scales.

Experimental and field studies indicate that the relative position of a western hemlock seedling within a gap, gap size, slope, and aspect contribute to moisture and insolation variability (Spies et al., 1992). At the landscape scale, western hemlock occurrence is generally negatively correlated with southern aspects (Figure 14.5). This topographic signature becomes more apparent with decreasing latitude. A second scale of pattern is correlated with light and temperature gradients within gaps. A north to south zonation of light and moisture has been identified within Douglas

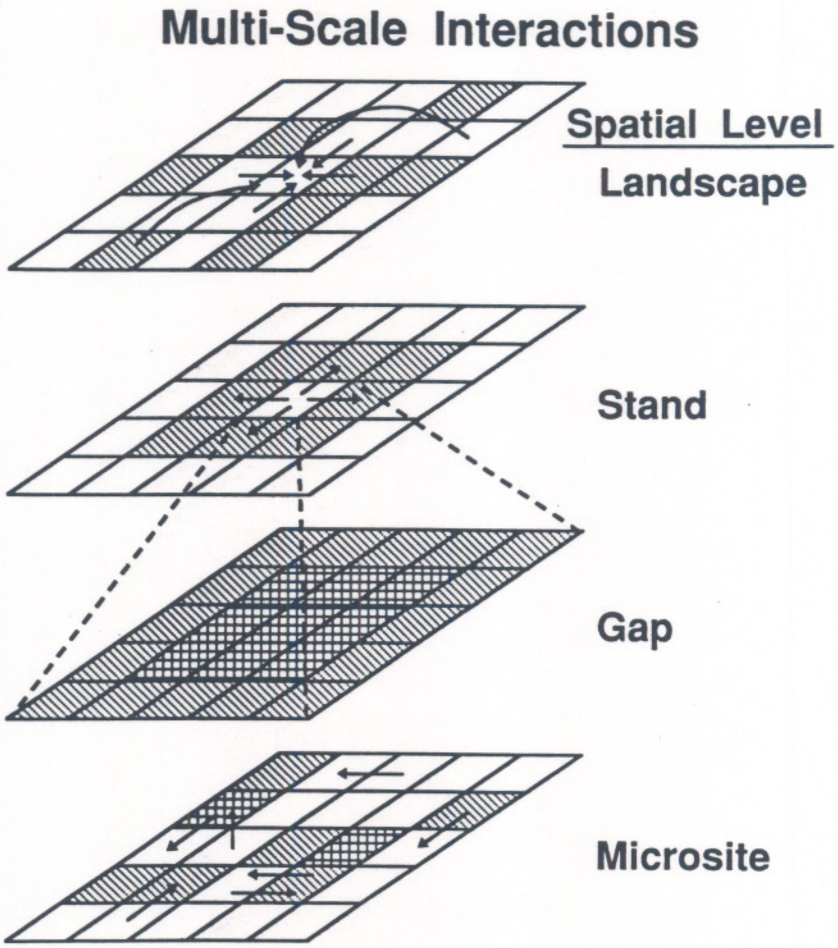


Figure 14.4. Patterns are created by a connecting hierarchy of relationships in the spatial and temporal domains. This figure illustrates how processes such as seedling regeneration may be affected by patterns at several scales.

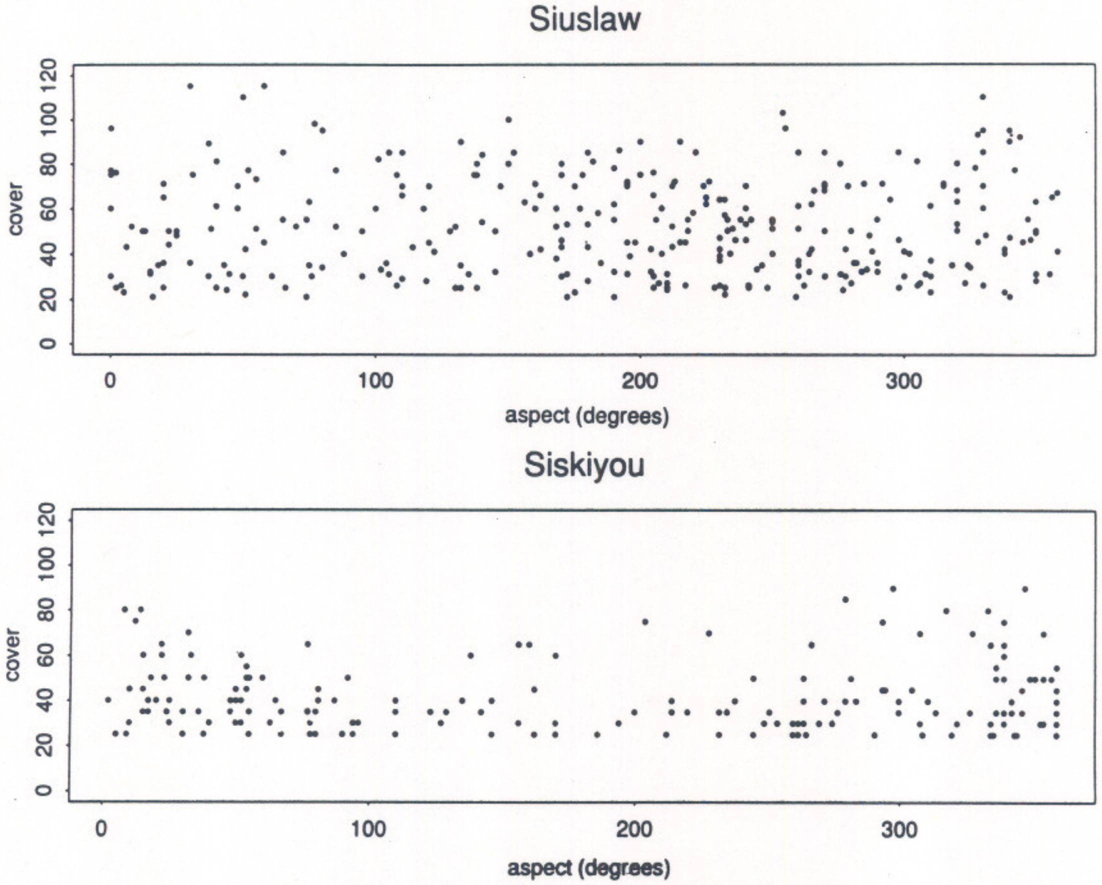


Figure 14.5. Percent cover hemlock (*Tsuga heterophylla*) plotted as a function of aspect (degrees) for forests at two latitudes in western Oregon. The data are derived from the Siuslaw (northwest) and Siskyou (south central) National Forest inventories. The cover-aspect pattern is more pronounced in the southern forest (i.e., Siskyou National Forest).

fir gaps on flat slopes (Figure 14.6; Gray, 1995). This within-gap gradient will vary with gap size and adjacent tree height. The interception of incoming solar radiation and precipitation by canopy trees creates a zonation of moisture, light, and radiation orthogonal to the north–south azimuth within the gap. Accordingly, seedling survivorship varies differentially along the gradient. However, environmental zonation is not consistent among all gaps. Because the amount of incoming solar radiation reaching the forest floor is a function of the geometry and adjacent tree size, the zonation created by direct light is predicted only in moderate to large gaps (>25 meters in diameter) and on slopes less than 50% (M. Easter, personal communication). A difference in hemlock seedling survivorship is expected when northern and southern aspects are compared under these conditions; lower moisture stress and leaf temperatures on northern slopes increase the likelihood of seedling survivability. On steep, southern slopes, increased exposure can generally exceed hemlock seedling tolerance and successful establishment is retarded. As a result, environmental differentiation effected by gap size is overridden by large-scale

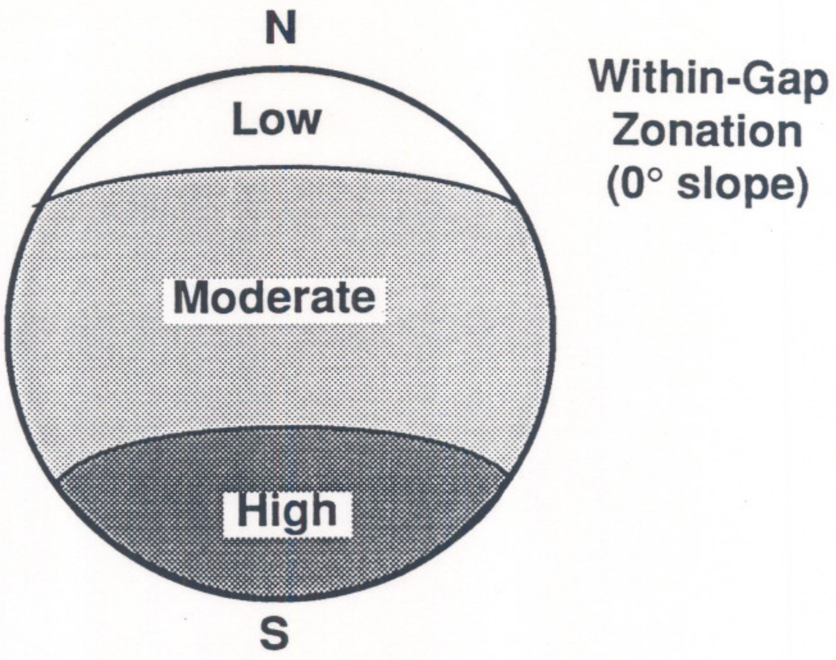


Figure 14.6. Seedling establishment zonation within a gap at zero slope. High, moderate, and low refer to relative levels of predicted seedling survivability.

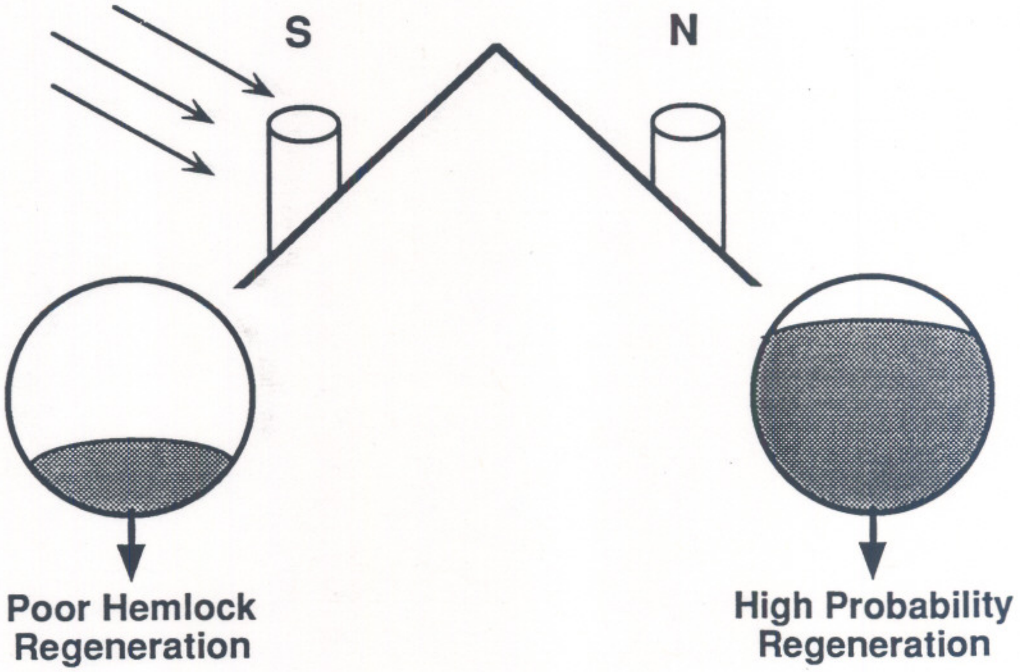


Figure 14.7. The predicted, combined effects of gap and topographic-level constraints on hemlock seedling survivability.

topographic factors when a threshold slope grade is exceeded (Figure 14.7).

These relationships may be viewed within the landscape context. A set of stand condition maps were created based on Thematic Mapper satellite imagery, classified according to age and structure. Companion elevational maps were developed for the Douglas fir dominant forest in the H.J. Andrews Experimental Forest located in central Oregon (Fiorella & Ripple, 1992). Old-growth Douglas-fir dominant stands characterized on average by moderate-to-large gaps were overlaid on slope and aspect maps derived from the topographic GIS coverage. The intersection of these maps predicts potential sites where the probability of hemlock seedling establishment is high (Figure 14.8). Thus, the distribution of hemlock seedling survival at the landscape scale may be viewed as controlled by both within-gap landscape interactions. Because the spatial distribution of seedlings predicted in the landscape depends on stand age, there is an implicit consideration of time where the timing and frequency

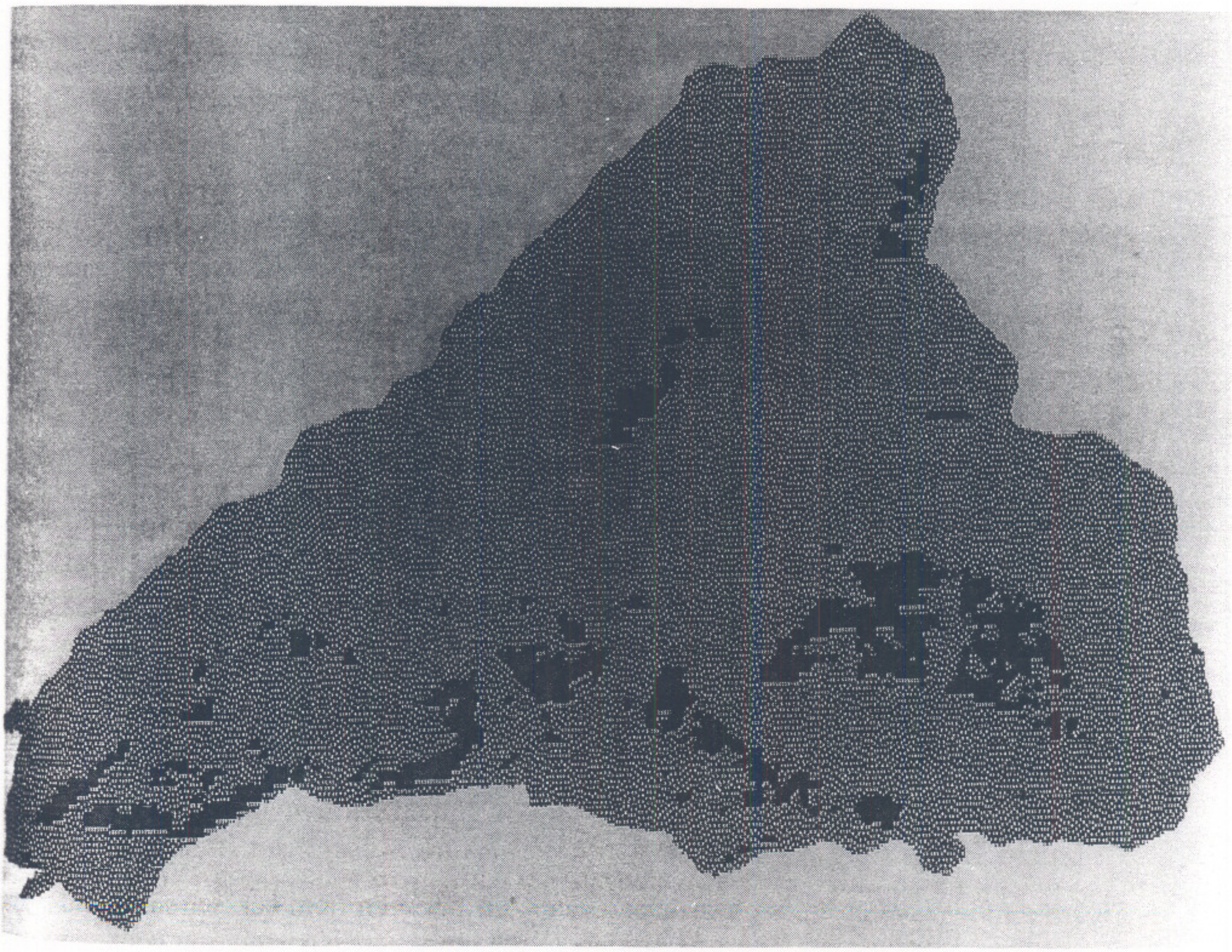


Figure 14.8. GIS map derived from the intersection of a satellite image-derived old-growth, slope and aspect maps depicting predicted distributions of high survivability sites of western hemlock (dark patches).

of disturbances characteristic of the area direct the distribution of stands of varying successional stages.

Temporal Heterogeneity

Disturbances such as wildfire, windthrow, flooding, and insect outbreaks also play an important role in imposing pattern on the landscape by redistributing resources (Morrison & Swanson, 1990; Spies & Franklin, 1991). Within-stand heterogeneity of resources (e.g., downed wood, canopy gap structure) reflects the integration and coupling of disturbance patterns (e.g., mortality due to wildfire, root pathogens) at several temporal and spatial scales. In a study comparing a set of old growth, mature, and young Douglas-fir dominant stands in the western Cascades, Oregon, hemlock seedling distribution showed a gradual increase with stand age and percent woody debris cover (Bradshaw, 1991). More interestingly,

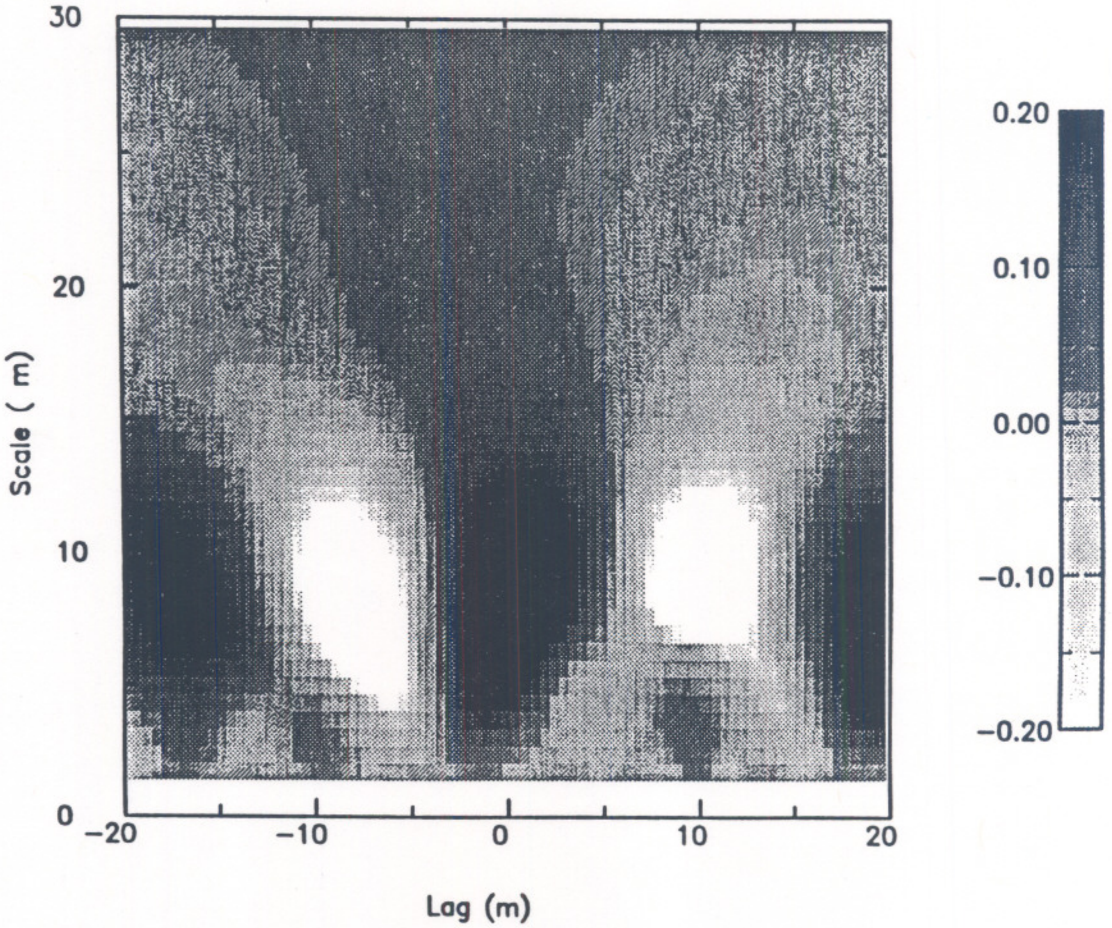


Figure 14.9. Wavelet cross-covariance calculated between hemlock seedling and downed log distributions. The *x*-axis refers to the lag at which correlation between the two variables occurs; the *y*-axis refers to the scale at which correlation occurs (meters). Downed logs and hemlock seedling distribution are correlated on average at approximately nine meters in this mature Douglas-fir stand.

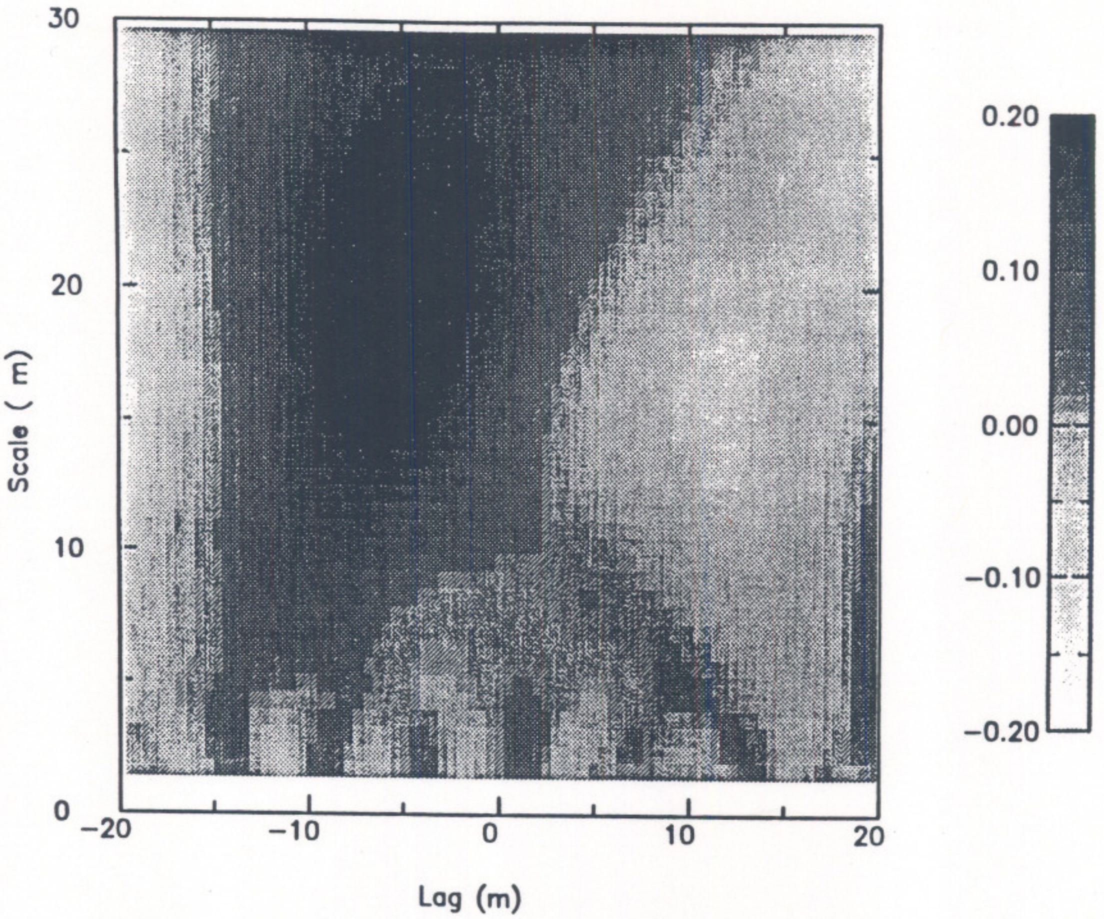


Figure 14.10. Wavelet cross-covariance calculated between hemlock seedling and downed log distributions. The *x*-axis refers to the lag at which correlation between the two variables occurs; the *y*-axis refers to the scale at which correlation occurs (meters). Downed logs and hemlock seedling distribution are correlated on average at 3 m and 18 m in this old growth Douglas-fir stand.

analyses quantifying the spatial distribution of hemlock seedling revealed a relationship between canopy and ground-level patterns. Hemlock seedling patches were correlated with patches of woody debris at different scales or patch sizes according to stand age and condition. In a mature stand characterized by high abundances of downed wood, hemlock seedling and wood occured coincidently in patches averaging 9 m (Figure 14.9).

In contrast, an old growth stand showed wood-hemlock correlation in patches at two different scales: 3 m and 18 m (Figure 14.10). The spatial distribution of hemlock seedlings and canopy gaps of the overstory were also correlated but at scales of 5 m and 25 m (Figure 14.11). These results suggest a coupled relationship between the distribution of hemlock seedlings in the understory and a composite pattern of patches related to the distribution of abiotic factors. The distribution of abiotic factors is in turn linked temporally by stand age and disturbance history.

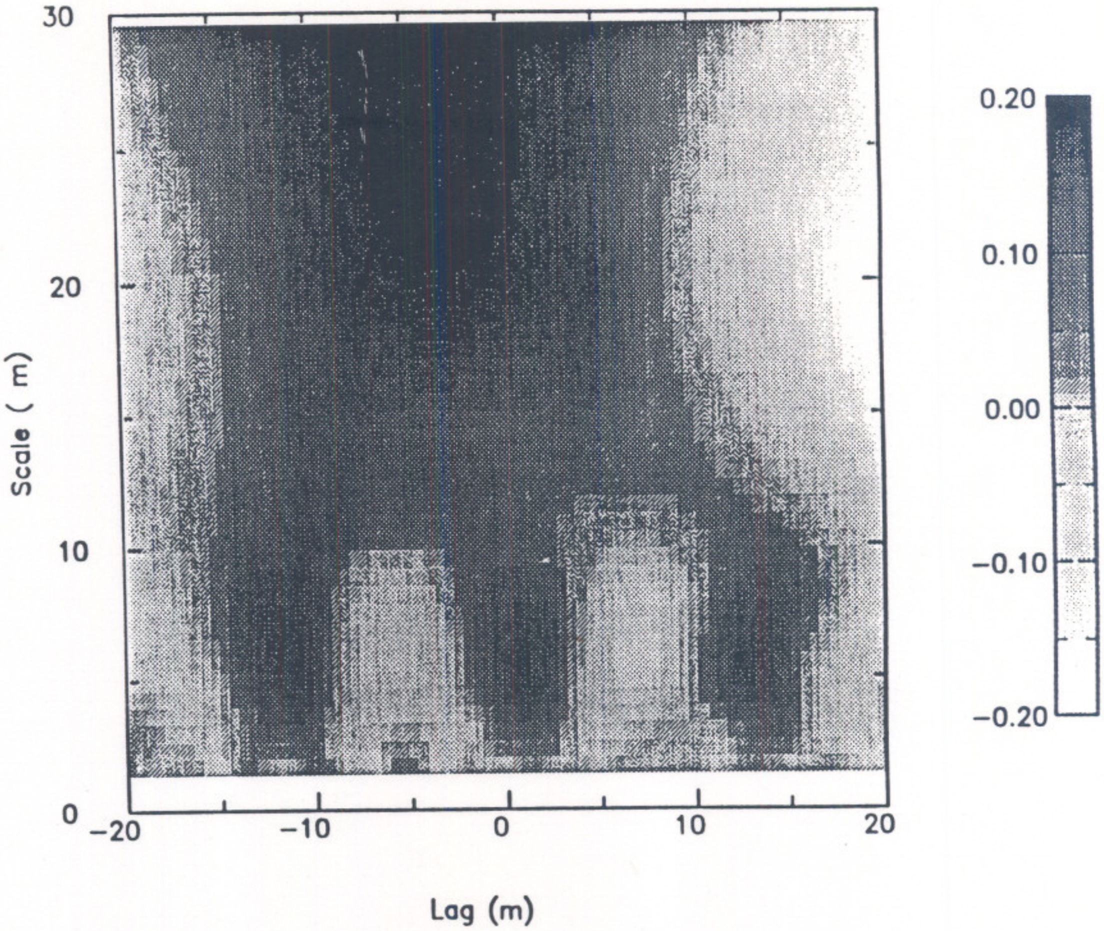


Figure 14.11. Wavelet cross-covariance calculated between hemlock seedling and downed log distributions. The *x*-axis refers to the lag at which correlation between the two variables occurs; the *y*-axis refers to the scale at which correlation occurs (meters). Overstory canopy gap and hemlock seedling distribution are correlated on average at 5 m and 25 m in this old growth Douglas-fir stand described in Figure 14.10.

From the geomorphic perspective, landforms processes influence ecosystem heterogeneity in several ways, by (1) modulating resource quality and availability (e.g., elevational modulation of temperature, nutrient distribution); (b) controlling flow of energy and material through the landscape (e.g., water movement); and (c) affecting the timing, frequency, and distribution of disturbances (e.g., wildfire, erosion, and wind; Grant et al., 1990; Swanson, Kratz, Caine, & Woodmansee, 1988). The timing distribution, and spatial arrangement of land movement and disturbance in general relates to the "range of natural variability," that is, a set of conditions or states that an ecosystem may have occupied prior to influence of European settlers (Swanson et al., 1994). Successional patterns and forest stand mosaics vary with disturbance intensity, location, and extent reflecting local and regional controls of climate, geology, vegetation dynamics (Delcourt, Delcourt, & Webb, 1983). It is instructive to view these processes from two perspectives of the temporal domain—frequency and duration. This distinction falls out naturally when viewed from a time series perspective; pattern can be described in terms of the peak structure (i.e., frequency) and in terms of the length or width of the peak (i.e., duration). Frequency and duration of disturbance will affect the type and rate of recovery in the ecosytem.

The frequency and duration characterizing a disturbance event may not always be commensurate or dependent on the same variables. Duration of a wildfire is primarily a function of several factors, including fuel load, topography, and present climate conditions (i.e., precipitation and wind; Agee and Huff, 1987; Morrison and Swanson, 1990). Although fire frequency is also a function of the same factors, it is constrained by frequency of initiation events, such as lightning strikes (i.e., elevation and combustible snags). Similarly, the frequency and rate of propagation of bark beetle infestation in PNW forests is strongly influenced by the order of disturbance events; large concentrations of downed wood or stressed live trees resulting from windthrow events and drought conditions, respectively, can initiate epidemic outbreaks. Frequency of infestation events (approximately every 20 to 30 yrs) is related to the probablities of these two types of disturbances and the order in which they occur (Bradshaw & Garman, 1994). In contrast, the duration of an infestation event is more dependent on the overall landscape composition and connectivity (i.e., an outbreak will only be sustained if there is available appropriate material). However, although infestation initiation may require a forest stand which has sustained physiological stress (e.g., drought), the spread can be sufficiently severe as to attack apparently healthy, live trees (i.e., a threshold condition may be breached) (Bedard, 1950). Duration of an outbreak may be expected to be dependent on the area and perhaps spatial pattern of the stand and landscape composition.

Modeling Anthropogenic Effects on Landscape Heterogeneity

In the previous section, landscape heterogeneity in the Pacific Northwest temperate forests was described in terms of pattern-generating processes within a spatial and temporal context. However, a glance at most regional satellite imagery reveals that the most striking source of landscape heterogeneity is anthropogenically derived patterns of historic land-use and land-conversion patterns. With the intensive and extensive resource extraction sustained over the recent decades, the temperate forests are markedly fragmented (Franklin and Forman, 1987). The implementation of a national policy of fire suppression has also contributed to the alteration of landscape dynamics by favoring species composition to fire intolerants and increasing the probability of insect outbreak (Borchers, 1994). In contrast to natural disturbance patterns, such human activities as timber harvesting and road construction are geometric in shape and occupy large areas of the landscape for sustained periods of time simoultaneously (Ripple, Bradshaw, & Spies, 1991). To examine the effects of such increased heterogenity and loss of connectivity in the landscape, we employ a simple heuristic model. A binary state (i.e., patch-matrix) model was constructed to observe how landscape rates and composition changes as fine-scale spatial pattern varies under different landscape conditions. Applications of the model and approach are discussed for two cases—disturbance propagation (e.g., bark beetle infestation) and seedling regeneration to which we refer for purposes of the present discussion as "dissipative" and "restorative" processes, respectively. Both seedling regeneration and bark beetle infestation are important agents sculpting landscape dynamics in the PNW (Franklin, Cromack, Denison et al., 1988; Furniss & Carolin, 1980; Harmon, Ferrell, & Franklin,

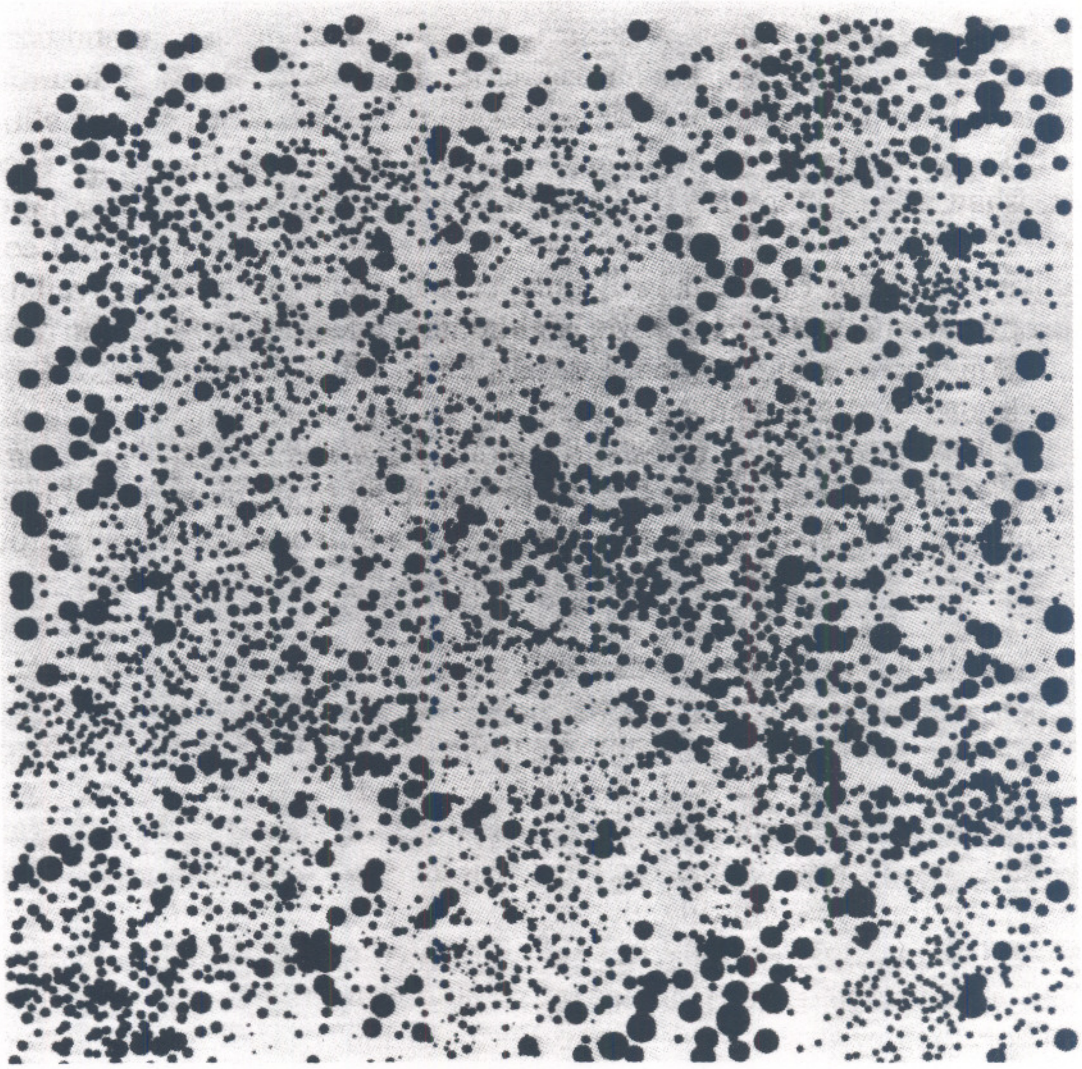


Figure 14.12. An example of the generated landscapes used in the model: small patch size.

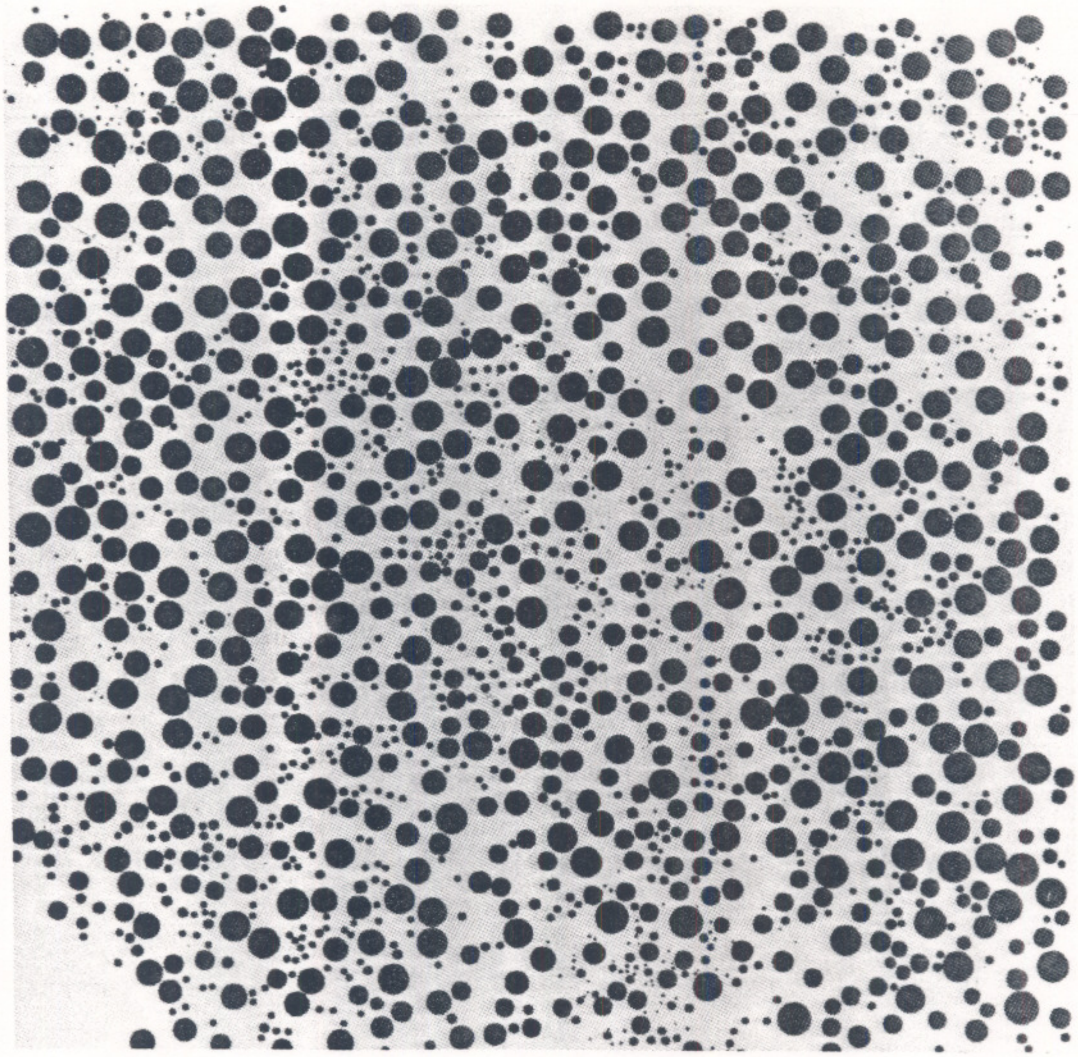


Figure 14.13. An example of the generated landscapes used in the model: large patch size.

1990). The term dissipative is used to connote a process which drives the forested system to an unforested state or one which deviates significantly from the present successional trajectory; restorative is used to denote processes which drive or sustain the system in its forested state. Although seedling regeneration initiated in canopy gaps may entail species replacement (e.g., replacement of standing Douglas fir to hemlock), it is nonetheless forested, and hence the process is considered "restorative" in the present context.

The model is constructed to test the hypothesis that local interactions between fine-scale features (e.g., tree aggregates, disturbance loci, gaps) and the matrix (e.g., intact forest) can alter the rate and direction of landscape change significantly. The landscape is defined as a set of randomly generated patches of homogeneous composition dispersed within a homogenous forest matrix (Figures 14.12 and 14.13). Two elements of spatial pattern are varied—mean patch size and patch-matrix contrast, as defined below. The initial landscapes have the same ratio of patch-to-matrix areas. Patterns resulting from patch-matrix contrast are examined by using a nearest-neighbor algorithm moved across the landscape of a given patch-size configuration. Depending on the cell type encountered (either patch or matrix) and the interaction algorithm applied, local change in landscape composition will occur. Patches are first-order approximations of harvested stands in a forest matrix; conversely, patches may be intact old growth stands within a matrix of young or harvested land (Figure 14.14).

Variability in patch size is achieved by specifying a mean patch radius and generating a normally distributed patch landscape. The patch-matrix contrast is varied in two ways: (1) radius of influence and (2) matrix susceptibility. A small radius of influence implies that only cells located in the immediate neighborhood of the patch will change; a large radius of influence implies that a larger zone of influence is exterted by the patch on the matrix. A difference in radii of influence is intended to correspond to rapid local change. Matrix susceptibility is defined as the tendency for the matrix to become patch. High susceptibility corresponds to an asymmetry in the direction of change between patch and matrix (i.e., low resistance of the matrix to resist patch-induced change) (Figure 14.15).

Results

The greatest difference exerted by these three parameters is associated with matrix susceptibility values. Under conditions of low susceptibility, the landscape changes over to matrix (Figure 14.16). Conversely, under conditions of high susceptibility, all four variants asymptotically approach a landscape composed of patch composition (Figure 14.17). Within each category, the effects of patch size and radius of influence have a lesser impact, but trends are visible. In the low susceptibility case (Figure 14.6b), the presence of a small radius of influence for patches of both sizes causes the landscape to converge to the forest matrix more rapidly in comparison to conditions where the radius of influence is high. As indicated by the case of small patches, total patch area increases. However, this trend reverses and the landscape eventually converges to forest matrix. In contrast (Figure 14.6a), patch size and radii of influence under conditions of high susceptibility appear to have a less noticeable effect on landscape change behavior; the rate and direction of change are dominated by the condition of high-matrix susceptibility and convergance is much more rapid. The experiment illustrates that local interactions and spatial relationships can effect vastly different landscape development and composition despite differences in local patterns. This experiment also illustrates the concept of a threshold; namely, the direction of landscape

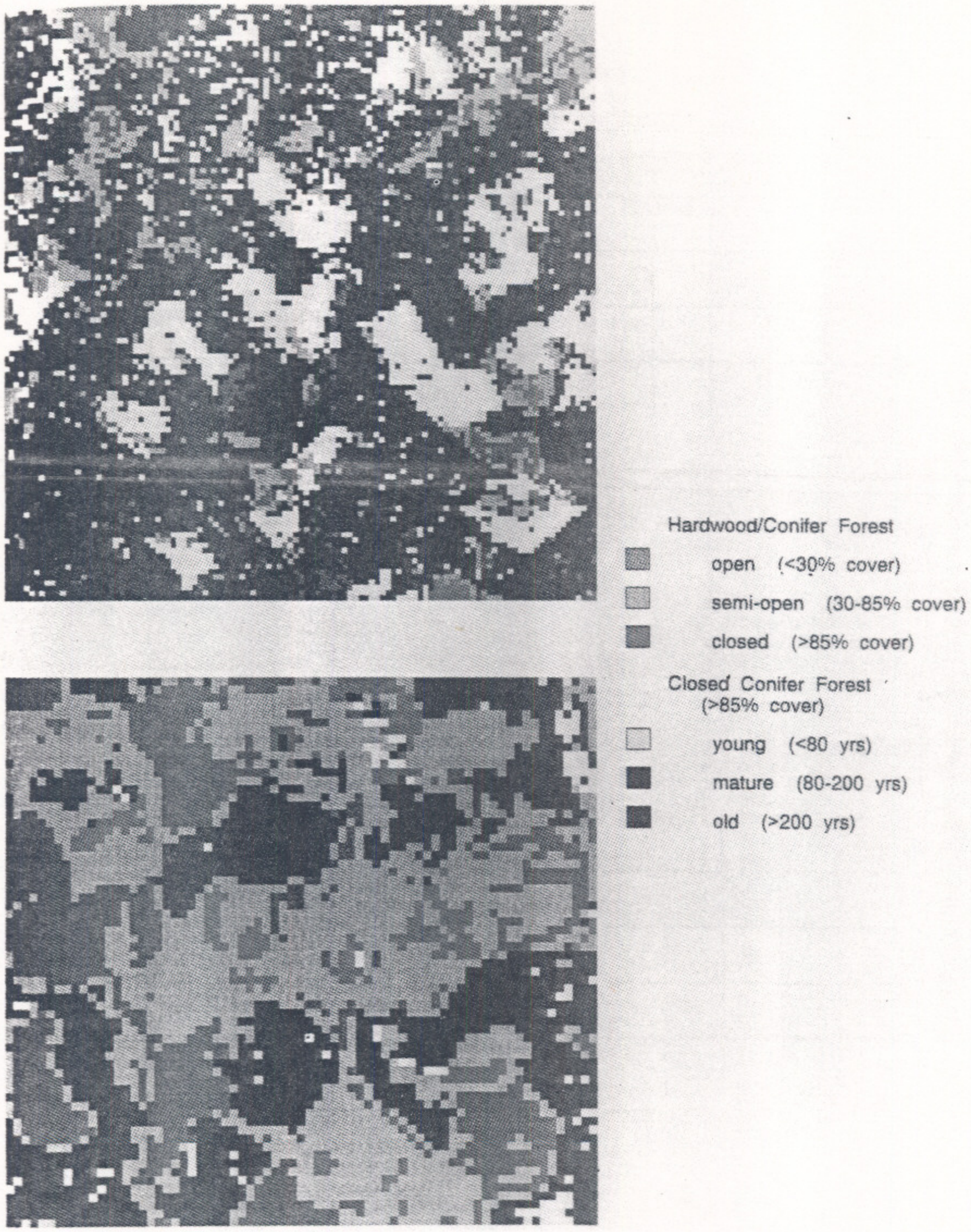


Figure 14.14. Classified thematic mapper satellite imagery depicting patch-matrix landscape for two representative forests in the Western Cascades, Oregon.

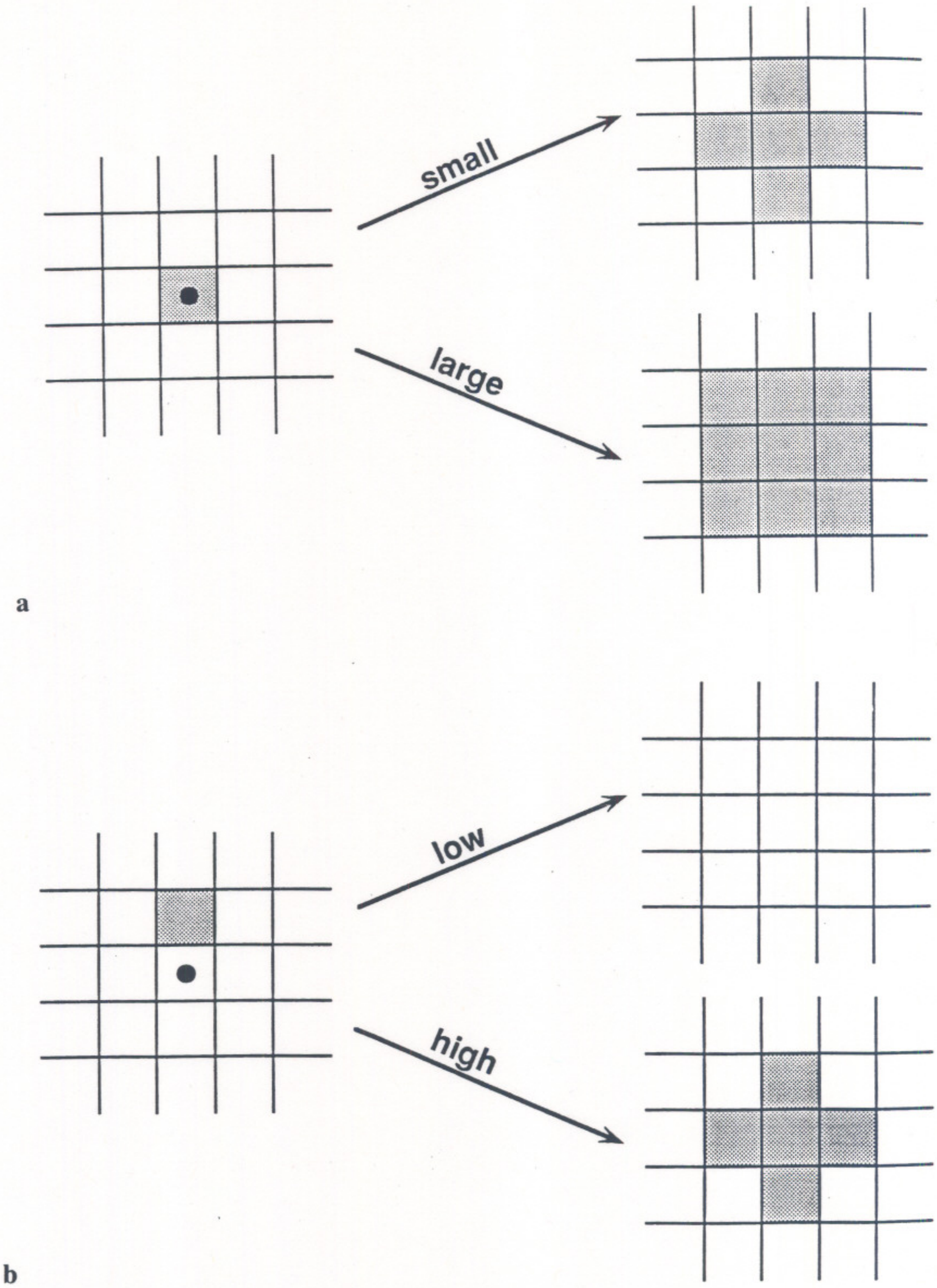
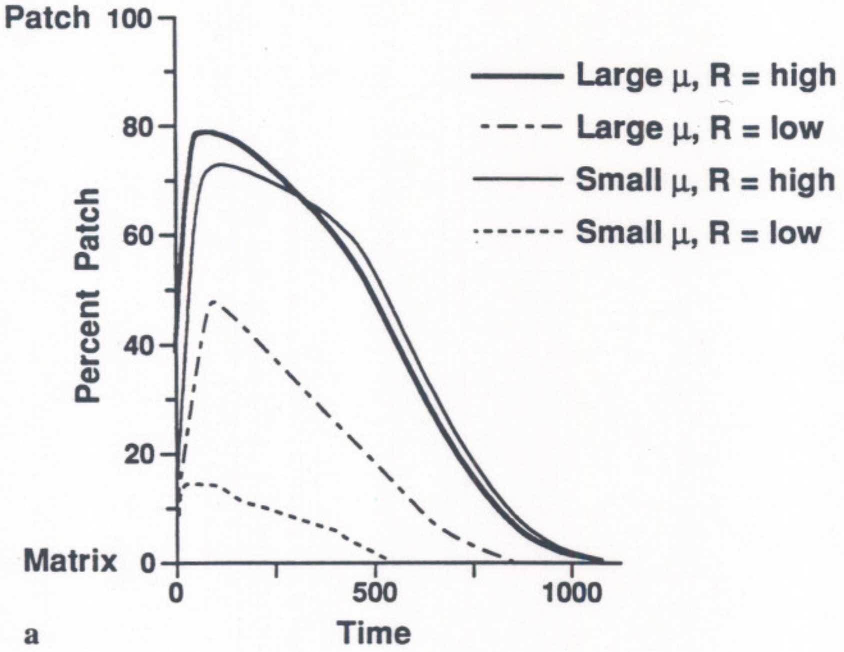


Figure 14.15. Rules describing two levels of patch-matrix interactions: (a) radius of influence and (b) matrix susceptibility. Two levels were considered in each case.

change may alter dramatically relative to initial perturbation magnitude (i.e., incremental change of spatial parameter).

As discussed, the forests of the PNW are significantly more fragmented prior to the settlement of Europeans. The present landscape is largely



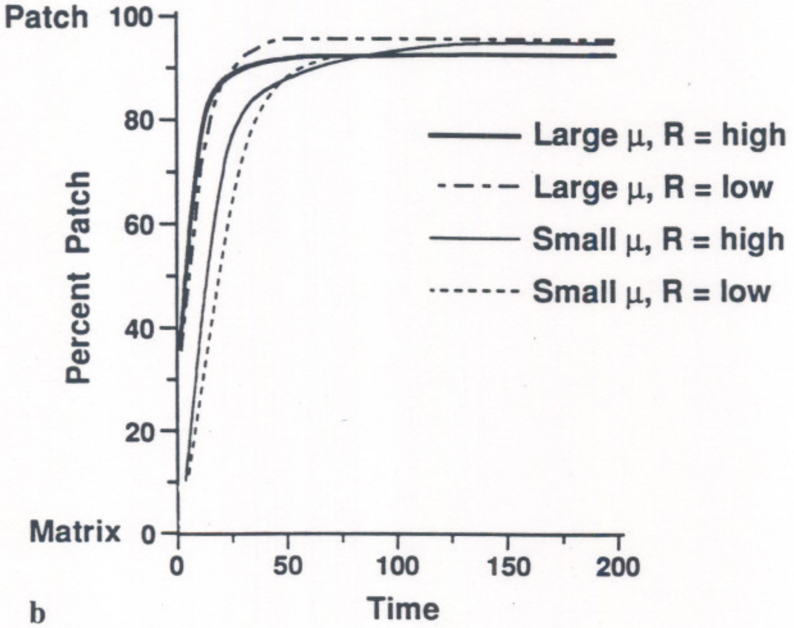


Figure 14.16. Resultant dynamics for the case of (a) high matrix susceptibility, and (b) low matrix susceptibility for low and high mean patch size radii and low and high conditions of small and large radii of influence (*R*). μ is the average patch size.

composed of patches within a matrix of varying composition and successional age. Each patch, as referred in the model, may be regarded as a potential disturbance locus (e.g., initiation site for insect outbreak) or refugia of faunal populations, respectively. Disturbance sites represent patches of downed wood remaining from previous wildfire or windthrow events from which insect outbreak may initiate. In such a disturbance setting, matrix susceptibility can be viewed as the tendency for Douglas fir trees to resist bark beetle infestation. In a heterogeneous, vital old growth stand, matrix susceptibility would be expected to be relatively low disturbance spread where would eventually die out despite initial patch size and potential rate of spread. Thus, the high matrix-patch contrast would act to insulate and isolate patches and retard disturbance spread. On the other hand, a landscape characterized by high susceptibility might correspond to aggregates of stressed trees (e.g., densely grouped young conifers). The weakened forest matrix would be less effective at resisting an outbreak. According to the model, propagation would occur locally at a faster rate. Levels of matrix heterogeneity, landscape connectivity, and dispersal capabilities of the insect would interact to determine the rate of spread.

In a second scenario, we consider conifer regeneration in a patchy landscape. In this case, the old growth and mature stands constitute the patches; the matrix is composed of young conifer and deciduous stands. The potential for conifer seedling establishment would be relatively high if the surrounding matrix was open and resource availability was not blocked by the presence of dense alder stands. In this case, matrix susceptibility would be considered high. Conversely, the presence of thick alder stands in the matrix would render seedling establishment more difficult and retard conifer regeneration. A similar scenario would be applicable for the dispersal patterns of faunal communities in the patch-matrix landscape.

Conclusions

Terrestrial ecology is now at the juncture where field and experimental analyses may be combined with the concepts of patch dynamics and hierarchy theory to develop a coherent spatially explicit, across-scale understanding of forest dynamics. Understanding what controls the rate and direction of local interactions as a function across spatial scales will be critical to developing appropriate management and conservation plans. We have engaged in a simple experiment to evaluate the effects of two elements of spatial pattern (i.e., patch-matrix contrast and patch size) on the rate and direction of landscape change. Two processes characteristic of Pacific Northwest forests, disturbance and regeneration, were discussed within the model context.

The model results suggest that anthopogenically introduced heterogeneity at a local level can dominate overall landscape change. Deviations in local patch-matrix interactions and pattern can effect significantly different rates of landscape change and the outcome of landscape composition. A differential in rates of change has several implications. If the rate of change effected by local patch-matrix interactions is slow relative to larger-scale phenomena (e.g., physiological response to global climate change), there is greater probability that the original successional trajectory will be altered. This phenomenon is illustrated with the topography-gap decoupling which may occur in the case of hemlock seedling regeneration and also in the case of understory vegetation response (Bradshaw, 1991; Bradshaw and Spies, 1992).

Landscape and regional model development should identify and evaluate critical components of pattern and their potential interactions over time. Depending on the particular landscape and ecological process, certain elements are more likely to exert influence than others (e.g., patch size versus patch–patch connectivity). Once again, while seeking for general principles, accomodation for the idiosyncracies of each ecosystem is necessary to fully capture system dynamics. It remains to determine to what extent local interactions and patterns influence variability observed within the region. Within the context of global change, several questions emerge. For example, as one moves latitudinally in the Northwest, the dominance of given landscape processes and patterns change accordingly. Will the effects of fine-scale change (e.g., stand-level land conversion) be uniform throughout the region? Will a change in regional climate multiply the effects of disturbance or will a threshold be reached and result in negative feedback shifting to a different dynamic regime? Will rates of change be constant throughout the region? Clearly, the construction of simple spatially and temporally explicit models in conjunction with large-scale field studies will contribute to our understanding.

Acknowledgments. The authors would like to thank Barbara Marks for programming assistance, William J. Ripple (ERSAL) for provision of satellite imagery, and Mark Harmon, and Mark Easter for helpful comments and discussion. Research has been conducted in part under the auspices of LTER site studies, H.J. Andrews Experimental Forest (NSF BSR 90 11663).

References

Agee, J.K., and Huff, M.H. 1987. Fuel succession in a western hemlock/Douglas-fir forest. *Can J For Res*, 17, 697–704.

Alaback, P.B., and McClellan, M.H. 1993. Effects of global warming on managed coastal ecosystem of western North America. In H.A. Moonpy, E.R. Fuentes, and B.I. Kronberg (eds.), *Earth System Responses to Global Change: Contrasts Between North and South America* (pp. 299–303). New York: Academic Press.

Bedard, W.D. 1950. The Douglas-fir beetle. U.S.D.A. Circular No. 918.

Borchers, J.G. 1994. A hierarchical context for sustaining ecosystem health. In R.G. Jaindl and T.M. Quigley (eds.), *Search for a Solution: Sustaining the Land, People, and the Economy of the Blue Mountains*. American Forests Publications.

Bradshaw, G.A. 1991. *Hierarchical Analysis of Patterns and Processes of Douglas-Fir Forests*. Unpublished doctoral dissertation, Oregon State University.

Bradshaw, G.A., and Garman, S. 1994. Detecting fine-scale disturbance in forested ecosystems as measured by large-scale landscape patterns. In W.K. Michener, J.W. Brunt, and S.G. Stafford (eds.), *Environmental Information Management and Analysis: Ecosystem to Global Scales* (pp. 533–550). London: Taylor and Francis.

Bradshaw, G.A., and Spies, T.A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. *J Ecol*, 80, 205–215.

Delcourt, H.R., Delcourt, P.A., and Webb III, T. 1983. Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quat Sci Rev*, 1, 153–175.

Fiorella, M., and Ripple, W. 1993. Determining successional stage of temperate coniferous forests with landsort satellite data. *Programmetric Engineering and Remote Lensing*, 59(2), 239–246.

Franklin, J.F., and Dyrness, C.T. 1973. *Natural Vegetation of Oregon and Washington*. U.S.D.A., Forest Service, General Technical Report PNW-8.

Franklin, J.F., Cromack, Jr., K., Denison, W., Mckee, A., Maser, C., Sedell, J., Swanson, F., and Juday, G. 1981. *Ecological Characteristics of Old-Growth Douglas-Fir forests*. Portland, OR: U.S.D.A., Forest Service, PNW Forest and Range Experiment Station. General Technichal Report PNW-118.

Franklin, J.F., Swanson, F.J., Harmon, M.E., et al. 1991. Effects of global climate change on forests in northwestern North America. In R. Peters and T. Lovejoy (eds.), *Climate Change and Biological Diversity*.

Franklin, J.F., and Forman, R.T.T. 1987. Creating landscape patterns by cutting: ecological consequences and principles. *Land Ecol*, 1, 5–18.

Furniss, R.L., and Carolin, V.M. 1980. *Western Forest Insects*. Washington, DC: U.S.D.A., Forest Service, Miscellaneous Publication No. 1339.

Goodchild, M., Parks, B.O. and Steyaert, L.T. 1993. *Environmental Modelling with GIS*. New York: Oxford University Press.

Grant, G.E., Swanson, F.J., and Wolman, M.G. 1990. Pattern and origin of stepped-bed morphology in high-gradient streams, Western Cascades, Oregon. *Geol Soc Am Bull*, 102, 340–352.

Gray, A.N. 1995. *Tree Seedling Establishment on Heterogeneous Microsites in Douglas-Fir Forest Canopy Gaps*. Unpublished doctoral dissertation. Oregon State University.

Harmon, M.E., Ferrell, W.K., and Franklin, J.F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science*, 247, 699–702.

Harris, L.D. 1984. The fragmented forest: Island biogeographical theory and the preservation of biotic diversity Chicago: University of Chicago Press.

Kolasa, J., and Pickett, S.T.A. (eds.), 1991. *Ecological Heterogeneity*. New York: Springer-Verlag.

Michener, W.K., Brunt, J.W., and Stafford, S.G. 1994. *Environmental Information Management and Analysis: Ecosystem to Global Scales*. Bristol, PA: Taylor & Francis.

Moloney, K.A., Morin, A., and Levin, S.A. 1991. Interpreting ecological patterns generated through simple stochastic processes. *Land Ecol*, 5(3), 163–174.

Morrison, P.H., and Swanson, F.J. 1990. *Fire History and Pattern in a Cascade Range Landscape*. Portland, OR: U.S.D.A., Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-254.

O'Neill, R.V., DeAngelis, D.L., Wade, J.B., and Allen, T.F.H. 1986. *A Hierarchical Concept of Ecosystems. Princeton, NJ: Princeton University Press.*

Pickett, S.T.A., and White, P.S. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Orlando, FL: Academic Press.

Powell, T.M. 1989. Physical and biological scales of variability in lakes, estuaries, and coastal ocean. In J. Roughgarden, R.M. May, and S.A. Levin (eds.), *Perspectives in Ecological Theory*. Princeton, NJ: Princeton University Press.

Ripple, W.J., Bradshaw, G.A., and Spies, T.A. Measuring landscape patterns in the Cascade Range of Oregon, USA. *Biol Conserv*, 57, 73–88.

Spies, T.A., Ripple, W.J., and Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecol Appl*, 4(3), 555–568.

Spies, T.A., Easter, M.J., and Gray, A.N. 1992. Light, temperature, and initial vegetation responses to experimental gaps in coniferous forests. *Bull Ecol Soc Am*, 77th Annual ESA Meeting, August 9–13, p. 352.

Spies, T.A., and Franklin, J.F. 1991. The structure of natural, young, mature, and old-growth forests in Washington and Oregon. In L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff (eds.), *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests* (pp. 91–109). Portland OR: U.S.D.A., Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-285.

Spies, T.A., and Franklin, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology*, 70(3), 543–545.

Spies, T.A., and Franklin, J.F. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology*, 69(6), 1689–1702.

Spies, T.A., Franklin, J.F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can J For Res*, 20, 649–658.

Spies, T.A., Ripple, W.J., and Bradshaw, G.A. Dynamics and pattern of a managed coniferous forest landscape. *Ecol Appl*, 4(3), 555–568.

Swanson, F.J. 1981. Fire and geomorphic processes. In *Proceedings, Fire Regimes and Ecosystems Conference: December 11–15, 1979*. Washington, DC: U.S.D.A., Forest Service, General Technical Report WO-26.

Swanson, F.J., Franklin, J.F., and Sedell, J.R. 1990. Landscape patterns, disturbance and management in the Pacific Northwest, USA. In Zoenfeldt and Forman (eds.), *Changing Landscapes: An Ecological Perspective* (pp. 191–213). New York: Springer-Verlag.

Swanson, F.J., Kratz, T.K., Caine, N., and Woodmansee, R.G. 1988. Landform effects on ecosystem patterns and processes: Geomorphic features of the earth's surface regulate the distribution of organisms and processes. *BioScience*, 38(2), 92–98.

U.S.D.A., Forest Service. 1993. *Forest Ecosystem Management: An Ecological, Economic, and Social Assessment. A Report of the Forest Ecosystem Management Assessment Team (FEMAT)*. Washington, DC: U.S.D.A., Forest Service.

Wiens, J.A. 1976. Population responses to patchy environments. *Ann Rev Ecol Sys*, 7, 81–120.

Richard G. Lawford Paul B. Alaback
Eduardo Fuentes
Editors

High-Latitude Rainforests and Associated Ecosystems of the West Coast of the Americas

Climate, Hydrology, Ecology, and Conservation

With 83 Illustrations

Springer

Richard G. Lawford
Office of Global Programs
National Oceanic and Atmospheric
Administration
1100 Wayne Avenue
Silver Spring, MD 20920-5603, USA

Paul B. Alaback
School of Forestry
Montana Forest and Conservation
Experiment Station
University of Montana
Missoula, MT 59812-1063, USA

Eduardo Fuentes
Catholic University
Laboratory of Ecology
Castilla 114-D
Santiago
Chile

Cover Illustration: Schematic of the integrated effects of climatic, hydrological, and biological processes on ecosystems along the west coast of the Americas. Artwork prepared by Mr. Philip Gregory of the National Hydrology Research Centre in Saskatoon, Saskatchewan, Canada.

Library of Congress Cataloging in Publication Data
High-latitude rainforests and associated ecosystems of the West Coast of the Americas : climate, hydrology, ecology, and conservation / Richard G. Lawford, Paul Alaback, Eduardo Fuentes, editors.
p. cm.—(Ecological studies : vol. 116)
ISBN 0-387-94487-7 (hardcover)
1. Rain forest ecology—America. 2. Rain forests—America. 3. Rain forest conservation—America. I. Lawford, Richard G. II. Alaback, Paul B. III. Fuentes, Eduardo. IV. Series: Ecological studies : v. 116.
QH101.H55 1995
574.5′2642′097—dc20 95-5547

Printed on acid-free paper.

Acquiring editor: Robert C. Garber
Production coordinated by Chernow Editorial Services, Inc., and managed by Terry Kornak; manufacturing supervised by Joe Quatela.
Typeset by Best-set Typesetter Ltd., Hong Kong.
Printed and bound by Braun-Brumfield, Inc., Ann Arbor, MI.
Printed in the United States of America.

9 8 7 6 5 4 3 2 1

ISBN 0-387-94487-7 Springer-Verlag New York Berlin Heidelberg