7

Regional Population Dynamics

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Abstract

The population dynamics of the southern pine beetle (SPB) exhibit characteristic fluctuations between relatively long endemic and shorter outbreak periods. Populations exhibit complex and hierarchical spatial structure with beetles and larvae aggregating within individual trees, infestations with multiple infested trees, and regional outbreaks that comprise a large number of spatially distinct infestations. Every year at least some part of the Southern United States experiences outbreaks, and the large and unpredictable timber losses associated with these make the SPB the most important pest of southern forests. This chapter reviews the mechanisms that may drive SPB populations at a regional scale. More specifically, it focuses on the initiation and decline of outbreaks, the patterns of damage within them, and the utility of this knowledge for managing the SPB.

Keywords

population dynamics
region
southern pine beetle

7.1. INTRODUCTION

Previous chapters have discussed the population dynamics of southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) at the spatial scale of a single tree, within a single stand or infestation, and across a broader landscape. A feature of this organization is that each viewpoint is intrinsically related —populations within trees drive stand level (infestation) dynamics, which in turn drive landscape-scale dynamics. In addition, each of these spatial units is associated with a distinct temporal scale. For example, population dynamics within a single tree may operate over approximately 30-120 days, a single infestation may last for 90 days to a year, while an outbreak within a landscape typically occurs between 1 and 3 years.

One outstanding challenge for SPB population biology is to integrate information at each of these basic spatial and temporal units into a complete and coherent picture of SPB dynamics. Another significant challenge is to understand how these biological processes ultimately impact humans and the management of the SPB. This chapter deals with SPB population dynamics at a regional scale. Although a definition of region is at least contentious, for the purposes of this paper it is defined as a spatial unit that allows the study and understanding of a complete, and as far as is possible, endogenous cycle of population dynamics from endemic to epidemic and back to endemic phases. The next section provides a historical overview of SPB outbreaks and discusses the appropriate spatial and temporal scales to study regional dynamics.

The question of what causes SPB outbreaks is central to a discussion of regional dynamics and has both economic and intrinsic ecological implications. The fluctuations characteristic of the SPB are an interesting case of population dynamics. This chapter also discusses hypotheses that may explain the causes of these outbreak dynamics and evaluates the evidence for each. Since this chapter takes a regional view, these hypotheses are evaluated based on factors capable of driving rapid population growth but also the subsequent decline of populations. In other words, they must account for the fact that populations are approximately stable in the long-term, but that stability is maintained by a finer scale temporal pattern of population increases and declines. However, in addition to intrinsic ecological interest, SPB research is also driven by its importance as a pest. The key components of this pestilence are large-scale tree mortality, depression of regional timber prices, and the disruption of local economies (see chapter 14 on economic impacts). Also important, the location and timing of SPB damage is largely unpredictable and pulsed. If the total damage caused by the SPB were metered out evenly through space and time, it is unlikely that the SPB would be such an important pest. A key to managing SPB pestilence is therefore to understand how regional population dynamics drive this spatio-temporal pattern of tree mortality. This chapter concludes by discussing how current knowledge of regional population dynamics could be used or are currently being used to manage the SPB.

7.2. HISTORICAL PERSPECTIVE

Figure 7.1 shows the historical record of SPB activity (counties in outbreak status) between 1960 and 2000 throughout the Southeastern United States. Outbreak status is defined as one or more SPB infestation per 1,000 acres of appropriate host type. In turn, an infestation, or spot, is defined as greater than 10 contiguously infested trees. Visually, the record shows a number of key features of the SPB problem:

1. Between 1960 and 2000, SPB outbreaks have occurred at least somewhere in the Southern United States.
2. There is considerable variation from year to year in the number of counties experiencing outbreak conditions, hence the severity of the regional or nationwide SPB problem.
3. The spatial pattern of outbreaks shifts from year to year, but outbreaks tend to be spatially and temporally correlated. In other words:
    a. Areas with SPB activity tend to be spatially and temporally aggregated (outbreaks tend to extend over a number of contiguous counties).
    b. A county is more likely to experience an outbreak in the current year if it experienced one the previous year.
    c. Counties bordering existing outbreaks are more likely to experience an outbreak the following year.

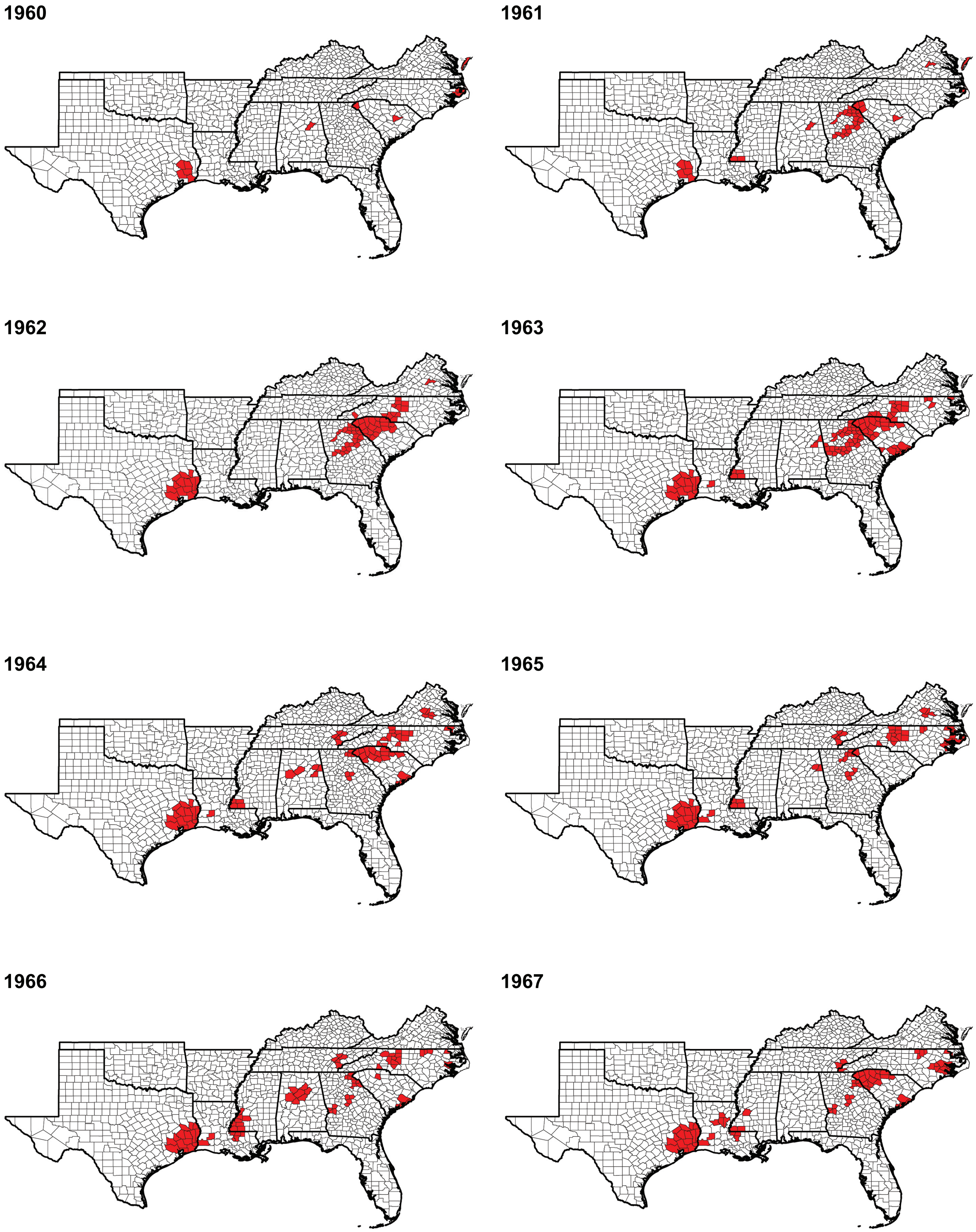


Figure 7.1—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)

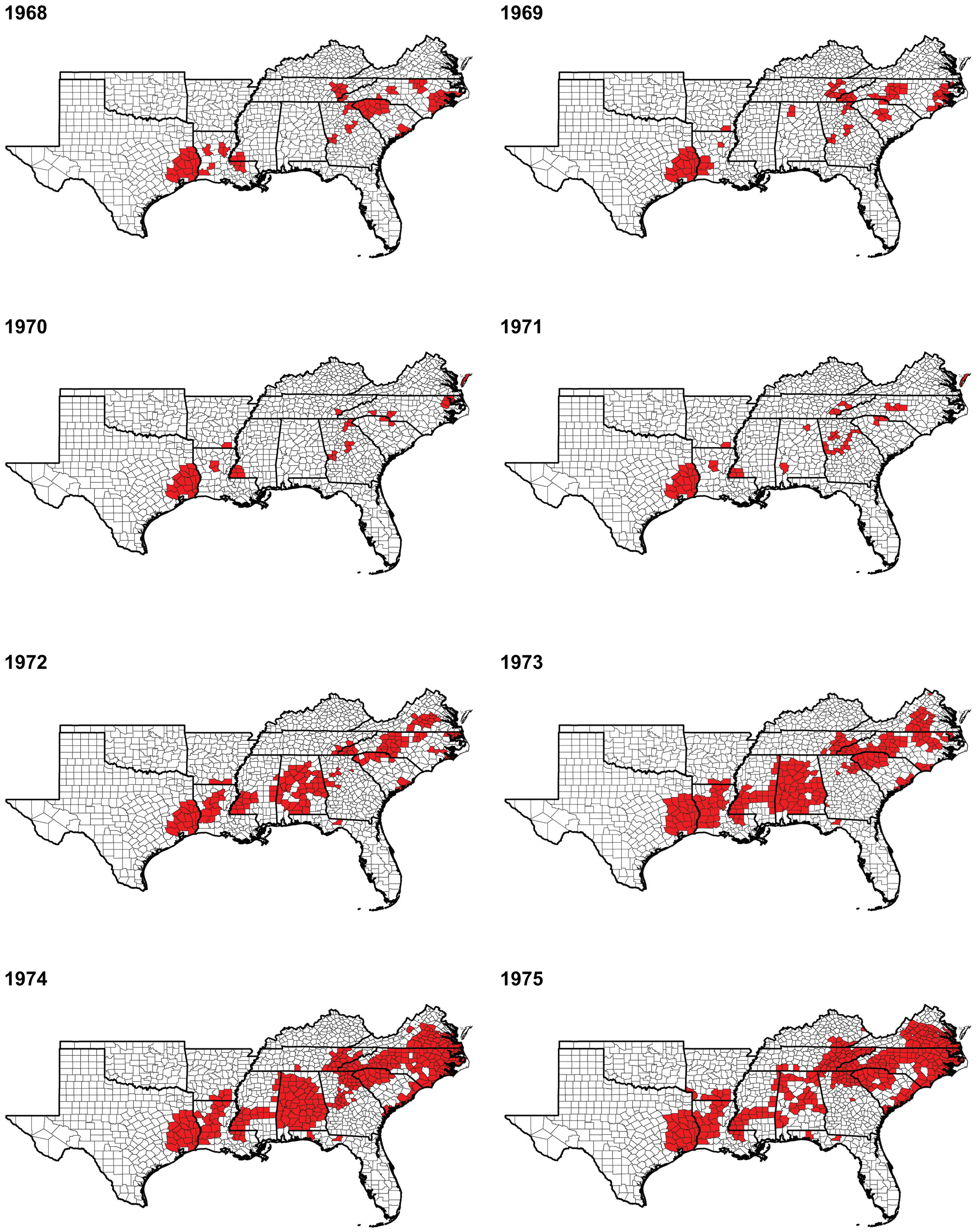
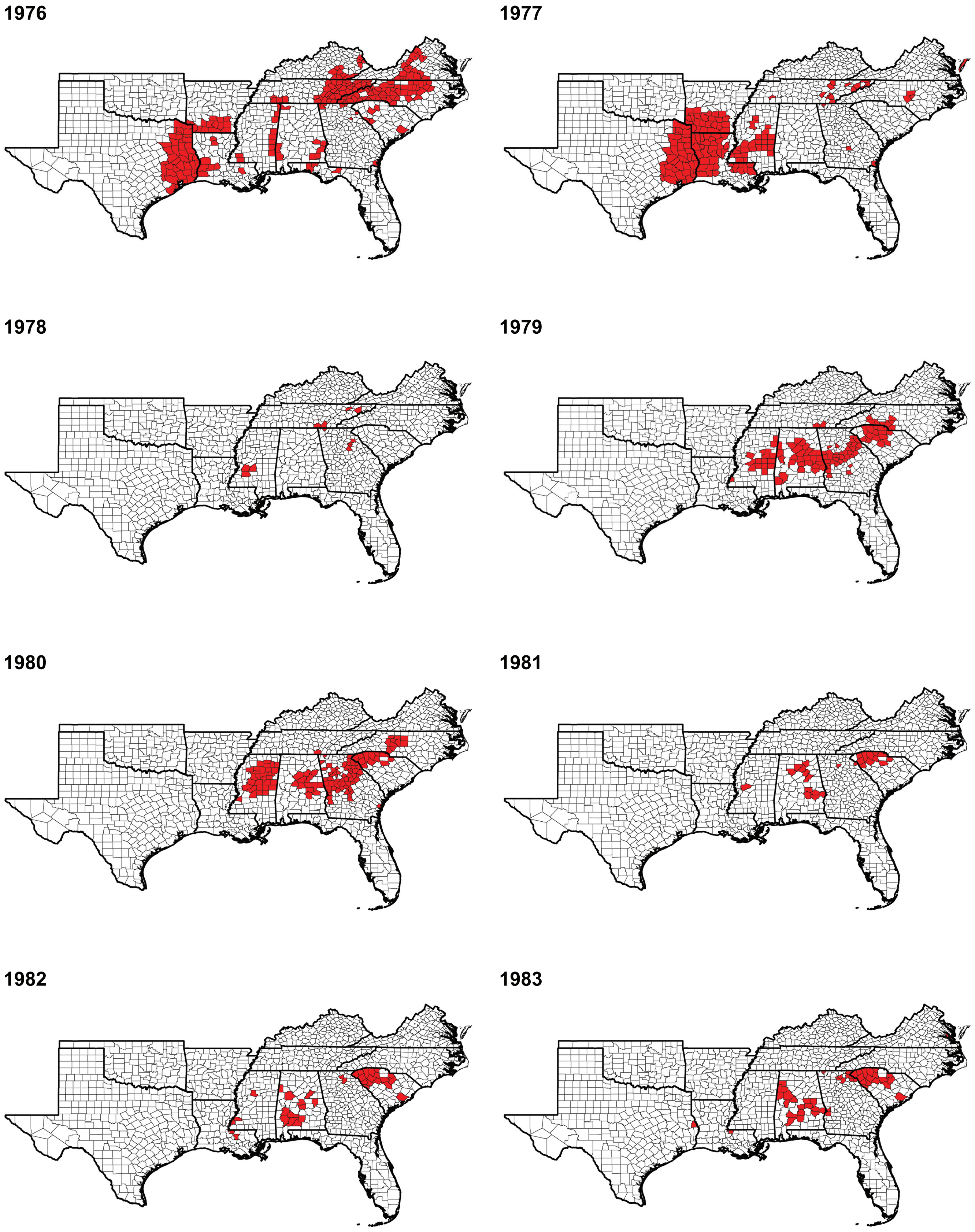


Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)



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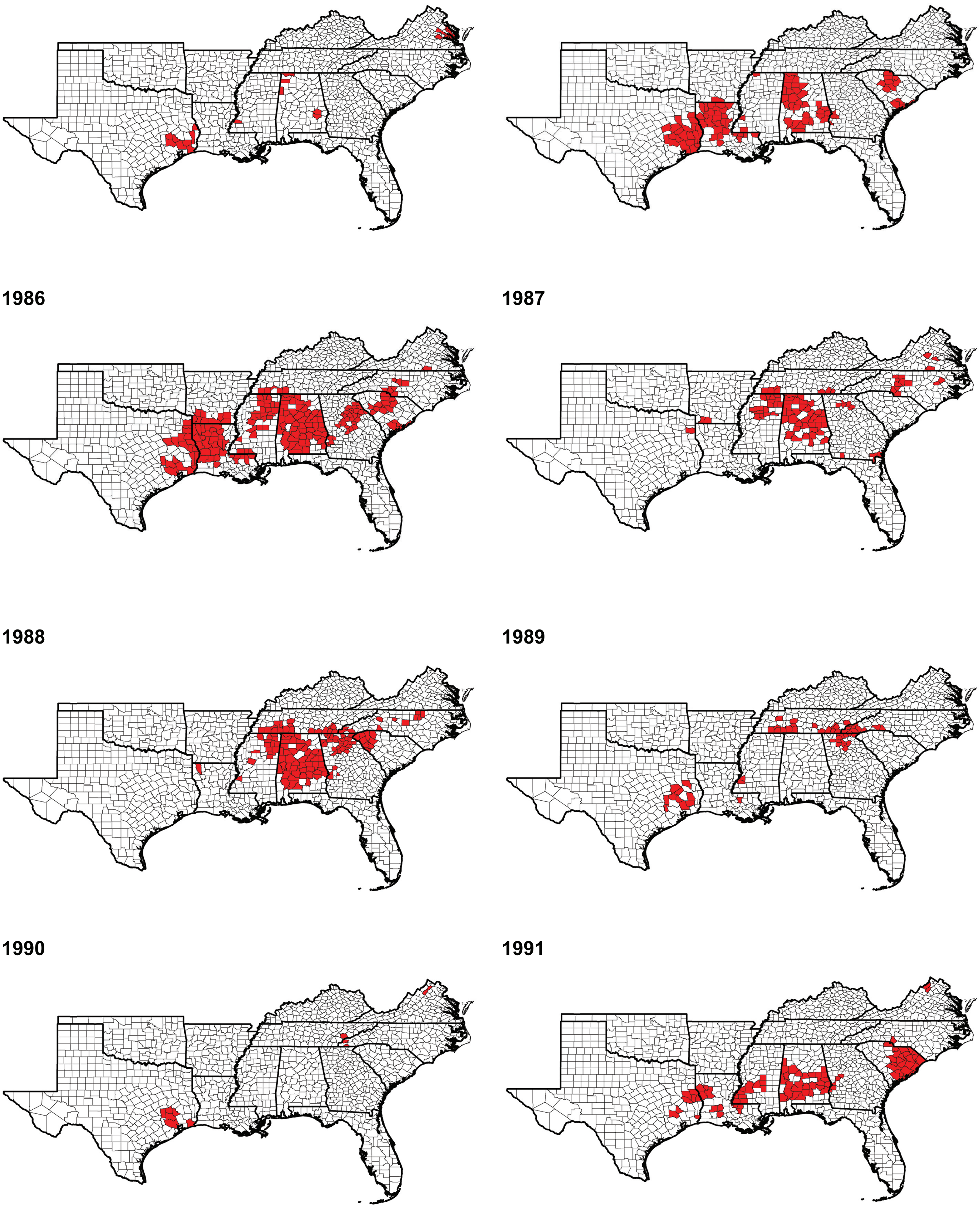

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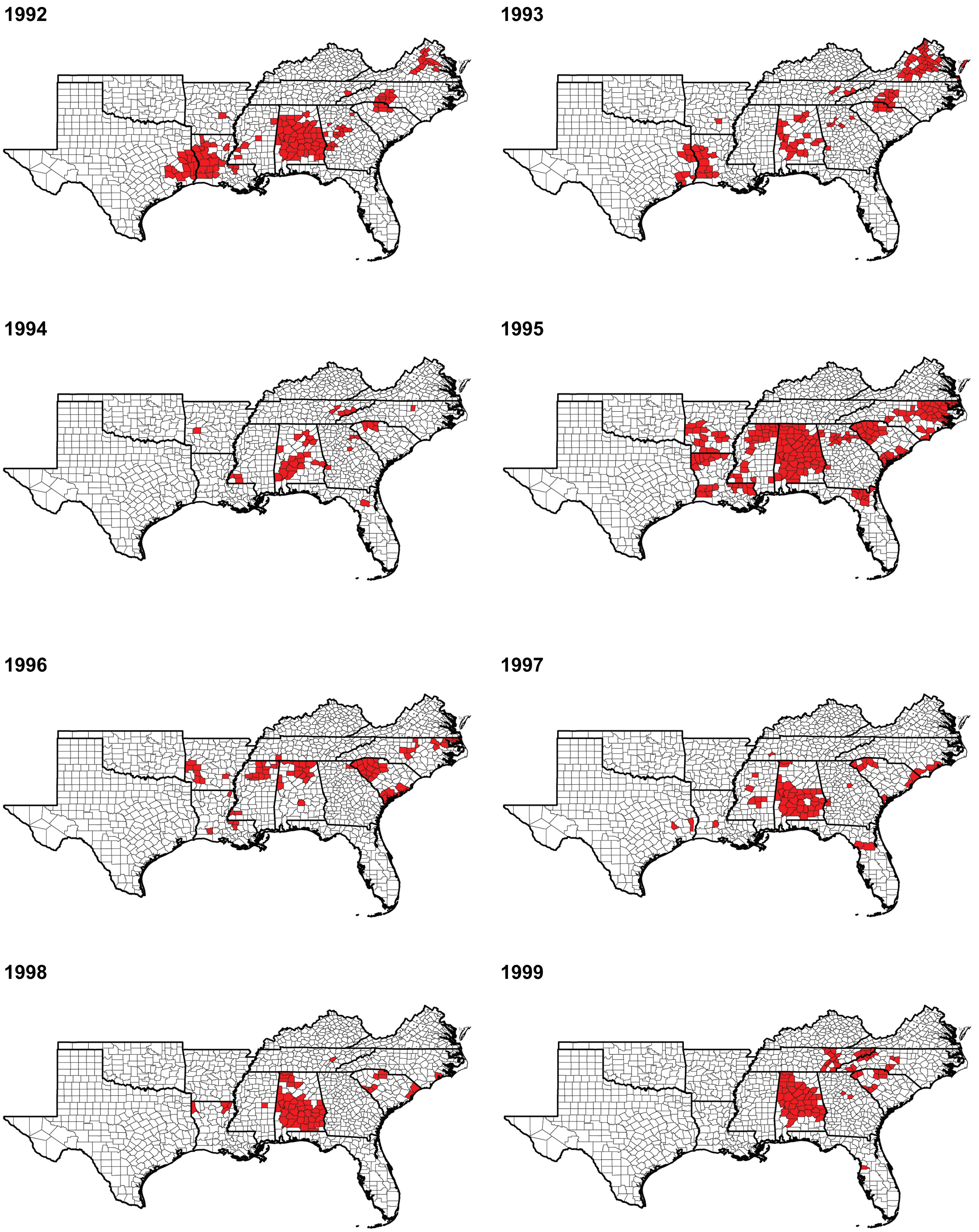
Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)



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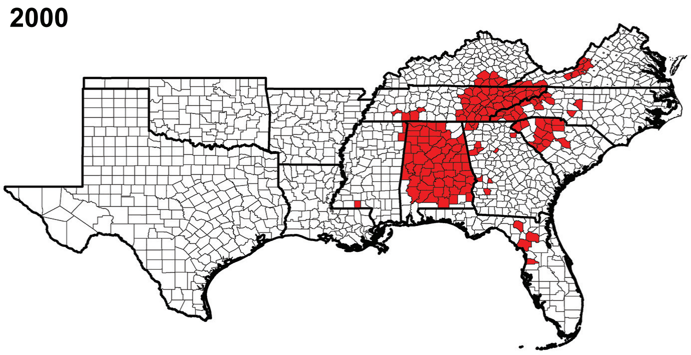

Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red.

4. Despite this spatial and temporal correlation, in some years outbreaks appear to occur spontaneously within a region; i.e., a county may become active even when spatially and temporally separated from previous outbreaks.

Figure 7.2 summarizes the detail presented in Figure 7.1 by reporting the frequency of outbreaks occurring in each county. Here the temporal pattern is lost, but areas that experience frequent outbreaks are clearly visible. These areas include East Texas, western Mississippi, central Alabama and northwest North Carolina.

7.2.1. Regional Patterns of SPB damage

Southern pine beetle population dynamics are complex and have strong spatial and temporal components. Figure 7.3 uses infestation counts and interpretations from known outbreaks to illustrate this concept approximately. Using the number of infestations per unit area as an index of population size, temporal fluctuations in the dynamics of the SPB within the Southeastern United States are relatively stable through time compared to fluctuations in populations within a single county (Hardin County, Texas), which in turn are more stable than for a single km^2 area. In other words, any observed pattern of population dynamics changes with the spatial scale of the observation. Figure 7.3 therefore highlights the importance of choosing the correct spatial and temporal scales for a study. A number of factors may affect this choice, including the availability of data, the known biology of the organism, and the socioeconomic implications (pestilence) of an organism's dynamics.

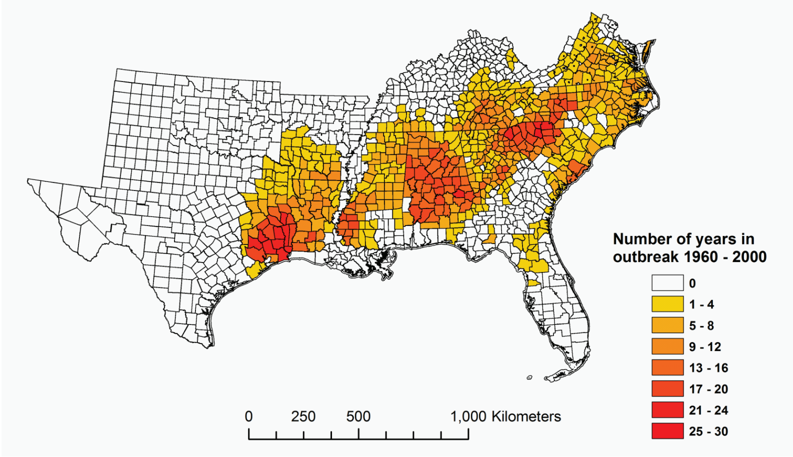

Figure 7.2—County map showing outbreak frequency in the Southeastern United States between 1960 and 2000.

Data Constraints

Although Figures 7.1 and 7.2 are useful summaries of SPB activity and abundance, the grain of the maps mask important information about the dynamics of the insect and the ecology that drives it. Central to this problem are precise practical and ecological definitions of both "infestation" and "outbreak." Practical definitions are relatively easy. An infestation is usually defined as a cluster of greater than 10 contiguous dead trees, while an outbreak occurs when greater than 1 in 1,000 acres of available host type incur an infestation (Gumpertz and others 2000). However, ecologically these definitions lack clarity. Whereas the spatial and temporal delineation of a population within a tree is very clear, for infestations and outbreaks this clarity is blurred. Infestations often grow into one another to create a large, single area of contiguous tree mortality or split into one or more divergent, active heads. Similarly, given the county level outbreak patterns illustrated in Figure 7.1, it would be reasonable to question the precise nature of the spatial pattern of infestations for a single year within a county. Figure 7.4 illustrates two possible, and contrasting, spatial patterns that might be extrapolated from county level maps, using 1990 as an example. Each would suggest very different spatial and temporal definitions for what constitutes a single, self-contained population. Similarly, Figure 7.5 illustrates three possibilities for the spatial and temporal pattern of infestations within an outbreak.

The complex spatial and temporal dynamics of the SPB therefore drive much of the difficulty of

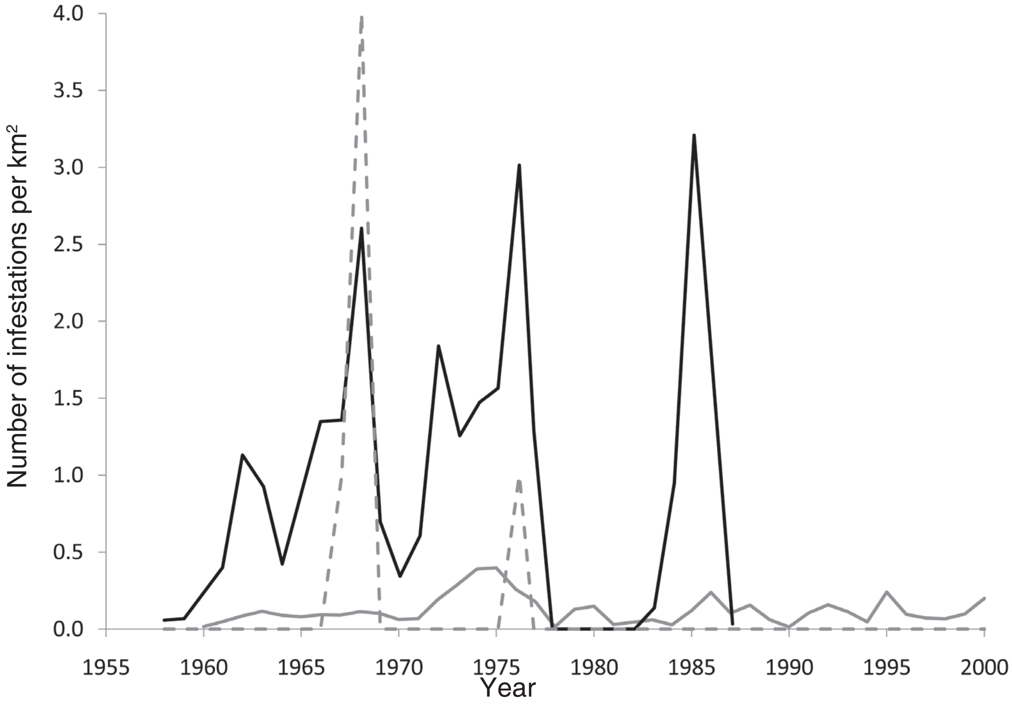

Figure 7.3—Graph illustrating how changes in spatial scale lead to changes in an observed temporal pattern of populations. Each line shows the number of infestations normalized to a single km^2 area. The solid grey line shows a relatively stable temporal pattern of infestations across the whole Southeastern United States. The solid black line shows the number of infestations in Hardin County, East Texas, and the dashed grey line shows the number of infestations in a single km^2 area of the Bankhead National Forest, Alabama. The graph and the pestilence of SPB illustrates the importance of spatial models of SPB populations.

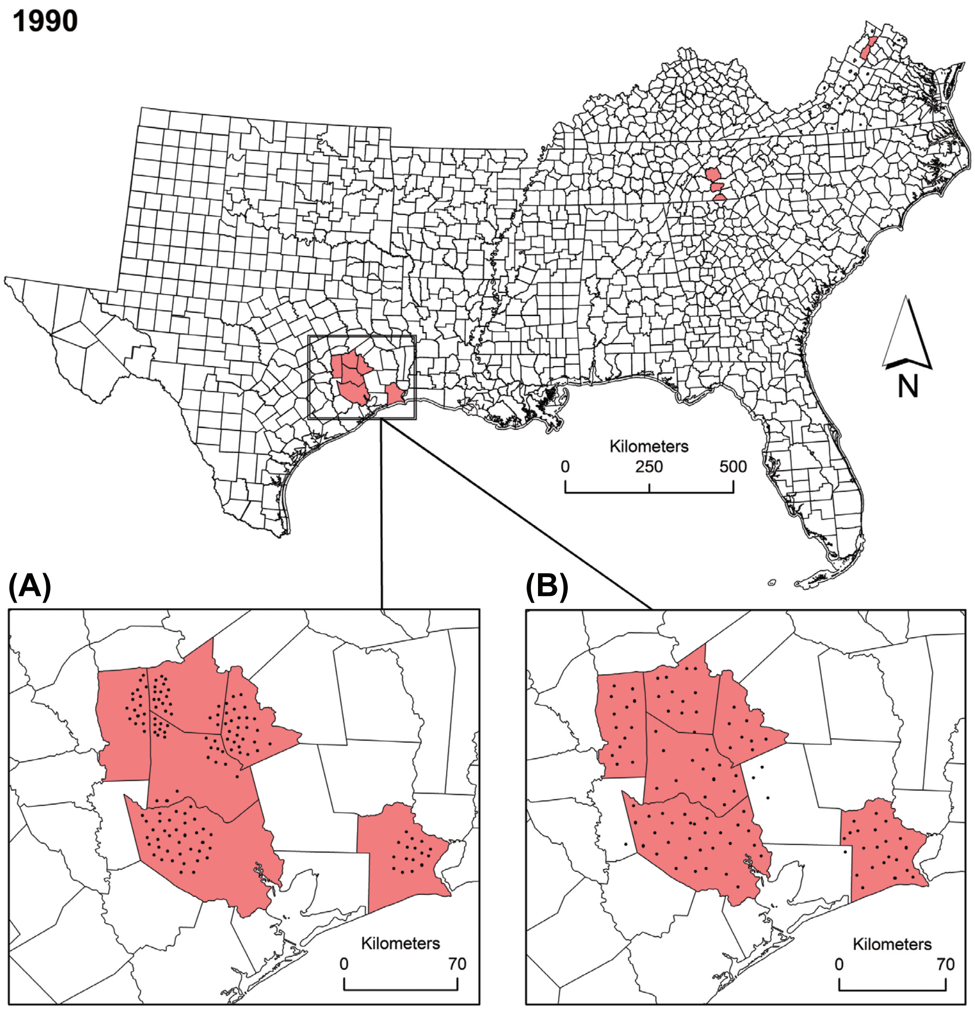

Figure 7.4—Two plausible patterns of the structure of infestations within an outbreak, extrapolated from county level observations as displayed in Figure 7.1; (A) illustrates a number of discrete, delineated populations. Each pattern is likely to be driven by different population processes particularly dispersal; (B) shows a homogenous pattern of infestations. Since the actual pattern of infestations within counties is unknown, the figure cautions against over interpreting the data displayed in Figure 7.1.

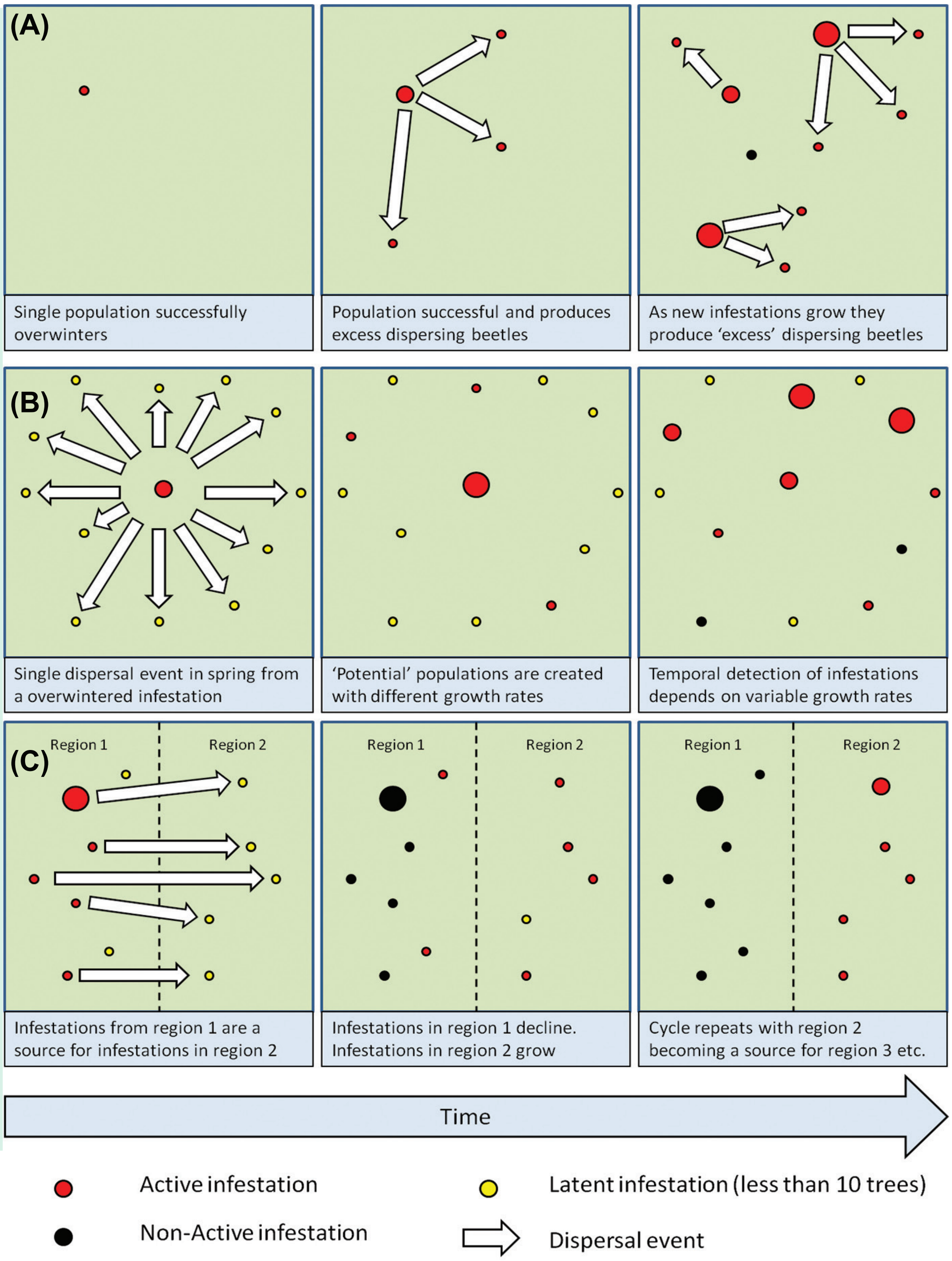

Figure 7.5—Diagram showing three plausible mechanisms of outbreak initiation and expansion. In the top panel (A) a single infestation (in early spring) grows and produces an excess number of beetles, which disperse across the landscape to initiate new infestations. In the second panel (B) a single infestation (possibly one that has successfully overwintered) leads to a single migration event and the initiation of new infestations. Through time, some of these infestations are successful and grow quickly; others grow more slowly and some die out. The final panel (C) illustrates a situation of mass movement from one region to another. To a large extent, the mechanisms in each panel represent the endpoints of a continuum, and owing to the difficulties of studying SPB, the exact spatiotemporal details of the pattern is unknown. One of the goals of population research is to understand how changes in basic ecological processes such as fecundity, survival, development, and dispersal relate to changes in the observed spatiotemporal structure of the population.

studying the insect and collecting and interpreting data. In truth, a complete picture of a typical outbreak is unknown because of these difficulties. First, the small size of the SPB and the sheer area of forested areas also make dispersal of individuals and the delineation of discrete populations difficult to determine accurately. Second, population dynamics tend to be observed indirectly through the symptoms of damage (the reddening of tree crowns) rather than the actual abundance of the insect. This reddening of tree crowns may also only appear some time after trees have actually been killed (Billings and Kibbe 1978), the delay depending on factors such as temperature, water availability, and the frequency that surveys are carried out. In short, however accurately field surveys are performed, measures of SPB population dynamics are indirect and subject to considerable errors. Finally, the geographic range of the SPB includes areas with different physical, vegetative, and climatic characteristics, and a landscape under constant change. In any analysis of population data, researchers must make allowances for all the variables deemed important. In effect, there are no true replicate or controlled data sets available for the study of large-scale SPB populations.

Spatial Scale and the Biology of SPB

Ideally, population dynamics should be described using simple, parsimonious ecological mechanisms for a system that is as enclosed or self-contained as possible. The hypothetical patterns shown in Figures 7.4 and 7.5 are driven by simple biological mechanisms such as quantities and timings of births, deaths, development, and dispersal. One goal of population ecology is to link basic life history of individuals to realized pattern of population dynamics, and in an applied context, to use this basic level of understanding to predict, prevent, and manage populations. Much of the difference in pattern illustrated by Figures 7.4 and 7.5 is likely driven by the timing and amount of dispersal away from growing infestations to initiate new ones. Figure 7.5A illustrates a situation where an outbreak is initiated by relatively few infestations, which grow throughout the season, producing excess beetles that initiate new infestations. In contrast, Figure 7.5B illustrates a situation where a number of infestations exist simultaneously at the beginning of an outbreak, some of which grow to large size and some of which decline before they become detected. Figure 7.5C illustrates a final hypothesis where the size of a regional population remains relatively constant through time and outbreaks occur as a population moves from one active region to an adjacent one. Each pattern must be driven by very different mechanistic population processes (e.g., development, survival, reproduction, and dispersal). Understanding these mechanisms is therefore crucial to predicting when and where SPB outbreaks are likely to occur in the future.

SPB Pestilence and Spatial Scale

Since the SPB is important as an applied problem, an appropriate spatial scale of study could be selected based on the outstanding needs of managing the population. For example, using the spatial hierarchy outlined in this text, within-tree populations of the SPB are relatively easy to study and relatively well understood but offer little direct value for practical management. Population dynamics within an infestation are also relatively easy to study and relatively well understood and offer some practical value in understanding the intrinsic hazard of particular stands should they become infested. Populations within a landscape and at a regional scale are, however, much more difficult to study, but arguably offer the most benefit for managing the SPB. In particular, regional scale dynamics are dominated by fluctuations between outbreaks and nonoutbreaks that cause massive, pulsed timber losses. This glut of timber may lead to depressed timber prices and costs of restoring forests that have long-term effects on local economies. Socioeconomic effects are therefore driven by the loss of value that occurs when trees are killed by the SPB at a regional scale.

Defining an Appropriate Regional Scale

The following sections describe three hypotheses that could explain regional fluctuations in SPB populations and the transition from endemic to outbreak and back to endemic populations. For clarity, regional is defined as a spatial scale of between 2500 km^2 (a typical southeastern county and the smallest outbreak given Figure 7.1) to 150 000 km^2 (corresponding to roughly size the size of the largest outbreak area). This scale is relevant to the economic impact of SPB dynamics, but also because it is probably large enough that the dynamics of the population can be described endogenously. However, since we have neither definitive patterns of SPB populations through space and time nor absolute knowledge of its life history and behavior, this definition may be subject to future debate. The remainder of this chapter will discuss how basic life history processes of births, deaths, development, and dispersal (for which other chapters in this text describe much valuable detail) may lead to the characteristic and economically important fluctuations of SPB populations at this regional scale.

7.3. REGIONAL POPULATION DYNAMICS

Several hypotheses have been proposed to explain the periodic outbreaks of SPB. The most significant of these are:

1. Outbreaks are driven by predator-prey interactions.
2. Outbreaks are driven by host interaction and intraspecific competition.
3. Outbreaks are driven by annual and geographic variations in weather.

It is noteworthy that after approximately 50 years of study, none of these hypotheses have been unanimously accepted by SPB researchers. To a large part, this can be explained by the inherent difficulties involved in studying the SPB and devising long-term, large-scale experiments to test hypotheses. As a result, much of our knowledge of the SPB has been derived through experiments at spatial and temporal scales where the insect is easy to study (for example, within-tree or within-infestation dynamics). This section presents a detailed review of mechanisms important to each hypothesis and an interpretation of how these pieces of SPB ecology might be pieced together to form a cohesive view of regional dynamics.

7.3.1. Predator-Prey and Interspecific Competition as Drivers of Regional Outbreaks

The most complete explanation for the pattern of population cycles displayed by the SPB involves delayed density-dependence driven by insect predators. In delayed density-dependence, the rate of population change in a given year is inversely related to the size of the population during one or more previous years. Using time series data collected from 1958 to 1990, Turchin and others (1991) developed statistical and mechanistic models to show that cycles in the abundance of the SPB in East Texas can be explained by delayed density-dependence with a lag of 1 and 2 years. In other words, the rate of population growth or decline in any given year is inversely related to the size of the population 1 and 2 years previously. They hypothesized that natural enemies are the principal drivers of this density-dependant effect. Subsequently, a 5-year experimental test of this hypothesis found that survival of SPB broods was significantly higher in trees protected from predators than in control trees (Turchin and others 1999b). In addition, they found that annual changes in the population density of the SPB (detected using a broader network of pheromone traps) were correlated with changes in predation (see chapter 29 for an alternative explanation).

Although these experiments did not explicitly identify a predator that drives this system, the clerid beetle *Thanasimus dubius* is generally considered one of the SPB's most important regulators based on its direct observations and association with SPB populations (Reeve 1997), predation of SPB adults, and dispersal capabilities (Cronin and others 1999). However, ecologically significant predation may not be limited to this species alone. The aggregation of the SPB into infestations, resulting in locally high population densities, offers a potentially large resource for predators and competitors to exploit. It is therefore not surprising that a complex of predators and interspecific competitors are known to associate with SPB infestations (Moser 1971).

Spatial detail is not explicitly included in the model of Turchin and others (1991), but regulation by predators or competitors must involve mechanisms that explain the efficiency with which they are able to locate infestations. As with any model, some imagination and interpretation are needed to conceptualize the mechanics of these real-world details and evaluate whether its assumptions are ecologically plausible. In particular, it is interesting to speculate whether infested trees will always be located by predators, given the dispersal capabilities of both species. Inefficient prey location might cause infestations that escape predation to exhibit increased population growth and possibly outbreaks. By introducing more ecological detail (e.g., dispersal of both predators and prey) it is possible that the model will exhibit quite different behavior. Such arguments serve as a reminder that, by definition, no model can represent a complete description of an ecological system. In particular, given the importance of space and unpredictability to SPB pestilence and management, a major criticism of Turchin and others (1991) delayed density-dependence model is that it is capable of explaining regional outbreaks, but does so without considering the spatial pattern of infestations within an outbreak. It would be interesting to find whether the delayed density-dependence hypothesis would be strengthened or weakened by a spatially explicit version of the original model.

Although delayed density-dependence is most often associated with predation, it may also be driven by other ecological factors. For example, Hofstetter and others (2005) highlight significant interactions between SPB, *Tarsonemus* mites (phoretic parasites of the SPB), and blue stain fungi (*Ophiostoma minus*). The latter species often infects the phloem of infested trees and inhibits the development and survival of SPB brood, and its spread appears to be facilitated by the presence of *Tarsonemus* mites on the SPB. Moreover, the authors conclude that the potential for population regulation by blue stain fungi is greater than that measured for clerid beetles. They suggest that an increase from 8 to 49 percent blue stain infestation corresponds to an 85 percent decline in progeny per beetle; whereas high densities (relevant to field observations) of predators reduce SPB survival by about 60 percent (although it should be pointed out that the overall effects on a population depend not only on the amount by which a life history process is reduced, but also on which life history process and which lifestage is affected). Although not as comprehensively studied as the predator-prey (clerid-SPB) system, it is possible that these interactions at the scale of individual trees may drive the kind of regional delayed density effect proposed by Turchin and others (1991) model.

One of the strengths of the predator-prey hypothesis is that there is supporting evidence from a variety of spatial scales. For example, Turchin and others' (1991) original model provides a simple, regional explanation of more detailed predator-prey processes that have been measured at the scale of an infestation or an individual tree. The belief fostered by this body of research has led to practical methods of monitoring and predicting SPB outbreaks. Since 1987 a Southwide network of pheromone traps has been employed to capture SPB individuals and its main clerid predator (Billings 1988). The results from this long-term ongoing survey have been used to predict likely trends and levels of SPB populations during the next season. One of the advantages of such prediction is that the results can be used to effectively plan aerial and ground surveys important for region-wide control. Weekly counts of adult SPB and clerids are recorded for 4 consecutive weeks in spring (marked locally by the flowering of dogwood *Cornus florida*). Data from each state are sent to a central location for analyses and predictions of SPB infestation trend and relative population level for the current year. These predictions are based on mean numbers of SPB per trap per day and percent SPB (defined as the number of SPB divided by the combined number of SPB plus clerids caught per trap and expressed as a percentage) (Billings 1988).This index is plotted onto the SPB prediction chart (Figure 7.6) to provide a prediction of SPB population trend or level.

Table 7.1 shows that this prediction system is fairly accurate. Actual SPB infestation trends and levels are obtained by comparing the number of spots reported in a given locality or State in the current year with the number reported for the same locality or State in the previous year. The model allows annual population trend to be predicted between 62 and 80 percent of cases, where a case represents a prediction for a State in a given year, while prediction of actual SPB population level is less successful (between 32 and 85 percent). When interpreting these success rates one should be wary that a base level of prediction will be roughly 33.3 percent; i.e., with three categories one would expect to be correct one in three times if a prediction were made entirely randomly (though one should also consider that long periods of endemic population phases suggest that it is also inherently more likely that there will be no changes to the population trends). One less tangible measure of the success of this survey is that most States in the South continue to remain involved with data collection and reporting, suggesting that the work involved with the monitoring system is worthwhile.

The success of this regional monitoring program is evidence for the importance of predator-prey interactions as a driver of SPB dynamics. However, it is also instructive to consider exactly how this practical, predictive index fits into an ecological explanation of the hypothesis. The predator-driven delayed density-dependence model (Reeve 1997; Turchin and others 1991, 1999) suggests that at a regional level there should be relationships between the relative size of the predator population and SPB rates of increase, a gradual buildup of SPB numbers through time, a predictive relationship between current populations and populations 2 years earlier, and a strong cyclical component (i.e., consistent periodicity) to SPB outbreaks. Currently, however, the predictive index uses only the first of these characteristics (i.e., a relative measure of predator density). Given the complex nature of the SPB system, it is argued that a large part of the belief in any predictive index stems as much from its relationship to the theoretical, ecological underpinnings of the system as to a statistical analysis of its success.

7.3.2. Host Dynamics and Intraspecific Competition as a Driver of Regional Outbreaks

The ecology of the SPB is intrinsically tied to the biology of its host. A population cycle within a single tree begins with adults congregating and attacking a suitable host, which produces a defensive resin to "pitch out" beetles. During initial colonization, SPB mortality may be high and attacks may be unsuccessful. However, if the tree's defenses are overcome, attacking beetles will produce tunnels and galleries within the phloem that eventually girdle the tree and kill it. Eggs are laid within these galleries, and after some period of time—most likely driven by the decline in nutritional quality of the host and the density of eggs— the original attacking adults reemerge to target another potential host. Finally, the eggs develop through larval, pupal, and teneral adult stages before emerging from their natal tree in search of a fresh host to complete the cycle.

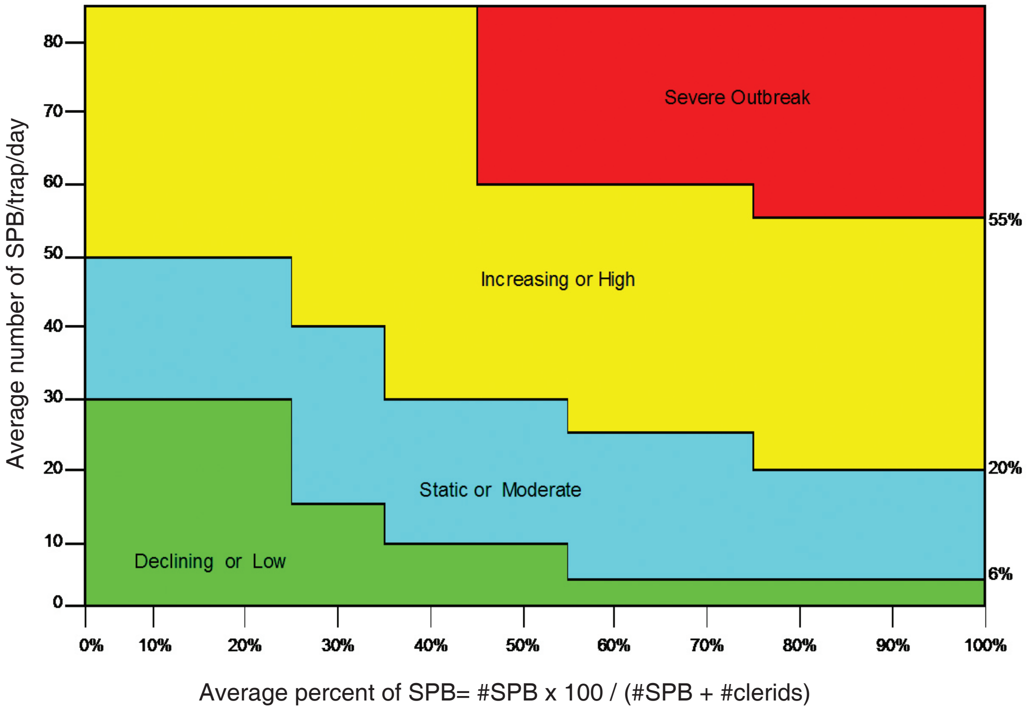

Figure 7.6—Graph used to determine regional risk (separated into outbreak risk, increasing, static, and declining population trends) using trapping data for predators and SPB.

Table 7.1—Prediction accuracy of predator-SPB regional risk prediction. The upper table shows the accuracy of predictions for the trend in SPB predictions (i.e., whether populations are declining, static, or increasing), and the lower table illustrates results of predicting the density of the SPB population (low, moderate, or high).

Predicted	Actual		
	Declining	Static	Increasing
Declining	80% (84/105)	9% (6/67)	23% (17/73)
Static	10% (10/105)	76% (51/67)	15% (11/73)
Increasing	10% (11/105)	15% (10/67)	62% (45/73)

Predicted	Actual		
	Low	Moderate	High
Low	85% (84/157)	38% (6/63)	12% (3/25)
Moderate	14% (10/157)	54% (51/63)	56% (14/25)
High	1% (11/157)	8% (10/63)	32% (8/25)

This simple, descriptive view of a population cycle masks many details important to a full understanding of regional population dynamics, including:

1. How many beetles does it take to kill a tree?
2. How do attacking beetles select a potential host?
3. Do trees have different susceptibilities or abilities to defend themselves, and what drives this characteristic?
4. Do different trees have different nutritional value to developing SPB?
5. How does the nutritional value of an infested tree decline through time, and what drives this decline?
6. How do beetles locate and target hosts across infestations (short distances) and across landscapes?

These questions form much of the ecological detail required to understand the dynamics between the SPB and its hosts and ultimately the initiation of outbreaks. The importance of host dynamics was discovered early in human-SPB interactions when foresters and early SPB researchers observed that SPB infestations occur more frequently in some stand types compared to others. Over time, researchers have used these observations to develop practical risk models that can be used to assess the risk of a stand becoming infested, based on characteristics of the host pines such as tree density (BA), age, tree size (DBH), and crown ratio (see chapter 22). These models are the underpinning for understanding the type of trees or stands in the forest that are most vulnerable to SPB damage. Given this information, it is reasonable to assume (though this assumption remains largely unevaluated) that the conditional state of the forest environment (host trees) drives the initiation and the severity of SPB outbreaks. An outstanding need of SPB research is to bridge the gap between these empirical observations and the population ecology that drives the presence of the SPB in certain stands and contributes to regional outbreaks.

One of the central tenets of the SPB-host hypothesis is that the vulnerability of a host tree is a function of both its innate susceptibility (driven, for example, by genetics, resin production, and *in situ* growing conditions) and the local density of attacking SPB individuals. Figure 7.7 illustrates this concept. It shows that a highly resistant tree may be successfully colonized if there are enough beetles available to overcome its defenses. Equally, trees with low resistance may require relatively few beetles for successful colonization.

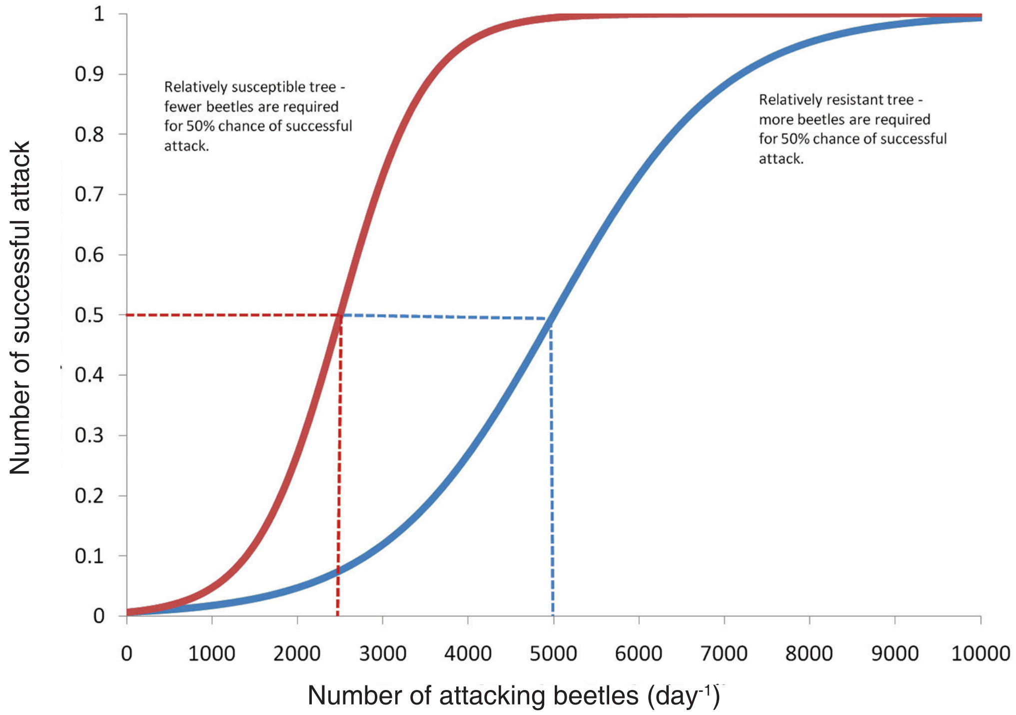

Figure 7.7—Graph illustrating a conceptual view of tree susceptibility to SPB attacks. The graph provides a mathematical description of attack success driven by population size. The red and black lines show relatively susceptible and resistant trees, respectively. Susceptibility can be described by curves at any point on the x-axis – shifts to the left indicate increased susceptibility (e.g., lightning-struck trees), and to the right, increased resistance to attack. These conceptual models are based on dose-response functions common in toxicology studies.

A number of authors have shown, empirically and experimentally, that damaged trees (for example, from lightning strikes) are readily colonized by SPB (Coulson and others 1986, 1999b; Rykiel and others 1988), and that relatively few attacking beetles are needed to overcome their defenses. One of the central tenets to the SPB-host hypothesis is that the forest environment is a distinctly heterogeneous environment, comprising a mix of hosts that vary greatly through both space and time in their vulnerability to SPB attack. Many researchers believe that damaged, highly susceptible trees are responsible for both the maintenance of low density populations within a region and the initiation of infestations. For example, Lovelady and others (1991) suggest that these trees are numerous enough to provide temporal steppingstones for endemic, low-density SPB populations. It is thought that under these conditions, relatively few progeny beetles are produced, making it unlikely that they are able to overcome the defenses of healthy, neighboring hosts such that populations are effectively regulated by the availability of such trees. However, if a number of vulnerable trees occur in close proximity through time and space, and/or a number of generations can be completed in close proximity, local populations may increase to densities capable of attacking more resilient hosts, serving as an epicenter of an infestation and outbreak. During epidemic phases, damaged trees may attract large numbers of dispersing beetles, as demonstrated by Coulson and others (1986). Under these circumstances, it may not be necessary for populations to complete several generations before surrounding trees become infested. During epidemic phases, then, vulnerable trees may act as attractors for beetles that have dispersed away from their natal infestations, thereby concentrating populations and serving as epicenters for new infestations.

Another detail important to the SPB-host dynamics is intraspecific competition. The importance of intraspecific competition is ecologically intuitive, given that host trees are a limited resource in the forest, both at high and at low population densities, and that the location and attack of hosts increase the risk of beetle mortality. Different types of competition have been characterized at different stages of tree colonization:

1. Contest competition: In established infestations, large numbers of adults may attack a tree in a relatively short period of time. Under these circumstances, parents tend to spend less time in the tree (reemerge after a shorter period of time), and hence construct less gallery and lay fewer eggs. This has been characterized as a form of contest competition because the organism is actively moderating its behavior to efficiently compete for resources (in this case by moving to another tree). In the SPB this behavior is thought to occur in response to pheromones that repel attacking beetles from colonized to uninfested trees (Payne 1980).
2. Scramble competition: At high larval densities (as a result of high adult attack densities) individuals (because of their sedentary nature) must compete for increasingly limited resources. As a result, larval mortality increases, and it is possible that the next generation of adults emerge with a lower fitness (Reeve and others 1998).

Intraspecific competition may be an important factor in driving the aggressive spread of a single infestation, the initiation of new infestations, and the decline of infestations. Southern pine beetle adults may respond to high adult densities by switching attacks to neighboring trees, thus accelerating the rate of spread of infestations, or possibly by dispersing more widely into the landscape to initiate new infestations (as suggested by Figure 7.5B).

Intuitively, optimal host-switching behavior must be underpinned by a set of tradeoffs involving the relative costs of using an established, currently infested host and the risk of progeny experiencing scramble competition during late developmental stages vs. switching to the attack of a fresh host and the risk of direct mortality associated with finding a suitable host and overcoming its defenses. Population densities within infestations may decline when mechanisms that regulate intraspecific competition break down; i.e., cease to be optimal. For example, the timing of changes in the focus of attacking beetles may sometimes be suboptimal, leading to overcrowding, competition for limited resources, and increased scramble competition. Reeve and others (1998) suggest that this may occur at attack densities of greater than 6 beetles/100 cm^2 of bark surface, densities that have regularly been observed in established infestations (Fargo and others 1978, Lih and Stephen 1996). In turn, suboptimal responses to competition during initial tree colonization may be explained by uncertainty in future environmental conditions that the population will experience. For example, seasonal changes in weather (which drives the emergence of the next generation of attacking adults) or the availability of suitable host trees may both affect the ability of the SPB to efficiently allocate resources between trees.

The role of temperature in the development, fecundity, and survival of SPB is well known (and discussed in the next section). Across its range, the SPB exists within a seasonal climate that may include high and low temperatures that exceed its thermal tolerance. Interannual variations in these seasonal cycles may be responsible for outbreaks (discussed in the next section). However, seasonal temperatures may also interact with the ability of the SPB to locate and attack fresh hosts. For example, extreme temperatures, either high summer or low winter, slow down population processes and curtail population growth. This seasonal dormancy may lead to lower densities of attacking adults, and in line with Figure 7.7, a reduction in the probability that the population will successfully attack a new host. The opposite may also be true. During periods of optimal temperatures, emergence may be concentrated within shorter time spans, leading to a higher local density of attacking adults and increased probability of successful colonization. In both cases it is easy to see how these processes may act synergistically with the presence of suitable hosts. In the case of suboptimal population growth, if a reduction in attacking beetles occurs in addition to the depletion of susceptible hosts, population decline may be exacerbated. Such an event might occur at a stand boundary, for example. Similarly, the simultaneous occurrence of a lightning-struck tree (or any highly vulnerable one) and a sustained period of weather conducive to population growth might create conditions suitable for multitree infestations, which in turn could be precursors to a regional outbreak.

7.3.3. Weather as a Driver of Outbreak Dynamics

Temperature has been shown to drive the reproduction, survival, and especially the development of the SPB (Gagne 1980, Wagner and others 1984a). The time taken for a single generation of the SPB to develop ranges from approximately 100 days at 15 °C to about 30 days at 30 °C (see Figure 7.8). Weather has been shown to directly affect SPB flight thresholds (Moser and Dell 1979a, Moser and Thompson 1986) and the survival of dispersing SPB. Drought, flooding, hurricanes, lightning, and ice storms may also indirectly drive SPB population dynamics by affecting the vulnerability of hosts. Seasonal variations in weather are therefore undoubtedly responsible for many consistent characteristics of SPB

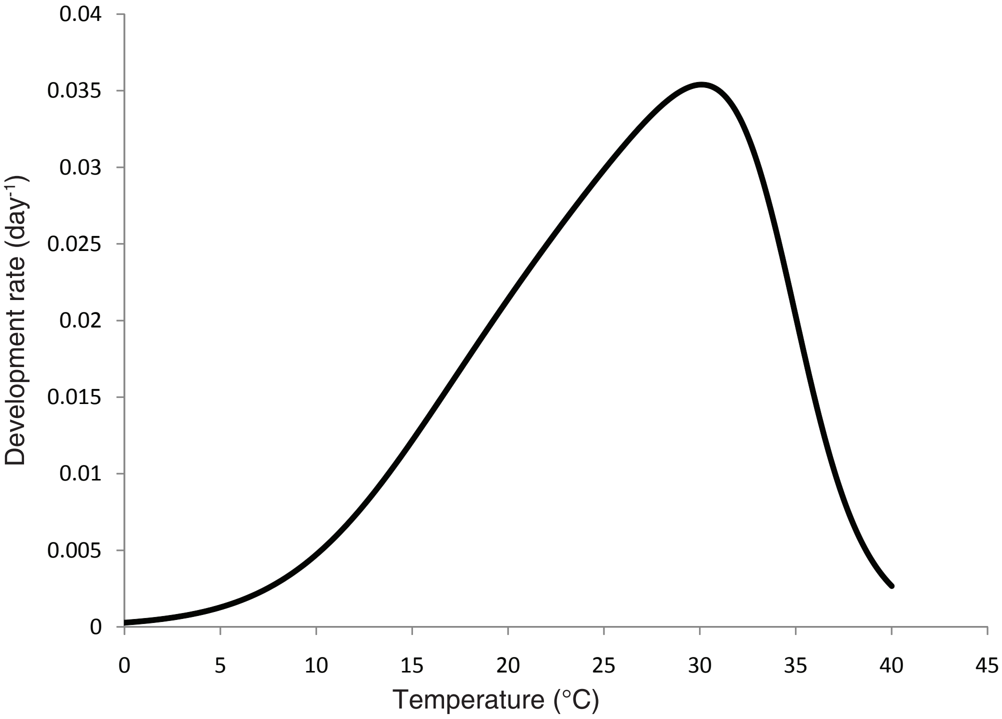

Figure 7.8—Graph showing the relationship between development rate (development time-1) and rearing temperature. Development is optimal at approximately 30 °C leading to a development time of approximately 1/0.035 = 29 days. Note that development rate rapidly drops off at temperatures above 35 °C, but at suboptimal temperatures the effect is more gradual.

dynamics such as the length of generations, the timing of infestation enlargement (mainly during the spring and autumn), the decline of infestations during winter, and the utilization of lightning-struck trees. In short, given empirical and experimental knowledge, there is no doubt that temperature and other seasonal weather factors are significant drivers of SPB population dynamics.

However, the most important questions for regional dynamics are:

1. The extent to which climate is responsible for differences in the frequency of outbreaks between regions
2. The extent to which interannual variations in weather drives outbreaks dynamics (endemic-epidemic transitions)

Figure 7.9A shows the average number of generations of the SPB (voltinism) expected to occur across its range, based on local temperatures. Cross-referenced with Figures 7.2 and 7.3 (showing regional outbreak frequency), the map suggests that areas of high SPB activity tend to coincide with areas that have host incidence and areas that support a large number of generations. However, this observation is not universally true. For example, southern Georgia has considerable areas of host and climatic conditions conducive to six or seven SPB generations per year, but has relatively low outbreak frequency. Similarly, the mountainous regions of North Carolina are predicted to support relatively few generations per year, yet exhibit considerable outbreak frequency. In short, regional differences in climate driving voltinism of the SPB does not, at least at first glance, appear to be a particularly strong predictor of the frequency of outbreaks.

Figure 7.9B shows the interannual variation in the voltinism of the SPB across its range, expressed as a standard deviation of the mean development time (as shown in Figure 7.9A). A practical interpretation of this map suggests that, even in areas with relatively large annual variation in voltinism (namely, southern Alabama, southern Georgia, and East Texas), an extra generation (above the mean) is expected approximately 1 year out of 40 or 2.5 percent of all years (note that approximately 95 percent of the time voltinism will be within two standard deviations of the mean, with the remaining 5 percent being split between an unusually high or low number of generations). Put simply, annual variation in SPB voltinism is relatively low. On this evidence alone, it would appear unlikely that such small changes in year-to-year voltinism are responsible for initiating outbreaks.

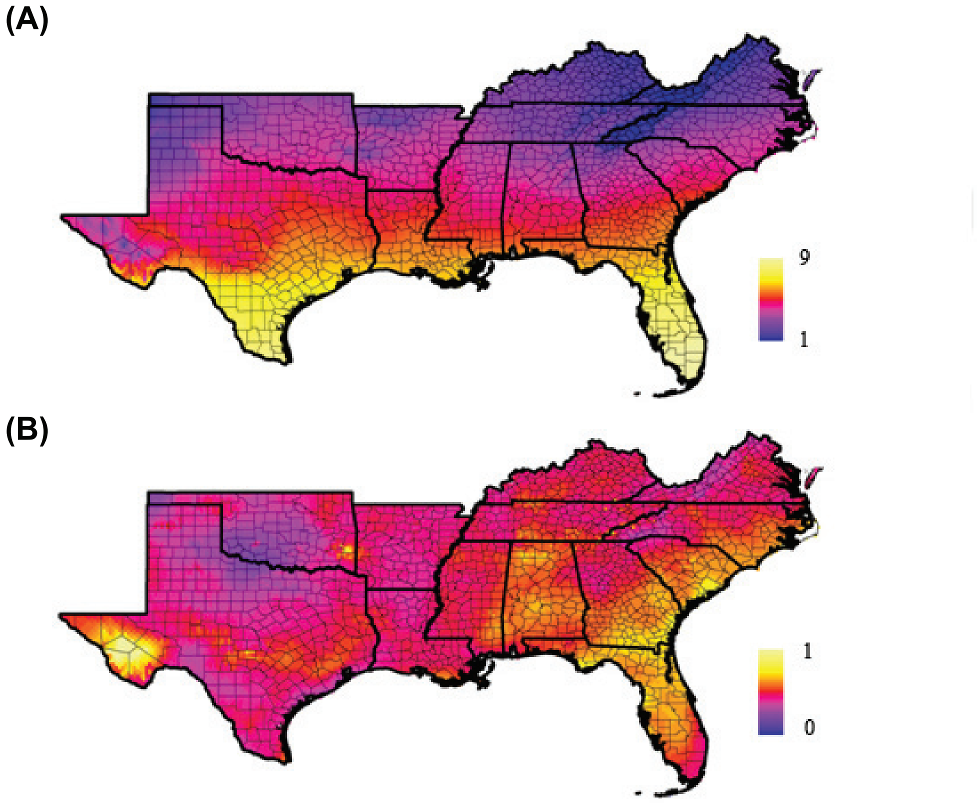

Figure 7.9—(A) Mean, and (B) Standard Deviation, of annual SPB voltinism across the Southeastern United States.

Why Weather May Still be Important Driver of Population Dynamics

Before the role of climate in driving outbreak dynamics is dismissed entirely, it is important to understand why its effects may be difficult to uncover. First, Figure 7.9 shows a single, surrogate measure of population performance – namely, voltinism. It is an assumption that areas that support the greatest number of generations are most suitable for SPB populations. Given that the SPB is an obligatory host killer, an essential (and costly in terms of mortality) part of its population dynamics is the need to continually locate fresh hosts in what is most likely to be a resource-limited environment. Under such conditions, it is possible that fewer generations might actually increase the stability of populations. Figure 7.9 may also be misleading in the sense that it reports only whether a county is in outbreak rather than the severity of the outbreak. It is possible that voltinism (or any other measure of population performance) is more relevant to the severity of an outbreak than the frequency with which outbreaks occur.

Second, statistical methods allow hypotheses to be formulated (for example, that annual voltinism is related to outbreak frequency) and then tested, given observations and data. However, climate (or weather) includes a large number of variables and dimensions and infinite ways by which they could be summarized as inputs into statistical models. For example, Figure 7.9 uses annual temperature, arbitrarily bounded by January 1 and December 31, as the input to the voltinism model. Yet it is possible that a different temporal timeframe might be a more appropriate driver of outbreaks. For example, a 2- or 3-year stretch of weather might be proposed as a better predictor of outbreaks perhaps representing a period more conducive to a buildup of SPB populations. Alternatively, the minimum length of time it takes for the SPB to complete one, two, or three generations, or weather patterns that influence other important life history processes such as overwintering (or high temperature) survival or host vitality (e.g., flooding, drought, storms) may be considered more important for driving outbreaks. In each case, although it is possible to test a proposed hypothesis against observed data, it is not possible to eliminate the importance of every possible interpretation or summary of climate.

Other authors have explored the relationship between outbreaks and weather with varying results. For example Gan (2004), using a model fit to county level data, found significant relationships between various temperature indices (lagged spring, summer, fall, and winter temperatures, and precipitation) and SPB infestation rates. He concludes that temperature has a greater effect on outbreak risk than precipitation and discusses these results in the context of global climate change. Working at the finer spatial scale of East Texas, Friedenberg and others (2008) developed a model that bridges the gap between exogenous and endogenous population regulation. The model uses delayed and direct density functions, and under certain assumptions about the nature of this density-dependence, found the number of infestations (used as a measure of population growth) was negatively affected by consecutive daily temperatures above 32 ^{o}C and by either higher than average or lower than average winter temperatures.

Given that seasonal weather patterns drive much of SPB population dynamics, it is difficult to believe that annual or regional variations in weather do not exert some effects on outbreak frequency or severity. Perhaps the most important deficiency in this hypothesis is the reliance on empirical studies alone. In contrast, evidence for delayed density-dependant predator-prey interactions comprises a theoretical model demonstrating how delayed density-dependence can result in outbreak dynamics—a fit of this model to empirical infestation data and detailed, *in situ*, experimental studies showing the population level effects of predation. Given the essential characteristics of the SPB problem (a large geographic range, regional data collection, a small insect in an extensive forest landscape, and infrequent outbreaks with both frequency and severity dimensions), it is argued that, even with 50 years of data, empirical studies alone are unlikely to uncover (and foster belief) climatic indices that can explain patterns of outbreaks. Like the predator-prey hypothesis, the climate-driven hypothesis warrants a bottom-up approach that pieces together the detailed life history processes of the SPB (which are undeniably driven by temperature) to form a coherent hypothesis for regional dynamics.

7.4. CONCLUSIONS

In previous sections, the population ecology of the SPB was organized around three theories that represent the conventional wisdom of how, when, and why regional outbreaks occur. Although no firm conclusions can be made about which of these (or to what extent each of them) is responsible for the characteristic patterns of SPB damage, a wealth of detailed ecological information exists about the population ecology of this species. One challenge for ecologists is to piece together existing knowledge into coherent, quantitative models of SPB population dynamics. Another is to use these models to identify deficiencies in our current knowledge of the SPB and devise experiments or observations capable of filling these knowledge gaps.

Although there is merit to understanding SPB population dynamics from a purely academic point of view, research into SPB damage is largely driven by its importance as a pest of southern forests. This pestilence is driven by the value of forest products and the magnitude and spatiotemporal unpredictability of SPB damage. However, given the importance of the SPB as a pest, it is also important to address how this knowledge can be used to manage future outbreaks. Regional population dynamics are particularly important for SPB management, and the hypotheses presented here have very different implications. In all cases, the ecological objective is to understand what drives regional outbreaks and the pattern of damage that comprises them. Management should include elements of prediction (forecasting when and where damage will occur), prevention (taking steps to reduce future damage), and remediation (accepting damage will happen but limiting its effects) based on this ecological knowledge.

Often, prediction of SPB damage is seen as the ultimate goal of SPB ecological research. However, it is likely that each of the hypotheses discussed in the previous section would need to be applied in different ways to enable it to be used in effective regional management plans. For example, even if population dynamics were found to be entirely driven by temperature, it is possible that the inherent unpredictability of long-range weather might prevent this knowledge being used to make practically useful predictions. If this were the case, the most valuable use of this knowledge would be to direct SPB management resources away from prediction towards methods of reducing its impacts. In contrast, knowledge from predator-prey research is currently being used to predict future SPB activity but probably offers little hope for prevention. Uniquely, knowledge from SPB-host research is currently used to predict and prevent damage (via risk models).

This chapter has taken a mechanistic, modeling approach to the description of regional SPB dynamics. In most cases, these models are qualitative and conceptual rather than quantitative. The reasons for this stem largely from the difficulty of observing the SPB and collecting data at all relevant spatial scales. Although quantitative models can be difficult to interpret without real-world data to validate results, the mechanisms by which SPB populations shift between small, benign endemic populations and problematic outbreaks are central to the SPB problem, and one of its defining characteristics. Any successful regional model should therefore recreate the aggregated pattern of trees within infestations and the disaggregated pattern of infestations within a landscape. Preferably, this pattern should be driven by a self-contained, endogenous population: Population dynamics should be determined by interactions between a defined environment and the SPB, rather than through open-ended processes such as immigration or emigration. Although it is relatively easy to model steady-state or infinitely growing or declining populations, repeated patterns of growth and decline are much more difficult to mimic. A theme of this chapter is that each of the hypotheses discussed is underpinned by considerable ecological detail (much of which is described in other chapters of this text), but that this detail may be interpreted or integrated in different ways. The advantage of a quantitative approach over the largely conceptual models described here is that the rigor of a mathematical formulation leads to unequivocal outputs. Although a quantitative model that reproduces population cycles is not necessarily correct, it would at least demonstrate that the ecological mechanisms it incorporates are capable of producing the endemic-outbreak dynamics so typical of SPB populations. Of the three hypotheses presented here, the only one that has been described quantitatively, and for which SPB-like population cycles can be demonstrated even theoretically, is the predator-prey explanation. Arguably, this shortfall in competing quantitative models represents the biggest barrier to understanding regional SPB dynamics and the translation of this knowledge to more effective management strategies.