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Population Dynamics of Southern Pine Beetle in Forest Landscapes

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Abstract

Southern pine beetle (SPB) is an important pest of Southeastern United States pine forests. Periodic regional outbreaks are characterized by localized areas of tree mortality (infestations) surrounded by areas with little or no damage. Ultimately, this spatiotemporal pattern of tree mortality is driven by the dynamics of SPB populations—more specifically, by rates of survival, reproduction, development, and dispersal. In turn these rates are driven by the interaction between SPB and its hosts, predators, and climate. In this chapter, the relationship between these factors and SPB population ecology are discussed. Particular emphasis is placed on mechanisms that could explain the temporal changes of the population from outbreak to nonoutbreak phases, the dispersal of SPB across a complex forest landscape, and the importance of interpreting the environment using current knowledge of SPB ecology.

6.1. INTRODUCTION

Like all organisms, the population dynamics of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) are intrinsically tied to its spatial and temporal environment. The pattern of damage exhibited by SPB is patchy (heterogeneous) through both space and time. SPB population dynamics exhibit two phases: an endemic phase, when populations are so low that damage is almost undetectable within the forest, and an epidemic phase, when populations reach high densities and tree mortality is considerable. During epidemic phases or outbreaks, damage is aggregated into discrete areas (infestations or spots) that occur within a much larger area of unaffected forest landscape. This pattern is a crucial component of the pestilence of the SPB. This heterogeneity ensures that some areas of the forest (hence individuals who manage it) will incur damage while others do not.

One possible explanation for the patchiness of SPB damage is that it is driven by the heterogeneity of the forest landscape itself. Figure 6.1 shows the juxtaposition of different land uses within a typical East Texas landscape where SPB outbreaks are prevalent. This heterogeneity may be driven by a number of factors including the dynamics of tree growth and forest management; natural disturbances such as logging, fire, weather damage, and pests (including the SPB); and socioeconomically driven land management (for example, forestry and agriculture). The survival, development, reproduction, and movement of the SPB are intrinsically tied to such forest landscapes. It is these processes that ultimately lead to high density populations, tree mortality, and pestilence. However, the biggest problem with interpreting Figure 6.1 is the temptation to visualize this landscape from a human point of view. The central thesis of this chapter is that to understand SPB population dynamics, this environment needs to be interpreted with reference to the life history, behavior, and ecology of SPB.

The goal of this chapter is to review the population and life history processes that drive SPB population dynamics across forest landscapes. These processes include development, survival, and reproduction; movement of SPB within and between infestations; interaction between the SPB and its hosts; and the interaction between the SPB and its predators. Practically, the extensive nature of forest ecosystems and the cryptic nature and small size of the SPB make it

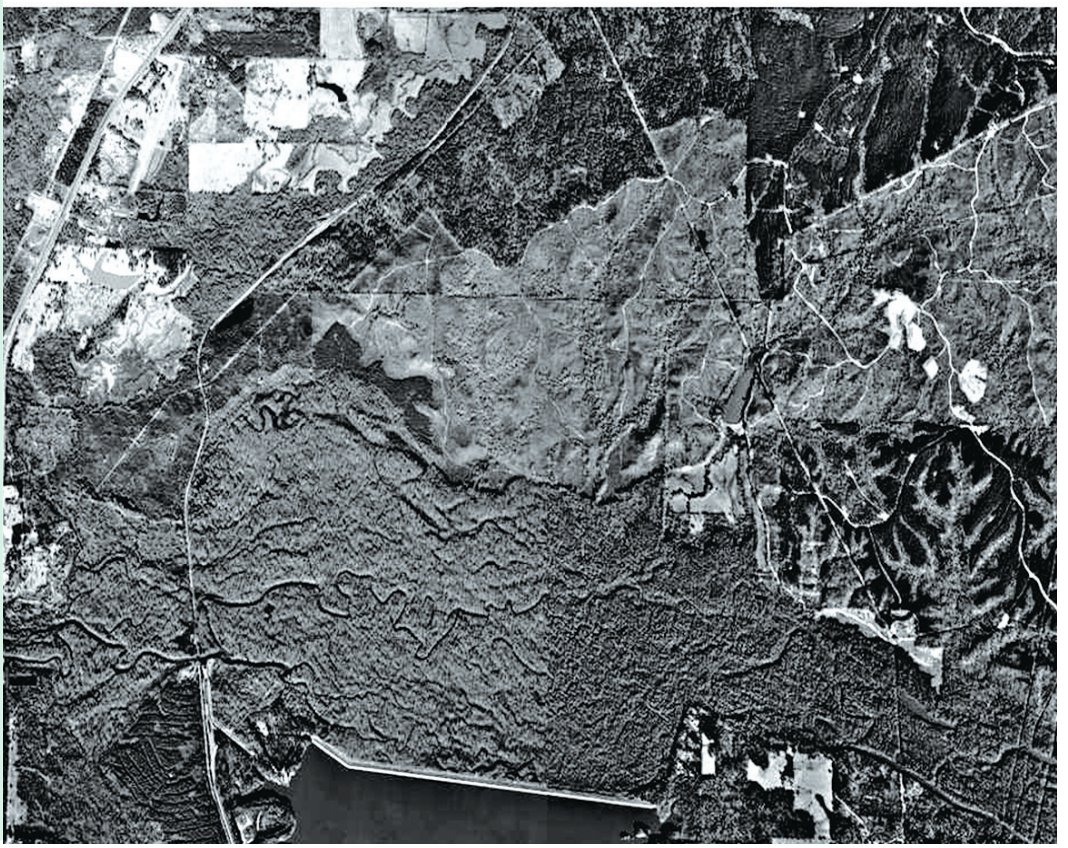

Figure 6.1—Photograph of a typical East Texas forest landscape. The image shows a mosaic of different land types including forest, pasture, urban areas, and water. Forest patches of various sizes and shapes can be seen with boundaries delineated by roads, creeks, or different land uses. Within this matrix, forest patches may be further classified by tree species, planting densities, age, and the type of management. The landscape is also dynamic, experiencing seasonal changes in temperature, soil water, and tree growth, and longer term changes caused by growth and management. One of the goals of SPB ecology is to understand the factors that drive population dynamics and damage, and thus be able to interpret landscapes such as the one depicted at right from the point of view of the beetle. (image courtesy of the USGS)

difficult to measure SPB population dynamics directly. However, many of these life-history processes can be measured independently. With some interpretation and speculation, this knowledge can be integrated into an overview of population dynamics useful for understanding and managing SPB damage. This "bottom-up" approach to understanding the SPB equips forest managers to understand why certain areas of forest incur damage while others do not. By focusing on the agent of damage itself (SPB) rather than just on the properties of the forest, this approach also arms forest managers with the knowledge needed to determine the extent and pattern of future SPB outbreaks.

6.1.1. The Range of SPB and the Physical Landscapes it Inhabits

The core range of the SPB extends from East Texas, across the Gulf States to Florida, and northwards to Virginia (Figure 6.2). Within this range, large variations occur in climate, topography, and the composition (abundance) and configuration (pattern) of host species. This large geographic range suggests that the life-history processes of the SPB (movement, development, reproduction, and longevity) define an organism capable of exploiting a wide variety of landscapes and climates.

Figure 6.3 shows patterns of SPB damage throughout its range between 1960 and 2000. A feature of this spatial and temporal pattern is that outbreaks do not occur at the same frequency throughout the SPB's range. An outbreak is formally defined as at least one SPB infestation per 405 Ha (Gumpertz and others 2000). The simplest explanation for differences in outbreak frequency is that they are driven by the amount of SPB hosts in a region. However, SPB outbreaks are only weakly (if at all) related to the abundance of potential hosts (Gumpertz and others 2000). A number of researchers have explored other simple hypotheses that might explain the spatial pattern of outbreaks. For

Figure 6.2—Geographic range of SPB. (redrawn from Payne 1981 by E. Takow)

example, Gumpertz and others (2000) used saw timber volume, along with other variables such as climate, elevation, and longitude, to develop a logistic regression model for the incidence of outbreaks in North Carolina, South Carolina, and Georgia. Similarly, Gan (2004) developed a statistical model that incorporated 16 selected climatic variables in an attempt to predict outbreak frequency. One conclusion from these studies is that SPB incidence and damage is not strongly related to any single, simple property of the landscape. Rather, it would appear that SPB damage is driven by complex population dynamics that we currently do not fully understand.

6.1.2. Why are Landscape Population Dynamics Important for SPB Management?

Patterns of SPB damage have both spatial and temporal components. Outbreaks occur infrequently through time (at periods of between 5 and 15 years depending on geographic location), with each outbreak comprising a number of discrete infestations, or spots, and localized damage. A number of statistical models have been developed to explain or predict the likelihood of infestations occurring in a particular area based on the local characteristics of the forest (e.g., soils, landform, and the age, BA, and DBH distribution of trees). Some of these models are reviewed in chapter 22. However, despite the utility of these models for SPB management, one trend that emerges is that although they can tell us which stands are most likely to incur damage (i.e., risk), they are unable to predict exactly where and when infestations will occur.

This lack of predictive power can be attributed to the fact that current models are missing vital information needed to fully describe the system. This missing information may fall into one of the following categories:

1. It is not possible to measure environmental variables accurately enough or at resolutions fine enough to permit accurate predictions.
2. Environmental variables used in these models are not those that are most relevant to SPB damage.
3. The models fail to account for the dynamic nature of the agent of damage itself—namely, SPB population dynamics.

Points 2 and 3 are especially relevant to this chapter. First, properties of the forest most relevant to SPB dynamics should be identified by understanding the basic population ecology of the SPB. This ecology includes mechanisms of host location; the speed, longevity, and habitat preferences during dispersal; and the relationship between life-history processes (development, survival, and reproduction) and temperature. Understanding the ecology of the SPB will undoubtedly lead to a different interpretation of the forest landscape as first registered by the human eye (Figure 6.1) and is arguably the first step in formulating hypotheses

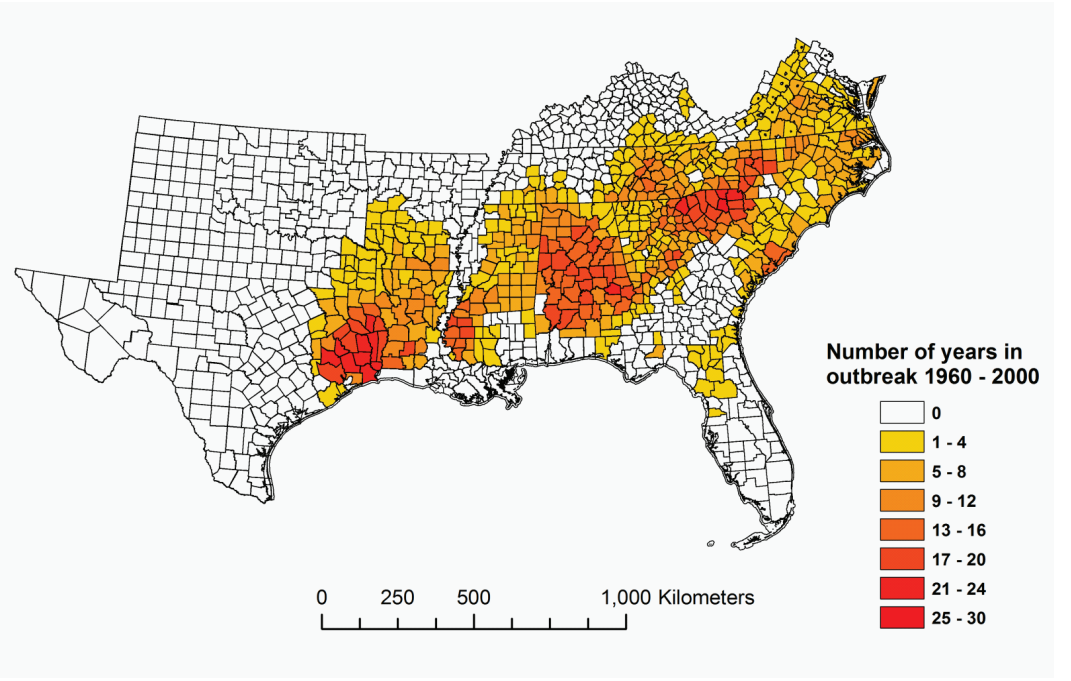

Figure 6.3—Map showing the number of outbreaks experienced by counties across the Southeastern United States between 1960 and 2000.

and models that explain the dynamics of SPB populations. Second, tree mortality is ultimately driven by changes in the abundance of SPB populations at a single point in space and time. Understanding the environmental factors that drive these changes should allow more effective SPB management.

Is it Necessary to Understand Population Dynamics to Predict Damage?

A fundamental question that surrounds SPB management is whether it is necessary to understand the dynamics of their populations in order to predict where damage will occur. More specifically, two competing hypotheses might be proposed:

H1. SPB populations are either homogeneously distributed through space and time, or are able to rapidly and efficiently disperse and/or locate potential hosts such that static, measurable properties of the forest (measurements of host suitability) become the most important factors for predicting future damage.

H2. SPB populations are unevenly distributed through space and time, have limited host-finding and dispersal ability such that patterns of damage can only be predicted by understanding the spatial and temporal patterns of the population.

These hypotheses mark endpoints of a continuum. Hypothesis 1 suggests that predictions for when and where damage will occur can be made by only measuring properties of the forest landscape, assuming the most relevant variables are measured. In contrast, Hypothesis 2 suggests that predicting the location and timing of damage depends upon both the properties of the landscape and the temporal and spatial distribution of beetles within the landscape. Given knowledge of SPB outbreaks, it is clear that H1 cannot be entirely correct. For a given region, SPB populations fluctuate between endemic and outbreak phases. In addition, outbreaks tend to occur locally such that the spatial extent of an outbreak can be defined.

Hypothesis 2 has important consequences for understanding the validity of current SPB management tools. Most risk models (reviewed in chapter 22) use only static properties of the forest to predict damage. In a sense, they estimate the potential for damage. Their formulation assumes that during outbreaks, populations are homogeneously distributed across a landscape. They also assume equal population densities during each outbreak, and since they do not account for variations in population dynamics through time, outputs from these models represent the long-term average probability that a stand or forest will become damaged (see following section).

If current risk models are correctly interpreted, they remain useful tools for SPB management. However, it is clear that many of their assumptions can be contested, given current knowledge of SPB population dynamics. In addition, there are many questions important for SPB management that cannot be addressed using existing risk models. These include:

1. How does the structure of the forest landscape affect SPB dispersal and the initiation of new infestations?
2. To what extent is the outbreak frequency of the SPB predictable?
3. To what extent are active infestations contagious?
4. Do regional SPB populations become locally extinct during nonoutbreak periods?

As mentioned previously, it is the patchiness and current unpredictability of damage that largely characterizes SPB pestilence. The challenge for population ecologists is to develop models (herein "model" refers to either a conceptual or a mathematical explanation of a process) that explain fluctuations in the abundance of SPB populations through space and time, and how these dynamics contribute to patterns of tree mortality.

6.1.3. Population Regulation

One central debate in SPB population ecology surrounds the mechanisms by which populations are regulated. Without some form of regulation (changes in the vital rates of the organism), populations either grow or decline infinitely. Southern pine beetle populations do neither. Instead they fluctuate from periods of high density populations (outbreaks), to extended periods of low density populations (endemic). Two classes of regulatory mechanisms have been suggested to explain these fluctuations. Proponents of exogenous regulation suggest that population dynamics are largely regulated by density-independent factors such as

weather. Endogenous regulation suggests that the dynamics of the SPB are influenced by density-dependant effects such as the reciprocal relationship between predators, hosts, or intra-specific competition.

Many SPB management issues can only be answered with full confidence if all of the mechanisms that cause populations to oscillate between low and high densities are understood. However, to make inroads into the SPB problem it is necessary to break down the complexity of population dynamics into discrete units. For example, it is possible to model SPB populations within infestations in order to understand the growth of infestations and to produce practically useful estimates of damage. Such models may be useful even if they do not attempt to explain why an infestation occurred, or do not account for immigration and emigration. Similarly it is useful to model populations at low densities in order to understand the dynamics of extinction within a region, or to develop simple temporal models that ignore the effects of space in order to investigate density-dependant effects (Turchin and others 1991). In all cases, the art of modeling (whether models are conceptual or mathematical) is to simplify population dynamics by choosing a level of complexity that contributes to an improved understanding of the system.

6.2. DRIVERS OF POPULATION DYNAMICS

The majority of data for the SPB have been collected from active infestations where SPBs are relatively easy to study. However, epidemic populations comprise only a fraction (but the most visible one) of SPB's population dynamics. It could be argued that the most important phase for understanding SPB dynamics is the endemic phase. An understanding of SPB populations between outbreaks and the factors that contribute to the shift from endemic to outbreak conditions is currently not well developed.

In the absence of data from endemic populations, conceptual or mathematical models must be built using life-history processes that can be more easily studied. The following sections deal with data and conceptual models that contribute to an understanding of how and why populations of the SPB oscillate from low density (endemic) to high density (epidemic) proportions. More specifically, they deal with mechanisms that could explain:

1. How and why SPB populations are regulated at low densities (between outbreaks).
2. How changes to this system (either endogenous or exogenous) lead to an increase in population growth rate and relatively short periods of high density populations.
3. How and why the system reverts back to an extended period of low density population dynamics.

6.2.1. Temperature and Climate

Figure 6.4 shows the time taken for SPB to develop at constant temperatures. Development is optimal at approximately 30 ^{o}C, and there is a reduction in development at temperatures above and below this mark. Similar relationships have been measured for reproduction and survival. Because of these relationships, temperature has long been proposed as an important regulator of SPB population dynamics, and there is little doubt that seasonal changes in temperature drive much of its dynamics. For example, at the onset of outbreaks, SPB infestations tend to be detected within the landscape in spring or autumn, when temperatures fluctuate around the optimum for development. Conversely, population activity and the initiation of new infestations tend to decline in midsummer and winter when temperatures become unfavorable for population growth.

These seasonal declines are a consistent and important component of SPB population dynamics. During winter, low temperatures curtail development and reproduction, and therefore population growth. Reductions in developmental processes affect the emergence of new individuals. Whereas under optimum conditions, a generation may be completed in 30 days, during winter it may take more than 90 days (Wagner and others 1984a). This extended development time may have a number of consequences. First, all other things being equal, extended development times and lower reproduction lead to a reduction in population growth rate (Birt and others 2009). Second, because there is intrapopulation variability in the development rates of individuals, longer development times increase the period over which emergence occurs. At optimal temperatures, individuals of the same age develop quickly and will emerge over a short period of time; whereas at low temperatures, individuals develop slowly and will

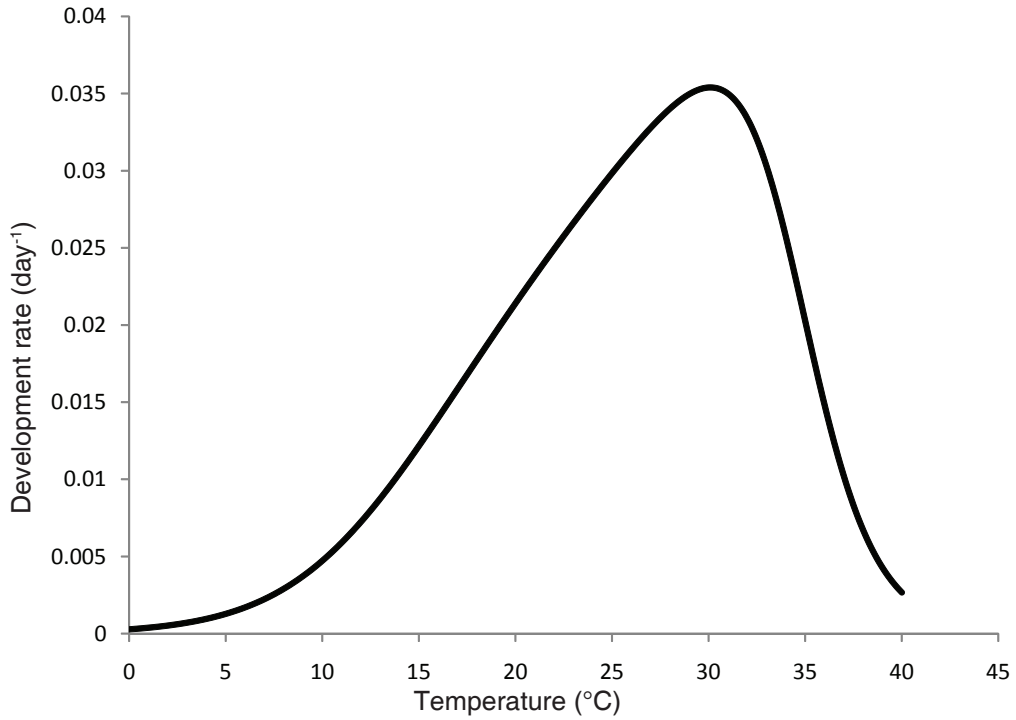

Figure 6.4—Graph showing the relationship between development rate (development time-1) and rearing temperature. Development is optimal at approximately 30 °C, leading to a development time of approximately 1/0.035 = 29 days. Note that development rate rapidly drops off at temperatures above 35 °C, but at sub-optimal temperatures the effect is more gradual. The graph serves as a basis to understand how seasonal climate (high summer temperatures and low winter temperatures) may curtail population growth by effectively halting development.

emerge over a much longer period of time. Low temperatures may also reduce the range of flight (Moser and Dell 1979a, Moser and Thompson 1986). Together, these interruptions to patterns of emergence are likely to reduce host-finding success and may be significant for populations at both endemic and outbreak conditions. Within infestations (epidemic populations), a reduction in attacking individuals may reduce the ability of the local population to overcome defenses of trees in the immediate vicinity. During endemic population phases, a decrease in attacking individuals may affect the ability of the population to locate and colonize highly susceptible hosts within a broader landscape (for example, lightning-struck trees).

Temperature may also have a direct effect on the mortality of individuals within a population. In the laboratory, 1 or 2 days of exposure to extreme low temperatures (-5 to -12 °C) causes >50 percent mortality (Lombardero and others 2000a). Through most of its range, such temperatures will occur infrequently, especially considering that bark may buffer temperatures by 1 to 4 °C (Tran and others 2007). But at high altitudes or in northern portions of its range, or during colder winters, extreme low temperatures may have significant effects on SPB overwintering. For example, Ragenovich (1980) recorded 95 percent brood mortality in areas of the Southern Appalachians that experienced temperatures <-20 °C. Ungerer and others (1999) suggest that the northernmost range of SPB is marked by a region where approximately 9 out of 10 winters experience minimum temperatures of -16 °C or less.

Extremely high temperatures may also directly increase mortality. For example, two of the methods used to manage active infestations, cut-and-leave and cut-and-top treatments, affect the microclimate of host trees and the mortality of brood stages within them (Fettig and others 2007). Such treatments are thought to reduce the emergence of attacking beetles within an infestation and the dispersal of individuals away from an infestation, thereby curtailing growth of infestations and outbreaks. In southern portions of its range, temperatures above the optimum for development (35 °C) and above its thermal tolerance (40 °C) may often occur.

Year to year differences in the overwintering (or high temperature) success of the SPB may affect the spatial distribution of SPB populations within a landscape and the ability of the population to outsource the following spring. Severe winters (or summers) may cause significant mortality of the SPB within a defined region, and population recovery may only occur following immigration from refuge populations that escaped the mortality. Under milder conditions, mortality may still occur, but at lower rates. In both cases, the effect could be to uniformly reduce the size of the population within every infested tree in the landscape or, possibly in conjunction

with landscape heterogeneity, temperature may impart differential effects on each meta-population (each actively infested tree in the landscape). In the latter case, in addition to reducing the overall size of a regional population, low temperatures may serve to disaggregate infested trees and thus reduce the distance between actively infested trees in the landscape. Such effects may be especially important where topographical features (for example, mountains) may buffer excessive temperatures. Considering the importance of aggregation for SPB populations (see following sections), changes to the spatial pattern of meta-populations may have an important role to play in the broadscale and long-term dynamics of the species.

Although temperature has clear, demonstrable effects on both directly measured population dynamics and the life history of individuals, its role in the mechanisms that lead to endemic-epidemic-endemic oscillations is contentious. The principal difficulty with this hypothesis is that it would require long-term and broadscale growth of the population to be close to zero. It suggests that in the long run (for example, over a 100-year period), the population should not significantly grow or decline, but within this period local populations would occasionally be driven (by year-to-year variations in climate) to epidemic levels and then return to endemic levels. More specifically, a temporary increase in growth rate would have to be followed by a corresponding decrease in order to complete the cycle to an original population size. This is plausible for predictable, seasonal dynamics where spring, summer, or autumn growth might be offset by winter (or high summer) declines. It is less likely that interannual variation in environmental conditions (alternate sequences of favorable and unfavorable conditions) are capable of driving the characteristic temporal patterns of outbreak and nonoutbreak conditions.

Another criticism of this model is that strong, consistent relationships between climate and SPB outbreaks have rarely been demonstrated. Gan (2004) did find relationships between selected climatic variables (including temperature and precipitation) and outbreaks, but the statistical model used does not necessarily point to these variables as direct drivers of population growth. Despite the difficulties of a pure hypothesis of climatic regulation, there can be little doubt that climate (temperature in particular) is an important driver of SPB population dynamics. However, it is suggested that the most likely role of climate is that it works synergistically with another regulatory mechanism. Two plausible mechanisms are discussed in the following sections—namely predator-prey and host availability. In both cases, it is possible that interannual variations in climate may act as a catalyst for these other processes.

6.2.2. Predator-Prey Dynamics

The most complete explanation of SPB population regulation involves the interaction between SPB populations and its predators. Turchin and others (1991) developed statistical and mechanistic models suggesting that patterns of SPB populations in East Texas are more attributable to delayed density-dependant effects (with a time lag of 2 years) than inter-annual differences in climate. In other words, the rate of population change in a given year is negatively related to the size of the population 1 and 2 years previously. Predator-prey interaction (a lag between the rate of change in predator populations in response to the abundance of their prey) is one mechanism that can drive delayed density dependence.

There is considerable evidence that predators can exert significant pressure on SPB populations. Populations of the SPB tend to be associated with a wide variety of potential SPB predators and competitors (Moser and others 1971). *Thanasimus dubius*, commonly associated with SPB populations, has been observed to exert considerable mortality on adult bark beetles on external bark surfaces (Reeve 1997). It is also considerably more mobile than the SPB, which suggests that it may be capable of efficiently locating its prey over large distances (Cronin and others 2000). The most compelling evidence for predator-prey regulation (in particular the delayed density independence known to cause cycles) comes from a 5-year field study (Turchin and others 1999b) where significant differences were found between survival rates of the SPB in trees where predators were excluded by cages vs. populations exposed to predators. More specifically, in agreement with a model of delayed density dependence, low density SPB populations were less affected by predation, whereas at high SPB densities (i.e., at the peak of SPB activity and during the first year of SPB decline) predator-induced mortality increased considerably.

The evidence that SPB populations are regulated by predator-prey mediated delayed density dependence is thorough but by no means conclusive. In particular, there is no evidence for delayed density population cycles outside of East Texas. Ideally, SPB population dynamics should be explained by a universal model, with mechanisms and parameters that are consistent throughout the range of the SPB. The model proposed by Turchin and others (1991) exhibits quasi-periodic cycles of approximately 6 years. However, the frequency of SPB outbreaks varies considerably across the United States (see Figure 6.3). To account for changes in these interoutbreak periods, the model will require a different set of parameters for different locations. To maintain plausibility, regional differences in these parameters must be explicable in terms of differences in climate, landscape structure, or some other measurable variable. Similarly, although the predator-prey hypothesis has driven much experimental work, these results have not yet been incorporated into detailed, explicit mathematical models that test the robustness of Turchin and others' (1991) original model. For example, a number of researchers have measured the growth rates of populations within individual trees with and without predators (Reeve and others 1998). In the original model, the rate of increase of the population corresponded to the number of infestations in the landscape rather than for the growth rates of populations within individual trees. It is argued that the plausibility of the hypothesis will be increased if these delayed density mechanisms can be demonstrated using finer scale population processes such as temperature-dependant development, reproduction, survival, and dispersal. In particular, these detailed mechanisms should be able to explain the characteristic spatio-temporal patterns of tree mortality of aggregated infestations during outbreaks and scarcity of damage during nonoutbreak conditions.

6.2.3. Host Availability

Southern pine beetle populations might also be driven by the availability of hosts. This might occur during both outbreak and low-density periods. The rapid growth rates of populations within infestations and the observation that free-flying, adult SPBs are relatively short-lived (Gagne 1980, Ragenovich and Coster 1974) suggest that a constant availability of new hosts is necessary in order to sustain the growth of an infestation and, in turn, outbreaks. For endemic populations, dynamics might be driven by a balance between the growth rate of a population occupying an infested tree and the mortality costs associated with emerging individuals that need to locate new hosts.

Central to a host-limitation hypothesis is the idea that there are differences in the susceptibility of SPB hosts within a forested landscape. These differences may occur through space and time and could be driven by climatic conditions such as drought, flooding, lightning strikes, or other tree stressors; genetic differences in hosts including different species; or the age, size, or density of trees or stands. In such cases, the functional heterogeneity of the landscape might be best envisaged as a complex mosaic of susceptible and nonsusceptible host patches. As such, the potential for SPB population growth and the spatial and temporal pattern of damage will depend on the arrangement and abundance of these susceptible hosts through space and time and the ability of the SPB to locate and utilize them.

It is widely acknowledged that host-finding (location and successful attack) depends on both the numbers of attacking individuals and the intrinsic susceptibility of a host. Figure 6.5 shows a conceptual model of this behavior inspired by dose-response relationships in toxicological studies. This model suggests that high population densities (large numbers of attacking individuals) will increase the probability of a new host becoming infested. But it also indicates that low density populations may also be capable of overcoming the defenses of highly susceptible trees; for example, those damaged by lightning (Coulson and others 1999b). Shifts along the x-axis represent differences in the susceptibility of hosts in the landscape (left shifts leading to increased susceptibility and vice versa). This conceptual model of susceptibility may help to explain the pattern of endemic and outbreak dynamics. Most directly, the decline of an infestation could be driven by the depletion of susceptible hosts, but also by the number of attacking beetles available in the local population. In turn, the number of attacking beetles in the environment may be driven by seasonal changes in climate or increased predation (see sections above). Such mechanisms could begin to explain how small changes in climate might lead to the much larger changes in population growth rate necessary to drive an entire population cycle. For example, endemic-to-outbreak transitions might occur when conditions conspire to create local population densities large enough to

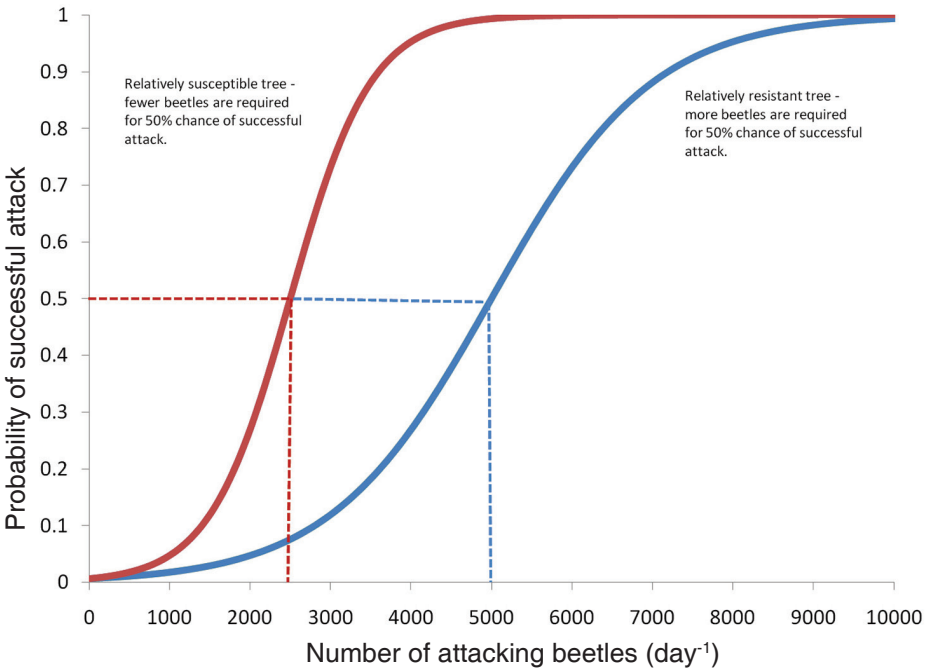

Figure 6.5—Graphs illustrating a conceptual view of tree susceptibility to SPB attacks. The graph describes mathematically how the probability of a successful attack may depend on the number of beetles available for attack, and some measure of the inherent susceptibility of the tree. The red and black 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. The models are based on dose-response functions common in toxicology studies.

overcome otherwise resistant trees, with the subsequent return to endemic conditions occurring through a combination of seasonal interruption of population dynamics and a reduction in the most susceptible trees in the landscape.

One problem with the host susceptibility hypothesis is that it relies upon a model that is highly conceptual. Unlike the predator-prey hypothesis, no mathematical representations exist with which to test its likelihood. Such representation is important in order to test the validity of conceptual, qualitative logic and turn it into testable and quantitative ideas. Nevertheless, there are large amounts of empirical data that suggest that at least some parts of SPB population dynamics are driven by interactions with its hosts. Most notably, SPB risk models are based on site conditions within a stand. Factors such as basal area (crowding of trees leading to increased stress and susceptibility) and soil conditions (the ability of the soil to drain or hold water and moderate water stress) have been shown to be important determinants of where infestations are likely to occur (see Lorio 1980b for a review).

The role of lightning-struck trees as highly susceptible hosts and sources of SPB populations has also been extensively studied. Using explosive detonator cord, Miller (1983) simulated lightning strikes in loblolly pine trees at various times between March and December, and within 10 days observed colonization of the tree first by black turpentine beetle (*Dendroctonus terebrans*), followed by *Ips calligraphus*, and finally SPB. In a similar study Coulson and others (1986) simulated lightning damage in 40 trees in East Texas and observed that bark beetles (including the SPB) colonized each tree. This colonization occurred after 6 months for trees injured in February and 5 days for trees injured in June, August, and September. In addition, approximately half of the disturbed and subsequently colonized trees spawned multiple tree infestations in neighboring untreated trees (two infestations grew to 45 and 35 infested trees). Lovelady and others (1991) extended these studies by exploring the availability of lightning-struck hosts in an East Texas landscape. They conclude that during endemic periods, lightning-struck trees are sufficiently available, both temporally and spatially, to provide an important refuge for the SPB and a mechanism for population persistence. However, during epidemic phases a large number of infestations occurred in areas that were not subject to lightning strikes, suggesting that the SPB is able to exploit less susceptible hosts at high population densities. Rykiel and others (1988) propose a conceptual model for the propagation and amplification of lightning strike damage by the SPB into large-scale forest disturbances. They conclude that lightning alone is unlikely to cause epidemic beetle outbreaks, but attribute outbreaks to synergies between lightning and other factors such as climate and the average susceptibility of a landscape. In turn, they suggest that average landscape susceptibility (an aggregate

measure of the composition and susceptibility of hosts within a landscape) is driven by a feedback loop involving the damage caused by SPB outbreaks, leading to depletion of suitable hosts, followed by regeneration of the forest and a return to conditions ripe for another outbreak.

Host Susceptibility, Population Dynamics, and Risk Models

Lightning-struck trees, water stress, wind and storm damage, silviculture, and tree genetics may all contribute toward a forest landscape comprising trees or stands with different susceptibility to the SPB. The SPB has also been observed to attack felled green timber (Moser and others 1987), preferentially select trees with active red cockaded woodpecker cavities (Conner and others 2001b), and utilize trees infested by other bark beetle species.

SPB risk models quantify the likelihood that damage will occur within one particular location over another. They characterize the heterogeneity of the forest landscape, usually based on properties of a stand. These models are usually based on historical data sets that document properties of stands (for example, soil, vegetation characteristics, slope, and aspect) that did or did not incur damage during an outbreak. Simple statistical models are then used to weigh these variables by importance and to estimate risk to damage in other unsampled stands. Stand level risk models have been successful tools for SPB managers over the last 30 years but cannot provide definitive, 100 percent accurate measures of infestations or damage. Many of the reasons for this are related to the population dynamics of the SPB.

First, these risk models only measure static properties of the forest and do not account for the agent of damage itself—SPB populations. Consequently, it is feasible that during an outbreak, a stand that a model predicts is at high risk (through an assessment of its physical and silvicultural characteristics) does not incur damage because it is under no pressure from dispersing beetles. Paine and others (1984) present a similar argument and a conceptual model that illustrates the concept of stand risk.

A more subtle problem arises because data used to develop risk models may be collected from a number of different outbreaks. In some years or locations, outbreaks may be severe, leading to high population densities and, if the relationships in Figure 6.5 are to be believed, a higher probability that a stand of a given susceptibility will be infested. It follows that data sets used to develop risk models may be biased by regional population size. Although it is difficult to experimentally control population size, increased knowledge of the spatial and temporal dynamics of populations during outbreaks may help to account for errors in the risk model and allow them to be applied more objectively and successfully.

Second, although it is known that the SPB preferentially attack certain hosts, it is not fully understood why this occurs. In other words, it is not possible to consistently predict the location of susceptible hosts in the landscape because the direct mechanisms involved in tree susceptibility are currently unknown. For example, susceptibility might be broken down into a number of factors including:

1. The influence of trees or silviculture on host-finding (for example, stand location, production of green leaf volatiles, relationship between stand structure, and pheromone diffusion)
2. Defenses against attack and reproduction (for example, measurements of resin flow and chemical defenses)
3. Nutritional value (for example, nutrient content, phloem thickness, and water balance) and its influence on brood survival

Many of these factors may also vary seasonally or over shorter time frames. The challenge for SPB ecologists is to develop repeatable methods to measure these factors and to relate them to relevant SPB life-history processes and population success. In the absence of knowledge of these susceptibility mechanisms, risk models usually use surrogate measurements of susceptibility such as basal area (presumably an indicator of competition among hosts and potentially stress), soil type or depth (which may indicate the likelihood of flooding or drought), or age (a possible indicator of nutritional status). These surrogate measures are used because they are relatively easy to measure. But as aggregate measurements of a stand, they may not always be indicative of susceptible trees. For example, high basal area stands might not be particularly susceptible (stressed) if other environmental conditions remain near optimal. Conversely, within a large stand, there may be localized anomalies (e.g., flooding or drought) that lead to small patches of susceptible trees that could serve as epicenters of SPB activity.

Such conditions may be driven by fine-scale, practically immeasurable differences in site conditions; for example, soils or topography.

By developing a more detailed understanding of SPB population dynamics, it should be possible to increase the accuracy of the next generation of risk models. Understanding the spatial and temporal distribution of populations during outbreaks should drive the measurement of forest conditions at the most appropriate scales and resolutions. And an enhanced, more fundamental understanding of why certain trees become infested may drive the development of novel ways to measure forest heterogeneity. Most of all, a most basic knowledge of SPB population dynamics clarifies what the results of current risk models actually mean and how they should be used. Given the discussion above, it is perhaps not surprising that risk models are unable to indicate exactly where damage will occur. However, far from diminishing the utility of these models, it is argued that this fact adds value by clarifying how their success should be measured (e.g., what level of predictive accuracy is acceptable) and how their results should be interpreted so that they can be used for practical management.

SPB as an Optimum Organism

In simple population models, faster development rates among individuals in the population (all other processes being equal) contribute to greater population growth rates (Birt and others 2009, Nylin and Gotthard 1998). Because they must kill the trees they infest, progeny of successfully reproducing adults must continually find hosts to ensure population persistence. This presents a paradox for low density vs. high density populations. At high densities (for example, within infestations), optimum development rates should lead to increased population growth because hosts are plentiful (the Allee effect is in play). However, at low population densities this may not be the case. If the growth of endemic populations is regulated by a limited supply of highly susceptible hosts (for example, lightning-struck trees), then rapid turnover of the population (shorter development times) may not be optimal. During nonoutbreak periods, or periods when there are fewer attacking individuals, it is conceivable that population persistence involves changes in life-history processes that mitigate the problem of locating hosts. For example, Coppedge and others (1995) and Wagner and others (1984a) found differences between the body mass of individuals collected at different times of the year. This may be an adaptive response to increase host-finding efficiency, and this extra mass may be explained by longer development times (Atkinson and Sibly 1997). Such plasticity has been observed and extensively studied in a number of other arthropods (Peckarsky and others 2001). Other important adaptive mechanisms might involve second generation individuals reproducing in their natal tree, or synchronized emergence after periods of unfavorable population growth. Although speculative, such arguments are a reminder that, by the nature of the system, most of the observations and data collected for the SPB are from epidemic populations.

6.3. SPB DISPERSAL AND HOST FINDING

The SPB must kill a host in order to successfully reproduce. Over much of its range, warm, moist conditions lead to rapid decomposition of dead trees, curtailing the length of time that a host remains nutritionally favorable. During endemic periods, individuals must continually locate hosts that may be sparsely distributed across the forest landscape. During outbreaks, and in particular within active infestations, competition for nutritional resources (Reeve and others 1998) may drive the location of fresh hosts both within an infested stand and within the broader forest landscape. The SPB's ability to efficiently disperse, locate hosts, and generally utilize a heterogeneous spatial environment is therefore a critical component of its population ecology.

6.3.1. Dispersal

Because of its small size, it is difficult to observe the movement of SPB individuals directly, especially during endemic periods. As a result, movement must be inferred using properties of the system that are measurable (e.g., mark-recapture data) and models of movement. Figure 6.6 shows a simple model that encapsulates one of the fundamental aspects of SPB movement and its impact for population dynamics. The graph describes differences in the density of SPB populations if individuals were to move different straight line distances from a source population (for example, their natal tree) and follows a simple mathematical relationship between the area of a circle with radius r and the local density of a population. Although it does not explicitly represent the movement of

the SPB, it illustrates a fundamental tradeoff for populations exploiting a heterogeneous forest landscape. If individuals move large distances from a natal tree, population densities become diluted, but moving smaller distances may severely limit the ability to locate fresh hosts. These reductions in population densities are important. At the very least, the success of a sexually reproducing population requires the presence of males and females, an event that is likely to become increasingly difficult as population densities decrease. But for the SPB in particular, the efficiency of host location and successful colonization is increased when large numbers of individuals are able to attack *en masse.*

The model illustrated by Figure 6.6 demonstrates some simple, physical consequences of diffusion. Mean SPB dispersal, measured using mark-recapture experiments, has been estimated at approximately 0.25 km, with some individuals moving greater than 1 km from their release site (Turchin and Thoeny 1993). Gara (1967) and Moore and others (1979) found marked beetles at approximately 0.3 km and 1.6 km away from a release site. Mark-recapture studies actually measure the endpoints of beetle movement (or spatial distribution) after a given period of time. In turn, these endpoints are driven by a number of more fundamental processes including:

1. Speed of movement expressed as distance per unit time
2. The amount of time a beetle spends dispersing, driven by motivational states and the loss of beetles from the dispersing population
3. The directionality or tortuosity of movement; for example, does it move in long straight lines or in shorter, non-directed hops

Flight Speed and Time Spent Dispersing

Tethered SPB flight experiments have recorded average flight durations of at least 1 hour during which time individuals covered an average of approximately 1 km (Kinn 1986). Although these experiments do not allow the SPB to exhibit natural behavior (for example, it is unclear whether flight is terminated because beetles are exhausted or whether these durations are indicators of true dispersal behavior), they do yield useful estimates of flight speed (13 m/minute). To place this figure into perspective, the flight speed of honeybees has been estimated between 200 and 300 m/minute (Nachtigall and others 1995).

Flight activity has been shown to be dependent on weather conditions. Moser and Dell (1979a) developed a predictive model of flight based on trap counts and estimated the minimum temperature threshold for flight as 14 ^{o}C. Moser and Thompson (1986) suggest that the threshold may be even lower (approximately 5 ^{o}C) and suggest that discrepancies between these values may be caused by solar insulation. They also estimate maximum temperature thresholds of approximately 38 ^{o}C and suggest that rainfall may also reduce flight activity. Given the relatively slow flight speed of the SPB, it is also suggested that wind may have a large impact upon flight activity, or at least the ability of the SPB to undertake directed flights. In these flight activity studies, the SPB were captured in a network of baited traps, and the number of captures related to weather conditions. Trapping success is therefore dependant on the average size of the dispersing population, in part driven by patterns of emergence and reemergence within the entire population. However, the size of this dispersing population and the length of time an individual spends dispersing may be affected (reduced) by two additional factors: mortality and successful host location. Southern pine beetle adults are short-lived and are unlikely to survive more than 7 days as dispersing adults, but this background mortality may be driven by additional factors such as the weather conditions, the heterogeneity of the landscape (amount of nonhost landscape), and predation. The size of the dispersing population may also be affected by the time it takes for dispersing individuals to locate and colonize a host. In turn, this may vary according to whether dispersal is within an active infestation (with high densities of attacking individuals) such that individuals are able to readily find suitable hosts. Changes in population size and losses from the dispersing population may therefore bias results from trapping experiments and movement patterns inferred from them.

The size of the dispersing population relative to the total population (population within trees) may be a strong indicator of the efficiency of an SPB population. Dispersing individuals, though clearly important for population persistence, are unable to produce offspring and therefore do not make immediate contributions to population growth. In addition, the process of dispersal

is costly both in terms of energy expenditure and mortality costs. This suggests that the motivation for dispersal is primarily to find fresh hosts and possibly to escape the effects of competition and predation. This motivational state, along with constraints imposed by beetle morphology and physiology (limitations of flight), and the forest landscape provides the backbone necessary for understanding fine-scale dispersal behavior.

Flight Directionality

The directionality of SPB movement is another fundamental driver of SPB spatial distribution. Host selection by insects has been broken down into a series of four steps: host-habitat finding, host recognition, host acceptance, and host suitability (Kogan 1994, Strom and others 1999). The speed and tortuosity of movement, in both two and three dimensions, of a dispersing population is important because it is related to the ability of individuals to sample or encounter potential hosts and conspecifics. Little is known about this fine-scale movement behavior. For example, it is not known whether individuals undertake large numbers of short flights, moving from tree to tree to continuously evaluate potential hosts, or whether they undertake flights of relatively longer durations before landing on a host.

Kinn (1986) observed that in an absence of an attractant or at distances greater than 20-25 feet (6.1-7.6 m) from an attractant, SPB will tend to disperse (meaning long range dispersal) (Gara 1967, Gara and Coster 1968). Under such conditions beetles tended to fly upwards at a steep angle of ascent. In contrast, individuals within the range of an attractant were observed to fly 1-5 m above the forest floor. Given the model outlined in Figure 6.6, it is plausible that the SPB employs different behaviors while dispersing within infestations (high density populations) compared with long-range dispersal. A number of authors have noted that infestations occur in the direction of prevailing winds, suggesting that long-range dispersal may occur above the canopy. It has also been suggested that the heterogeneity of the landscape itself may affect the speed and directionality of dispersal; for example, Turchin and Thoeny (1993) found aggregation of beetles within stands with high basal areas, and it is possible that understory development, the height of forest canopies, and the juxtaposition of different stands may also lead to marked three-dimensional corridors that affect SPB dispersal.

6.3.2. Host Location and Selection Mechanisms

The need to find new hosts each generation, the dilution of local population densities, and

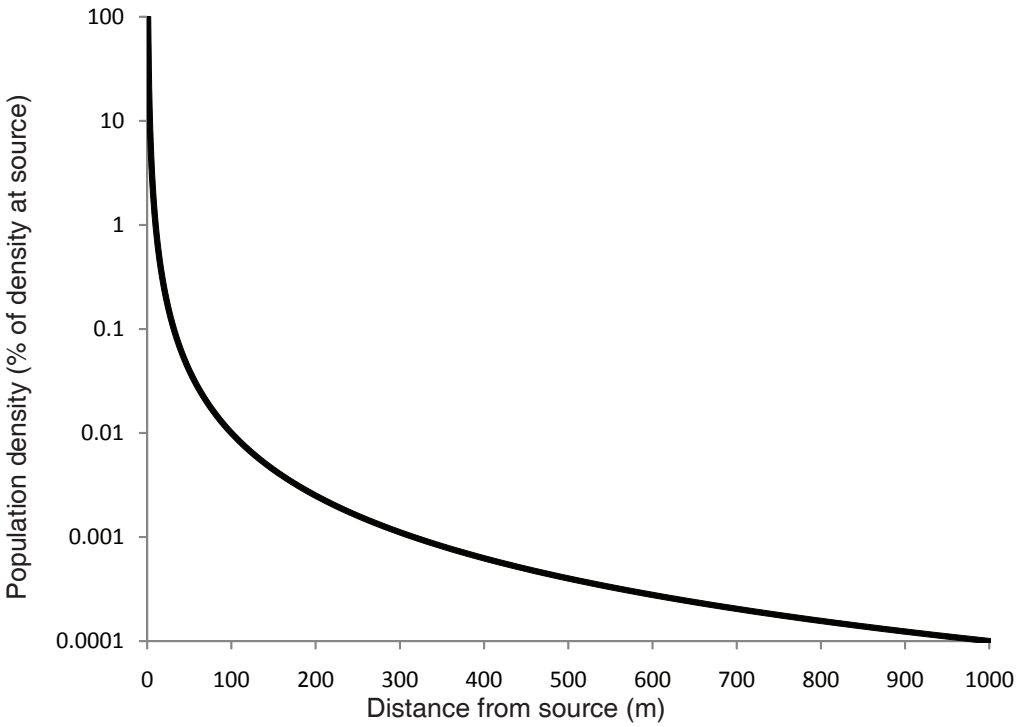

Figure 6.6—A simple model for the reduction in population density (individuals per unit square) with distance *r* from a population source. Note the use of log10 scale on the y-axis. The relationship is based on a fixed number of individuals evenly distributed over the area of a circle with radius *r* so does not account for a gradient of population density from a point source.

the speed and fine-scale movement behavior of dispersal drive much of the spatial distribution of SPB populations. But for the SPB, the ability to detect and respond to chemical (either host volatiles or pheromones) or visual cues in order to locate hosts is another important component of dispersal, hence population dynamics. Figure 6.6 is relevant as a base for exploring the relationship between movement and local SPB densities, and highlights the importance of chemical or visual cues for increasing the efficiency of host-finding and beetle aggregation. These host-finding mechanisms therefore provide much of the detail necessary to fully understand SPB dispersal. An indepth discussion of the role of chemical and visual cues for host-finding has been discussed elsewhere in this volume, and this review will focus on the consequences of these mechanisms.

Host volatiles alone (α-pinene) are unlikely to attract SPB (Payne 1980), especially over large distances. As a result, beetles are most likely to locate fresh unattacked hosts through a process of random searching. However, once a suitable host has been located, pheromones produced by attacking beetles (most notably frontalin) attract conspecifics and drive the aggregation of beetles. Although no detailed experiments have been conducted (Byers 1989b), it is reasonable to assume that the concentration of pheromones increases as the host accumulates individuals. It follows that the attractiveness of new, actively infested trees may follow a positive feedback loop driven by the spatial and temporal distribution of beetles around the host. In two dimensions, this might be conceptualized as a radius of pheromone influence—individuals that move within this radius will become affected by the chemical. Figure 6.6 suggests the importance of this process to the SPB. As individuals disperse further away from a population source, the likelihood of finding a conspecific by chance are greatly reduced. For low density, endemic populations, assuming susceptible hosts are rare and the mortality costs associated with attacking a fresh host are high, any mechanism that facilitates aggregation is likely to be important for population growth. Byers (1996) developed a model of host-finding based on these concepts and concludes that host-finding efficiency is greatly increased when this feedback mechanism occurs, and that even endemic populations may be able to locate rare, highly susceptible hosts relatively efficiently. The model could also be expanded to three-dimensional space. Here, this area of influence could be envisaged as a volume of influence that may extend above the forest canopy but is bounded by the forest floor or understory. The extent, shape, and longevity of such plumes are likely to be driven by wind, humidity, canopy closure, rainfall, and temperature. While quantification of the diffusion of pheromones and the attractiveness of beetles is difficult to measure, this three-dimensional view of the forest may be useful for understanding the potential advantages of dispersal above or below canopies.

In addition to driving the aggregation of beetle populations, it is possible that chemical cues affect SPB populations in other ways. For example, assuming that aggregation pheromones are driven by the presence of SPB, they also present a consistent cue that can be used by predators. Clerid beetles and *Monochamus* spp. have been shown to respond to chemicals associated with beetles (Allison and others 2001, 2003; Mizell and others 1984), while parasitoids also use chemical cues to distinguish between preferred life stages within such trees (Sullivan and others 2003).

Populations of the SPB are also often associated with other pine beetle species (for example, *Ips* spp., *Dendroctonus terebrans*). Each species minimizes competition by occupying different niches within infested trees (Wagner and others 1985), but as species colonize suitable hosts they may also facilitate host location and successful attack by the SPB. The extent to which olfactory cues are used interspecifically is subject to debate. Payne and others (1991) found a behavioral response by SPB to compounds produced by *D. terebrans* but not to those produced by *Ips spp*. In contrast, *Ips* spp. did respond to SPB compounds. Whether the SPB is a pioneer species in such guilds or makes use of trees already weakened by other species, the fine-scale interactions between species within the guild of southern pine bark beetles may be important for understanding broadscale SPB populations.

Although aggregation of beetles is important for host attack, intraspecific competition occurs in high density populations (Reeve and others 1998). Here, antiaggregation pheromones may serve to repel beetles from an infested host that is either too old or contains excessively high populations densities, such as may occur within large infestations. Antiaggregation effects are interesting not only for driving the

ecology of SPB populations but also for direct management. Within infestations they drive the mechanisms that cause attacks to switch from infested hosts to fresh hosts; hence, the magnitude of damage within an infestation. Possibly of greater importance, it is conceivable that they drive the mechanisms that determine the timing and amount of dispersal away from active infestations and thus affect the contagion of infestations. A paradox for SPB populations is that assuming the benefit of aggregation, it is unclear how it can be advantageous for individuals or genotypes to move away from high density population sources (infestations). Assuming a high cost of dispersal and the rapid reduction in population density away from an infestation, it is difficult to see how it would be advantageous for individuals to intentionally move away from infestations. The following hypotheses might be proposed:

1. Emigration is unintentional. It may be caused by strong winds affecting the SPB's ability to undertake directional flight or by a breakdown in pheromone communication during periods of unfavorable weather, or by an infestation growing too large too quickly and leaving infested trees (therefore individuals emerging from them) too far away from pheromone sources at the head of the infestation.

2. Emigration is a response to predation.

3. Emigration is a response to seasonality, a factor that consistently leads to a reduction in local population densities. If densities become too low to overcome the defenses of local trees, the dispersal may be a more optimal strategy.

4. Emigration is a response to intraspecific competition and occurs when the mortality costs associated with dispersal are lower than those associated with competition.

These hypotheses are speculative but are also testable. Depending on the hypothesis, emigration will be proportional to population growth, related to measurable weather indices or to predator numbers. In the case of a response to intraspecific competition, one might expect that during early stages of infestations, individual beetles will tend to remain within an infestation because they have a high value for infestation growth, and emigration as a proportion of the population size will increase as the population density within each tree increases. In turn, densities of within-tree individuals might increase as a result of changes in the susceptibility of trees (for example, if the infestation reaches a stand boundary) or as a result of other environmental changes such as seasonal temperature changes that interrupt the emergence of beetles, reduce the Allee effect, and thus limit the availability of new hosts.

However speculative these hypotheses may be, understanding why beetles disperse is important to understanding when and where damage will occur. Armed with knowledge of why the SPB disperses, it is possible to develop robust models, whether conceptual or mathematical, driven by the motivational state of the organism. In turn, these motivational states are likely to be driven by local environmental conditions including population size, temperature, and predation that may drive different dispersal strategies across the SPB's range. One of the tools that ecologists can use to complete this process is to measure, map, and visualize the landscape from the SPB's rather than human perspectives. Population models often assume that organisms move or behave in predefined ways, usually based on real-world measurements. But armed with an SPB-centric view of the environment, a method based around the concept of SPB populations seeking to optimize environmental resources may offer a fruitful perspective to the problem. Such concepts clearly depend on strong concepts of what an optimal behavior actually is (maximized population growth, population persistence, or the success of individuals or genotypes) and on the tradeoffs and limitations of certain life-history processes. Clearly 100-percent survival and infinite reproduction would be optimal but unrealistic. For the SPB, one of these tradeoffs (dispersal distance) is readily apparent and may be the cornerstone necessary to understand complete SPB population dynamics.

6.4. CONCLUSIONS

Southern pine beetle population dynamics are complex. After 40-plus years of study there are no definitive explanations for why populations oscillate between high density (outbreaks or epidemics) and low density (endemic) populations. They are also difficult to study directly, which makes it imperative that processes that can be or have been measured are integrated into more complete descriptions of population dynamics. One conclusion from this review is that although much is known about

the ecology of the SPB, there are still too many unknowns for a complete, definitive model of population dynamics to be developed. Given the difficulty of studying SPB populations directly, it is suggested that much can be gained by piecing together these ecological processes into more comprehensive models of dynamics.

How these observations are pieced together is important. In the long run, it is desirable to develop models capable of explaining the entire dynamics of the SPB—models that include spatial and temporal dynamics and that explain the characteristic patterns of outbreak and nonoutbreak dynamics. But realistically, these real-life processes are complex. In the short term, smaller modules of SPB population processes can be developed; for example, models of infestation growth, dispersal and host-finding, population regulation, contagion of infestations, and so on. These smaller portions of population dynamics are relatively easy to develop, understand, and validate compared to models representing complete SPB dynamics. Some may also have an immediate practical value for SPB management. Most important, once models are assembled and documented they provide tangible, testable descriptions of population dynamics. Since there are a large number of ways in which SPB ecology can be interpreted, the development of multiple working models, each with respective merits and weaknesses, should greatly contribute to overall understanding of SPB population ecology.

Throughout this review, the word "model" refers to a conceptual or mathematical explanation of how some components of the SPB system work. Three conceptual models have been proposed that offer an explanation for changes in SPB populations. A number of other models have been proposed that describe dispersal and host location. These conceptual models are an important first step to understanding SPB dynamics. However, population ecology is a quantitative disciple. It links quantitative rules for reproduction, death, and movement to changes in the number or distribution of individuals through space and time. The advantage of mathematical over conceptual models is that they demand a logical integrity that helps to translate conceptual models into testable ideas. At present, the predator-prey hypothesis is the only complete model of population regulation that has been represented in this way (Turchin and others 1991). At the very least, the model demonstrates that a predator-prey model is capable of explaining the oscillations shown by SPB populations. By incorporating an error term in the model, the authors allow for the fact that the model parameters (population growth) may be affected by other unexplained factors (e.g., climatic variations, changes in host susceptibility), some of which are also discussed in this chapter. These are ecological details currently only implied by the predator-prey model, and that need further explanation and research.

One of the conclusions of this chapter is that SPB dynamics are complex. But this complexity arises because many processes are responsible for driving patterns of birth, death, and movement. More specifically, the importance of each proposed mechanism changes according to the spatial or temporal scale at which a population is studied. Over a single year, changes in temperature clearly play an important role in population dynamics. During endemic phases, the availability of highly susceptible trees and the ability of the SPB to find them may be the important factors. Within infestations, temperature, the size of the attacking population, and its effect on host susceptibility (the Allee effect) may drive overall patterns of damage. And within an infestation, populations in a single tree may be primarily driven by competition and predation. This complexity, driven by the spatial and temporal scale of any particular study, is likely one reason why SPB dynamics are currently not well understood. An advantage of a quantitative approach is that it disambiguates the spatial and temporal scale of any conceptual model and clarifies the importance of different processes and mechanisms.

Finally, data is required in order to test and evaluate models. Southern pine beetle populations are difficult to study directly, but spatial distributions of beetles can be estimated using trapping experiments or by documenting visible signs of tree mortality. In addition to population or damage data, measurements are required that document the state of the forest, predator populations, climate topography, or any other factors that could be important drivers of population dynamics. To extract maximum value, the spatiotemporal scale and resolution of all data sets should be comparable, and the data sets should be well documented and readily available to researchers. Given the complexity of the SPB system, it is doubtful whether any individual, using observation and experience

alone, could ever effectively organize the vast amounts of information associated with the SPB. Extensively managed forests, a large geographic range, infrequent and unpredictable outbreaks, and the importance of both spatial and temporal dimensions present large challenges for data collection and organization. In a given year, outbreaks might occur simultaneously at opposite ends of SPB's geographic range. These outbreaks might occur in landscapes with very different environmental conditions, and each may exhibit subtle differences in the spatial and temporal patterns of damage detectable only through meticulous observation or data collection. Some outbreaks may be so severe that it is impossible to document each infestation in detail without using complex sampling methods. The organization of this information is imperative for understanding the SPB problem at all scales. Advances in GPS technology and Web-based data entry, storage, and retrieval tools are beginning to address these problems (see chapter 21). When populated with data, these tools should provide an unprecedented overview of SPB damage and population dynamics viewable at any number of spatial and temporal scales, and provide a comprehensive overview of historical SPB activity necessary to further the development of improved population models.