Simulating the effects of the southern pine beetle on regional dynamics 60 years into the future

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ABSTRACT

We developed a spatially explicit model that simulated future southern pine beetle (*Dendroctonus frontalis*, SPB) dynamics and pine forest management for a real landscape over 60 years to inform regional forest management. The SPB has a considerable effect on forest dynamics in the Southeastern United States, especially in loblolly pine (*Pinus taeda*) stands that are managed for timber production. Regional outbreaks of SPB occur in bursts resulting in elimination of entire stands and major economic loss. These outbreaks are often interspersed with decades of inactivity, making long-term modeling of SPB dynamics challenging. Forest management techniques, including thinning, have proven effective and are often recommended as a way to prevent SPB attack, yet the robustness of current management practices to long-term SPB dynamics has not been examined. We used data from previously documented SPB infestations and forest inventory data to model four scenarios of SPB dynamics and pine forest management. We incorporated two levels of beetle pressure: a background low level, and a higher level in which SPB had the potential to spread among pine stands. For each level of beetle pressure, we modeled two scenarios of forest management: one assuming forests would be managed continuously via thinning, and one with a reduction in thinning. For our study area in Georgia, Florida, and Alabama, we found that beetle pressure and forest management both influenced the landscape effects of SPB. Under increased SPB pressure, even with continuous management, the area of pine forests affected across the region was six times greater than under baseline SPB levels. However, under high SPB pressure, continuous management decreased the area affected by nearly half compared with reduced management. By incorporating a range of forest and SPB dynamics over long time scales, our results extend previous modeling studies, and inform forest managers and policy-makers about the potential future effects of SPB. Our model can also be used to investigate the effects of additional scenarios on SPB dynamics, such as alternative management or climate change.

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1. Introduction

Bark beetles (Curculionidae: Scolytinae) are one of the most important factors in the biology of pine ecosystems around the world. Several bark beetle species found in the Northern Hemisphere are currently undergoing their largest outbreaks in recorded history, and, in the process, are changing societal and political perceptions of forest stability and value (Lieutier et al., 2004; Price et al., 2010). The effect of bark beetles on forests occurs in bursts associated with outbreaks, interspersed with decades of relative inactivity. As such, only when the complete forest development cycle is observed over decades to centuries does it become apparent that tree mortality caused by bark beetles can dwarf that caused by fire or the timber industry (Kurz et al., 2008). We simulated bark beetle dynamics 60 years into the future in the Southeastern United States to examine the likely long-term effects on the region's pine forests.

In the pine-dominated Southeastern US, the southern pine beetle (*D. frontalis*, SPB) is the forest pest with the greatest effect on the large-scale dynamics of tree populations (Ciesla, 2011). The

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SPB is a native species usually present at low levels throughout its range. It has evolved sophisticated strategies to mass-attack and overwhelm healthy trees. Thanks to their complex pheromone communication (Wood, 1982) and association with mutualistic and phytopathogenic fungi (Paine et al., 1997), beetle populations are able to increase rapidly under suitable conditions. This rapid population growth can lead to large-scale outbreaks of SPB. The most destructive SPB outbreaks result in elimination of entire pine stands and can affect the majority of pine trees across large geographic regions. For example, in the 1960s, 70s and 80s, several large-scale outbreaks spanning multiple states killed the equivalent of over 4 billion board feet of pine timber, resulting in multi-million dollar losses (Flamm et al., 1986). Large-scale outbreaks of SPB can also affect species of conservation interest that depend on pine trees for habitat. These species include the Federally-endangered Red-cockaded Woodpecker (*Picoides borealis*, Conner and Rudolph, 1995; Tchakerian and Coulson, 2011). The amount of damage likely caused by SPB in the future thus has large implications for forest management and policy because of potential impacts to forest health, fire risk and endangered species, but has been relatively unexplored. We developed a simulation model to examine the dynamics of SPB and pine stands under alternative future scenarios that will inform regional management and policy.

Many models that simulate the dynamics of conifer-dominated landscapes and bark beetles exist, but when considered alone, each is inadequate for jointly modeling forest and beetle dynamics in a way that can inform regional planning and policies. Existing approaches, however, can be a foundation for models that are more appropriate for regional decision-making. Modeling SPB dynamics has resulted in sophisticated software applications simulating beetle development and population outbreaks (Coulson et al., 1989; Lih et al., 1995; Bishir et al., 2009) at small extents (i.e., individual forest stands). Only recently has the accumulated data on past SPB infestations, combined with GIS technology, made it possible to generate larger-scale models, such as the recent projections of SPB hazard for the Southeast done by the USDA Forest Service (2010b). Despite the large extent and high resolution of those regional models, they are still relatively static predictions of tree mortality based on recent environmental conditions and the current condition of pine trees. Cairns et al. (2008a,b) successfully integrated forest succession and disturbance into spatially explicit models of SPB infestations. However, the landscapes they modeled were simulated (non-empirical) and relatively limited in extent (2600–10,000 ha) compared to the Southeastern US as a whole. Developing models that incorporate dynamic processes like the model of Cairns et al. (2008a,b) for large empirical landscapes on which management decisions are actually being made is key for informing regional forest management and policy.

The factors controlling SPB populations are diverse, interact across spatial and temporal scales, contain a large amount of spatial and temporal autocorrelation and stochasticity, and often differ significantly among regions (Hicks, 1980; Gumpertz et al., 2000). However, several factors influence the dynamics of SPB universally across its range. First, although the beetle can attack all pine species within its range, the species that suffers the greatest mortality and sustains the largest outbreaks is loblolly pine (*P. taeda*), especially when the trees are planted in high-density monocultures (Payne, 1980). In addition, the age of trees in a stand influences SPB outbreaks, with older trees generally being more susceptible (DeAngelis et al., 1986; Ylioja et al., 2005). Forest management techniques, including thinning, have proven effective and are often recommended as a way to prevent SPB attack and reduce the probability and rate of growth once an infestation arises (Fettig et al., 2007). Yet, to our knowledge, no one has ever tested, in a modeling framework, the robustness of current management practices to long-term beetle dynamics.

Table 1

The four scenarios of southern pine beetle (SPB) population pressure and management intensity modeled, with their corresponding research questions.

SPB pressure	Management level	
	Current thinning	Reduced thinning
Low beetle pressure	Scenario 1, baseline dynamics with current level of thinning	Scenario 2, Question 1: Does forest thinning to prevent SPB have the same effect on the landscape under low and high beetle pressure? (Compared with Scenario 1)
High beetle pressure	Scenario 3, Question 2: Is current forest thinning sufficient to protect the landscape in the case of large SPB pressure? (Compared with Scenario 1)	Scenario 4, Question 1: Does forest thinning to prevent SPB have the same effect on the landscape under low and high beetle pressure? (Compared with Scenario 3)

Here we present a model that simulates the interaction between SPB dynamics and forest management, while incorporating extrinsic variation in beetle densities. We modeled SPB dynamics and forest management in empirical landscapes for a large region in the Southeast Coastal Plain. We projected a set of potential scenarios at substantial spatial and temporal scales: across 2.5 million ha (25,000 km^2) in Alabama, Mississippi, and Florida, and for 60 years of vegetation development using a spatially explicit state-and-transition simulation model. State-and-transition models (Horn, 1975) have become increasingly important and popular tools for investigating scenarios of disturbance and natural resource management across regions (Provencher et al., 2007; Bestelmeyer et al., 2004). The discrete representation of vegetation stages, disturbances, and management actions simplifies ecological complexity, while still incorporating the roles of important processes. Therefore, these models are useful means by which both scientists and land managers can explore alternative scenarios of management and disturbance (Forbis et al., 2006; Strand, 2007). Spatial versions of state-and-transition models have also become popular because they can readily visualize results across real landscapes at regional extents (Provencher et al., 2007; Strand, 2009; Elkie et al., 2009).

In our model, SPB infestations are a function of stand successional stage (age), management history, and proximity to prior outbreaks. Implementing a mechanistic model of the beetle's dynamics across a regional extent and over several decades is not feasible because of the multiple interacting non-linear factors associated with SPB infestations. Instead, we emulated outbreak probabilities from previously documented cases of SPB population behavior in planted loblolly pine forests in our focal region. This implementation has the advantage of being based on actual observed historical scenarios, while simulating the non-linear dynamics of the SPB effect on the landscape over a 60-year period. We included two levels of SPB pressure: a low background level, and a higher level in which SPB had the potential to spread among pine stands. To test the robustness of current forest management practices, we also included two levels of management: a high probability of forest thinning that reflects current management levels, and a reduction in thinning relative to current levels. Our model allowed us to answer two questions about the joint dynamics of forest development, bark beetle outbreak effect, and preventative forest management actions (see also Table 1):

1. Will current levels of forest thinning have the same effect on beetle activity under low and high beetle pressure? Our hypothesis was H_{0a}: The level of future SPB infestation will be the same under low and high SPB pressure. The alternative hypothesis was

H_{1a}: The level of future SPB infestation will be different under low and high SPB pressure.

2. Is current intensive forest thinning sufficient to protect the landscape in the case of large SPB pressure? We answered this question by testing the hypothesis: H_{0b}: In the two scenarios in which the landscape is managed by intensive thinning, the level of future SPB infestation will be similar regardless of SPB pressure. The alternative hypothesis was H_{1b}: More pine stands will be affected by the SPB under high SPB pressure, despite intensive thinning.

Our work provides critical information for forest managers and policy-makers regarding the potential future effects of SPB on southeastern pine forests at a regional extent under alternative empirical scenarios of management and beetle population pressure.

2. Methods

2.1. Study area

We modeled SPB infestations across a region of the Southeast Coastal Plain of the US, corresponding to the Dougherty Plain ecoregion (Environmental Protection Agency, 2004). This region covers portions of southwestern Georgia, southeastern Alabama and the Florida Panhandle (Fig. 1). Pine plantations cover approximately 24% of the Dougherty Plain (Southeast Gap Analysis Project, 2008) and comprise the second most common land cover in the region today, behind row crops (25% of the landscape). The pine plantations in the Dougherty Plain are typically dense monocultures of loblolly pine (USDA Forest Service, 2010a). The remaining portions of the Dougherty Plain are dominantly pasture, developed land, or other plant communities, including floodplain forests and naturally regenerating longleaf pine forests.

2.2. Model framework

To model the impacts of southern pine beetle infestations on planted loblolly pine forests, we used a state-and-transition simulation framework developed with the Vegetation Dynamics Development Tool (VDDT, Version 6.0, ESSA Technologies Ltd, 2007) integrated into a spatially explicit landscape dynamics modeling environment (TELSA, ESSA Technologies Ltd, 2008). We implemented VDDT and TELSA in a way that is typical of most other uses of these tools. There are four main inputs to TELSA: (1) an aspatial state-and-transition simulation model for planted pine developed using VDDT, (2) a polygon map showing the distribution of planted pine in the landscape, (3) an initial age and corresponding successional stage for each polygon, and (4) an initial structural stage for each polygon.

In VDDT, vegetation states are defined by their successional stage (e.g. early, mid- and late succession) and by their structure (e.g. density of trees or amount of canopy). Transitions among states occur due to succession, disturbance, or management actions, and are simulated in a semi-Markov framework on an annual time step. For each early and mid-succession state, there is one deterministic successional pathway to another state, and the timing of succession depends only on the time in the state. Disturbances (such as SPB infestations) and management actions (including forest thinning or harvest) occur according to user-defined probabilities that can vary among states. At each time step, a polygon may stay in the same state, undergo succession, or undergo a disturbance or management event, according to the probabilities defined in the model.

In TELSA, the state-and-transition model is applied to a polygon map that defines the location of the modeled vegetation type on the landscape. The initial age and structure of vegetation within each polygon are used to determine the polygon's initial vegetation state in the model. At each time step, disturbances and management actions occur at random locations on the landscape according to the defined probabilities. Disturbances can be spatially constrained to occur on polygons adjacent to other polygons that have been disturbed in the past. The spatial distribution of the vegetation (though not the model state) in the landscape is static throughout the simulation. The TELSA model algorithms are described in more detail by Kurz et al. (2000) and ESSA Technologies Ltd (2008).

2.3. Aspatial state-and-transition simulation model for planted pine

For our landscape, we developed a state-and-transition simulation model for planted loblolly pine stands that distinguished states based on their age and whether they had undergone a first thinning (Fig. 2, Table 2). We created three successional stages: early, mid- and late succession. Early succession included young stands up to 21 years old, the age by which most managed stands have been thinned (USDA Forest Service, 2010a). Mid-succession stages were stands 22–40 years old, during which time harvest occurs on most commercial plantations. Late succession included stands older than 40 years.

Structural states were defined for mid- and late succession, and represented thinned and non-thinned stands. Thinned stands had a basal area <18.3 m^2/ha, which is the level recommended for prevention of SPB infestations (Fettig et al., 2007; Nowak et al., 2008), while non-thinned stands had a higher basal area. In the model, if thinning occurs in the early succession stage, a stand follows the "thinned" pathway, and is not susceptible to SPB infestations in the mid- and late succession stages. This is the usual pathway for managed loblolly pine stands in the Southeast. In reality, thinning does not completely eliminate SPB activity in a stand; however, in this model, we are not tracking the small SPB infestations that may occur in thinned stands and do not change overall stand structural characteristics (see following paragraph). If the first thinning is not applied, a stand follows a "non-thinned" successional pathway in which it is susceptible to SPB in mid- and late succession. A second thinning event can occur in mid- or late succession stands between ages 22 and 27, no fewer than ten years after the first thinning. Harvest can occur in mid- or late succession stands anytime beginning at age 30, no fewer than five years after the last thinning.

Non-managed mid- and late succession states in our model were susceptible to infestations of SPB. Three types of infestation were considered, and two were included explicitly in our model (Fig. 2). First, a single-year infestation of a small number of trees, also known as a "spot", can occur in a stand. We did not include this single spot infestation explicitly in our model because a single spot is usually much smaller than a forest stand, has little effect on the structure of the stand, and rarely produces elevated beetle activity in the next year. A second type of SPB infestation (hereafter, "SPB infestation"), which was included in our model, occurs when two or more spots appear in the same stand in a given year. These infestations are defined as incipient outbreaks in the Forest Service SPB dataset, which includes the annual area infested by county since the 1960s (Pye et al., 2008). When a mid- or late succession non-thinned stand experiences such an SPB infestation, it enters the mid- or late succession "beetle-infested" state in our model. Beetle-infested stands may either stay infested, return naturally (probabilistically) to the non-thinned, non-infested state, be successfully treated with direct control methods to remove the infestation (Billings, 1980) and return to the non-thinned, non-infested state, or may be harvested. A stand in the beetle-infested
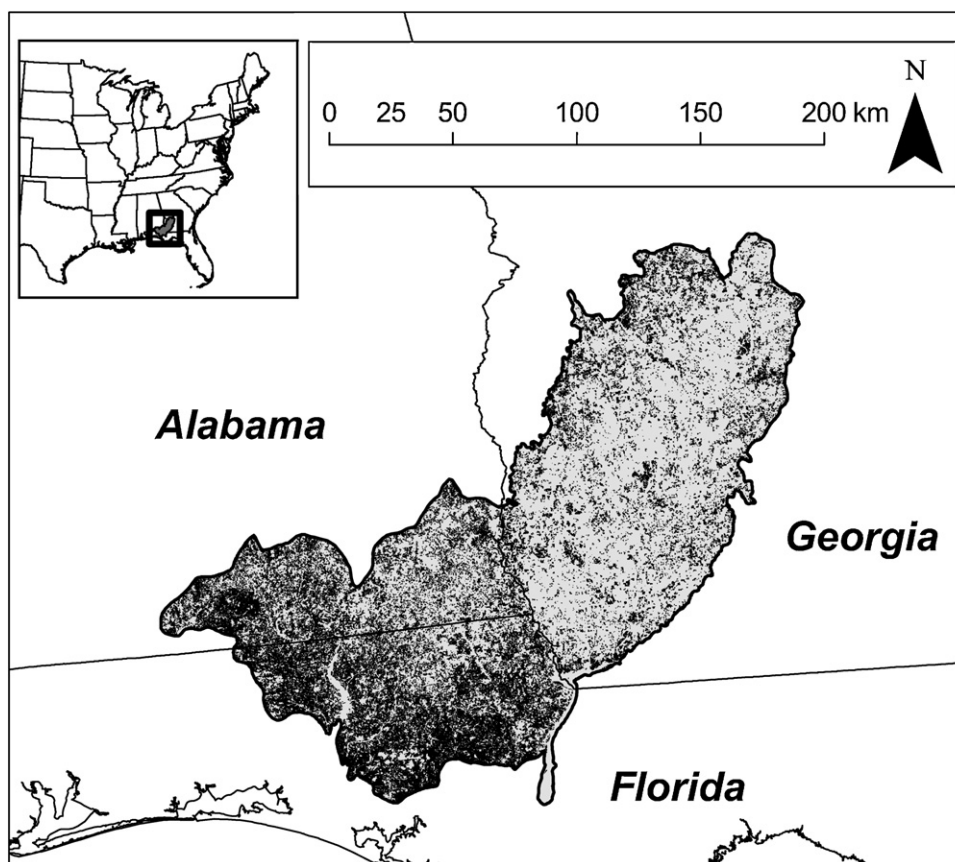
Fig. 1. Study area in the Dougherty Plain ecoregion, shaded in gray. Mapped planted pine stands on which we simulated southern pine beetle dynamics are indicated in black.

Table 2
Disturbance and management transitions[a] for scenario 1, low beetle pressure with current thinning.

From state	Transition	To state	Prob	Min age	Max age	TSD[b]
Early	Thinning	Early	0.091	12	21	≥11
	Alternative succession	Thinned mid	1	21	21	<11
Non-thinned mid	Thinning	Thinned mid	0.022	22	27	0
	Harvest	Early	0.036	30	40	0
	SPB infestation[c]	Beetle infested mid	0.0125	22	40	0
Non-thinned late	Harvest	Early	0.036	41	999	0
	SPB infestation[c]	Beetle infested late	0.025	41	999	0
Thinned mid	Thinning	Thinned mid	0.091	22	27	≥10
	Harvest	Early	0.149	30	40	≥5
Thinnned late	Harvest	Early	0.149	41	999	0
Beetle-infested mid	Harvest	Early	0.036	30	40	≥5
	SPB inactivity[d]	Non-thinned mid	0.22	22	40	0
	Successful treatment[e]	Non-thinned mid	0.74	22	40	0
	SPB large infestation[f]	Early	0.004	22	40	0
Beetle-infested late	Harvest	Early	0.036	41	999	0
	SPB inactivity[d]	Non- thinned late	0.22	41	999	0
	Successful treatment[e]	Non- thinned late	0.70	41	999	0
	SPB large infestation[f]	Early	0.008	41	999	0

[a] All transition probabilities are from the FIA database (USDA Forest Service, 2010a) unless otherwise indicated.
[b] TSD stands for "time since disturbance" and is the number of time steps needed following a disturbance for the event to occur.
[c] Average of probabilities in Daniels et al. (1979), Reed et al. (1982) and Duncan and Linhoss (2005).
[d] Reed et al.'s (1981) formula, averaged for numbers of trees between 1 and 100.
[e] Average of success rates for proven SPB direct control methods is 95% (Clarke, 2011). We calculated that all active infestations (1−0.22 = 0.78) are treated with 95% effectiveness in mid-succession (0.78 × 0.95 = 0.74) and used lower probability of success in late succession (0.70).
[f] Less than 20% of infestations that do not become inactive or are not treated effectively cause enough mortality to reset succession (Billings, 1980).
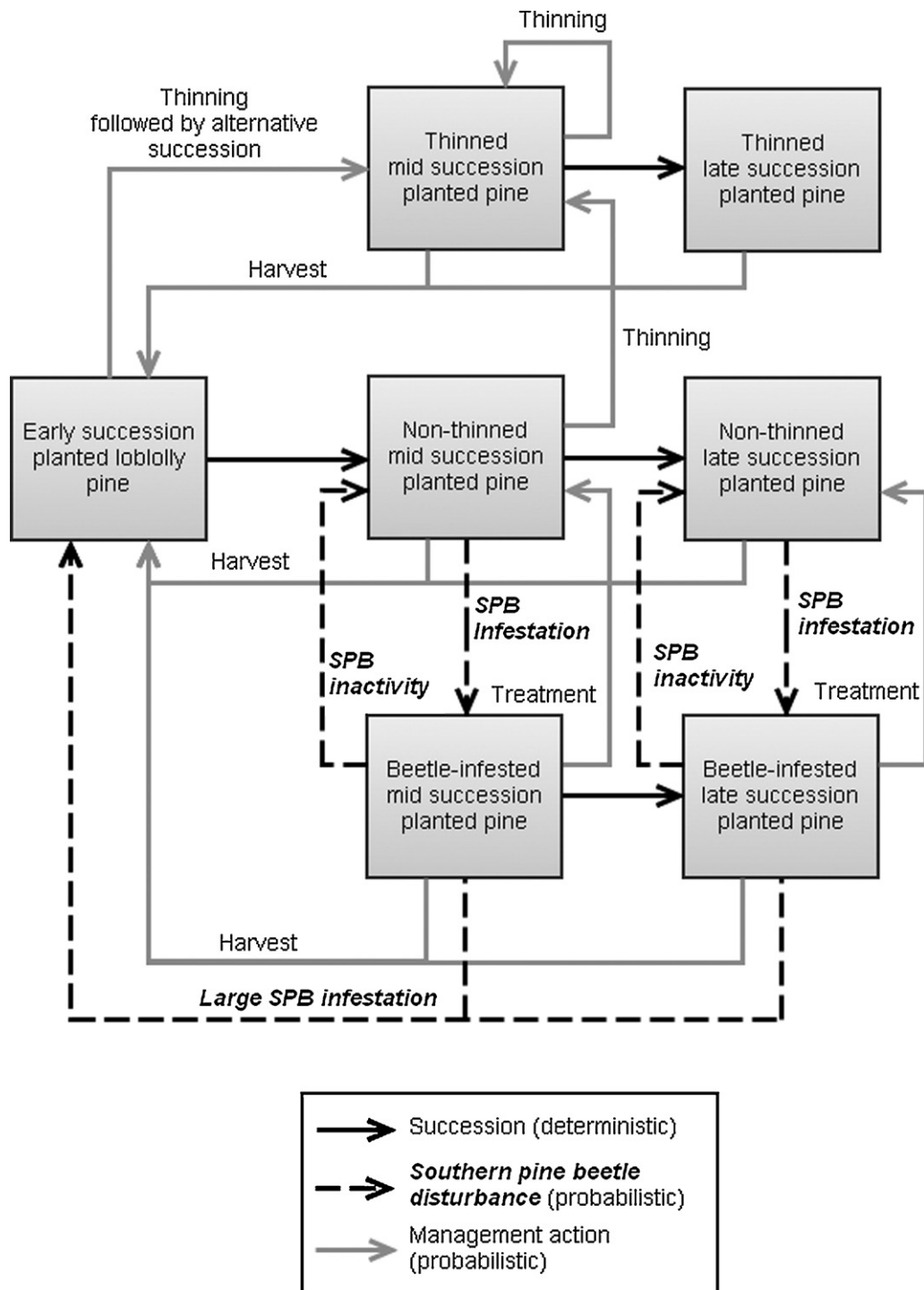
Fig. 2. State-and-transition model for planted pine showing probabilistic transitions associated with southern pine beetle infestation, forest thinning, and harvest.

state is also susceptible to the third type of infestation, a "large SPB infestation", in which the entire stand is affected by SPB, and it returns to early succession.

2.4. Input spatial data

A polygon map of planted pine in the Dougherty Plain region was the primary spatial input to TELSA. We delineated planted pine polygons in the region using image segmentation in combination with a land cover map. First, we used eCognition (Definiens Imaging, 2004) to perform image segmentation on multispectral Landsat TM images from the growing seasons of 2000–2002 that had been used for mapping the 2001 NLCD and Southeast Gap Analysis Program's (GAP) land cover maps (Homer et al., 2004; Huang et al., 2002). The eCognition software groups adjacent image pixels into polygons based on their spectral similarity. We included a 2-km buffer beyond the study area boundary in order to minimize edge effects within the region during our simulations. The result was a polygon data layer, which we attributed with the majority land cover based on the 2001 Southeast GAP land cover map (Southeast Gap Analysis Project, 2008) using ArcGIS (Environmental Systems Research Institute, 1999–2009).
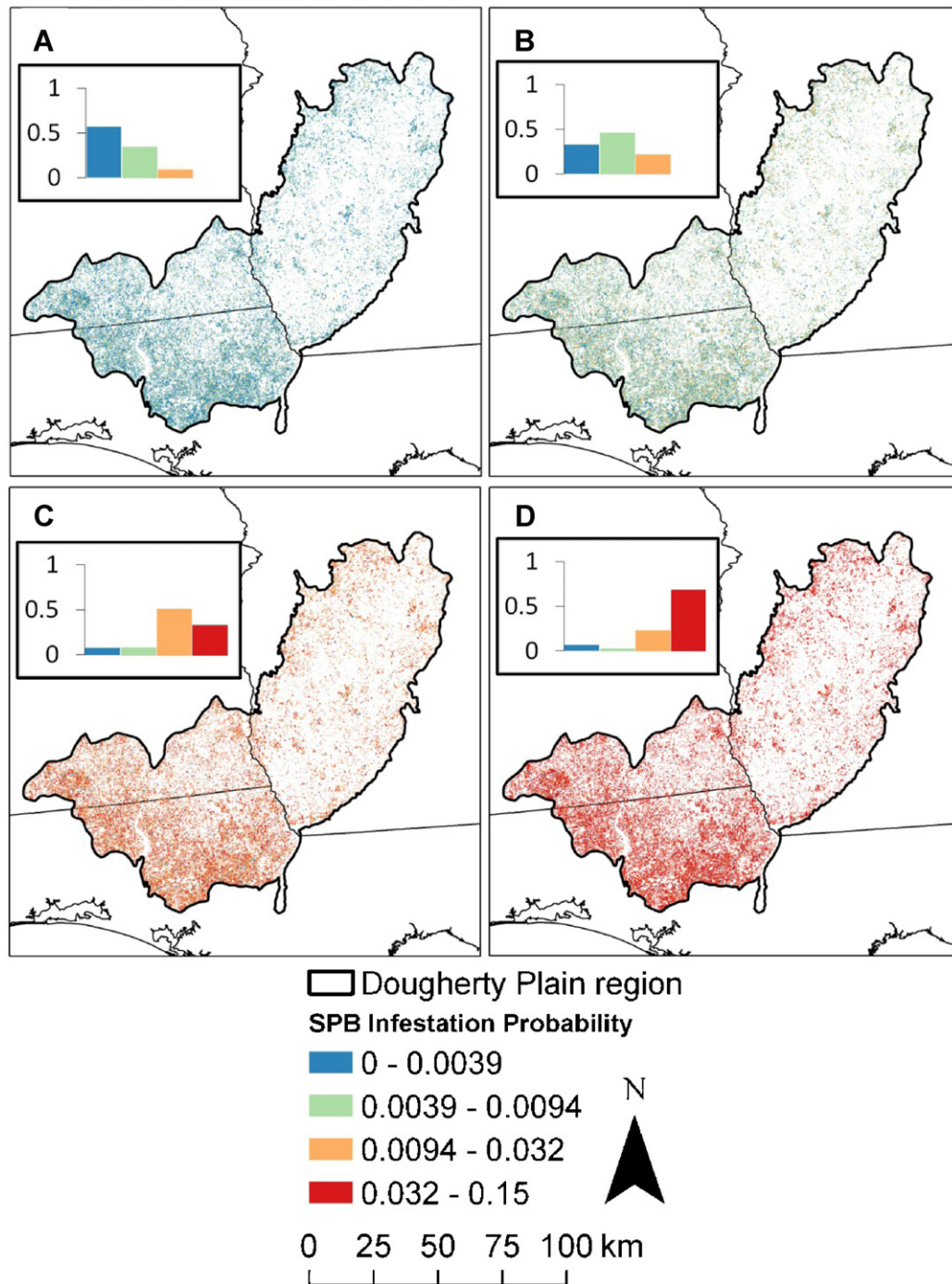
Fig. 3. Average SPB infestation probabilities for the simulated region over 60 years under (A) scenario 1, low beetle pressure and current thinning, (B) scenario 2, low beetle pressure and reduced thinning, (C) scenario 3, high beetle pressure and current thinning, and (D) scenario 4, high beetle pressure and reduced thinning. Bar graphs indicate proportions of planted pine in the region in each range of probabilities. Probabilities were averaged across all time steps for all Monte Carlo simulations.

We identified a polygon as planted pine and included it in our simulations if the majority of its land cover was classified as Evergreen Plantations or Managed Pine in the land cover map. We delineated 81,114 planted pine polygons covering 685,300 ha in the Dougherty Plain region (Fig. 3). Our model assumes that these polygons will remain plantations throughout the simulation.

The model-specific spatial inputs to TELSA are an initial age for each polygon, and an initial structural stage corresponding to management history or beetle activity (thinned, non-thinned, beetle-infested) for each polygon in mid- or late succession. We assigned these initial conditions based on the US Forest Service

(USFS) Forest Inventory and Analysis (FIA) data from planted loblolly pine stands across the counties in the Dougherty Plain region (USDA Forest Service, 2010a). Because these inventory data did not allow us to map the initial conditions of each stand directly, we randomly assigned initial ages to polygons in our region to match the age distribution of FIA plots. Based on age, we assigned the appropriate successional stage (early, mid-, or late) to each polygon. To mid- and late succession polygons we also assigned an initial structural stage of thinned or non-thinned to match the proportions of FIA plots above or below 18.3 m^2/ha basal area.

Table 3
Changes to disturbance probabilities in each scenario. Blank indicates probabilities left unchanged from Table 2.

Scenario	Multipliers				Probability
	SPB infestation, mid-succession[a]	SPB infestation, late succession[a]	SPB inactivity[b]	Initial thinning	Adjacent infestation[c]
1. Low SPB pressure, current thinning (baseline)	All probabilities as in Table 2				
2. Low SPB pressure, reduced thinning	–	–	–	0.1	–
3. High SPB pressure, current thinning	4.8	7.2	0.19	–	0.45
4. High SPB pressure, reduced thinning	4.8	7.2	0.19	0.1	0.45

[a] Based on Daniels et al.'s (1979) probabilities for disturbed stands.
[b] Reed et al.'s (1981) formula, averaged for numbers of trees between 50 and 100.
[c] For polygons that were adjacent to polygons in an SPB-infested state, the probability of infestation was replaced with the probability listed here. This probability is the proportion of variation in infestation status explained by the parameter "previous year" in statistical models by Duehl (2008).

2.5. Modeled spatial scenarios of southern pine beetle infestation

We constructed our model to illustrate the interaction of two factors at two levels each: density of the SPB population (low background density, and high outbreak-like density), and different management approaches (a high probability of thinning, according to contemporary standards, and a reduced probability of thinning). The combination of these levels provides four scenarios (Table 1). Scenarios 1 and 2 both assume baseline, low SPB pressure, and only differ in whether or not continuous beetle suppression is applied throughout the landscape. Scenarios 3 and 4 are like 1 and 2, respectively, but assume elevated beetle pressure.

For all state classes in our model, we derived annual probabilities of thinning and harvest from planted loblolly pine plots in the USFS FIA database (USDA Forest Service, 2010a) for the counties in our study area. We calculated average annual thinning and harvest probabilities (Table 2) and assumed all probabilities were constant over our model simulation period. According to FIA data, stands that had been thinned had a higher probability of being harvested. In model scenarios with reduced initial thinning, we multiplied the probability of thinning by 10% (Table 3) to represent a 90% reduction in thinning. In those scenarios, we assumed that thinning to prevent SPB ceased, but a small amount of thinning occurring in the landscape for timber management would still occur.

We derived probabilities representing SPB behavior and direct control from previously published literature (see Tables 2 and 3 footnotes). We first derived probabilities for scenarios with low SPB pressure (Table 2) and then used multipliers to modify those probabilities for scenarios with high SPB pressure (Table 3). In all scenarios, SPB infestations were a function of the successional stage of forest stands, as well as management history. In the scenarios with high SPB pressure, the probability of SPB infestation also depended on proximity to previous infestations (Duehl, 2008; Duehl et al., 2011). In those scenarios, the probability of infestation for polygons that were adjacent to a previous infestation was increased (Table 3).

2.6. Model output

We modeled the four SPB infestation scenarios over 100 time steps initially, but the model projections were qualitatively unchanged after 60 time steps so we report results for 60 time steps here. Because our initial conditions correspond to the condition and structure of our landscape in the year 2000, model output represents the period 2000–2060. The stochastic disturbance and management events lead to potentially varying landscape composition among TELSA outputs for the same scenario. Therefore, we simulated each scenario 30 times using a variable random seed. This allowed us to quantify the range of variability in landscape composition within a scenario due to model stochasticity, and make meaningful comparisons among scenarios.

The response variable in each scenario is the proportion of the landscape infested by SPB, which we calculated by aggregating SPB infestations and large infestations in each time step. For our first question about the effect of forest thinning under low and high SPB pressure, the test criterion is whether or not the change in proportion of the landscape affected by SPB in scenario 1 compared with scenario 2 is significantly different from a comparison between scenarios 3 and 4 (Table 1). For the test criterion for question 2 about whether current thinning is sufficient to protect the landscape from a significant increase in infestations under high SPB pressure, we compared the response variable for scenarios 1 and 3, the scenarios with current, high levels of management (Table 1).

2.7. Sensitivity analysis

We conducted a sensitivity analysis to test whether beetle pressure and management significantly affect the model outcome, using a range of values of each. To test sensitivity of the model to beetle pressure, in addition to low and high levels of beetle pressure, we used multipliers that were twice as high and half as high as those in the empirical probabilities for the high beetle pressure scenario. For thinning, we added levels of 0%, 50% and 200% current levels to the two levels in our model (Appendix A). We combined the four levels of beetle pressure and five levels of thinning management, for a total of twenty simulations over 100 years. We compared model outputs using the same response variable described above: the proportion of the landscape infested by SPB.

3. Results

We modeled SPB dynamics from the year 2000 to 2060. We tracked the state class of each polygon every ten modeled time steps (Fig. 4), as well as the SPB disturbance transitions that occurred each modeled time step (Fig. 5). Modeled results indicate a difference among scenarios in the probability that a polygon became infested by SPB in a given year (Fig. 3; see also Appendix B). When infestation probabilities for each polygon were averaged across all time steps for all Monte Carlo simulations, the median annual infestation probability for an individual polygon under scenario 1 was 0.0039, under scenario 2 was 0.0061, under scenario 3 was 0.023, and under scenario 4 was 0.043. According to the same averaged probabilities, the highest median annual infestation probability was 0.15 for a single polygon under scenario 4.

To determine whether thinning for SPB prevention has the same effect on the landscape under low and high SPB pressure, we compared the change in the proportion of the landscape affected by SPB due to thinning between scenarios 1 and 2 (low SPB pressure) with the change between scenarios 3 and 4 (high SPB pressure). In both pairs of scenarios, the proportions affected were no different for the first few years of the simulation (until 2008 and 2009 under low and high SPB pressure, respectively) but the differences became greater over time. Across the 60-year time
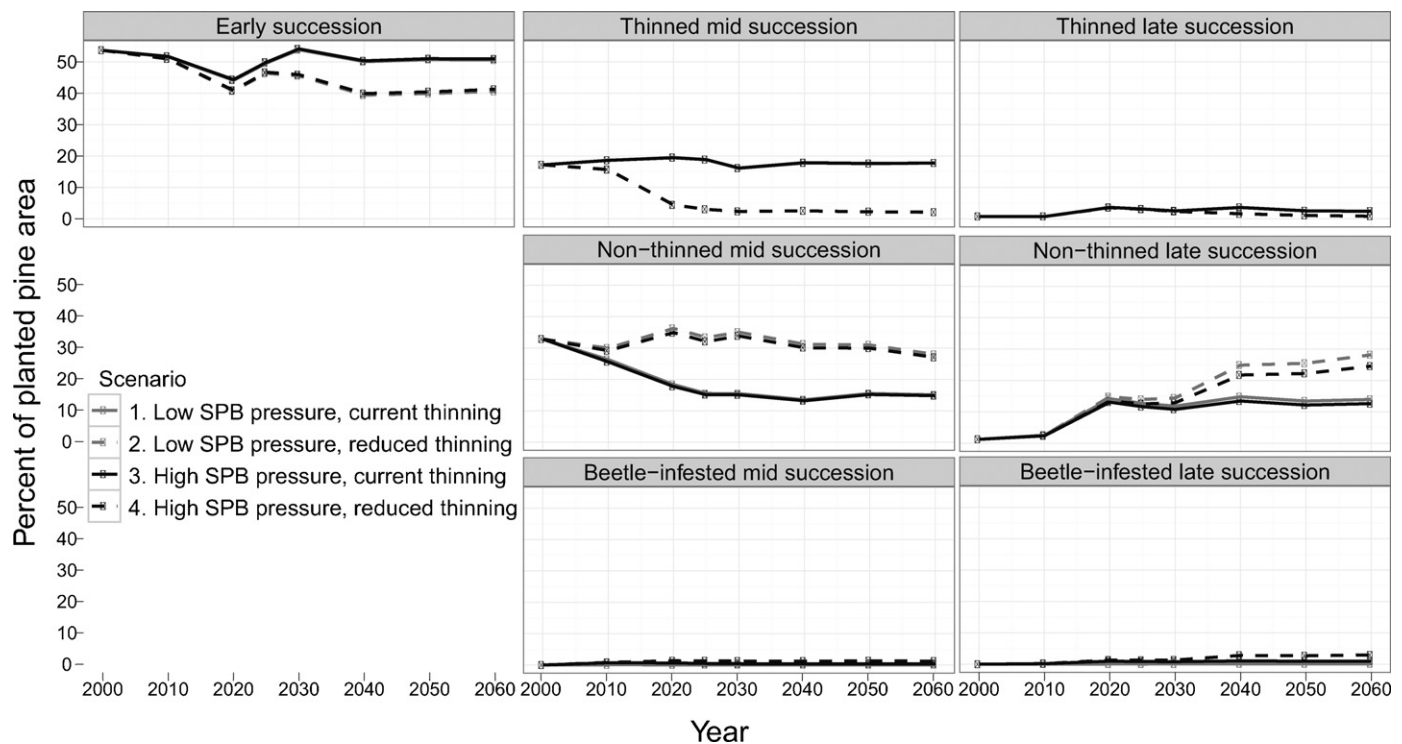
Fig. 4. Percentage of planted pine in the study region in each of the seven state classes across the 60-year simulation for the four modeled scenarios. Lines show the mean of 30 Monte Carlo simulations.

series under high beetle pressure, higher levels of thinning resulted in a larger decrease in the amount of the landscape affected by SPB (43% decrease on average in any year between scenarios 3 and 4) than under low beetle pressure (38% decrease between scenarios 2 and 1; Fig. 5). In other words, thinning made a bigger difference in the region when beetle pressure was high.

To determine whether current management is sufficient to protect the landscape from high SPB pressure, we compared scenarios 1 and 3, which incorporated current high levels of forest thinning for SPB prevention. Across the 60-year projection for every Monte Carlo simulation, the percent of planted pine infested by SPB in scenario 3, which included high SPB pressure, was greater than that under scenario 1, which included low SPB pressure (Fig. 5). On average under scenarios 1 and 3, respectively, SPB affected 0.5% and 3% of the landscape annually, corresponding to areas of 3400

and 20,500 ha. This represents a sixfold increase in the area affected under high versus low SPB pressure under current management.

Sensitivity analysis indicated both beetle pressure and thinning influence the proportion of the landscape infested by SPB (Appendix C). Generally, the higher the level of SPB pressure, the higher the proportion of planted pine that was affected in the simulations. However, both the level of thinning and the level of SPB pressure interacted to influence the proportion of planted pine affected by SPB by approximately year 2050. For example, the simulation with slightly reduced SPB pressure (high SPB pressure × 0.5) but no thinning had higher levels of infestation than under the scenario with much higher SPB pressure (high SPB pressure × 2) but increased thinning (200% of current) after year 2050. In addition, analysis showed that for any single level of thinning, as beetle pressure increased, SPB infestations increased. Therefore, no level
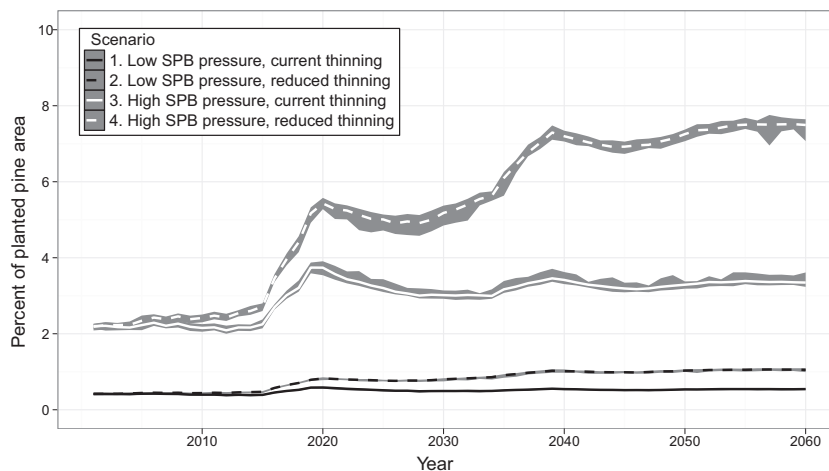

Fig. 5. Percentage of planted pine in the study region becoming infested by SPB (experiencing either an "SPB infestation" or "Large SPB infestation" disturbance transition) over the 60-year simulation for the four modeled scenarios. Lines represent the mean, and shaded gray represents the range of projections from 30 Monte Carlo simulations.

of thinning we modeled was sufficient to prevent all landscape changes due to high beetle pressure. Similarly, regardless of the level of SPB pressure, a decrease in thinning led to an increase in SPB infestation.

4. Discussion

We developed a model to simulate southern pine beetle dynamics for a real landscape over a temporal extent that spans the lifetime of a planted loblolly pine forest stand. Our model incorporates disturbance and management probabilities from recent data, and allows testing of alternate disturbance and management scenarios. Our results highlight the joint influence of forest thinning and beetle pressure on landscape dynamics in the Southeast. Model outputs indicate that if SPB pressure is increased in the future, the effect of SPB on planted pine across the region will be greater than under the baseline level of SPB pressure even with continuous management. However, when beetle pressure is increased, continuous management decreases the SPB effect by nearly half, and thinning is likely to have a slightly greater effect on suppression than it does under lower SPB pressure.

The increase in the proportion of the region affected by SPB under both management scenarios with high beetle pressure has implications for forest management in the Dougherty Plain. In particular, under current management levels, the area affected by SPB was six times higher than under low SPB pressure. This suggests that even when thinning during early succession is widespread, more money and resources will be required for direct control methods to treat SPB infestations if beetle pressure is elevated (Billings, 1980). This cost, in addition to the potential for a loss in harvest value from forests that have been infested, means that costs to forest managers will likely be substantially greater under high beetle pressure. In addition, while habitat may be enhanced under elevated beetle pressure for some species such as Northern Bobwhite (*Colinus virginianus*) that prefer open forest canopies, many species are likely negatively affected by SPB infestations, including the federally-endangered Red-cockaded Woodpecker and mammals such as the eastern gray squirrel (*Sciurus carolinensis*; Tchakerian and Coulson, 2011). Therefore, if SPB pressure is elevated in the future, it is likely to impact loblolly pine forest ecosystems as well as the forest industry in the region.

Despite the increase in area affected under high beetle pressure, in all four scenarios SPB infestations occurred on a relatively small portion of the Dougherty Plain planted pine forests annually: a maximum of 7.8% under scenario 4, which incorporated high beetle pressure and reduced management. Furthermore, most polygons under all four scenarios had a low probability of becoming infested in a given year. These results are in contrast to the large outbreaks that have occurred in the Southeast in the past four decades. Yet, the relatively small effect of SPB projected in our simulations is not unexpected in this region. First, high-density pine plantations in the region are fragmented, especially compared with other areas in the Southeast. Thus, the potential for SPB infestations to spread is reduced. Second, the current abundance of young as well as thinned stands that are less susceptible to SPB throughout the Southeast may have led to decreased SPB activity recently, compared with the past (Duerr and Mistretta, 2011). In the future, a level of SPB infestation in the region that is higher than we simulated will be more likely if fragmentation decreases or the age class distribution becomes older. Additionally, the initial ages and management status we mapped were based on randomly assigned conditions that matched the distribution of conditions in forest inventory data. In reality, age or management status may be similar for stands in close proximity, leading to slightly higher potential for spreading infestations. However, the high degree of fragmentation of pine forests in the Dougherty Plain likely prevents most infestations from spreading.

Our results are broadly consistent with, but extend the results from, previous modeling studies. Like our results, the USDA Forest Service's southern pine beetle hazard maps show a relatively low current hazard for much of the Dougherty Plain (Fig. 6). In that assessment, 66% of the region was mapped as forested, and 74% of that forested area was mapped as having very low or low hazard currently. Of the remaining forested area, 19% had moderate or moderate/high hazard, and 6% had high or very high hazard (USDA Forest Service, 2010b). Our models extend this effort by projecting the effect of SPB into the future. Cairns et al. (2008a,b) found that SPB infestations in simulated landscapes were positively correlated with the degree of aggregation of pine trees. We suggest this correlation may explain the low probability of SPB infestation in our results in an empirical landscape.

A major assumption in our model is that forest thinning prevents SPB infestations. There is much support in the scientific literature for this assumption. Thinning dense pine stands promotes tree vigor, reducing a stand's susceptibility to SPB infestation as well as subsequent growth of infestations (Fettig et al., 2007). In experimental studies, substantially more trees were infested in non-thinned stands than in thinned stands, though a small number of trees were infested by SPB in thinned stands (Schowalter and Turchin, 1993; Turchin et al., 1999). However, our model only includes larger infestations, not the smaller infestations or "spots" that affect only a small number of trees in a stand. Therefore, by modeling thinned stands as not susceptible to infestation we are sufficiently capturing the difference in SPB dynamics between thinned and non-thinned stands.

We are not modeling the mechanisms underlying beetle activity, but are incorporating probabilities based on data from past SPB outbreak events and forest management to understand the potential effects of SPB under potential future scenarios. SPB dynamics result from factors that interact at multiple spatial and temporal scales and some, such as the influence of climate, are not yet fully understood by ecologists. Although a mechanistic model of SPB activity for the region was not feasible, by simulating a suite of scenarios informed by real data, we were able to project a range of potential future landscape conditions that can serve as a template for exploring the effect of SPB under various forest management policies.

The state-and-transition simulation model we developed will be useful for forest managers and policy makers in the Southeast because it is straightforward to conceptualize and can be easily modified to simulate conditions in another region or under alternative scenarios. In the future, our model will be expanded to simulate SPB dynamics in other regions and under additional scenarios. Particularly important will be areas such as the piedmont of Georgia, where high SPB risk has been reported and where past SPB outbreak records with sufficient resolution are available. In addition, the model should be extended to evaluate economic tradeoffs in costs of SPB management versus potential cost of SPB damage under different scenarios. For example, increasing acceptance of forest thinning promoted by the Federally coordinated Southern Pine Beetle Prevention Program (Nowak et al., 2008) has led to a decrease in the frequency of SPB outbreaks across the Southeastern US (Fettig et al., 2007). By associating each management action and SPB disturbance with a monetary cost, our model could evaluate the economic consequences of implementing the program.

The ultimate goal of our modeling effort is to couple the landscape dynamics model developed here with other models of landscape and ecosystem change. In particular, incorporating the effect of climate change on SPB dynamics will be important. Some effects of climate on SPB are known. Too little or too much
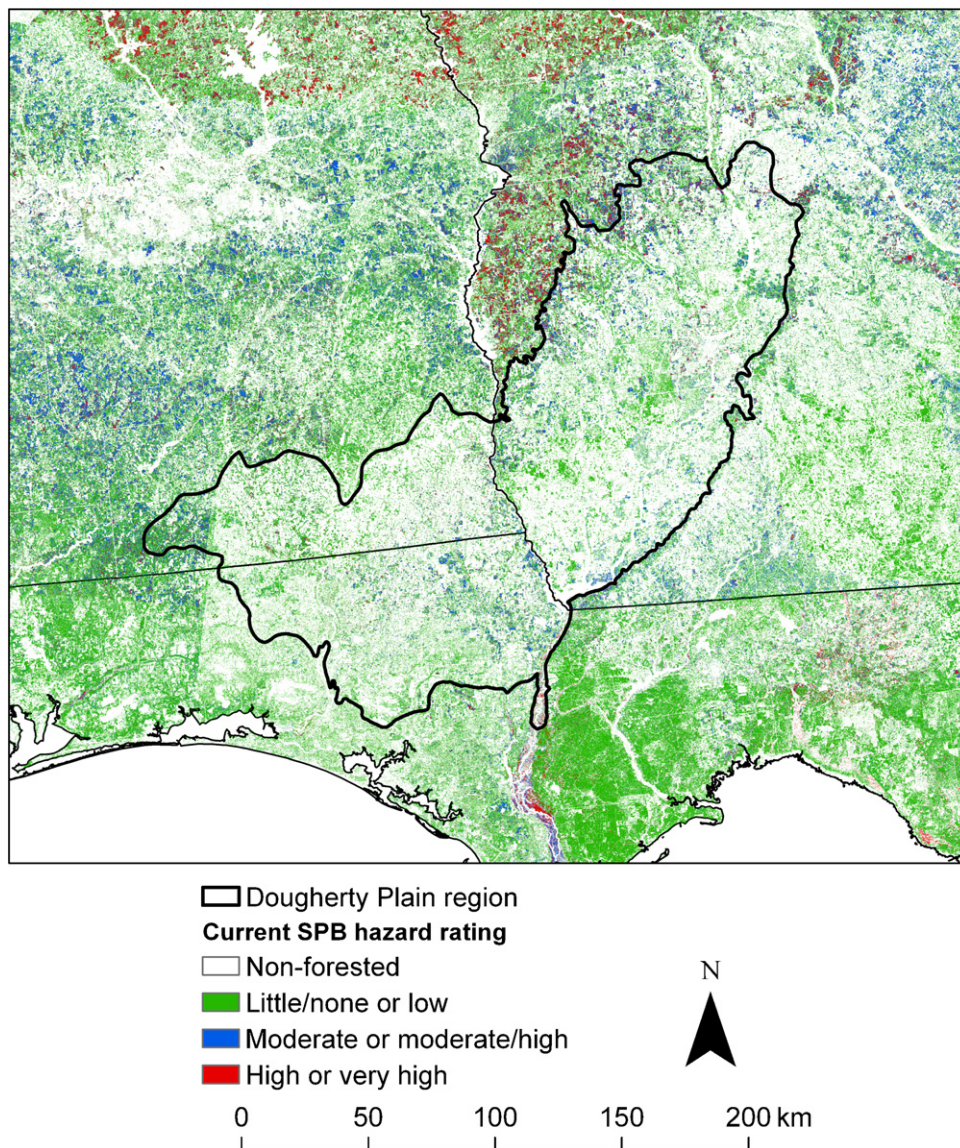
Fig. 6. Map of SPB hazard for the study region. Hazard data were produced by the USDA Forest Service (2010b).

precipitation can weaken tree defense mechanisms and lead to beetle outbreaks (Kalkstein, 1976). Elevated temperatures can also trigger outbreaks by increasing the number of beetle generations per season (Ungerer et al., 1999) as well as their overwintering success (Tran et al., 2007). However, the effect of climate on SPB at a regional scale is not completely understood, and data are currently not sufficient to predict future activity (Duerr and Mistretta, 2011, but see Gan, 2004). Nonetheless, our model can be a starting point for a more comprehensive simulation of potential ecosystem changes to inform forest managers and policy-makers about strategies to ensure the future of their forests.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.06.037.

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