

Disturbance propagation by bark beetles as an episodic landscape phenomenon

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Abstract

Landscapes are the resultant of ecological processes and events operating on many different space-time scales. Large scale disturbance is recognized as a major influence on landscape patterns, but the impact of small scale events is often overlooked. We develop an hierarchical framework to relate lightning and bark beetle population dynamics to the southern pine forest landscape using the concepts of disturbance propagation and amplification. The low level lightning disturbance can be propagated to the landscape level when weather and forest stand structure facilitate bark beetle epidemics. We identify epidemics as biotically-driven episodes that alter landscape structure. The concept of the landscape as the spatial dimension of these episodes is represented in a conceptual model linking insect-host and landscape mosaic interactions.

Introduction

Landscape dynamics are influenced by complex abiotic and biotic interactions that lead to changes in the structure and function of ecological systems (Forman and Godron 1986). Disturbance is a major factor affecting landscape dynamics. However, disturbance can be subtle as well as dramatic and may involve translation of effects across hierarchical levels of organization. Episodic disturbance changes the landscape and these changes in turn influence the spatial and temporal pattern of future disturbances. In the southern pine forest of the United States, the southern pine bark beetle guild restructures the landscape, both by its herbivory and the response of foresters to the ravages of these insects on commercial forestry.

Disturbances occurring at lower hierarchical levels are not expected to produce detectable effects at higher levels. O'Neill *et al.* (1986), for example, say

that 'lower levels are constrained because they are unable to affect the behavior of the higher level', and that 'the greater the number of levels separating two scales of interest, the less will be the recognizable influence of lower-level behavior on a higher level in the system'. Allen and Starr (1982) suggest that the explanatory principles that apply to a set of observations are scale-dependent. Therefore, there is no reason to expect disturbance at one level to bear any simple relation to disturbance at a higher level. However, we postulate that lower level disturbances can be amplified and propagated by ecological processes to produce significant effects at higher levels. In particular, a disturbance acting at the level of individuals may be propagated through hierarchical levels as a result of population processes. Hierarchy theory has not addressed in detail the circumstances that might lead to attenuation or amplification, although amplification is considered unlikely (Allen and Starr 1982). We also

suggest that when propagation occurs, the nature of the disturbance changes as higher levels are affected. Propagation across levels of an hierarchy implies that the disturbance and its effects will be viewed differently as the level of observation changes. The disturbances we will be concerned with are lightning and bark beetle epidemics.

The intricate ecological processes by which a landscape is shaped can be difficult to interrelate. Our purpose here is to weave together the threads of species life history, insect-host interactions, disturbance, and hierarchy concepts to develop a framework that relates bark beetle population dynamics to the landscape dynamics of the southern pine forest. We begin with definition of important terms. Next we introduce the bark beetles, their pertinent life history characteristics, and the major features of their interaction with pine trees. Disturbance considerations are then examined to develop the concepts of disturbance propagation and conversion in an hierarchical context. Lastly, we suggest a feedback mechanism that conceptually integrates landscape dynamics with episodic bark beetle epidemics.

Definitions

A landscape is a heterogeneous land area composed of a cluster of interacting ecosystems or an ecological mosaic (Forman and Godron 1986). For our purposes, the mosaic consists of forest stands of varying sizes and stages of development and non-forest patches such as farmland.

An episode is an event that is distinctive and separate although part of a larger series, *i.e.*, a situation that is integral to but conceptually separable from a continuous process or stream of events. By this definition, bark beetle herbivory, which results in dead pine trees, is the larger series or continuous process, while an epidemic is recognizable as a distinctive event or episode. Disturbances that cause landscape changes are generally thought of as grand scale abiotic events that initiate succession. However, biotic events can also have a major impact on the landscape, and we characterize bark beetle epidemics as biotically-driven episodes in

Table 1. General disturbance characteristics

1. Type: what is it
2. Initial predominant effect: what does it do
3. Mode of action: how does it do it
4. Organizational level: what is affected
5. Scope: how big is it
6. Duration: how long does it last
7. Intensity: how much damage does it do
8. Timing relations: when does it occur
9. Frequency: how often does it occur
10. Reliability/predictability: does it always occur within a particular interval and when will it recur

contrast to abiotically-driven episodes.

Currently, there is no single widely accepted definition of disturbance (Mooney and Godron 1983; Pickett and White 1985; Rykiel 1985) because the ecological content of disturbance can be further specified by a variety of characteristics (Table 1) and descriptors (Table 2). Disturbance causes a sudden change in the behavior or properties of a system. Obviously, the qualifier 'sudden' is related to the time frame over which the system is observed and its characteristic behavioral frequencies. We define disturbance broadly as a physical force, a process, or an event that causes a sudden deviation in system behavior or a change in system properties.

It is important to distinguish between the original cause of a disruption or change (White and Pickett 1985) and its effects. In general, we use the term disturbance to identify the cause of a change. We separate the effect of a disturbance, a measurable deviation in the value of an ecological variable in relation to a reference condition, from the disturbance itself (Rykiel 1985).

Scale refers to a frame of reference derived from the level of resolution and the set of objects used to identify the system of interest and describe its attributes (Allen *et al.* 1984). For our purpose, levels of ecological organization (e.g., individual, population, community, ecosystem) denote scale.

Attenuation means a reduction of severity, lessening of strength, or decrease in magnitude. Amplification means an expansion, intensification, or increase in magnitude. We use these terms to indicate that the impact of a disturbance and its effects can be lessened (attenuated) or increased (ampli-

Table 2. Classification of disturbance descriptors

Category: general disturbance effect

1. destruction: loss of an existing ecological quantity, usually biomass; applied to any ecological level
2. discomposition: alteration of species composition by adding, removing, expanding, or reducing one or several species, often selectively; usually at the population and community levels
3. interference: alteration of energy flow, nutrient cycling, and information processes required for normal function, typically applied to interference with reproductive processes; usually at individual and population levels

Origin: in a system-environment dichotomy

1. external: originating in the environment (exogenous)
2. internal: originating and acting within the system (endogenous)

Nature: in a physical (non-living)-physiological (living) dichotomy

1. abiotic
2. biotic

Echelon: ecological levels of organization

1. individual
2. population
3. biotic community
4. ecosystem
5. landscape

Locus: in a multispecies system, distribution of disturbance impact immediately after occurrence

1. distributed: most or all species affected, but not necessarily equally
2. targeted: one or a few species affected, most not affected
3. diffuse: structurally or functionally distributed within the system
4. patchy: structurally or functionally targeted, creating patches within the system

Impact: in a multispecies system

1. direct: species directly affected by disturbance
2. indirect: species affected by propagation of disturbance effects through ecological processes

Response: in a population context

1. density dependent: response to disturbance or level of effect depends on population density
 2. density independent: response or level of effect is independent of population density
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fied) by ecological processes that vary with hierarchical level.

Bark beetle-pine tree interaction

'Bark beetles' include several genera and many species of the family Scolytidae that feed in the subcortical region of host trees. The southern pine bark beetle (*Dendroctonus frontalis* Zimmerman) (Thatcher *et al.* 1982) is responsible for much of the damage to southern pines. Beetles must locate and colonize a live host tree, normally a mature pine. Successful colonization ultimately results in the death of the host tree, which is usually caused by

fungi inoculated into the tree by the beetles. About 90% of the beetles' life cycle is spent within a pine tree. The host provides the beetles with a food supply (phloem) and a relatively protected environment in which to mate and rear offspring. Bark beetle life span is relatively short and dependent on the temperature regime (Wagner *et al.* 1984). The probability of adult survival outside a host tree decreases rapidly and is reduced to 1% within eight days (Pope *et al.* 1980), which indicates the importance of locating a suitable host.

Under ideal conditions, beetle development from egg deposition to adult emergence from a host tree can take place in as little as 30 to 40 days (Thatcher

and Conner 1985). The number of beetles may increase tenfold in a single generation and, in the southern United States, up to seven overlapping generations may develop in a single year. Thus, sparse populations can increase to outbreak numbers within a growing season. Epidemics are believed to occur at approximately 10 year intervals, although there is significant variation, and epidemic populations may be found somewhere within the beetles range virtually every year (Payne 1982).

A large number of beetles are usually required to attack and colonize a healthy pine because of the tree's defensive mechanisms (Sharpe *et al.* 1985). The colonization process (Coulson 1979) involves interaction of adult insects with host defenses (Blanche *et al.* 1983; Hodges *et al.* 1985). Conditions that diminish the effectiveness of the host's defenses (Cates and Alexander 1982) enhance colonization and influence both the initiation and growth of infestations. When oviposition is completed, the attacking adults either die in the tree or re-emerge. Both re-emerged adults and brood adults are capable of colonizing hosts.

When a tree has been fully occupied by beetles, the attacks of newly-arriving as well as emerging beetles shift to nearby pines leading to 'spot' growth or spread. A spot is one or more adjacent dead and dying trees forming a recognizable group. In any given year, isolated spots of beetle attacked trees are scattered throughout the landscape. Generally, these small infestations die out without any treatment.

A number of factors have been identified as contributing to the susceptibility of pine trees to beetle attack. Anything that weakens the defensive capacity of a pine tree can increase its susceptibility to bark beetle attack. We focus on lightning because it is a common natural disturbance in the southern pine forest. In a comparison of weather-related disturbances associated with beetle spots, lightning was by far the most important (Hicks 1982). It is not uncommon for more than 50% of the bark beetle spots to be associated with lightning strikes during the summer months (Thatcher and Connor 1985). Lightning-struck trees also produce volatile compounds that may aid the beetles in detecting them (Payne and Coulson 1985). Lightning thus

plays an important role in the epidemiology of pine bark beetles (Coulson *et al.* 1983; Hodges and Pickard 1971).

Lightning simulation

Lightning can cause several different ecological effects. The intense electrical discharge initiates fires that can consume considerable amounts of the living and dead biomass of an ecosystem or landscape. A tree can also be destroyed by lightning without starting a fire, or be damaged but not killed. The surviving lightning-struck tree is severely stressed physiologically. We focus on this last effect because bark beetles can colonize lightning-damaged trees more easily than healthy trees.

To investigate the response of pine bark beetles to lightning-struck trees, the damage done by lightning was simulated by winding detonating cord around individual trees and setting off an explosion (Coulson *et al.* 1986). Although there is no way to duplicate the effects of lightning exactly, the resulting wound was remarkably similar to that observed on lightning-struck trees. We hypothesized that the effect of the lightning disturbance (both real and simulated) was to render the tree unable to defend itself from pine bark beetle attack.

Twenty plots consisting of three loblolly pines each were established in the Piney Woods region of east Texas (Coulson *et al.* 1986). A group of five plots was treated in each of four seasonal trials (Fig. 1). Two of the pines in each plot were disturbed and the third tree served as a control. Although the study area had a history of bark beetle activity, there were no visually detectable infestations at the beginning of the study. All forty treated trees in the experiment were located and attacked by bark beetles, although the length of the colonization period varied by season of disturbance (Fig. 1). None of the control trees were colonized except as a result of spot growth initiated by colonization of the treated trees. In 10 of the 20 plots, only the treated trees were successfully colonized and in two plots, only one additional tree was colonized. However, eight plots developed into multiple tree infestations (Fig. 1).

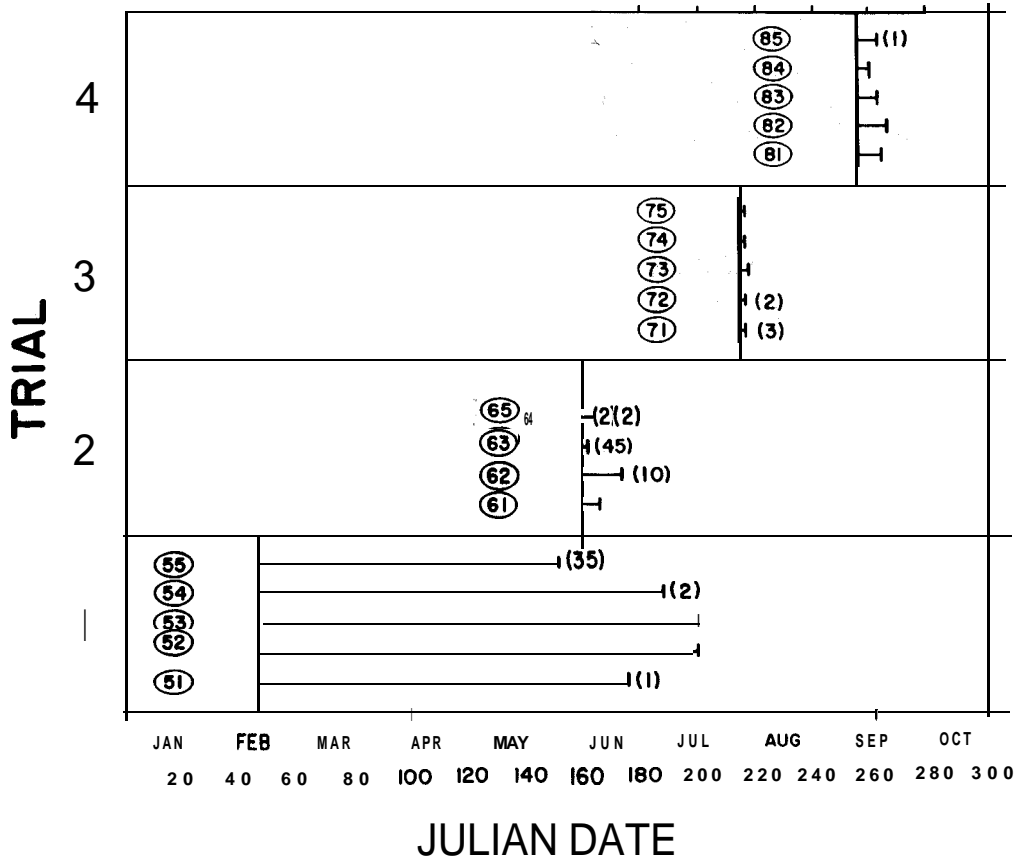


Fig. 1. Response of bark beetles to host disturbance for 20 plots in four seasonal trials. The length of the horizontal lines represents the time between treatment of the trees and mass colonization by bark beetles. All treated trees were colonized. Numbers in parentheses indicate trees colonized in excess of the two treated trees in each plot. Modified from Coulson *et al.* 1986.

The experimental results indicate two important points for our discussion. First, trees damaged by simulated lightning strikes in the winter persisted as suitable hosts attracting bark beetles for up to 150 days after the disturbance before finally succumbing to accumulated attacks. These trees served as refuges for beetles during a period when beetle activity is much reduced: During warmer seasons when beetles are most active, the time required for successful colonization was considerably shortened (Fig. 1).

Second, the damaged trees served as epicenters for the development of larger infestations. One winter treatment (plot 55, Fig. 1) and one late spring treatment (plot 63, Fig. 1) developed into significant infestations. While late spring is the period of greatest beetle activity, the results demonstrate

that trees damaged in winter can also serve as foci for beetle population development. Infestations can therefore develop from latent centers. In essence, disturbance of individual trees provides resources for pine bark beetle survival and subsequent population growth even when beetle activity is normally low as in winter.

For lightning to provide resources to maintain endemic beetle populations, the disturbance regime must generate an adequate number of lightning-struck trees. Based on historical records on the occurrence, intensity, and duration of thunderstorms, Coulson *et al.* (1983) arrived at an estimated range of 28 to 112 strikes per km² of forest during the course of a year. Beetles may disperse up to 10 km under certain conditions such as wind storms. From the experimental results (Coulson *et al.* 1986) and

the expected occurrence of lightning strikes (Coulson *et al.* 1983), we conclude that the lightning disturbance regime provides an ample supply of lightning-struck trees which are readily located and easily colonized by bark beetles.

Lightning disturbance and bark beetle life history

From a hierarchical perspective, lightning can be characterized as a low level disturbance that damages individual trees. It is not the disturbance itself to which beetles respond, but the effect of the disturbance. This effect persists through time as a 'record' of the disturbance event, and in this case, can be measured in terms of the tree's ability to defend itself from attack. A lightning-damaged tree may eventually heal and recover its defensive capability if the tree goes undiscovered by bark beetles.

The beetles operate on a temporal scale of months and a spatial scale of hectares. The translation of the lightning disturbance from the level of individuals to populations is possible because the information of the original disturbance event is encoded in a tree in the form of its response to the shock and electrochemical damage of the lightning strike. This information persists for months. The subpopulation of lightning-struck trees is spatially distributed at the scale of hectares. The ecological encoding of the disturbance thus translates the instantaneous lightning bolt striking an individual tree in the forest to the space-time scale of the bark beetle life cycle.

At the level of individuals, lightning is essentially a random disturbance and any given tree in a forest has a very low probability of being struck. Clearly, bark beetles cannot rely on particular trees being hit by lightning. When the level of observation shifts from individuals to populations, however, the effect of the lightning disturbance regime is to generate a subpopulation of lightning-struck trees within the forest. The disturbance regime assures that a supply of readily colonizable trees are present. While, the production of lightning-struck trees appears unpredictable at the scale of individuals, at the scale of populations, production of these trees appears quite reliable for bark beetles.

Disturbance propagation and amplification

Propagation and patch dynamics

If lightning was the only natural disturbance occurring in the southern pine forest, endemic population levels of bark beetles could be maintained by the disturbance-life history interaction we have described. The result is a continual creation of small gaps centered around lightning-struck trees and varying in size depending on the local availability of host trees. Gap phase succession then leads to a steady-state mosaic of patches related to bark beetle activity. From this perspective, bark beetles appear to be the disturbance responsible for creating the patches, and thus, a disturbance affecting the structure and function of the entire ecosystem.

This interaction can be viewed as propagation of a low level disturbance (lightning) of individuals (pine trees) to the higher level of ecosystem dynamics. Disturbance propagation will always be accompanied by changes in the nature and effects of the disturbance because boundaries between hierarchical levels are being crossed. In this case, the nature of the disturbance changes from abiotic (lightning) to biotic (bark beetles), and the disturbance effects change from physiological damage to an individual tree to creation of patches (bark beetle spots) in the forest ecosystem initiating gap phase succession. Lightning is directly related to ecosystem dynamics by providing the epicenter for beetle activity. The beetles propagate the lightning disturbance by creating patches that influence ecosystem dynamics.

Amplification and forest succession

Under favorable conditions, however, beetle populations can expand rapidly to produce an epidemic in which large numbers of pine trees are killed. An epidemic is not qualitatively different from normal bark beetle herbivory, but is quantitatively much greater and is therefore recognized as an episode. During an epidemic episode, individual spots can expand in size and coalesce producing damage over large areas.

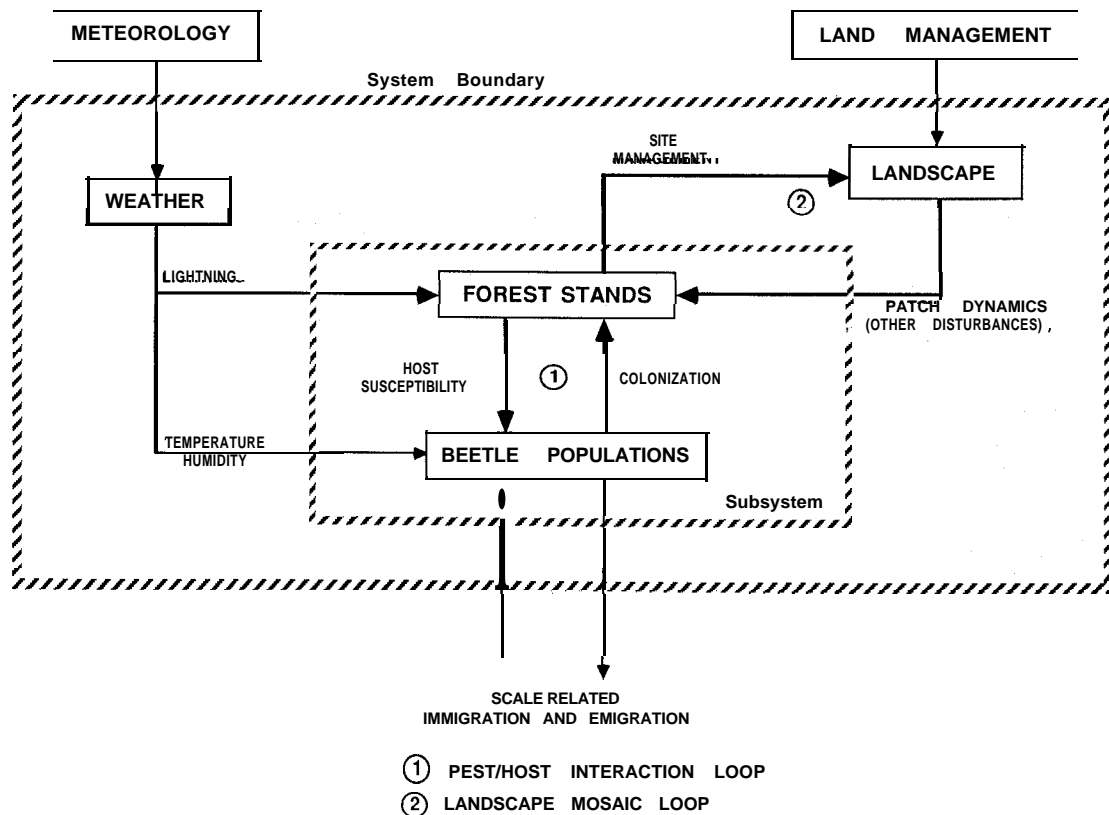


Fig. 2. Conceptual model of major interacting subsystems involved in the epidemiology of southern bark beetles. The beetle population level is linked to the landscape level by forest stands through two feedback loops, the pest/host interaction (loop 1) and the landscape mosaic interaction (loop 2). Source: Coulson *et al.* 1985.

At the ecosystem level, the effects of an epidemic are quite different from non-epidemic effects. A mature forest stand is destroyed and secondary succession is initiated (in actuality, foresters often intervene to re-establish a pine stand and inhibit natural succession). The quasi steady state of patch dynamics is replaced by large scale successional processes. In effect, the bark beetles not only propagate the original lightning disturbance, but under appropriate conditions, amplify it increasing the effects apparent at the higher ecosystem level. Amplification results from the interaction of lightning-generated patches with other critical factors. Lightning by itself is insufficient to cause a beetle epidemic.

Some conditions that facilitate amplification are illustrated by the Pest-Host Interaction Loop (Coulson *et al.* 1985) in Fig. 2. In particular,

weather conditions affect this interaction by influencing both beetle development rates and host susceptibility (Gagne *et al.* 1980). Moderate water stress, e.g., may actually decrease a pine tree's susceptibility to colonization, while prolonged stress increases susceptibility (Sharpe *et al.* 1985). In addition, the structure of a forest stand in terms of species composition, stand age, and age-class distribution (Miller and Keen 1960) affects vulnerability to bark beetle attack (Waring and Pitman 1985; Mitchell *et al.* 1983) of the entire stand. Modification of stand structure, by thinning e.g., can reduce physiological stress on the trees (Waring and Pitman 1983) and lead to increased tree vigor (Waring and Pitman 1985), which effectively attenuates bark beetle herbivory. Lightning in effect short-circuits the complex pest-host interaction by providing the bark beetles with a defenseless host.

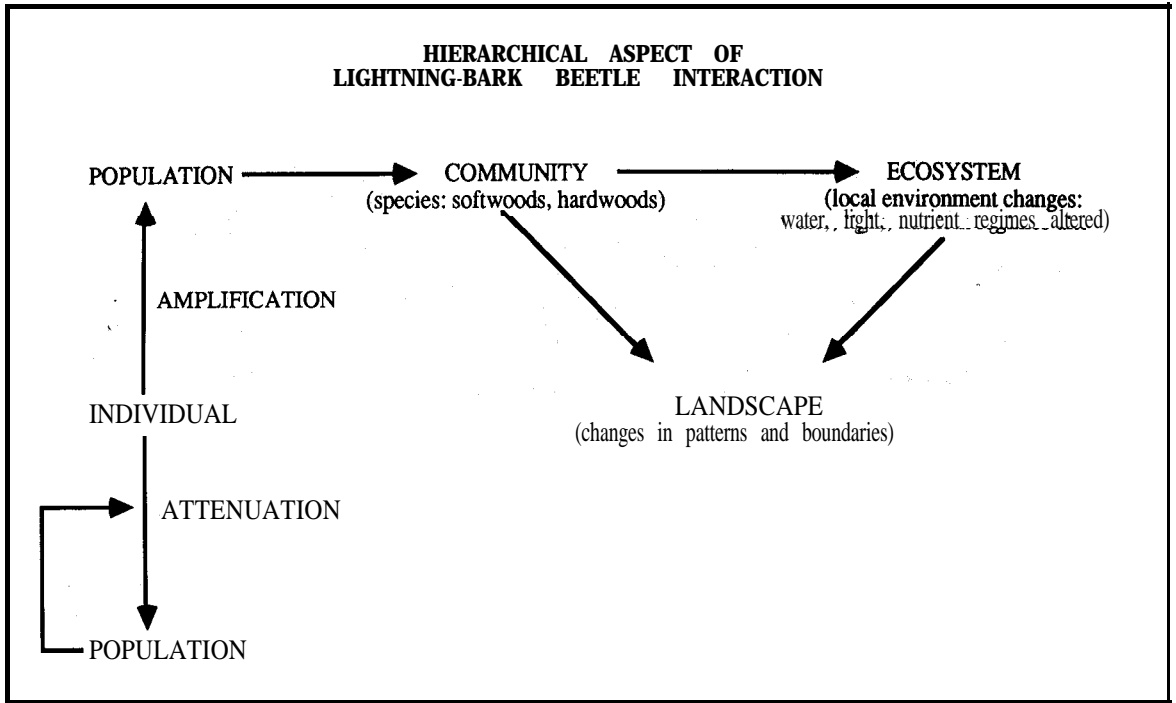


Fig. 3. Conceptual model of hierarchical relationships involved in disturbance propagation by bark beetles. Propagation involves ecological amplification of the abiotic disturbance that is attenuated under normal conditions. See text for further explanation.

Landscape and regional interactions

Landscape interactions affect disturbance propagation and amplification in at least two ways. First, the existing structure of the landscape influences the spread of bark beetle infestations. This structure includes both non-forested areas and the distribution of forest stands (both managed and unmanaged) with varying structural characteristics. Second, bark beetle epidemics in turn alter the landscape creating a feedback loop that influences both the temporal and spatial characteristics of future epidemics (Fig. 2). In addition, the structure of the landscape is profoundly influenced by forest management practices and non-forest land uses. The landscape effect is illustrated conceptually as the Landscape Mosaic Loop in Fig. 2.

The severity of a bark beetle epidemic can be measured in terms of stand damage. When severe, essentially all the merchantable trees in a stand will be killed. However, severity can also be related to the landscape and region levels. The loss of a single

stand may be locally important but have essentially no effect at the regional scale. The vulnerability of any given stand is related to the types of surrounding ecosystems in the landscape as well as the structural and functional characteristics of that stand. Vulnerability is generally associated with high basal area, dense stocking, and mature trees (40-60 years old). Disturbance amplification by bark beetles can be greatly affected by the juxtaposition of forest stands of different ages, by the distribution of forest stands among other landscape components, and by dispersion of vulnerable stands throughout a region such as east Texas. The nature of the interactions among the ecosystems comprising the landscape will obviously be altered by a bark beetle epidemic.

Although they are often viewed only as temporal events, episodes have both temporal and spatial dimensions. For bark beetle epidemics, the landscape represents the spatial dimension. First, forest stands in certain locations in the landscape, such as low lying areas e.g., are more prone to bark beetle

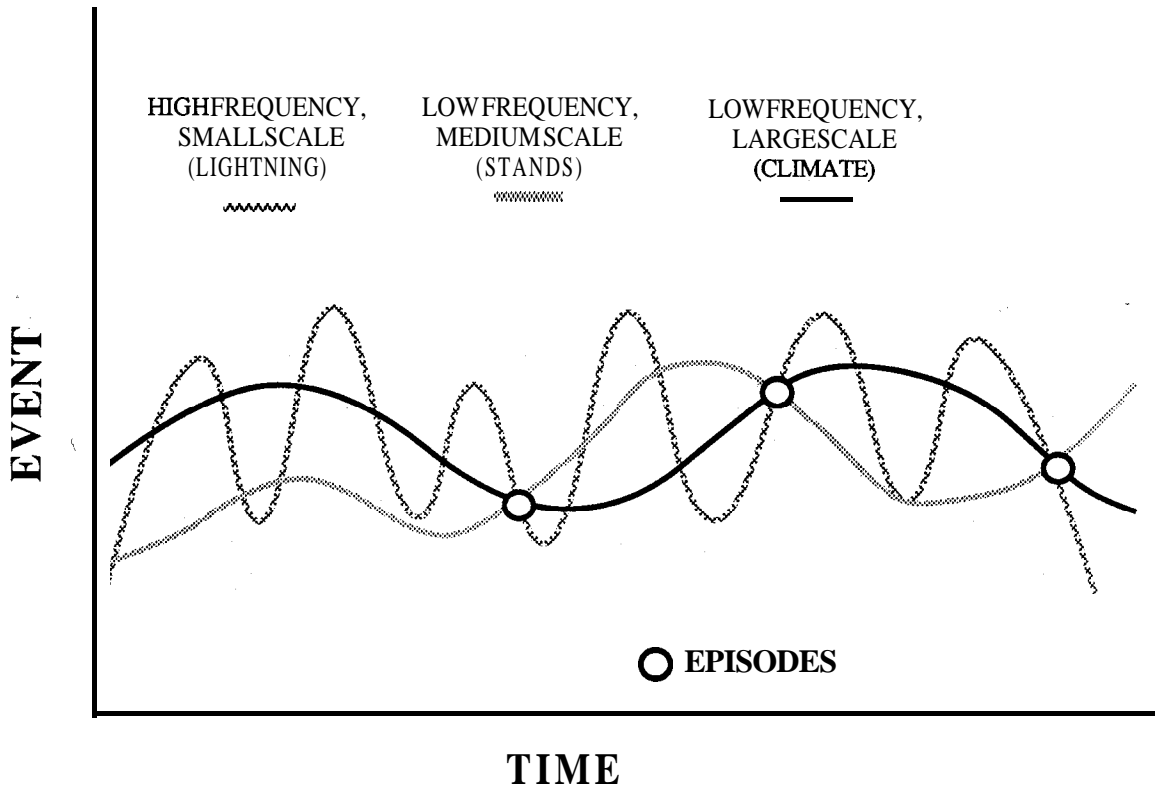


Fig. 4. Graphical model of the interaction of three factors (lightning disturbance regime, availability of vulnerable stands, and climate regime) involved in producing bark beetle epidemics. Factors are represented in terms of frequency and scale to suggest a hierarchical relationship of events. Episodes occur when key factors converge to create the necessary conditions for an epidemic.

attacks. Second, an area in which the pines have recently been destroyed will not be the site of another epidemic for several decades. The dispersion of vulnerable stands in space is a characteristic of the landscape and region levels that influences the rate of spread of epidemics and the amount of damage that occurs. We believe that the coupling of the pest-host interaction loop with the landscape mosaic loop (Fig. 2) is essential to understand the nature and effects of bark beetle epidemics as a part of the larger regional ecological dynamics. Very little study has been devoted to the effects of bark beetles on southern pine forest landscapes. The spatial and temporal characteristics of the lightning disturbance regime are also poorly known in relation to landscapes. However, vulnerable pine stands contain the tall mature trees that are more likely to be struck.

Hierarchical considerations

The interactions we have described can be represented in a conceptual model of hierarchical levels (Fig. 3). The levels are simply those traditionally used in ecology, and progress from individual to ecosystem and landscape. This model summarizes our contention that the low level abiotic disturbance of lightning can be propagated to higher levels of organization by bark beetles. In this process, bark beetles amplify the original disturbance and become themselves a disturbance to the forest ecosystem altering its relation to the landscape. In effect, the beetles propagate the disturbance across hierarchical levels.

We wish to emphasize three points. We see no reason why events low in an ecological hierarchy would be unable to affect higher levels (indeed, even to destroy the higher level's structure and com-

pletely alter its function). The bark beetle population operates at a much faster rate and lower hierarchical level than the forest ecosystem of which the beetle population is but one small part. In the case of an epidemic, whatever constraints are imposed by a higher level are circumvented. It is a general problem for hierarchy theory to elucidate this phenomenon.

Second, the principle of incorporation (e.g., Urban *et al.* 1987) suggests that steady state dynamics are more likely to be observed at the landscape or regional levels. That is, at these levels, the disturbance regimes of lightning and bark beetle epidemics are incorporated into landscape behavior and act as constraints on landscape patterning. Under these conditions, an equilibrium pattern may emerge that has part of its roots in the lightning-bark beetle-pine tree interaction. This idea further suggests that the equilibrium landscape pattern will be altered if the factors that affect disturbance amplification are altered.

Third, bark beetle epidemics illustrate the concept of biotically-driven episodes. In contrast to the large abiotic disturbance that resets the ecological system to some initial condition from which recovery proceeds, the biotic disturbance arises from within the system. We propose that these episodes are a result of the confluence of events operating at different space-time scales (Fig. 4) that represent a hierarchy of dynamic processes.

Conclusions

Ecologists often think of disturbance or other episodes as abiotically driven and patch dynamics as recovery. However, episodes can be driven by biotic interactions and small patches can grow to large patches before an episode subsides. Biotically-driven episodes represent an increase in amplitude of otherwise normal ecological events. At one scale, these episodes differ only quantitatively from normal events (beetles are always eating some pine trees). At a higher scale (or level), they differ from normal events qualitatively as well in their impact on the ecosystem and landscape (beetles usually do not eat the whole forest).

An apparently random low level disturbance can provide a reliable supply of resources for a species when considered at an appropriate scale. The particular characteristics of a disturbance (Table 1), not just the type of disturbance, determine the kinds of resources that become available. Conversely, the life history attributes of a species determine its ability to respond to the particular characteristics of a disturbance or disturbance regime and the resources that are made available. Reliability emerges as a scale-dependent factor that may only be apparent at one particular scale for a given ecological system. Resources that appear unreliable at one scale may be reliable at another.

Any disturbance which is considered exogenous to a system (Table 2) can be conceived to be an endogenous disturbance simply by raising the level of organization (passive incorporation (Urban *et al.* 1987)) i.e., by creating a larger system and incorporating the putative disturbance within it. While the significance attached to the disturbance changes as the hierarchical level observed is raised, the fact that a disturbance has occurred does not change.

Disturbance propagation generally involves a change in the nature and characteristics of the disturbance as the level of observation changes. A low level disturbance can be propagated to higher levels and amplified. Lightning is an exogenous targeted impulse disturbance (Table 2) to an individual tree. The effect of this disturbance is inconsequential at the level of the forest ecosystem unless it is amplified and distributed by bark beetles (or fire). When this occurs, the significance of the event may only be interpretable at the landscape level.

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