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

Table 1
The classification accuracy of the two statistical models. The CART model with limited variables performed best both in terms of overall accuracy and also in classification agreement. The variable numbers of total counties stem from missing variables in some years and the variables chosen by the models.

	Total miss-classified	Total counties	Overall classification accuracy (%)	Cohen's kappa
CART	1546	23,432	90.4	0.46
CART limited variables	2508	34,291	92.7	0.48
Logistic all	2909	37,657	92.3	0.41

crystallization points (Lombardero et al., 2000a). Thus, in addition to minimum winter temperature, we determined the day during the winter when minimum temperature was the most different from the average minimum over the previous 20 days. That minimum temperature, the relative minimum, and its difference from the average minimum over the previous 20 days were recorded. These temperatures were linked to infestations recorded in the following summer.

Average temperature and total precipitation were calculated for the whole year and also seasonally for winter (December–February), spring (March–May), summer (June–August), and fall (September–November). The previous year's seasonal precipitation was considered as an explanatory variable for the current year's infestations. In the case of precipitation, the departure from the average over all the years examined and the previous year's precipitation were also calculated. For both of these values the previous year, 2 years ago and total for the previous 2 years were calculated; the latter consisted of adding the previous two together. This enabled the model to account for drought or wet periods lasting multiple years.

Temperature was also used to calculate voltinism or the number of generations per year. We used the G-function (Powell et al., 2000; Powell and Logan, 2005) to calculate the number of generations that should occur given a specific temperature regime. Two additional variables, winter and spring seasonal focusing, were generated to depict how oviposition times are related to emergence over the course of both seasons. These variables were linked to infestations in the same year. Changes in emergence occur because temperature-mediated development occurs at different rates across insect life stages. This can cause certain developmental stages to predominate and lead to synchronized emergence. These two variables show how 15 days of oviposition relate to emergence. The focusing variables were calculated by following development hourly and using the G-function to see how 15 days of oviposition lead to emergence and oviposition in the next generation (Duehl, 2008; Powell et al., 2000); essentially, if emergence is over a shorter period focusing has occurred, while a longer period indicates defocusing. Winter focusing was based on eggs laid between October 15th and October 30th and spring focusing was calculated from eggs laid between March 3rd and March 18th. We hypothesized that winter focusing leads to synchronous spring emergence and attack with more outbreaks in counties experiencing these conditions. In contrast, spring focusing decreases synchronization, creating a more continuous searching population better able to compete for ephemeral resources.

2.2. Analysis procedures

All of the listed variables were organized into a spreadsheet such that each county was linked to all the variables for each year. To determine how these variables related to the occurrence of infestations, we employed two different statistical models. We used stepwise logistic regression in SAS (with SLENTRY and SLSTAY set to 1) to construct a sequence of reduced models, and Akaike's Information Criterion (AIC) to pick the best model (Allison, 1999; Hosmer and Lemeshow, 2005; SAS, 2000–2004). We then dropped highly correlated variables and refitted the model. Beginning with

the model fit before removing correlated variables allowed us to determine the most predictive variables out of the full set before eliminating redundancies. The second statistical model we considered was a Classification and Regression Tree (CART) analysis. We used R to run this statistic and chose this method because CART shows the natural breaks in the data and the relative predictive power of specific variables along with their hierarchical relationships (CRAN, 2010). We selected a cut point of 1% to prevent overfitting and to identify the most critical factors underlying data (Breiman et al., 1984).

3. Results and discussion

Both statistical models considered in this analysis were successful in separating infested from un-infested counties. The distribution of those infested versus un-infested counties over all recorded years was unbalanced between groups, with only about 10% of counties showing infestation in a given year. Because of the imbalance, the statistical models made better predictions of the relatively common un-infested counties while not handling the uncommon infested counties as well (Table 1). For example with the full CART model, looking at the producers errors of those counties the model classified as un-infested, only 1% was in error, while of those classified infested, 63% was erroneous.

The CART method finds natural breaks and hierarchical structure and while it may not have performed better than logistic regression, it was able to show specific relationships between explanatory variables. Logistic regression instead fits a curve using the best variables together and then classifies counties by their infestation probabilities, showing the relative influence of individual variables but not identifying cutoff points within variables. We used a 0.5 probability threshold, classifying counties with a probability of infestation greater than 0.5 as infested and those with less than 0.5 as un-infested (Allison, 1999). The imbalance between infested and un-infested counties hindered the ability of the model to explain much of the variation in the data (Hosmer and Lemeshow, 2005).

In CART the variable defining the root node is the best separator of infested versus un-infested counties. The additional variables selected are, in descending importance, the best at separating the remaining variability. CART requires the user to input a minimum increase in explanatory power for adding variables, which keeps the tree compact (Breiman et al., 1984). Applying the CART model to the complete data set generated the tree (Fig. 1) and the associated cross-validation classification table (Table 2). As with the logistic model, the accuracy for predicting un-infested counties was much higher than the accuracy when predicting infested counties. The tree showed that infestation history, relative minimum

Table 2
The classification accuracy of the CART model applied to the whole data set and selecting from all available variables. The model makes fewer errors when predicting uninfested counties than those that have infestations.

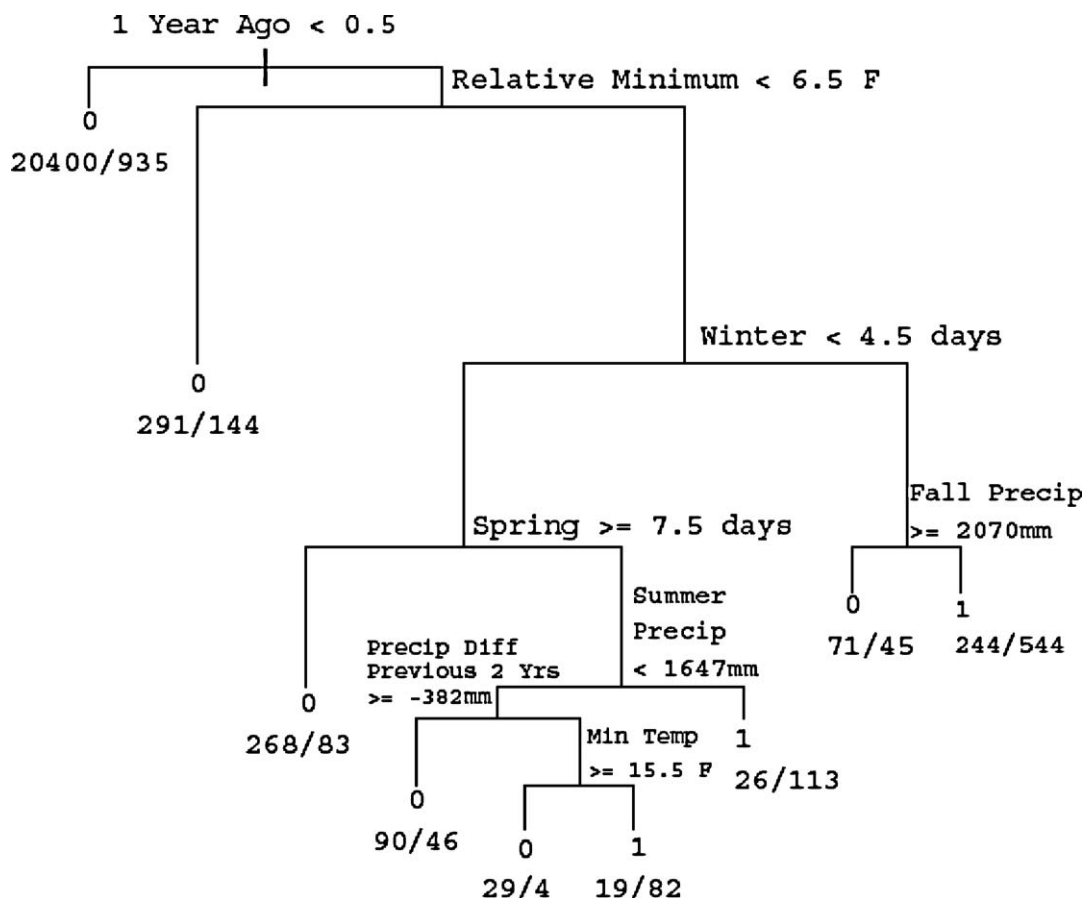| Predicted	Observed		
	0	1	Commission error (%)
0	21,147	289	1
1	1257	739	63
Omission error (%)	6	28	

Fig. 1. The CART selected using all the available variables and a cutoff point of 0.01 to prune the tree. *Legend*: 1 year ago, 0/1 was the county infested last year; relative minimum, coldest point on a winter day relative to average temperature over previous 15 days; winter, days of emergence from 15 days of oviposition October 15rd–30th; spring, days of emergence from 15 days of oviposition March 3rd–18th; fall precip, cm precipitation September–November; summer precip, cm precipitation June–August; precip diff previous 2 years, the departure from the average over all examined years for each of the previous 2 years summed together; min temp, lowest yearly temperature.

temperature, and winter focusing, in that order, were the important factors for predicting outbreaks.

We also tested the variables selected for the best logistic model in CART (Fig. 2 and Table 3). Again we determined that the infestation presence–absence data from 1 year ago were the best separator and had even more predictive ability in this case. Using limited variables increased the total model error along with omission error although commission error (the number of false positives) decreased. These patterns of results are similar to the logistic model that used the same variables.

The two models parsed out the predictive abilities of the variables in different ways but with similar result. CART did not use any of the landscape variables other than county history. After this variable for the initial branch, both CART runs we discussed here used temperature and then a precipitation variable. The inclusion of focusing, a variable based on temperature-mediated development, showed that there is an important link between emergence

synchronicity and temperature that influenced success. Logistic regression uses one equation to predict the log likelihood of infestation for a county. Thus, the circumstances where a particular variable may be important for prediction are unclear. The relative power of the variables is demonstrated by the size of their respective parameter estimates and chi square values, but this does not elucidate any hierarchical structure. We tested adding squared terms for the explanatory variables because of the non-linear fits between infestation probability and variable level. The squared terms were statistically significant (in terms of *p*-values) but did not affect classification accuracy enough to justify their inclusion.

The order of the seven variables added during the selection process for the logistic model primarily reflects the importance of infestation history. The county infestation occurrence in the previous year was the first variable selected, followed by forest cover and then the infestation status of the 20-county region surrounding the focal county. The fourth variable was focal county 6 years ago and the fifth variable was the total precipitation over the previous 2 years. Additional variables selected with AIC were discarded upon examination of the correlation matrix. It demonstrated that within families of variables – precipitation, temperature, land cover, and history – there were high correlations. The final model contains only the variables with the most influence from each family of explanatory variables (Table 4). The final logistic model (Table 4) was used to generate a classification table (Table 5). The classification table shows that logistic regression made fewer errors relative to infested counties than to un-infested counties.

Table 3
The classification accuracy of the CART model applied to the whole data set and selecting from the variables chosen for the logistic model. The overall accuracy is lower than the unconstrained model but more infested counties are classified correctly.

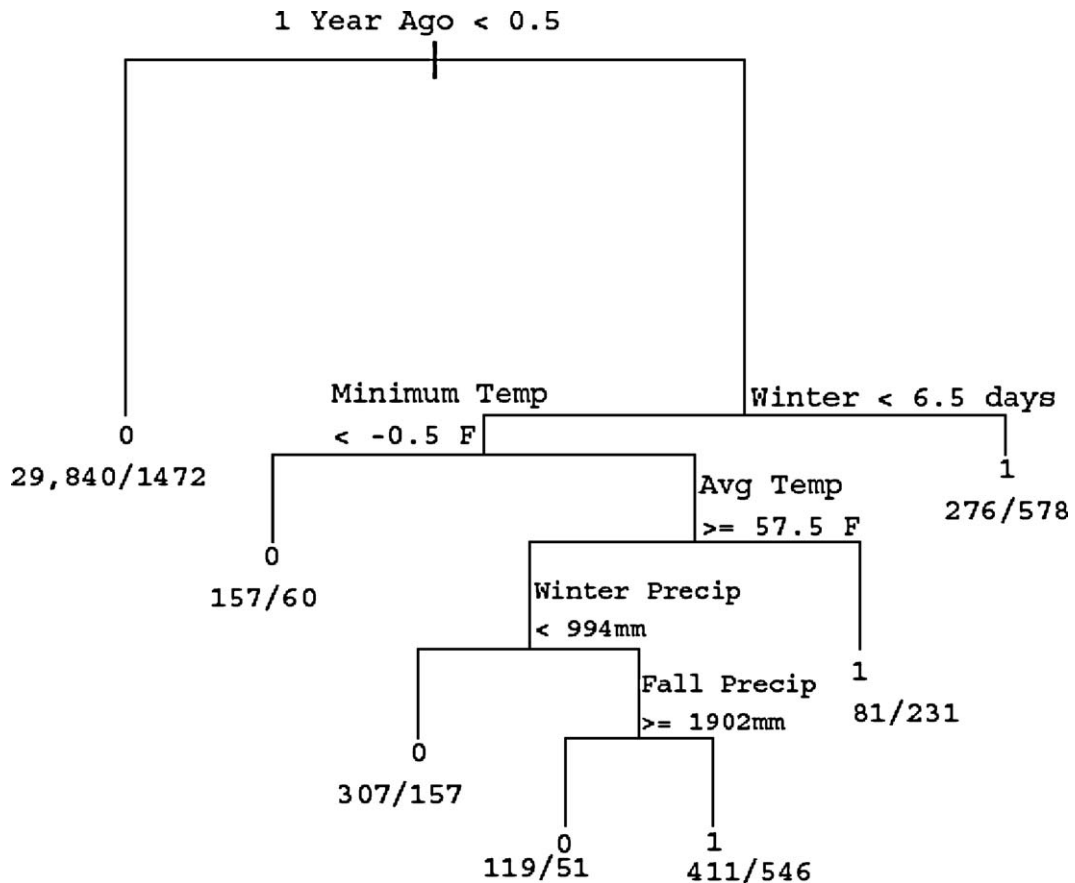| Predicted	Observed		
	0	1	Commission error (%)
0	30,428	768	2
1	1740	1355	56
Omission error (%)	5	36	

Fig. 2. The CART created from a limited set of variables and a cutoff point of 0.01 to prune the tree. 1 year ago, 0/1 was the county infested last year; winter, days of emergence from 15 days of oviposition October 15rd–30th; min temp, lowest yearly temperature; avg temp, average temperature over the year; winter precip, cm precipitation December–February; fall precip, cm precipitation September–November.

Table 4
The parameters chosen for logistic regression after consideration of the correlation table. The chi-square shows the relative influence of the different variables and the estimate shows the value of the parameter in the equation.

Parameter[a]	df	Estimate	Standard error	Wald chi-square	$p >$ chi-square
Intercept	1	2.24	0.35	40.90	<.0001
1 year ago	1	−1.96	0.06	931.27	<.0001
20 county region	1	−2.54	0.12	476.69	<.0001
6 years ago	1	−0.9690	0.057	291.7515	<.0001
Forest cover	1	−0.0007	0.00006	141.16	<.0001
Relative minimum	1	−0.0229	0.0026	76.59	<.0001
Total precip prv 2 years	1	−0.00008	0.000001	70.32	<.0001
Avg spring temp	1	0.0413	0.0059	49.46	<.0001

[a] 1 year ago, 0/1 was the county infested last year; 20 county region, percent of infested counties out of the nearest 20; 6 years ago, 0/1 was the county infested 6 years ago; forest cover, acres of forest in the county; relative minimum, coldest winter day relative to average over previous 15 days; total precip prv 2 years, total precipitation cm over the previous 2 years; avg spring temp, average temperature over March–May.

The accuracy of the models can be evaluated through a number of different measures. The overall classification accuracy was above 90% for all models, this was mainly due to accurate predictions of un-infested counties. These counties accounted for about 90% of

Table 5
The classification of infested (1) and un-infested (0) counties by logistic regression. Counties with a model prediction less than 0.5 were classified as un-infested while those higher were classified as infested.

Predicted	Observed		
	0	1	Commission error (%)
0	33,564	765	2
1	2144	1184	64
Omission error (%)	6	39	

all counties (Table 1). Another measure of classification agreement is Cohen's kappa, a more conservative measure representing how well a model performs relative to a random classification. Kappa values for our models ranged from 0.41 to 0.48, indicating that a disconnect existed between overall accuracy and prediction quality across classification groups. It is manifested as an over prediction of infestation although there was also a fair amount of false negatives.

4. Conclusions

This modeling exercise expanded the extent and breadth of variables examined for their influence on SPB infestation. Previous research (Gumpertz et al., 2000; Kalkstein, 1981; Kroll and Reeves, 1978; Mawby and Gold, 1984) elucidated many relationships between individual explanatory factors and the likelihood of

SPB infestation, but herein we demonstrated the relative power and hierarchical relationships between a suite of variables. The complexities of infestation formation and spread make it difficult to determine what factors are most important (Fettig et al., 2007). This analysis clearly showed that a consideration of local infestation history, followed by temperature and precipitation, will give the clearest picture of infestation likelihood. This is not different from current recommendations but is confirmed by a greater breadth and depth of data. Additionally, the specific relationships between the variables and infestation elucidated by this research give managers a broader basis to predict how infestations may develop or collapse in their stands.

Both models picked infestation history variables as the most important in the system, agreeing with our other work (Duehl, 2008) and also that of other authors (Gumpertz et al., 2000; Mawby and Gold, 1984). We showed that an infestation either in the previous year, further in the past or in the region around the focal county always increases the probability of infestation in the focal county. This contrasted with Gumpertz et al. (2000) by extending the range of prediction and in the logistic model, demonstrating the power of infestation 6 years ago. Although both approaches suggest that larger regional infestation patterns are important, in our case the infestation rate of the 20-county region and in Gumpertz et al. (2000) the neighborhood of spatial autocorrelation. At the county level, infestation history must implicitly capture many infestation related factors: sufficient populations of beetles, available host and suitable environmental conditions in the previous year. Beyond these factors the additional environmental variables added in the analyses capture changes that make a given year unique, specifically altering county level populations.

Climatic variables were ranked second in the level of importance with temperature leading precipitation in predictive power. Out of the temperature variables considered, seasonal average temperature, annual minimum temperature and relative minimum temperature were the most important variables. One management implication of our findings is that a very cold winter or a cold snap will decrease the likelihood of infestation even if there were high populations of beetles in the previous year (Ungerer et al., 1999). While average temperature likely correlated with the center SPB geographic range, minimum temperatures strongly influence yearly population success (Ungerer et al., 1999). The seasonal focusing variables also had explanatory power, indicating the temperature influences on development are important in determining population success (Powell et al., 2000). Of the precipitation variables considered, seasonal precipitation in the current year and the difference in precipitation over the previous 2 years from the average over all examined years were the most important. Precipitation can be related to how able a tree is to defend itself (Herms and Mattson, 1992), with the trees diverting more resources to secondary metabolism and defensive chemicals during periods of drought (Lombardero et al., 2000b). In general, high levels of fall precipitation lead to higher levels of infestation the following year. In some regions this may occur because soil saturation increases root anoxia, but in others high fall precipitation may result in healthier, faster growing trees that provide beetles with a more nutritious substrate (Lombardero et al., 2000b).

There are some differences in the predictions between the two models. The CART model did not select landscape structure variables (these only played a minor role in the logistic model), but instead captured appropriate locations through county infestation history. Additional explanatory power came not from landscape features but factors that were more varied year-to-year such as weather patterns. Yearly average temperature implicitly reflected certain landscape characteristics albeit indirectly, through such features as topography, proximity to water and latitude. Beetles are more successful in moderate conditions (Lorio, 1986; Wagner et al., 1983/1984) and average temperature may best approximate appropriate climate. Winter precipitation recharges the water table before trees begin transpiring in the spring. This measure may have stood in for the resistance characteristics of trees (Kalkstein, 1981; Lombardero et al., 2000b), particularly the resistance change from the previous year. Total precipitation difference over the previous 2 years captured water availability and may have been a good proxy for beetle population levels with both the previous year's success and current year's condition (Lombardero et al., 2000b).

Logistic regression added the percent of infested counties in the 20-county region to the previous year's history and increased prediction quality with greater spatial extent. Total precipitation over the previous 2 years was the environmental feature selected by the logistic model. The inclusion of infestation 6 years ago as an explanatory variable indicated that cycles of beetle activity may also play an important role in determining overall infestation likelihood (Duehl, 2008; Turchin et al., 1991).

The objective of determining the likelihood of range expansion and future infestation patterns can only be partially addressed. The SPB is most successful when it has abundant host material and large local populations. Additionally, examining the relationships between individual temperature variables and success shows that for the most part infestations will occur under average conditions within its current range (Duehl, 2008). Our analyses indicate that extreme conditions with the exception of drought, like those predicted to occur with climate change (IPCC, 2001), are less likely to lead to beetle success. To the north there are some susceptible hosts that have historically only experienced occasional infestations or been protected by extreme winter temperatures that could be exposed to consistent beetle populations. Beetle populations may also help regulate the distribution of certain tree species and changing climate will alter the frontiers of this relationship (Bentz et al., 2010). Additional research is needed to show how successful the SPB can be in alternate hosts. Given the preference for averages it is unlikely that the SPB will be highly successful outside of its native range. That said, changing climates will change the geographic location of historically average conditions as well as the physiological condition of the trees on the landscape. These impacts will have unknown consequences for forest, stand and individual tree resistance to insect damage.

These models can help managers determine the probability of SPB infestation in a county. However, the problem is that these models only explain a small amount of the total variability in infestation occurrence. Many infested and un-infested counties were misclassified by these methods. We examined the influences of landscape, precipitation and temperature at this scale in another publication (Duehl, 2008). Therein we demonstrated that each independent variable only explained a small amount of the variability in infestation occurrence. We hypothesized that a combined analysis would show that climatic, landscape and infestation history variables complement each other to explain more of the total variation in infestation occurrence than would be expected from their individual relationships. The analysis described here does show how the various individual explanatory variables fit together to explain infestation incidence, and the hierarchical relationships within those predictions. However, the variables used in this analysis still explain limited variability in the data. More research is needed to identify and capture other potentially important features of the system, such as natural enemies and smaller-scale landscape structure; these will enable the creation of a model more applicable to management. Until a more robust SPB prediction model is developed, managers should continue to utilize spring pheromone surveys (Billings, 1988) to predict shifts in SPB population trends, particularly to detect when outbreaks are likely to first occur or to collapse. They should also reference the FHTET SPB risk maps that incorporate landscape and climate variables (Krist et al., 2007).

Acknowledgements

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