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13. Modeling Landscape Disturbance

Monica G. Turner and Virginia H. Dale

13.1 Landscape Heterogeneity and Disturbance

Almost all landscapes are affected by natural or anthropogenic disturbances (e.g., Mooney and Godron 1983; Risser et al. 1984; Forman and Godron 1986; Pickett and White 1985; Turner 1987). The spatial spread of disturbance (e.g., fire, pests, pathogens, exotic species, and wind throw) across a landscape is an important ecological process that is influenced by landscape pattern (e.g., Turner 1987). Disturbance can be defined generally as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). Although the general role of ecological disturbance has received considerable attention (e.g., White 1979; Barrett and Rosenberg 1981; Paine and Levin 1981; Mooney and Godron 1983; Menges and Loucks 1984; Sousa 1984; Pickett and White 1985; Rykiel 1985), only recently have studies attempted to predict the relationship between landscape pattern and disturbance (Romme and Knight 1982; Knight 1987; Odum et al. 1987; Remillard et al. 1987; Turner and Bratton 1987; Franklin and Forman 1987; Foster 1988; Rykiel et al. 1988; Baker 1989a; Turner et al. 1989).

Disturbances operate in a heterogeneous manner in the landscape. Gradients of disturbance frequency and severity are often controlled by physical or vegetational features. For example, a study of the disturbance history of old-growth forests in New England between 1905 and 1985 found that site susceptibility to frequent

natural disturbances (e.g., windstorms, lightning, pathogens, and fire) was controlled by slope position and aspect (Foster 1988). Plant survival and recovery following the eruption of Mount St. Helens depended on (1) the nature of the volcanic disturbance the site experienced and (2) the aspect, time of snowmelt, and ongoing disturbances such as erosion (Adams et al. 1987). Some insect outbreaks are dependent on external conditions and tend to track environmental gradients in time or space (Berryman 1987).

Disturbances may spread from a local epicenter to cover large areas, and thus disturbance propagation may be enhanced or retarded by landscape heterogeneity. In forests of the Pacific Northwest, increased landscape heterogeneity due to "checkerboard" clear-cutting patterns enhances the susceptibility of old-growth forest to catastrophic windthrow (Franklin and Forman 1987). On a barrier island, the unusually close proximity of different habitats in the landscape appears to enhance the disturbance effects that result from introduced ungulate grazers in mature maritime forest (Turner and Bratton 1987). Landscape heterogeneity may also retard the spread of disturbance. In some coniferous forests, heterogeneity in the spatial patterns of forest by age class tends to retard the spread of fires (e.g., Givnish 1981). Other examples of disturbance types that may be impeded by landscape heterogeneity include pest outbreaks and erosional problems in agricultural landscapes, in which disturbance is generally enhanced by homogeneity.

Modeling and analytic methods are needed to better understand the relationship between landscape patterns and disturbance regimes. Disturbances operate at many scales simultaneously and play an important role in promoting the coexistence of species in the landscape (e.g., Watt 1947; Loucks 1970; Wiens 1977). Results from models that simulate disturbance and population persistence indicate that populations are stabilized at broad scales by spatial extent, heterogeneity, and dispersal (DeAngelis and Waterhouse 1987). However, the development of models that can project the spatial and temporal patterns of ecological communities across whole landscapes remains challenging.

In this chapter, we distinguish two views of landscape disturbance and examine the quantitative methods that are applied in each. First, we briefly consider disturbance effects that are spatially heterogeneous on the landscape (e.g., the patchy effects of a storm) and distinguish between modeling approaches that are spatially aggregated and those that are spatially explicit. Second, we consider the spatial spread of a disturbance (e.g., pests, pathogens, or fire) across a landscape. Two modeling approaches that we have developed, a probabilistic disturbance spread model and a coupled species model, are presented in detail. Finally, we discuss the new insights that have emerged from the use of these approaches, compare their applicability to different questions, and suggest future directions and research needs.

13.2 Models of the Heterogeneous Effects of Disturbance

Models of the heterogeneous effects of disturbance must explicitly recognize the variable nature of the landscape. There are at least two approaches to representing

this heterogeneity. First, information on landscape variability can be spatially aggregated in the models. In the aggregated approach, the landscape frequently is divided into homogeneous categories that may be based upon vegetation type, temperature or precipitation regime, elevation, land use, or time since disturbance. A second approach is a spatially explicit model of the map of landscape heterogeneity in which the geographic location and change in the attributes of each site are recorded and followed. The advantage of the spatially explicit approach is that the juxtaposition of sites and cover types can be considered.

13.2.1 Spatially Aggregated Approach

Markov transition models are examples of the spatially aggregated approach to modeling the effects of disturbances on heterogeneous landscapes. These models are stochastic in the sense that the probability of transition between two states is given an explicit value. For example, the probability of a disturbance resetting one community type to another type is assigned. The transition probability usually relates to a particular time period, such as the successional change from one vegetation type to another for a particular time since disturbance (Anderson 1966, Horn 1975). The Markov model can be applied at a variety of spatial scales. Applications have ranged from a spatial unit of less than a hectare (e.g., Austin 1980; Austin and Belbin 1981) to a few hundred hectares (e.g., Williams et al. 1969; Hobbs 1983; Lippe et al. 1985). Multiyear sequences of remote sensing data can be used to provide estimates of transition frequencies between ecological states, and these estimates can serve as inputs for Markov models (Hall et al. 1988). Hall et al. (1988) applied this method to examine disturbance frequencies in wilderness and managed areas in northern Minnesota boreal forests. The steady-state solution of the model (e.g., percentage of the landscape in different states) is determined by the frequency of disturbance.

Baker (1989a) used a Markov chain approach to examine potential long-term trends in the vegetation mosaic in the Boundary Waters Canoe Area, Minnesota, based on fire-year maps published by Heinselman (1973). The model was developed for heuristic purposes and assumed that the fire regime that occurred during the 141-year study period (1727–1868) remained constant into the future. Transitions occurred between forest age classes. Baker used the model to compare the final distribution of age classes at five spatial scales and to evaluate the presence of a stable mosaic and the minimum area needed for a stable mosaic to be observed. Similarity between the simulated final distributions of age classes and the steady-state final distribution was generally low across all spatial scales.

Tabular models have also been used to track spatial changes following disturbances. These models predict temporal changes in state variables for particular regions and ecosystems within each region. Such models are particularly useful when massive amounts of data are available and must be organized. A global environmental problem to which tabular models have been applied is estimating annual changes in terrestrial ecosystems following various patterns of land use change (Moore et al. 1981; Houghton et al. 1983, 1987; Detwiler and Hall 1988).

These models track the yearly changes of carbon in terrestrial vegetation, soils, and products removed from the land (e.g., lumber). The rates of buildup and decay of carbon can vary with geographic region, ecosystem type, and prior land use (the disturbance in these models). Time lags are generally associated with the growth and decay of the net flux of carbon. For each ecosystem, the model describes the response of vegetation and soils to different kinds of disturbances. Although these responses are aggregated by ecosystem type, if the spatial distribution of ecosystem types is known, then the spatial arrangement of response curves can be mapped.

Patch dynamics models of intertidal communities represent recovery from disturbance in a general manner (Levin and Paine 1974; Paine and Levin 1981). In these models, the landscape is considered to contain populations of patches representing disturbance gaps; in the absence of the disturbance, the landscape would ultimately be dominated by a single cover type. Disturbance patches may vary in size, and the age-size distributions of the patches are modeled over time based on the interaction between the disturbance rate (patch birth rate) and the recolonization rate (patch death rate). This theory projects patterns of intertidal patches in mussel beds to within 5% of observed values (Paine and Levin 1981). This approach may be generally applicable to disturbances that create gaps or patches in a variety of landscapes. DeAngelis and Waterhouse (1987) suggest that these models of "transient dynamics" may have practical applications in describing the dynamics of pest species over short periods of time when there is no basis for inferring the existence of an equilibrium point.

Spatially aggregated models of disturbance are useful for several reasons. Transition models are relatively simple and have been used extensively. From a pragmatic viewpoint, the results of matrix models may not differ significantly from continuous models for some purposes (Baker 1989b). However, spatially aggregated models of disturbance have several limitations. Disturbance events are often not spatially independent but are influenced by the surrounding environment. A Markov or tabular model does not incorporate these neighborhood effects. The frequency of disturbance may also not be constant through time but may vary, so dynamic transition probabilities might be required. Finally, as with all transition probability models, it is difficult to relate the probabilities to ecological mechanisms or processes. Baker (1989b) provides a detailed review of these approaches, their relative merits, and potential modifications to the model structures.

13.2.2 Spatially Explicit Models

Models that have spatial representation of heterogeneous landscape units and/or the processes that change following disturbance are referred to as spatially explicit models. There is great variation as to the detail with which the processes and spatial resolution are modeled.

The transient dynamics of disturbance patches have been examined in the presence of environmental gradients that control species reestablishment (Green 1989). Green (1989) simulated the patterns associated with fire, seed dispersal, and

the distributions of plants and resources by using approaches derived from cellular automata. A cellular automata model of a landscape consists of a fixed array in which each cell represents an area of the land surface and is assigned a state (Green 1983, Green et al. 1985). This grid cell approach is amenable to many sources of data, such as satellite imagery or raster data in a GIS, and enables processes that involve movement through space, such as fire, to be modeled (Green 1983). Fahrig has also simulated disturbances on a landscape represented in grid cell format, focusing particularly on the magnitude and recurrence interval of disturbance (see Chapter 17, this volume).

Green (1989) used a square grid (50 × 50) to simulate a forested landscape that was susceptible to fire. Based on the disturbance rules that were developed, the cells were assumed to represent an area ranging from 10 m to 100 m in diameter. Each cell was assumed to contain a single plant (at the smallest spatial scale) or a stand (at the larger scales). Fires were ignited at random locations and were elliptical in shape, with the frequency and size having Poisson and negative exponential distributions, respectively. Simulated fires created nonuniform patches into which species could disperse, creating a mosaic of different vegetation types that varied depending on whether dispersal was influenced by an environmental gradient. The actual spread of fire was not simulated, but the spatial patterns of fire and species dispersal were represented.

Another class of models that can be used to simulate landscape disturbance includes the individual-based forest succession models (Botkin et al. 1972; Shugart and West 1977). This approach assumes that small landscape units are unstable with respect to vegetation cover. These models incorporate ecological processes and track the birth, growth, and death of all trees in a small plot (≤1 ha). Tree growth is influenced by light availability, soil moisture, temperature, and competition. Although the spatial location of each tree within a given plot is not recorded, the spatial relationships between plots can be analyzed. Regional patterns of forest disturbance effects have been projected by extrapolating results from model plots within a homogenous area to a larger area and by considering a variety of homogeneous subunits (Shugart and Noble 1981; Dale and Gardner 1987). The effects of disturbance can be modeled by considering forest development with and without disturbance or with a variety of disturbance types. For example, Doyle (1981) modeled the effects of hurricane frequency and severity on the lower montane rain forest of Puerto Rico and confirmed the importance of hurricanes in maintaining a diverse composition and structure of the forest. By modeling the effects of fire, wind throws, insect outbreaks, and logging on Pacific Northwest forests, Dale et al. (1986) were able to compare the long-term effects on forest development of these disturbances.

A series of individual-based forest stand models can be arrayed in a grid to simulate the dynamics of a larger forested landscape. This approach was taken by Smith and Urban (1988) to simulate forest changes through time as a spatially interactive unit rather than as a series of independent plots. Smith and Urban did not study disturbance processes per se (all grid cells were initialized with no trees), but this approach is clearly amenable to studying gap-creating disturbances in a spatially-explicit manner.

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Spatially-explicit models of disturbance effects and patch dynamics are useful for several reasons (DeAngelis and Waterhouse 1987). First, the effects of the size, shape, and arrangement of disturbance patches on species responses can be directly addressed. Second, the local dynamics of patches can be studied empirically in the field, and thus patch-oriented models may generate hypotheses that can be experimentally tested. Finally, the creation and extinction of patches at small scales can also be extended to larger areas and temporal scales.

13.3 Models of the Spread of Disturbance

The approaches we have reviewed thus far have dealt with the spatial heterogeneity created by disturbances but have not considered the spread or propagation of a disturbance across a heterogeneous landscape. Understanding disturbance spread is important both from a practical standpoint (e.g., how far and how fast might a pest species be expected to spread?) and to predict more generally the dynamics of the vegetation mosaic in disturbed landscapes.

13.3.1 Gradient Models

One of the first spatially explicit disturbance spread models was the gradient model developed by Kessell (1976, 1977, 1979). The objective of the model is to predict the daily spread (i.e., distance traveled) of a fire front rather than to predict the spatial patterns that result from a disturbance. The model uses six environmental gradients (elevation, topographic moisture, time since last burn, primary succession, drainage, and alpine wind-snow exposure) and four categories of disturbance (intensity of last burn, slide disturbances, hydric disturbance, and influences of heavy winter grazing by ungulates) to predict the daily spread of fire in Glacier National Park. Linkages are achieved between a terrestrial resource inventory system, gradient models of the vegetation and fuel, a micrometeorological model, and a mechanistic fire behavior model (Rothermel 1972). Gradient analysis is used to estimate the vegetation and fuels present throughout a large area, and the fire behavior model is then run in each spatial cell. Postfire succession is simulated deterministically based on habitat types (Kessell 1979) or life history traits of the species (Cattelino et al. 1979).

13.3.2 Epidemiological Models

A class of models that may be applicable to the spatial spread of a disturbance is derived from the theory of epidemiology (Bailey 1975; see also Gardner and O'Neill, Chapter 11). Epidemiology, which deals with the spread of a disease from individual to individual through a population, predicts factors such as the rate of spread and the proportion of the population that is affected by the disease. Models are available that trace the spread of an epidemic through space (e.g., Bartlett 1955; Radcliffe 1973). However, spatial pattern is not included in these models; each site is considered to be equally susceptible to the disease. In other words, the theory considers the spread of a single disturbance initiation through a homogeneous population (or landscape) in which it is possible for a single individual (or site) to infect all others. Thus, in its general form, the "general epidemic" theory can be considered to be a neutral model with respect to the possible effects of spatial heterogeneity in the landscape on the spread of a disturbance. Gardner and O'Neill (Chapter 11, this volume) describe neutral landscape models in general and present the mathematics of epidemiology as adapted to landscape studies.

13.3.3 A Probabilistic Model of the Spread of Disturbance

Ecological disturbance regimes can be described by a variety of characteristics, including spatial distribution, frequency, return interval, rotation period, predictability, area, intensity, severity, and synergism (e.g., White and Pickett 1985; Rykiel 1985). These parameters can be used to simulate landscape disturbance, and simulation experiments that use ranges of values for several of these characteristics can offer some general insights into the interactions between landscape pattern and disturbance spread. The spatial movement or spread of disturbance is amenable to study by using simple probabilistic models.

13.3.3.1 Model Description

One approach to developing simple models of disturbance spread is to adapt the methods of percolation theory (Stauffer 1985) to landscape studies (Gardner et al. 1987). Consider a landscape that contains only two types of habitat: habitat that *is* susceptible to a particular disturbance (e.g., pine forests susceptible to bark beetle infestations) and habitat that *is not* susceptible to the disturbance (e.g., hardwood forests and grasslands). The spatial arrangement of the disturbance-susceptible habitat can be randomly generated on a landscape map at probability p, and the propagation of disturbances that spread within the susceptible habitat may then be studied. The spread of disturbance in these random landscapes can be considered as a neutral model (see Turner et al. 1989).

For our simple model, we have incorporated three disturbance characteristics: frequency, intensity, and severity. Each characteristic is represented as a probability that can range from zero to one. Disturbance frequency (f) is defined as the probability that a new disturbance will be initiated in a grid cell of susceptible habitat during the time period represented by the simulation (e.g., the probability of lightning striking a hectare of pine forest during a particular storm event or time period). Disturbance intensity (i) is defined as the probability that the disturbance, once initiated, will spread to adjacent sites of the same habitat. Disturbance severity (h) is the probability of the site being damaged or altered by the disturbances such that it cannot be "revisited" by the disturbance during the simulation. When severity is equal to one, all disturbed sites are altered (e.g., vegetation in all disturbed cells is completely consumed by a pest); if severity is less than one, then some sites are not altered and can be disturbed again (e.g., although a pest passes through a site, sufficient vegetation remains such that the pest can revisit the site).

Thus, the general model simulates the spread and effects of disturbance as a function of four parameters: (1) the proportion of the landscape occupied by the disturbance-prone cover type, (2) disturbance intensity, (3) disturbance frequency, and (4) disturbance severity. The model is conceptualized in terms of discrete units of space (grid cells) and discrete units of time (time steps), in which we assume that a disturbance can move a distance of one grid cell per time step. In the general model, units of space and time are not specified. To simulate particular types of disturbances, parameters can be estimated for particular spatial units (e.g., m^2 or ha) and time steps (e.g., day, week, or year).

13.3.3.2 Simulation Algorithm

Our simulation program is written in FORTRAN 77 to run on VAX computers. Each of the four parameters must be assigned a value at the beginning of the simulation. First, two-dimensional $m \times m$ landscape maps are randomly generated to represent the disturbance-susceptible habitat at different values of p. This is done by generating random numbers between 0 and 1, then filling each grid cell in the map based on whether the random number is greater or less than p. For large maps (we used 100 × 100 arrays), the probability p, can be estimated as the proportion of a landscape occupied by a disturbance-susceptible habitat. For example, if we wish to simulate a landscape that is 65% pine forest, the p value for generating the random distribution of that forest would be 0.65. The remainder of the landscape ($1 - p$) is considered to be unsuitable for the simulated disturbance. Thus, the landscape maps are composed of 10,000 cells, each of which is randomly designated as vulnerable or resistant to a disturbance.

Next, the pattern of the landscape is analyzed before a disturbance is simulated. The chapters in Section 2 of this volume present a variety of methods to quantify landscape pattern; any of these could be incorporated into a disturbance model. We have included the following measures: the number of habitat clusters, the size and shape (measured by the fractal dimension) of the largest cluster, and the amount of inner and outer edges in the landscape.

After the initial landscape is generated and its pattern quantified, disturbance is simulated as follows. Grid cells on the map are randomly disturbed at a given frequency without replacement until exactly fpm^2 disturbances are initiated. (This is because the number of grid cells of susceptible habitat is given by pm^2, and fpm^2 therefore gives the number of discrete disturbances that occur.) Sites that are disturbed can be altered based on the severity, h, such that they cannot be disturbed again during the simulation. Disturbances then spread randomly with an intensity, i, to nearest-neighbor cells of susceptible habitat (diagonal movement is not allowed). Of course, the disturbance cannot spread if none of the adjacent cells is of susceptible habitat. The process is continued in discrete time steps until the disturbance can no longer spread (i.e., it "goes out" or consumes all available habitat). The pattern of the disturbed landscape is then analyzed, and the number,

sizes, and shapes of clusters of the disturbed habitat and of the remaining undisturbed habitat are summarized.

Any combinations of the four parameters p, f, i, and h can be simulated. By selecting a variety of plausible values for each parameter, simulation experiments (sensu Fahrig, Chapter 17, this volume) can be conducted with the model. We used a factorial design in which all possible combinations of a set of parameter values were run, and each particular combination was replicated ten times. Because this model is probabilistic, the replicate runs (Monte Carlo approach) allow the predictions to be summarized and evaluated statistically.

13.3.3.3. Simulation Experiments

We present a few illustrative simulation experiments (see Turner et al. 1989 for additional information). In one set of simulations, disturbance frequency was simulated at three levels, $f = 0.01$, 0.10, and 0.50 (representing low, moderate, and high levels). For each frequency, ten replicates were simulated for paired combinations of low, moderate, and high disturbance intensity ($i = 0.25$, 0.50, 0.75) and low and high p ($p = 0.4$ and 0.8). The severity of the disturbance was fixed at 1.0, (i.e., once disturbed, a site could not be disturbed again during the simulation). The proportion of habitat affected by disturbance was influenced by disturbance frequency but varied qualitatively for landscapes above and below the critical threshold, p_c, when the susceptible habitat could extend across the landscape (Fig. 13.1). This threshold, p_c, is approximately 0.6 for large, square random maps and is empirically derived from percolation theory. When $p = 0.4$, an increase in disturbance frequency causes a substantial increase in the proportion of habitat affected, even when the probability of spread is low (Fig. 13.1). When $p = 0.8$, increasing frequency increases the amount of habitat affected only when probability of spread is low. If probability of spread is sufficiently high (e.g., $i = 0.75$), more than 90% of the habitat can be affected by disturbance of very low frequency.

In another set of simulations, disturbance frequency was fixed at $f = 0.01$, and the interaction between disturbance intensity and severity was examined in fragmented ($p = 0.4$) and connected ($p = 0.8$) landscapes. Disturbance severity was simulated at four levels ($h = 0.25$, 0.5, 0.75, and 1.0), and disturbance intensity was simulated at three levels ($i = 0.25$, 0.5, and 0.75). Disturbance intensity, i, was more important than severity, h, in determining the proportion of the susceptible habitat that was disturbed during the simulation (Fig. 13.2). However, for a given value of i, increased disturbance severity resulted in a greater percentage of the habitat being disturbed. The effect was not always proportional to the increase in h. For example, when $p = 0.4$ and $i = 0.75$, an increase in h from 0.75 to 1.0 resulted in a twofold increase in the percent of available habitat affected by the disturbance (Fig. 13.2). In general, as disturbance severity decreased below 0.75, the reductions in the percent of habitat disturbed tended to become smaller.

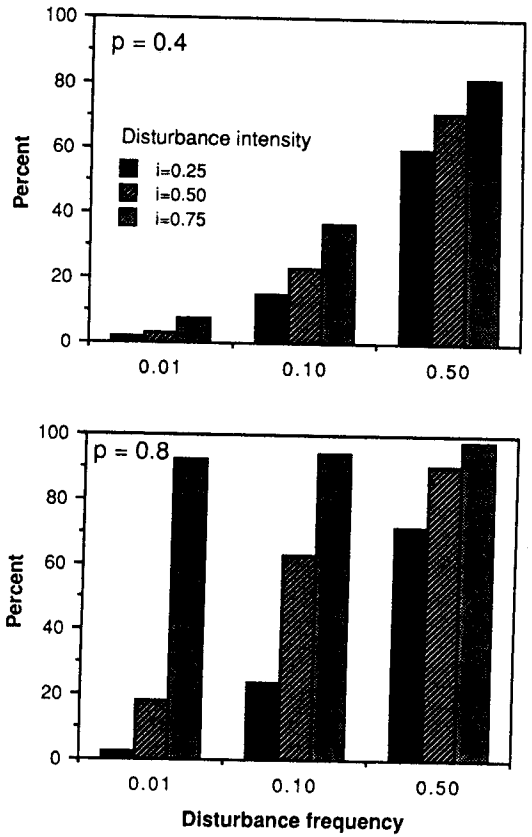

Figure 13.1. Mean (n = 10) percent of habitat disturbed as a function of both disturbance intensity and disturbance frequency for two initial probabilities (p) of occurrence of susceptible habitat (adapted from Turner et al. 1989).

13.3.3.4. New Insights from the Probabilistic Model

Simulation experiments in random landscapes suggest the existence of a threshold level of habitat connectivity that influences the spread of disturbance and its effects on the landscape. This insight may be of importance in resolving the question of whether disturbances are enhanced or inhibited by landscape heterogeneity because disturbance spread and effects depend on the interaction of several parameters. The distribution and spatial arrangement of the susceptible habitats help explain the differences. Habitats occupying less than the threshold, p_c, tend to be fragmented, with numerous small patches and low connectivity (Gardner et al. 1987). Disturbance propagation is constrained by this fragmented spatial pattern, and the number and sizes of patches are not substantially affected by the probability of spread. Habitats occupying more than p_c tend to be highly connected, forming continuous patches (Gardner et al. 1987). Disturbance can spread through the landscape even when frequency is relatively low.

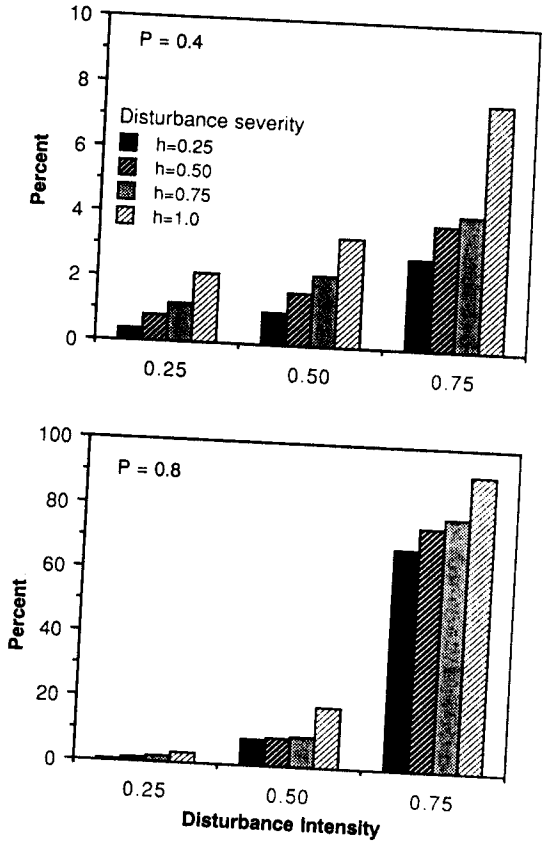

Figure 13.2. Mean (n = 10) percent of habitat disturbed as a function of disturbance intensity, i, and disturbance severity, h, for two initial probabilities of occurrence of susceptible habitat. Disturbance frequency, f, was held constant at 0.01.

Results from the simulation experiments may have implications for landscape management and conservation. For example, the persistence of less dominant habitats ($p \leq p_c$) that are susceptible to disturbance appears to depend upon disturbance frequency (f). Thus, the long-term viability of remnant forest stands or other dispersed patches of rare communities (e.g., cedar barrens and granite outcrops) in a landscape may therefore depend on the number of disturbances rather than on their probability of spread. A locally intense disturbance may

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eliminate a single habitat patch but have little effect on the persistence of that habitat in the landscape. In contrast, many disturbances over a large region could reduce or eliminate the habitat.

Habitats that are common may be easily fragmented by disturbances of only low to moderate intensity. Intermediate levels of disturbance intensity and frequency created greater patchiness in landscapes that were dominated by a disturbance-prone habitat. The interaction among *p*, *i*, and *f* may thus affect the landscape in ways that are counterintuitive. Large tracts of forest, for example, may be fragmented by disturbances of relatively low frequency (e.g., Franklin and Forman 1987). Structural changes associated with this fragmentation, such as the increased number of edges, may influence the susceptibility of the landscape to other disturbances (e.g., wind throw) or cause changes in the distribution and abundance of species.

13.3.3.5. Use and Interpretation of the Probabilistic Model

Key strengths of the probabilistic modeling approach are its generality and the ability to produce testable hypotheses. The general model can be applied to numerous types of disturbance that spread spatially across heterogeneous landscapes. The expected ranges of parameter values that will give certain types of disturbance spread and effects can be predicted. Importantly, the hypotheses generated by the model (e.g., the existence of thresholds in connectivity) can be tested quantitatively by using data for real landscapes and actual disturbance regimes. However, the present simulations must be interpreted and evaluated at the scale of the whole landscape, rather than on a site-by-site basis. Because the model is probabilistic, it is not designed to predict whether a particular hectare or plot will be disturbed; rather, the objective of the model is to predict disturbance patterns over a large area.

Appropriate spatial and temporal scales must be selected for particular landscapes and disturbance regimes. Discrete units of space and time must be specified explicitly to parameterize the model for any real landscape and disturbance. For example, to simulate the spread of pine bark beetles through a forested landscape, decisions must be made regarding the time step (e.g., weekly or monthly) and the size of a cell (e.g., 1 ha or 10 ha). The parameters must be estimated in the appropriate units (e.g., the probability of spreading 10 ha within one week).

The general model could be modified as follows to simulate a particular disturbance regime and to reflect local processes more accurately. First, habitats are often differentially susceptible to disturbance (for example, susceptiblity to fire increases with age in some coniferous forests) rather than displaying the Boolean "either-or" susceptibility that we have represented. Classes of susceptibility could be introduced, although they would increase the complexity of the model. For example, forests could be differentiated by age classes and assigned unique probabilities of being disturbed. Gradients of variability in edaphic conditions, such as elevation or moisture, might also be used to influence susceptibility to disturbance. Second, disturbances frequently tend to move directionally (e.g., fire

spreading with the prevailing winds). The tendency of a disturbance to spread in a particular direction could be incorporated by adding a bias factor, *B*, representing a probability of moving up, down, left, or right. In the random case, movement in all directions is equally probable, i.e., $B = 0.25$ (directional bias has been used by Gardner et al. [1989] to simulate the movement of organisms through a landscape). Third, ecological systems recover from disturbance within some duration of time. To simulate the long-term dynamics of a particular disturbance regime, a probability of recovery could be introduced, allowing sites to be disturbed again after a specified amount of time. Long-term recovery could also be simulated by using a transition matrix that assigned grid cells to new successional classes based on the elapsed time since the last disturbance.

13.3.4 Coupled Species Models

The spread of a pest or pathogen across a landscape represents a class of disturbance that involves the interaction of two or more species. One species causes the landscape disturbance by killing or reducing the growth or reproductive capacity of the other species. Such species frequently operate on different spatial and temporal scales. For example, the life cycle of phytophagous insects is generally on the order of days or weeks; yet outbreaks of these herbivores can drastically affect forest dynamics, which generally occur on the order of decades or longer. Models of the spread of such disturbances must take into account the different spatial and temporal dynamics of the two species. Coupled species models that operate at different spatial or temporal scales offer a means to consider the different scales as well as the different environmental factors affecting each species (Fig. 13.3).

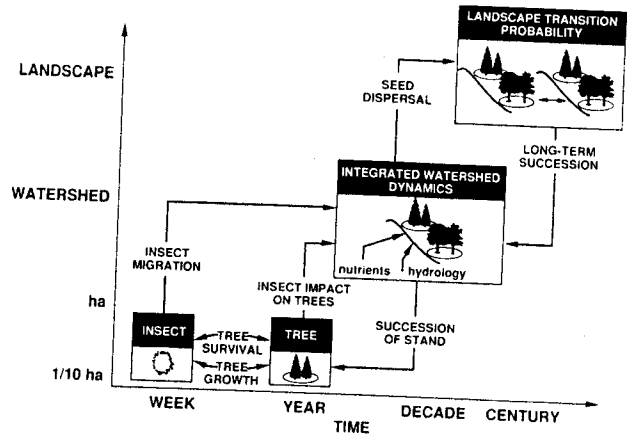

Figure 13.3. A diagram of coupled models that can address insect-tree interactions at a variety of spatial and temporal scales.

13.3.4.1 Model Description

Coupled models for tree and insect dynamics (Dale et al. 1990) have been developed by using Leslie matrix growth models (Leslie 1945, 1948; Usher 1966). The advantage of the Leslie model approach is that the dynamics of each of the life stages of the two species can be examined. Because the time scales of development for the trees and insects differ so greatly, it is necessary to use an approach that accommodates these differences. Two time scales were used simultaneously to model the tree-insect interactions: the trees were simulated with yearly time steps, while the insects were simulated with two-day time steps. The yearly time step for the tree corresponds to the annual growth rings of each tree. The two-day time step for the insects permits tracking instar development yet does not cause the simulation to be too slow (a daily time step would approximately double the simulation time).

The spatial dynamics of the coupled model are represented by implementing the tree and insect models for a series of patches or cells. Each cell can be separately parameterized to represent a spatial gradient of temperature or elevation in a linear or matrix framework. The cells interact by immigration and emigration of tree seeds and insect eggs and instars.

In the absence of insect predation, the forest patch is assumed to tend toward a stable steady state with a characteristic age structure. For simplicity, the tree population is described by the age-class vector $X(t) = (X_1, X_2, ..., X_5)$, where X_i is the number of trees in age class i and the age classes (or life stages) are one, two to five, six to thirty-five, thirty-six to sixty-five, and greater than sixty-six years old for a particular t (time in years). For each cell, the transitions of firs from one life stage to the next can be described by a Leslie matrix equation:

$$\mathbf{X}(t + 1) = \mathbf{P}\mathbf{X}(t) + \mathbf{I}_f, \tag{13.1}$$

or

$$\begin{bmatrix} X_1(t+1) \\ X_2(t+1) \\ X_3(t+1) \\ X_4(t+1) \\ X_5(t+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & f_4 & f_5 \\ p_{21} & p_{22} & 0 & 0 & 0 \\ 0 & p_{32} & p_{33} & 0 & 0 \\ 0 & 0 & p_{43} & p_{44} & 0 \\ 0 & 0 & 0 & p_{54} & p_{55} \end{bmatrix} \begin{bmatrix} X_1(t) \\ X_2(t) \\ X_3(t) \\ X_4(t) \\ X_5(t) \end{bmatrix} + \begin{bmatrix} I_s \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \tag{13.2}$$

where $p_{i+1,i}$ is the fraction of trees transferring from one life stage to the next stage per year, p_{ii} is the fraction remaining in age class i (where $p_{ii} + p_{i+1,i} \leq 1$), I_s is input of seeds from other plots, and f_i is the number of seeds produced per mature tree in age class i.

In actual simulations, this condensed life-stage model (Eq. 13.2) is expanded into an annual age class model. To make such a simulation, the p_{ij}'s are factored into annual probabilities in a manner similar to that of Harrison and Michie (1985). The complete Leslie matrix is 66 × 66 in size, with identical transition probabilities within each age class. Thus a seedling that sprouts in model-year one does not reach maturity until model-year thirty-six, unlike a traditional Leslie matrix, in which individuals could reach maturity by year four.

The insect population is modeled for each spatial cell under the assumption that the insect can easily disperse within the 0.1-ha cell. The insect population is divided into five life stages (Y_i): egg, first instar (crawler), second instar, third instar, and adult. The transition from one life stage to the next can be described by a Leslie matrix equation:

$$\mathbf{Y}(d + 1) = \mathbf{Q}\mathbf{Y}(d) + \mathbf{I}_a, \tag{13.3}$$

or

$$\begin{bmatrix} Y_1(d+1) \\ Y_2(d+1) \\ Y_3(d+1) \\ Y_4(d+1) \\ Y_5(d+1) \end{bmatrix} = \begin{bmatrix} q_{11} - E_{c1} & 0 & 0 & 0 & g_5 \\ q_{21} & q_{22} - E_{c2} & 0 & 0 & 0 \\ 0 & q_{32} & q_{33} & 0 & 0 \\ 0 & 0 & q_{43} & q_{44} & 0 \\ 0 & 0 & 0 & q_{54} & q_{55} \end{bmatrix} \begin{bmatrix} Y_1(d) \\ Y_2(d) \\ Y_3(d) \\ Y_4(d) \\ Y_5(d) \end{bmatrix} + \begin{bmatrix} I_{c1} \\ I_{c2} \\ 0 \\ 0 \\ 0 \end{bmatrix} \tag{13.4}$$

where I_{c1} and I_{c2} are the external inputs of passively transported eggs and the first instars, respectively, to a particular plot (c) from other cells (eggs dispersed per time step); $q_{j+1,j}$ and q_{jj} are the fraction of insect in life stage j that are transferred to life stage $j+1$ or that remain in life stage j, respectively, per time step (two days); E_{ci} is the fractional loss due to emigration from cell c; and g_5 is the number of eggs produced per mature adult. The ratio $q_{j+1,j}:q_{jj}$ indicates how rapidly insects move through their life stages. Because $(q_{j+1,j} + q_{jj})$ represents bidaily survivorship of insects starting the day in life stage j, the quantity

$$m_j = 1 - (q_{j+1,j} + q_{jj}) \tag{13.5}$$

represents bidaily mortality in that life stage. The model includes parameters for the average fecundity of adult insects and the export of insect eggs by passive wind dispersal.

The progression through life stages of the insects is highly dependent on temperature (Amman 1968; Greenback 1970). We approximated the mean development periods of the egg ($D_{T,e}$) and nymph ($D_{T,n}$) as:

$$D_{T,e} = 5.0 + 100 \exp(-0.10(T-4)) \tag{13.6}$$

$$D_{T,n} = 10.0 + 50 \exp(-0.25(T-4)) \tag{13.7}$$

where T is temperature in °C and $D_{T,e}$ and $D_{T,n}$ are measured in days. The term *nymphs* refers to all three instar stages so that $D_{T,n}$ measures the development time from the end of the egg stage to the beginning of the adult stage. No development is allowed to occur for values of T less than four.

The ratio $q_{21}:q_{11}$, or the rate of development of eggs, is expressed in terms of T through

$$\frac{q_{21}}{q_{11}} = \frac{1}{D_{T,e}} \tag{13.8}$$

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Mean daily temperature of a cell at time t is represented by a sine function:

$$T(d) = T_{ave} + T_{amp} * \sin\left[\frac{2\pi}{365}\ (d\text{-DAY}) + \frac{\pi}{2}\right] \qquad (13.9)$$

where T_{ave} is the average temperature, T_{amp} is the amplitude, and DAY is the time of the year with the maximum temperature. The actual temperature of a cell is $T(d)$ plus a factor that accounts for the variation of that cell temperature from the mean as a result of elevation.

Parasite-host interactions. The negative effects of the insect on the survival of trees (M_t) can be expressed as a cumulative effect, defined as the "effective insect days per tree" for year t, or

$$M_t = \sum_{d=1}^{183} \frac{[Y_2(d)+Y_3(d)+Y_4(d)+Y_5(d)] * f(T)\ W_d}{a_4X_4(t) + a_5X_5(t)} \qquad (13.10)$$

where $f(T)$ is 1 if the temperature exceeds 4°C but is 0 otherwise; W_d is two days; and a_i is the fraction of trees in each age class that are expected to be susceptible to insects ($a_i \leq 1$). Note that only trees of age classes four and five can be infected. The number of trees dying is calculated by fraction of trees transferring from one life stage to the next for susceptible age classes by $(1 + \alpha M_t)$, where α is the aphid mortality constant that determines how many of the susceptible trees are actually infected, e.g., $p_{55} = p_{55,0}/(1 + \alpha M_t)$.

The insects are assumed to be limited by the availability of host trees and by density-dependent regulation. When susceptible trees are removed as a result of natural or insect-induced mortality, a proportional number of insects are removed. Because $a_4X_4(t)$ and $a_5X_5(t)$ are the numbers of infected trees at year t and $1.0 - p_{44} - p_{54}$ and $1.0 - p_{55}$ are the mortalities in each of these stages, the fraction (f_r) of the first instar removed as a result of tree mortality is

$$f_r = a_4(1.0 - p_{44} - p_{54}) + a_5(1 - p_{55}) \qquad (13.11)$$

Only the first instar is removed because the adjustment occurs on January 1, when the first instar is the only insect life stage that is living.

The carrying capacity of insects is implemented by letting the daily average fecundity of adults, g_5 (eggs per two days per insect), be a density-dependent function of the number of insects present:

$$g_5 = [g_{5,0}/(1 + kY_2 + kY_3 + kY_4)] \qquad (13.12)$$

For example, to determine the value of k that results in a total carrying capacity of 50,000 we solve Eq. 13.12 for k using the equilibrium value

$$Y_2 + Y_3 + Y_4 + Y_5 = 50{,}000 \qquad (13.13)$$

to get

$$k = 0.000002\left[\frac{g_{5,0}\ q_{21}\ q_{32}\ q_{43}\ q_{54}}{(1-q_{11})(1-q_{22})(1-q_{33})(1-q_{44})(1-q_{55})} - 1.0\right] \qquad (13.14)$$

The value k, above, is appropriate for one tree. To calculate an effective value of k (termed k') for the whole cell, we take roughly the number of trees older than sixty-six years (X_5) and the number of trees between thirty-six and sixty-five years old (X_4) that exist in the cell at the given time, and we assume that the younger trees have half the carrying capacity of the older trees. Then $k' = k/(X_5+0.5X_4)$.

The tree-insect model is used to simulate long-term effects of the insect infestation on spatial patterns of the forests. Accomplishment of this objective requires the simultaneous modeling of many patches in different climate regimes and the dispersal of insects and tree seeds between the patches. Emigration of eggs and first instars from a cell to the adjacent cell are calculated by assuming that the number of emigrants is a linear function of the number of eggs and first instars in the patch. For example, the emigration of eggs from patch c is $E_{c1}Y_1(d)$, where E_{c1} is the dispersal coefficient (eggs dispersed per two days per insect). The number of immigrants into patch c is computed by summing the number of emigrants from the neighboring patches and multiplying by the probability that an emigrant from one patch becomes an immigrant to another. Thus,

$$I_{c1} = V_{c,c-1}E_{c-1,1}Y_{c-1,1}(d) + V_{c,c+1}E_{c+1,1}Y_{c+1,1}(d) \qquad (13.15)$$

where $V_{c,c-1}$ is the probability of an insect reaching patch c after leaving patch $c-1$, and the subscript c added to $Y_i(d)$ indicates the cell being referenced. Tree seed dispersal between patches is currently ignored; that is, $I_s = 0$ in Eq. 13.2. The model is flexible enough to simulate any desired configuration of a large number of patches.

13.3.4.2 Simulation Algorithm of the Coupled Species Model

The coupled tree-insect model was developed in Turbo-Pascal to run on a personal computer. A version of the model was also written in FORTRAN 77 to run on a Cray supercomputer so that numerous interacting patches could be simulated. Applying the model to specific landscapes requires obtaining data on the interaction of interest, including species transitions between age classes; inputs of seeds, eggs and instars from adjacent cells; effects of temperature on egg and nymph development or survival; insect fecundity; and temperature average and amplitude for the cells. The model projects the numbers of insects and trees by size class for each cell.

13.3.4.3 Simulation Experiment

The coupled tree-insect Leslie matrices have been applied to interactions between the exotic balsam woolly aphid (BWA) (*Adelges picae* Ratz.) and the endemic

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Fraser fir (*Abies fraseri* [Purch] Poir.) in the southern Appalachians (Dale et al. 1990). The effects of BWA on the small scale of a forest stand are deterministic because BWAs kill all mature fir trees in about three to nine years after initial infestation (Amman and Speers 1965). Prediction of the broad-scale effects of BWA in a forest region requires an assessment of (1) the population dynamics of the BWA and fir, (2) the prevailing physical conditions that affect the spread of aphids, and (3) the subsequent pattern of fir mortality. The coupled models can project patterns of fir mortality and recovery on an elevation gradient using site-specific environmental conditions and ecological interactions.

The patchiness of BWA outbreaks in the fir forest (Eagar 1984) suggests that a relatively small spatial scale is appropriate for describing dynamics both within and between cells. Here, the cell size of the model is set at 0.1 ha, but it can be adjusted easily. Choice of the cell size influences the parameter value for the proportion of propagules dispersed between cells.

The simulated time from infestation of a stand to adult tree mortality and the simulated equilibrium population sizes are comparable to observed values (Table 13.1). The model projects the growth of BWA populations within each cell and the subsequent demise of both the fir and the BWA as BWAs kill their host organisms. When mature BWAs in a cell are sufficient in number, eggs and crawlers are dispersed to adjacent cells. After the BWAs kill all the mature trees within a cell, the BWAs cannot survive in that cell. The absence of BWA allows any remaining fir seedlings and saplings to grow into mature trees. If BWAs are in adjacent cells when the surviving trees mature, then BWAs can reinvade and kill the adult trees. These patterns of fir and BWA dynamics are similar to those

Table 13.1. Model Results Compared to Measured Values for Data that Were Not Used in the Development of the Model Parameters

Characteristic	Model Result[a]	Measured Result	
		Value	Reference
Years after initial BWA infestation during which fir died	7–10	3–9	Amman and Speers (1965)
Equilibrium fir population number per 0.1 ha:			
Seedlings	1984	1991	Witter and Ragenovich (1986)
Trees older than 6 years	67	80[b]	

[a] Run under temperature conditions typical for 1600 m as calculated from regression equations in Shanks (1954) by using a monthly temperature record.
[b] Trees taller than 244 cm were measured and are assumed here to be older than 6 years.

observed in the southern Appalachian spruce-fir forests (Eagar 1984). The inclusion of long-distance BWA dispersal in the model would undoubtedly increase the likelihood of infestation of a cell.

Model simulations were run for a series of six cells intended to represent a transect on an elevation gradient from 1600 to 2000 m. For all cases the BWA eggs and the first instars were allowed to disperse directly between adjacent cells. The simulation experiment was used to examine two hypotheses about the observed pattern of fir mortality, which occurs first at lower and middle elevations (1300 to 1700 m) (Eagar 1978). The hypotheses are (1) the fir mortality pattern results from dispersal of BWA between mountains versus (2) the pattern results from temperature limitations on aphid development. The first hypothesis maintains that BWAs are more likely to be dispersed from a mountain top to trees at lower elevations on the adjacent mountain because BWAs are transported by winds that generally increase in velocity as they rise toward the summit and produce eddies on the leeward size in the vicinity of the lower elevation range of the fir (Eagar 1984). Wind velocities are too high for successful BWA deposition on the windward side, but they are mild enough on the leeward side. The gradual movement of BWAs up the slope is explained by dispersal of BWAs between adjacent stands. The second hypothesis is that BWAs are dispersed to all locations at the same time, but temperature acts to slow down the development rate of the BWA and the subsequent mortality of the fir at high elevations. The simulations project the effect on fir survival (1) when the BWA is introduced to the lowest elevation cell, with all cells having identical temperature conditions, and (2) when the BWA is introduced to all cells, with the cells having a temperature gradient. In the second case, the temperature of the cells decreased linearly as elevation increased, falling from 1.2°C above the mean January temperature for the lowest elevation cell to 0.8°C below the mean for the highest elevation cell.

The tests of the hypotheses that dispersal and temperature cause fir mortality to occur first on the lower slopes suggest that temperature is a major cause of the observed pattern (Fig. 13.4). In both tests, mature firs died earlier in the lowest elevation plot and later in the highest cell. The difference between the time of fir death in the low elevation plot and that in the high elevation plot was greater in tests of the temperature hypothesis. The final size of the simulated fir population in the highest elevation cell did not depend on whether the BWAs were introduced to the lowest cell or to cells at all elevations on the temperature gradient. The simulations suggest that both BWA dispersal and temperature constraints on BWA development influence the long-term pattern of fir mortality and recovery but that temperature has the more pronounced effect when only between-plot dispersal is included.

13.3.4.4 New Insights from the Coupled Species Model

Considering causes of fir distribution on a broad spatial scale requires reevaluation of the significance of physical and biological factors in the formation of the resulting patterns. In general, physical gradients are thought to be the major

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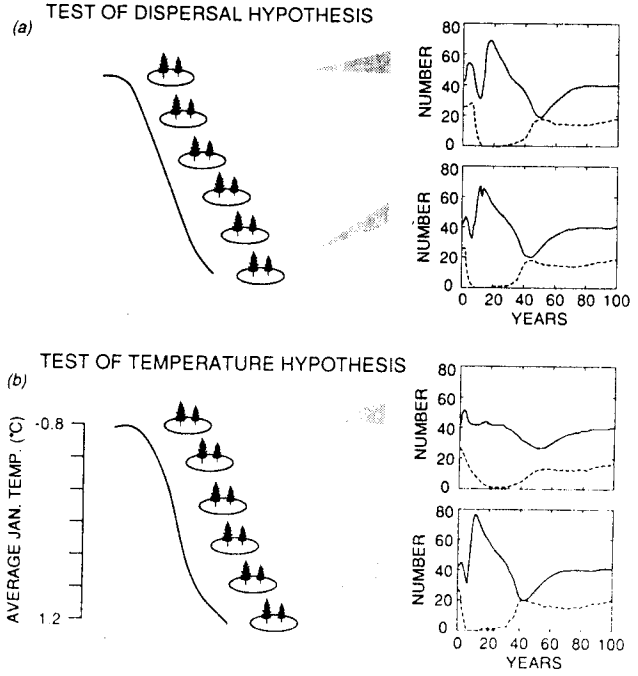

Figure 13.4. Number of fir trees by age class predicted over time for the highest and lowest elevation cells when (a) BWAs were introduced only to the lowest elevation plot and there were no temperature differences between the plots, and (b) BWAs were introduced to all plots and the plots were on a temperature gradient. The age classes depicted are trees between 5 and 35 years old (–) and trees older than 36 years (---).

determinants of pattern on the large scale, whereas biological factors may be more important at a smaller scale (Meentenmeyer and Box 1987). Whittaker (1956) has demonstrated that the general vegetation pattern in the Great Smoky Mountains is due to the physical gradients of moisture and topography (a complex gradient combining the effects of changes in precipitation, temperature, and insolation). This study builds upon the work of Whittaker by examining how a biotic disturbance can combine with physical gradients to affect vegetation pattern.

The model results show that patterns of fir mortality and spread of the BWA are strongly influenced by the relative density of fir and the prevailing temperature. Other computer simulation studies have concentrated more on the rate of dispersal have shown that persistence of both the predator and prey increased with (1) the prey's ability to disperse, (2) the predator's decreased ability to disperse (as long as the predators dispersed at some minimum level to keep ahead of exhausting their food supply), and (3) the total number of spatial cells (Caswell 1978; Hastings 1977). For the BWA-fir interaction there are a large number of cells possible over the extent of the southern Appalachians. The environmental diversity of the southern Appalachians could be simulated with the Leslie model by simulating temperature gradients of longitudinal transects.

The use of coupled tree and insect models that operate at different temporal scales has been effective in elucidating major determinants of Fraser fir distributions in the southern Appalachians. Analysis of broad-scale patterns should consider life-history characteristics of the major species as well as prevailing environmental conditions. The potential importance of small-scale interactions to broad-scale patterns has been demonstrated with the Leslie model. The model suggests that temperature can act at a small spatial and temporal scale to slow down the rate of development or to kill the BWA and thus indirectly affect fir distribution. The broad-scale implications of those results would be that temperature can act at a large resolution to limit the distribution of BWAs and thus affect the pattern of survival of fir. Therefore, predicted climate changes that would result from increases in atmospheric concentrations of CO_2 could have an indirect effect on the distribution of fir by altering the ranges where BWAs can survive.

13.4 Discussion

Each of the modeling approaches used to simulate the heterogeneous effects of disturbance or the spatial spread of disturbance across a landscape has advantages, limitations, and appropriate uses (Table 13.2). Spatially aggregated models of disturbance effects are applicable at many spatial and temporal scales and can be developed for a variety of landscape and disturbance types (Table 13.2). However, these models do not incorporate mechanisms, feedbacks, or spatial neighborhood effects. Furthermore, these models frequently imply the existence of an equilibrium state that may not exist. Spatially explicit models of disturbance effects may include more process representations and provide a means to follow the temporal changes in disturbance-created gaps or patches. These models may simulate the influence of environmental gradients on disturbance processes or the change in the size and age of disturbance patches.

Disturbance spread models are also spatially explicit, but they incorporate the spatial movement of a particular (or general) disturbance (Table 13.2). These models are particularly useful for exploring the effect of particular landscape patterns on the rate and extent of disturbance propagation. Numerical simulations are generally required in spread models because most approaches do not have an analytical solution. Models derived from epidemiology can be solved analytically, but only if the explicit pattern in the landscape is ignored. New approaches that use probabilistic models or coupled species models offer a means to address disturbances that occur at various scales.

The limitations of landscape disturbance models indicate that the relationship between landscape heterogeneity and disturbance requires additional research. The existing diversity of modeling approaches demonstrates that disturbance spread and effects can be modeled in a variety of ways. The most appropriate approach for a particular situation depends on the type of disturbance, degree of landscape heterogeneity, availability of data, and the desire to include mechanisms

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Table 13.2. Summary of Approaches to Modeling Landscape Disturbances

Approach	Applications	Advantages	Limitations
Heterogeneous Effects of Disturbance			
Spatially Aggregated Models			
Markov chain	Probabilistic disturbance events and subsequent species transitions.	Applicable at multiple scales and for many types of disturbances, organisms, and ecosystems.	Steady-state solution; no feedbacks or spatial neighborhood effects; many landscape changes not truly Markovian.
Tabular	Deterministic net changes in state variables in a region	Applicable at many scales and has been used globally; hierarchical data structure allows user to select appropriate level of detail.	No mechanisms, feedbacks, or neighborhood effects.
Patch dynamics	Disturbances that create gaps in homogeneous systems	Follows patch sizes and ages; general, applicable to many types of disturbance; has analytical solution; remote sensing and GIS data could be used.	Limited mechanistic detail (empirically determined patch birth and death rates); no interaction between patches.
Spatially Explicit Models			
Forest succession	Forest responses along environmental gradients	Processes represented; can be extrapolated to broader scales; already implemented with many types of disturbance.	Requires detailed information about species and sites to parameterize; lack of interaction between cells.
Cellular automata	General patch-creating disturbances	Has interaction between cells; includes disturbance, recovery, and environmental gradients; can be scaled for individual organisms or plots; includes size and shape of disturbance patches; can be used with remote sensing and GIS data.	Lack of mechanism (patch size determined empirically).
Spread of Disturbance			
Gradient modeling	Fire spread; disturbances that vary along environmental gradient.	Uses mechanistic model, recovery and spatial data; interaction between cells; remote sensing GIS data.	Requires much detailed data in advance; patch shapes not addressed.
Epidemiology	Spread through homogeneous landscapes	Analytical solution; predicts velocity of spread.	Assumes homogeneous landscape, difficult to adapt to patterned landscape; steady-state solution.
Probabilistic spread models	Spread of generic disturbance through patterned landscape	Can be scaled for individual organisms or plots; addresses patterned landscapes; can be run using grid-cell based data (e.g., satellite imagery, GIS data); processes can be incorporated.	Lack of mechanism and feedbacks; does not include differential susceptibility.
Coupled species models	Spread and effects of pests and pathogens; any interacting species.	Includes mechanisms and feedbacks and environmental effects; links species at different spatial and temporal scales; applicable to patterned landscapes.	Requires detailed information to parameterize model.

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or feedbacks. The complexity of disturbance effects remains difficult to predict, although progress is being made in determining the factors that control disturbance effects. Recent advances with geographic information systems (GIS) and satellite imagery will undoubtedly enhance the development of spatial models of disturbance because measures of landscape pattern are used both to parameterize models and as comparison against model predictions.

Predicting the spread of disturbance through landscapes and the resultant spatial pattern is of considerable current interest. It is likely that the pattern of the landscape prior to disturbance will be important at some times and not at others. For example, landscape pattern may influence the spread of disturbance when the disturbance occurs at low or moderate intensity but not at high intensity. The role of disturbance in creating landscape patterns is likely to receive greater attention regarding projected changes in the global environment. Altered disturbance regimes may be the proximal cause of large-scale changes in the environment (Clark 1988; Franklin et al. 1990), and new communities that become established may differ significantly from the undisturbed communities (Cwynar 1987; Dunwiddie 1986).

13.5 Summary

Natural and anthropogenic disturbances are common to many landscapes. The effects of disturbances frequently vary spatially across a landscape, creating a heterogeneous vegetation mosaic. Some disturbances propagate spatially and may be enhanced or retarded by the pattern of the landscape. Modeling and analytic methods are being developed to better understand and to predict the relationship between landscape patterns and disturbance regimes.

Two categories of landscape disturbance models are examined. First, we review models in which the heterogeneous effects of landscape disturbances are simulated. The models are further classified as "spatially aggregated," in which homogenous subunits of the landscape are treated together, and as "spatially explicit," in which the geographic location and change in attributes of each site are included. Spatially aggregated models (e.g., Markov chain and tabular models) are useful for addressing net disturbance effects and changes in the proportion of a land area that remains in a particular disturbance category. These models can also be used to explore the potential of a steady-state mosaic and can easily address the effects of altering the frequency of disturbance. However, the spatially aggregated models are unable to incorporate neighborhood effects. Spatially explicit models of disturbance effects do include the neighborhood effects but have differing levels of mechanism. The dynamics of disturbance-created gaps can be modeled, and the implication of changing the frequency, size, and responses to disturbance can be simulated.

The second class of models that we consider simulate the spread of disturbance. The gradient modeling approach (Kessell 1979) was one of the first spread models, and it linked several different submodels. Epidemiology theory has been used extensively to study the spread of diseases through populations, and this theory

can be modified to simulate landscape disturbances. However, epidemiology theory has difficulty incorporating the explicit effects of landscape pattern. A simple probabilistic spread model can be used to examine the frequency, intensity, and severity of disturbances in patterned landscapes and to generate hypotheses that can be tested with a variety of different disturbance regimes. However, to simulate specific disturbances or landscapes, a link to empirically measurable parameters or mechanisms must be incorporated. Coupled species models can be used to predict the spatial spread of a disturbance in which one species feeds on another and the interaction of the distribution of the host and the life history attributes of both species constrain the disturbance spread.

Each model category is suited to particular types of disturbances and spatial patterns. The mathematical construct of each model and its application determine the advantages and limitations of each approach. A summary of the approaches to modeling landscape disturbances indicates that more research is needed to elucidate the relationship between landscape heterogeneity and disturbance.

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