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Southern pine beetle regional outbreaks modeled on landscape, climate and infestation history

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ABSTRACT

The southern pine beetle (*Dendroctonus frontalis*, SPB) is the major insect pest of pine species in the southeastern United States. It attains outbreak population levels sufficient to mass attack host pines across the landscape at scales ranging from a single forest stand to interstate epidemics. This county level analysis selected and examined the best climatic and landscape variables for predicting infestations at regional scales. The analysis showed that, for a given county, the most important factor in predicting outbreaks was that the county was classified as in outbreak status in the previous year. Other important factors included minimum winter temperature and the greatest difference between the average of daily minimums and a subsequent low temperature point, precipitation history either seasonally in the previous year or difference from average over the previous 2 years, the synchronizing effect of seasonal temperatures on beetle populations and the relative percentage of total forest area composed of host species. The statistical models showed that climatic variables are stronger indicators of outbreak likelihood than landscape structure and cover variables. Average climatic conditions were more likely to lead to outbreaks than extreme conditions, supporting the notion of coupling between a native insect and its native host. Still, some extreme events (i.e., periods of very low temperature or very high precipitation) did precede beetle infestation. This analysis suggested that there are predisposing and inciting factors at the large scale but the driving factors leading to individual infestations operate at smaller scales.

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1. Introduction

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) is an important pest of pine forests in the southeastern United States (Thatcher et al., 1980). The beetle is primarily successful in loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*) pine species, although it can reproduce successfully in other pine species. A local outbreak of beetles will start in a single or a few trees and then spread to the surrounding trees, creating a “spot”. Southern pine beetles (SPBs) use aggregation pheromones to rapidly recruit conspecifics for mass attack and then begin to release anti-aggregation pheromones as the tree is fully occupied to prevent overcrowding. To successfully reproduce, the beetles first kill a host tree or colonize a recently killed tree. Under optimal environmental and host conditions, SPB populations may increase exponentially, infesting pine forests over large areas. Numerous studies have focused on stand level outbreaks and their control (see references cited in Fettig et al., 2007), and these studies allow us to understand the factors leading to local outbreaks and the steps that can be taken to limit spread and minimize infestation initiation. Stand density and tree age, among other stand-level factors, can increase susceptibility to infestation, but the true measure of risk is the concurrence of these predisposing and inciting factors with a population of locally dispersing beetles (Gara, 1967; Gara and Coster, 1968; Moser and Dell, 1980; Thatcher et al., 1980; Turchin et al., 1991; Turchin and Thoeny, 1993; Reeve, 1997). Outbreak data are collected by forest managers throughout the SPB’s range, and compiled by state or federal forest health specialists. These data have enabled previous studies to examine regional infestation patterns and predict average infestation distribution (Kalkstein, 1981; Kroll and Reeves, 1978; Mawby and Gold, 1984; McNulty et al., 1998; Gumpertz et al., 2000). Forest health enterprise team (FHTET) risk maps incorporate many of these findings at spatial scales that enable forest managers to evaluate the risk of infestation in their management area (Krist et al., 2007).

While some studies have predicted yearly infestations at the county level (Gumpertz et al., 2000; Kramer, 1993), these projects do not use all of the available county-level data or attempt to predict risk across the entire southeastern U.S. range of SPB. The county level is important for prediction because state level

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management recommendations are generally communicated at the county level for managers to implement within stands. This means that resources for monitoring, thinning and SPB prevention will be utilized more efficiently with an understanding of the year-by-year county-level risk. Certain resources are already available at this scale, such as the spring pheromone survey based on trap captures of SPB and natural enemies (Billings, 1988; Billings and Upton, 2008), and FHTET risk maps (Krist et al., 2007). This examination attempted to find important factors that are not already considered in these methods. Some of our earlier work demonstrated that county infestation history is an important and significant predictor of infestations, while factors relating to SPB generations are not (Duehl, 2008). The historical data utilized in these studies, along with climate and landscape data, will provide a more complete understanding of the determinants of SPB infestation rates across the southeastern United States.

There are certain large-scale phenomena that are important predictors of SPB infestation. At the regional level, extreme temperature events will lower infestation likelihood, while extreme precipitation events will increase infestation probability (Kalkstein, 1981). These variables are also important in predicting risk at the county level (Gumpertz et al., 2000). Minimum winter temperature is another important factor that maintains northern range limits (Lombardero et al., 2000a). Elevation drives many ecophysiological processes and relates to temperature and species distribution. Drought, at levels severe enough to limit the production of defensive compounds, is also an important factor inciting damage to stands (Lorio, 1986). The degree of host availability (i.e., the amount of host species forest cover in a county) also influences infestation occurrence (Gumpertz et al., 2000). Some stand-level factors are also significant. Stands where trees are in competition for resources are less able to resist attack (Billings et al., 1985; Lombardero et al., 2000b). Stand-level competition may be captured by proxy, with the amount of host and human population in a county accounting for management intensity. In the southeast, host stands where human population is low are many times managed forests, while higher human population indicates smaller stands and less forest management (Barlow et al., 1998). These factors were then tested in two statistical models as predictors of infested counties for all the years of available data (Price et al., 1992).

While some of the dynamics that occur in the SPB system can be captured at the scale of this study, others cannot. For example, predation, fungal competition and symbiosis, mite load and other factors cannot be considered with currently available data (Hofstetter et al., 2006; Klepzig et al., 2001; Reeve, 1997). While these small-scale factors are linked to infestation formation and expansion in localized outbreaks, their roles at the regional scale have not been determined.

Our objectives were to determine the best variables to predict SPB infestations at the county level, and to use these variables to make a regional model of infestation probability. This in depth look at the hierarchical relationships between many landscape, climatic and infestation history variables should aid managers with a better understanding of the factors influencing SPB success at the county level. Furthermore, this regional model will complement existing, smaller-scale models of within-stand risk, such as SPBMODEL and HOG (Lih and Stephen, 1987) and perhaps better inform other regional models (Krist et al., 2007).

2. Materials and methods

2.1. Data and processing

For this study, county-level SPB presence–absence data from Price et al. (1992) were supplemented by additional data from the USDA Forest Service. The temporal extent of the combined data was from 1960 to 2004 and their spatial extent covered the SPB's southeastern range from Texas to Virginia. While infestations occur on occasion further north and regularly in a discontinuous area of their range extending from Arizona through northern Nicaragua, we were unable to collect infestation data from these parts of the range. Additional variables used for this analysis were separated into four distinct groups: infestation history, land cover, human population and climate. The infestation history variables recorded for each county included regional infestation level and focal county history. Regional infestation level was the percent of the 20 counties nearest the focal county that were infested in the previous year. Focal county history was the infestation condition of the focal county itself in previous years. This included presence–absence data on county infestations in the previous year and 6, 7 and 9 years in the past to capture eruptive population cycles and delayed density dependence (Duehl, 2008). County level SPB infestations experience significant cycles during the years examined and natural enemy populations build up over the course of an infestation and these data capture both elements. The host species cover data were derived from county summaries of USDA Forest Service Forest Inventory and Analysis (FIA) data. These data have been collected and compiled since 1930 to inventory the condition of United States forests. The forest monitoring component of the FIA program uses remote sensing and ground surveys to get an estimation of forest cover and composition (USDA, 2010). Using FIA county cover estimates we were able to assure consistent data quality across states. Since FIA surveys were carried out approximately every 10 years over the time period examined, the values were linearly interpolated for the 10 years between surveys. Data collected from the county summaries were hectares of forest cover and hectares of host cover. We defined host as loblolly (*P. taeda* L.) and shortleaf pines (*P. echinata* Mill.). SPB can successfully reproduce and increase their population in other pines, but these two species are the most conducive to SPB success (Thatcher et al., 1980) and are both widely distributed and consistently surveyed. Additional information calculated for each year was percent change in both host and forest cover. Additionally, the number of hectares of host was divided by hectares of forest to get a proportional measurement of host relative to total forestland. The other variable tested that related to land form was the average elevation for the county derived from a 15-m digital elevation model (USGS, Seamless 2007).

Human population data were extracted from United States Census Bureau records (NHGIS, 2010). The variables considered were total population per county, population per 0.4 ha, percent population change from the previous measurement, and absolute value of the population change. Because Census data are collected and reported every 10 years, the latter two measures of population change for intervening years were calculated with linear interpolation.

Climate-related variables used in this study were derived from National Climatic Data Center Summary of the Day data. For each weather station, about 227 regional stations, the data available were minimum and maximum daily temperatures and daily precipitation in millimeters (NCDC, 2010). The counties were joined to the data collected at the weather station nearest to the county center (ESRI, 2004). We considered various spatial interpolations, but for weather data at this scale interpolation does not significantly increase accuracy (Jarvis and Stuart, 2001). The first variables tested were minimum yearly temperature and maximum yearly temperature. However, minimum yearly temperature only partially described the potential for cold temperature mortality of the SPB. A very cold day in November may cause mortality to less cold-tolerant life stages, while a colder day in January might not cause any mortality (Lombardero et al., 2000a). Insects can modulate their cold tolerance by desiccating and lowering their