

**FOREST RISK AND IRRUPTIVE INSECT PESTS:  
ECOLOGY FOR MANAGEMENT IN CHANGING TIMES**

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# FOREST RISK AND IRRUPTIVE INSECT PESTS: ECOLOGY FOR MANAGEMENT IN CHANGING TIMES

## Abstract

Many forest ecosystems can sustain—and even require—natural disturbances such as fire and insect outbreaks. Predicting when and how these events may occur is an essential tool for forest managers. For irregularly irruptive insects, prediction can be especially challenging. Using the southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) as a study system, I investigated risk of SPB infestation from host susceptibility and insect population perspectives, with particular attention to models that could be easily applied for management.

To understand the processes contributing to host susceptibility, I looked at tree defenses and forest structure across the New Jersey Pinelands. These pitch pine (*Pinus rigida*) forests present a relatively naïve environment for SPB, with the beetle's native range expanding northward from its usual habitat of loblolly and longleaf pine (*P. taeda*, *P. palustris*). Counter to findings in the southern states, stands on wetter sites had higher levels of resin defense, but these stands were mixed in their probability of infestation. Tree defenses appeared to be overridden by the effect of stand composition, with pure conifer stands being infested at a higher rate than mixed stands. High basal area, high tree density and moderate age/height also contributed to higher infestation probabilities.

Monitoring data on pests with irregular cycles can include many zeros, causing overdispersion. I utilized mixture models to test the effects of SPB and its predator (*Thanasimus dubius* Fabricius) on the occurrence of SPB infestations, using data from 13 southern states. A zero-inflated negative binomial distribution provided the best fit to the data overall. Outbreaks per forest-year were correctly predicted by our models 82% of the

time. The independent variables providing the best fit in the final model included: SPB this year and last year, predators this year, ratio of SPB to predators this year and last year, as well as host area per location and number of spots in the previous two years. We also found that a simpler model utilizing only SPB and SPB/predator ratio, although producing a higher AIC than the full model, resulted in nearly identical predicted zero and non-zero counts, as well as similar numbers of correct vs. incorrect predictions of outbreak status. The application of zero-inflated mixture models provides a promising new tool for understanding the biology and improving our capacity to predict the irregular.

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## Table of Contents

Abstract .....	ii
Acknowledgments .....	iv
Table of Contents .....	v
List of Tables .....	vii
List of Figures .....	ix
Introduction .....	1
<i>Literature cited</i> .....	6
 <b>Chapter 1:</b> Old pests in new places: Novel host susceptibility to a native bark beetle with an expanding range .....	9
<i>Introduction</i> .....	11
<i>Methods</i> .....	18
<i>Results</i> .....	22
<i>Discussion</i> .....	24
<i>Literature cited</i> .....	29
<i>Tables and figures</i> .....	39
 <b>Chapter 2:</b> Oleoresin defenses in pines: Finding landscape-scale proxies for risk of bark beetle attack .....	50
<i>Introduction</i> .....	52
<i>Methods</i> .....	59
<i>Results</i> .....	63
<i>Discussion</i> .....	66
<i>Literature cited</i> .....	72

<i>Tables and figures</i> .....	80
<i>Supplementary material</i> .....	87
 <b>Chapter 3: Predicting the irregular: Developing models to anticipate outbreaks in a tree-killing bark beetle</b> .....	92
<i>Introduction</i> .....	94
<i>Methods</i> .....	99
<i>Results</i> .....	103
<i>Discussion</i> .....	105
<i>Literature cited</i> .....	110
<i>Tables and figures</i> .....	116
<i>Supplementary material</i> .....	124
 Conclusion .....	129
<i>Literature cited</i> .....	131

## List of Tables

### CHAPTER 1

Table 1: Forest stand characteristics and the mechanisms of their influence on host susceptibility .....	39
Table 2: Correlation matrix of measured forest structure variables .....	40
Table 3: Loading matrix for the two principal component axes .....	42
Table 4: Means and standard deviations for measured forest structure variables .....	42

### CHAPTER 2

Table 1. Variance components, standard errors, and percent variance explained for random effects in resin flow model .....	80
--	----

#### *CHAPTER 2, SUPPLEMENTARY MATERIAL*

SMTTable 1. Ranges, means, and standard deviations for forest structure variables measured in soil type plots .....	87
---	----

### CHAPTER 3

Table 1: AIC values for count models .....	116
Table 2: AIC values for binomial models .....	117
Table 3: Parameter estimates for the final, best-fitting model.....	117
Table 4: Parameter estimates for the Texas model. ....	118
Table 5: Comparison of observed and expected counts for each of several models .....	118
Table 6: Comparison of outbreak status predictions between full best-fitting model and Texas model .....	118

#### *CHAPTER 3, SUPPLEMENTARY MATERIAL*

SMTTable 1. Comparison of univariate distributions for the dependent variable number of spots .....	124
SMTTable 2. Comparison between the offset of log(Host Area) and host area in hectares as a simple variable in the model .....	124



SMTable 3. AIC comparison among all models.....	124
SMTable 4. Predicted probabilities of numbers of spots for the full best fitting model and the simpler Texas model .....	125
SMTable 5. Observed vs. expected spots in selected forests .....	126
SMTable 6. Sensitivity analysis comparing low versus high values of all variables in the full best-fitting model. ....	127

## List of Figures

### CHAPTER 1

Figure 1: Distributions of primary SPB host species across the eastern U.S. ....	43
Figure 2: Map of southern New Jersey, public ownership, Pinelands, and sample forest cover .....	44
Figure 3: Spot locations for GIS analysis .....	45
Figure 4: Locations of control and spot plots .....	46
Figure 5: Regional distribution of area in each forest type.....	46
Figure 6: Infested vs. uninfested area within each forest type.....	47
Figure 7: Biplot showing distribution of variables along principal components 1 and 2 .	47
Figure 8: Logistic regression curves of infested vs. not infested status on principal components one and two.....	48
Figure 9: Means and standard errors from PCA of southern region uninfested and infested forest structure plots .....	49

### CHAPTER 2

Figure 1: Ranges of pine species in the eastern United States .....	81
Figure 2: Location of resin sampling plots .....	82
Figure 3: Wetland and upland resin sampling sites .....	83
Figure 4: Mean resin flow for six soil types across the Pinelands .....	83
Figure 5: Stand-level resin flow means and tree density .....	84
Figure 6: Mean resin flow with standard error in upland and wetland stands .....	84
Figure 7: Mean site index and resin flow for pitch pine in New Jersey, loblolly pine in Kisatchie National Forest, and Red pine in Itasca, Minnesota and west central Wisconsin .....	85
Figure 8: Resin flow comparison among different pine species .....	86

## CHAPTER 2, SUPPLEMENTARY MATERIAL

SMFigure 1: Boxplots for the forest structure variables measured in each sampling plot .....	89
SMFigure 2: Ages and heights of all individual trees sampled .....	91

## CHAPTER 3

Figure 1: Frequency distribution of numbers of spots per forest per year.....	119
Figure 2: Locations of SPB trapping sites .....	120
Figure 3: Rootograms (square root of frequency) comparing the univariate distributions of number of spots .....	121
Figure 4: Observed vs. expected frequencies of numbers of spots per range of values for selected forest ranger districts .....	122
Figure 5: Sensitivity analysis of full best-fitting model .....	123

## CHAPTER 3, SUPPLEMENTARY MATERIAL

SMFigure 1: Prediction chart currently in use for the annual SPB outbreak prediction system .....	128
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## **Introduction: Risk and Forest Insect Pests**

In the modern world, we are surrounded by the possibility of adverse events. From natural disasters such as earthquakes and hurricanes, to economic events such as recessions and stock market crashes, we are constantly trying to understand our level of *risk* of these events. In its simplest definition, risk is the “probability of loss or damage due to the occurrence of a hazard” (Kaplan and Garrick 1981, Jactel et al. 2012), i.e., it is a probabilistic framework usually presented as a range of possibilities characterized by some probability distribution. Kaplan and Garrick (1981) describe risk analysis as the answer to three questions: a) what can happen?; b) how likely is it to happen?; and c) if it does happen, what are the consequences? Risk thus comprises the related concepts of hazard, probability, and consequences. Fortunately for us, hazardous events tend to happen (relatively) infrequently, so risk is usually described by the tails of event occurrence distributions. Burgman (2005) notes that as scientists we tend to be focused on central tendencies—means and medians—and not the tails where hazards are found, whereas the assessment of risk is concerned with exactly these tails. How then do we think about and analyze these events?

In the study of natural hazards or disturbances, an important distinction is that some events are within the range of variation for that disturbance type and that particular ecosystem, while other events are catastrophic or extreme. One theoretical possibility for characterizing systems that experience disturbance is that of alternate attractors, or alternate stable states; the disturbance is present or absent depending on the state. Entomologists have theorized for decades that insect population fluctuations can be described by a system with two stable attractors at high and low population levels

(Takahashi 1964, Southwood and Comins 1976, Berryman 1987, Ives et al. 2008). More recently, the vocabulary of alternate attractors/stable states has become somewhat conflated with the literature on regime shifts and resilience (Scheffer and Carpenter 2003, Folke et al. 2004, Walker and Salt 2012). As these terms have been applied to conservation scenarios and other potentially catastrophic events, the theoretical framework of alternate attractors has been used to describe both expected fluctuations in native species, and unexpected or catastrophic events leading to permanent system shifts (Ludwig et al. 1997). The Canadian entomologist C.S. Holling has written papers in both the earlier theoretical literature (Holling 1973) and in the more applied resilience literature (e.g., Ludwig et al. 1997, Folke et al. 2004, Walker et al. 2004), suggesting that the two viewpoints are not incompatible. However, predicting risk in a natural resource management context requires that we specify the distinction between the two.

Hazards in the natural environment can include occasional or rare events that are integral to the functioning of the system. Forests prone to wildfire are often adapted to this natural disturbance, using it to advantage in reproduction, as well as in the provision of habitat and other ecosystem services. Serotinous pine cones, for example, only release their seeds when heated by fire. Understanding the distributions of the probability of fire has been integral to the understanding of fire risk in different kinds of forests (Clark 1996, Grissino-Mayer 1999). Similarly, native insect pests that display outbreak dynamics are natural disturbances to which the forest environment is adapted, often playing essential roles in ecosystem function (Strong et al. 1984, Carson et al. 2004, Speight et al. 2008). For forest managers, a fire or pest outbreak may represent a situation to be dealt with, but not necessarily one to be prevented or eradicated. The major fires in

Yellowstone National Park in 1988 turned out not to be outside the natural range of variation of fire occurrence for that forest type, and the system rebounded remarkably quickly following the event, obviating the need for post-fire rehabilitation (Turner et al. 2003). The spruce budworm system in eastern Canada likewise relies on regular disturbance cycles (Holling 1973). Early management efforts included pesticide spraying which eventually created such a buildup of mature trees and insects that a much larger than usual outbreak was inevitable. The eventual population explosion was only staved off by more and more spraying (Walker and Salt 2012). Managers eventually learned to implement a more cautious program of pesticide application which allowed a more natural mosaic of stand ages, and a decrease in the risk of an unmanageable outbreak that would cause so much damage that the system would not recover.

This example returns us to the idea that extreme disturbance events can push a system beyond the point of return to its original state. Disturbance adapted environments can withstand some range of variation in disturbance cycles or fluctuations, but extreme events may cause irreversible system change. The recent mountain pine beetle outbreak across the western US and Canada, for example, has been described as unprecedented in its scale and some wonder whether and how the forest will recover (Astrup et al. 2008), and whether permanent changes to carbon feedbacks have occurred (Kurz et al. 2008). For managers, predicting disturbance events is an important component of decision-making and resource allocation. It is therefore crucial to distinguish between two types of uncertainty—uncertainty due to variability, and uncertainty due to lack of knowledge, in this case the difficulty of predicting extreme, system-changing events. The purpose of the work that follows is to describe the former as completely as possible, while

acknowledging that perfect prediction is impossible and that the latter may yet occur. In other words, the prediction of risk in natural, disturbance-adapted environments focuses on that which can be known—i.e., the distribution of disturbance events given patterns and processes of the abiotic and biotic environment that contribute to that distribution, versus that which can possibly not be known; the distribution of extreme, system-changing events. Some workers are developing models for the prediction of these latter events (e.g., Denny et al. 2009, Burgman et al. 2012), but that is not the focus of the present research.

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) is an insect pest native to the southern United States, capable of killing thousands of hectares of trees during its periodic outbreaks. Due to its economic importance to the timber industry in the south, SPB has been intensively studied and monitored over the last 50 years. In the last decade, however, SPB has appeared less regularly throughout the south, with the primary major outbreak in the first decade of the 21<sup>st</sup> century occurring in New Jersey. Extensive SPB mortality was also detected for the first time on Long Island, New York in 2014 (Schlossberg 2014), with small-scale trap catches occurring farther to the north in Connecticut, Massachusetts, Rhode Island, and the Hudson Valley of New York (Kevin Dodds, personal communication). As SPB moves rapidly northward, it is critical to develop risk models that can be rapidly assimilated by managers encountering the beetle for the first time.

Hanewinkel et al. (2011) note that the study of insect outbreak risk necessitates both the study of host susceptibility and the population dynamics of the insect of interest. In the chapters that follow I investigate both these components of SPB outbreak risk, in

each case attempting to develop models and methods that can be utilized by forest managers with data that they are already accustomed to collecting, or for which the institution of new protocols would be relatively simple. In chapter 1, I analyze the impact of stand-level forest structure on the probability of SPB infestation. The pitch pine (*Pinus rigida*) forests of New Jersey represent a relatively naïve host environment for SPB, so this analysis enabled me to investigate whether relationships between forest structure and stand susceptibility that we know from the south would hold true in this new environment. In chapter 2, I focus on the defenses of the host tree, attempting to discern landscape-scale proxies that can be used to quantify variation in defense capabilities across the landscape. In addition, I compare resin defenses among pine species, and consider how well-defended naïve host species might be as SPB continues to move northward. In chapter 3, I develop models to understand the relationship between SPB, its clerid beetle predator (*Thanasimus dubius* Fabricius), and probability of outbreak. One of the difficulties in analyzing relatively rare events is that the data may present statistical challenges, such as the many zeros present in the SPB data due to years in which no SPB were detected. I used mixture models to find better fits to these overdispersed data. The goal in both the forest and population analyses was to increase our understanding of the uncertainty due to variability in this system, i.e., to develop predictive models based on probability distributions that can be known and interpreted to help in management decision-making.



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## Chapter One

### **Old pests in new places: Novel host susceptibility to a native bark beetle with an expanding range**

#### **Abstract**

Range expansion of native insect pests under climate change has the potential to move many species beyond their usual habitat. As resource managers attempt to respond to these “new” pests, methods are needed that can build on previous research and rapidly assess local impacts, while utilizing familiar metrics so that the wheel need not be invented with each new pest. Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) is a bark beetle native to the southeastern United States whose periodic outbreaks can kill thousands of hectares of trees, resulting in economic losses and degradation of ecosystem services. Over the past decade, a sustained outbreak in the New Jersey Pinelands has moved the northern limit of its range, switching from forests consisting primarily of loblolly, longleaf, and shortleaf pines (*Pinus taeda*, *P. palustris*, *P. echinata*) in the southeastern U.S. to one consisting primarily of pitch pine (*P. rigida*) along the mid-Atlantic seaboard. We sought to understand the effects of forest type and structure on the variation in susceptibility of stands to SPB infestation, using Pinelands-wide infestation and forest type data, in conjunction with field data collected in infested and uninfested plots. We found that among wetland conifer, wetland mixed pine/oak, upland (dry) conifer, and upland mixed pine/oak stands, those with a high percentage of pine were infested at a higher rate than mixed pine/hardwood stands, regardless of whether the stands were upland or wetland habitats. The effects of stand type (wetland or upland) were overridden by the effect of stand composition, with wetland pure conifer stands being disproportionately infested, and wetland mixed stands being

disproportionately uninfested. Research from the south has found that wet or waterlogged stands tend to be more susceptible to SPB, and that lowered tree defenses in such stands may be part of the mechanism, in accordance with the growth-differentiation balance hypothesis. In contrast, work in New Jersey has found that wetland pitch pine in fact are better defended, but our finding that wetland/upland status is less important than stand composition suggests that defenses may also be less important for susceptibility at the stand scale. Also in contrast to southern findings, site index did not predict infestation status. More in line with previous work in the south, we found that stand structure variables such as high pine and high total basal areas, high density between trees, and moderate age/height contributed to higher probabilities of infestation. These results suggest that thinning is an appropriate management strategy for forest managers seeking to build resilience to SPB, and that all else being equal, conifer stands should receive priority for management attention over mixed stands. Detected for the first time in large mortality events on Long Island in 2014, and in smaller trap catches in Massachusetts, Connecticut and Rhode Island, SPB continues to move northward. These results provide forest managers unaccustomed to dealing with this pest insect an easy method to assess their existing stands for risk, and to implement management strategies accordingly.

## **Introduction**

Outbreaking forest pest insects exhibit unusual population dynamics that can result in large-scale economic and landscape impacts (Berryman, 1987; Wallner, 1987). Many famously damaging forest pests are characterized by years of endemic population levels, in which their numbers are too low to result in widespread mortality, punctuated by years of epidemic, or “outbreak” population levels. Fluctuations of this kind have been studied by theoretical biologists since at least the 1960s (Holling, 1973; May, 1977; Takahashi, 1964). For forest managers, such outbreaking species pose immense challenges over the many thousands of hectares that can be affected in a single outbreak. Although native pest insect outbreaks can be considered natural agents of ecosystem dynamics and forest succession (Speight et al., 2008), they can also cause extensive economic damage (Cohen et al., 2016; Holmes, 1991; Pye et al., 2011), as well as non-monetary damage to recreational and aesthetic resources (Boyd et al., 2013). With climate change, the possibility of range expansions increases, bringing native pests into previously naïve habitats and exacerbating the effects of these pests on both managed and unmanaged forests (Dukes et al., 2009; Weed et al., 2013). These expansions can occur rapidly, with new pests moving into zones where local resource managers are unaccustomed to dealing with them. Under this scenario, determining management options can be challenging. Will research from the pest’s original habitat apply in the new habitat? What is the fastest way to integrate previous knowledge into current management options? Can data commonly collected by foresters and resource managers be used to obtain relatively rapid assessments of risk in naïve or novel habitats of native pests?

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) is a native pine bark beetle whose range extends from Central America to the mid-Atlantic states, and from southern Arizona to the southeastern seaboard. Since recognition of southern pine beetle in 1868, SPB outbreaks have occurred regularly throughout the south, causing significant economic damage (Clarke et al., 2016). Historical documents suggest that widespread outbreaks of a similar nature occurred during the 18<sup>th</sup> and 19<sup>th</sup> centuries, prior to identification of the species (Payne, 1980). The economic losses from such outbreaks can be enormous; for example, an outbreak in the eastern U.S. from 1999-2002 resulted in over 1 billion dollars just in the direct costs of lost timber (Clarke and Nowak, 2009). Since 2002, however, outbreaks have occurred much less frequently in the south, and with the exception of a few scattered, short events, SPB has remained at non-outbreak levels (Clarke et al., 2016). Just as the southern states settled into this longer non-outbreak period, an outbreak began in southern New Jersey. Although included in the northernmost extent of the beetle's historic range map, the region had not experienced a significant outbreak since the 1930s, when an outbreak occurred in both southern New Jersey and southern Pennsylvania (Knull, 1934; Wilent, 2005). The 2000s outbreak spread northward across New Jersey, causing an estimated 14,000 acres of damage in 2010 alone (New Jersey Department of Environmental Protection, unpublished data), a greater extent of damage than had previously been recorded. In the fall of 2014, SPB was detected for the first time on Long Island, New York (Schlossberg, 2014), and since then small numbers have been trapped in Connecticut, Rhode Island, and Massachusetts (Kevin Dodds, unpublished data). Although the latter three states have yet to detect tree mortality due to SPB, the extent of tree mortality on Long Island—where SPB had not

been previously detected—indicates that SPB’s range is continuing to expand. Northern distribution limits of SPB are constrained by the beetle’s ability to overwinter, emerging the following spring. Minimum annual temperatures at a given latitude thus play a key role in the northern range expansion of SPB (Trần et al., 2007). Both physiological and climatic models have shown the potential for SPB to expand northward into New England, given changing temperature regimes (Ungerer et al., 1999; Williams and Liebhold, 2002).

Host species of SPB have traditionally been identified as the southern yellow pines, also known as the diploxylon, or hard pines (Clarke et al., 2016; Hopkins, 1909; Payne, 1980). The four primary species of southern yellow pines are loblolly, longleaf, shortleaf, and slash pine (*Pinus taeda*, *P. palustris*, *P. echinata*, *P. elliottii*) (United States Forest Service Forest Products Laboratory, 1936). These four species comprise the main commercially significant species of pine for southern timber production, but other diploxylon pines have also been targets of SPB; these include Virginia, pitch, and table-mountain pine (*P. virginiana*, *P. rigida*, *P. pungens*), and more rarely red pine (*P. resinosa*) and pond pine (*P. serotina*) (Payne, 1980; Richardson, 1998).

Southern New Jersey is home to over 1 million acres of federally protected pine and mixed pine-oak forest, known as the New Jersey Pinelands National Reserve. As SPB expands its range northward, the potential host species change. While its primary hosts in the south are the four primary species of southern yellow pines, the primary pine species in New Jersey and on Long Island is pitch pine (*P. rigida*), whose distribution extends northward to Maine (Fig. 1, Little, 1971). SPB has been previously detected in pitch pine, and the southern extent of the pitch pine range distribution extends into the



traditional range of SPB, but its susceptibility to SPB outbreak has not been studied. As climate driven range expansions become more common, and insects move into regions of relatively naïve host species and likely different climates, it will be important to make effective use of existing knowledge. This raises the question of how well knowledge gained from research and experience in one region (historic range of outbreaks) can be applied to address management options in another recently occupied region.

A similar range expansion is taking place in mountain pine beetle (*Dendroctonus ponderosae* Hopkins), a related bark beetle species that killed millions of hectares of trees in the western U.S. and Canada during the 1990s-2000s. There has been range expansion of mountain pine beetle into jack pine (*P. banksiana*), a departure from its historic restriction to lodgepole pine (*P. contorta*) and other pines that only occur in western North America (Cullingham et al., 2011; de la Giroday et al., 2012). Chemical similarities between historical and novel host species probably facilitate host recognition in the newly occupied forest (Erbilgin et al., 2014), thus promoting effective aggregation by attacking beetles and the consequent expansion of the beetle into host species outside its native range (Burke and Carroll, 2016). Other work has shown that as beetles expanded their range into climate types that had not typically experienced bark beetle outbreaks, even within the same host, beetle reproductive success increased (Cudmore et al., 2010). Effects of landscape factors on dispersal into the novel environment (de la Giroday et al., 2011), potential effects of climate on historical and novel host distributions (Coops et al., 2012), and differential responses of historical and novel host defenses to beetle fungal associates (Arango-Velez et al., 2016) have also been investigated. Differences in host stand-level characteristics that may affect susceptibility

to the beetle, however, have not yet been explored in the novel hosts of either mountain pine beetle or southern pine beetle.

Risk assessments for insect outbreaks can typically be divided into two primary types: those focused on aspects of host susceptibility, and those focused on the population dynamics of the insect (Hanewinkel et al., 2011). In the case of SPB, a population-based risk assessment procedure has been in place since 1986 across the southern states (Billings and Upton, 2010). Spring trapping of both SPB and its primary predator, *Thanasimus dubius* Fabricius, takes place annually in forest stands throughout the south. Using these data, an assessment of summer outbreak risk is delivered to each cooperating forest management unit. While this method has proved relatively reliable, its success depends on a data collection infrastructure among many collaborators across state lines. As SPB moves northward, however, forest managers often face a rapid-response situation, in which detection of extensive mortality coincides with the first known occurrence of SPB in that state or region. Under these circumstances, it is next to impossible to implement standardized trapping procedures, not to mention acquiring the expertise required to identify and count the insects, and then to assess landscape-scale risk of infestation in that management unit. Here we focus on risk assessment related to host susceptibility, which can be evaluated in the context of standard forest health data already collected by most forest managers, and perhaps allow for risk assessment prior to the first large-scale mortality event in potential new locations.

Extensive work has been conducted on host susceptibility to SPB across the southern U.S., including standardized data collection from Virginia to Texas, funded in the 1970s by the Expanded Southern Pine Beetle Research and Applications Program

(ESPBRAP; Hicks Jr 1980, Coster and Searcy 1981). Although there was some regional variation, these southwide data show that, on average, certain stand characteristics are correlated with infestation by SPB. These include high basal area, high percent pine, high site moisture and/or site index, and the correlated variables of diameter at breast height, age, and height. Each of these characteristics is related to the biology of SPB aggregation behavior and the unfolding of an infestation. Unlike some bark beetle species, SPB attack healthy pines, forming discrete infestations, known as “spots,” within an outbreak area. Pine trees have evolved oleoresin defenses against such herbivores, so the initial attack phase in a new spot sometimes begins with a weakened tree, such as one struck by lightning (Coulson et al., 1986; Hodges and Pickard, 1971). If a local background population of SPB exists in the area, the pioneer beetles will be drawn to the tree; these in turn will begin producing a cocktail of at least five known pheromones that includes frontalin, the primary attractant component for drawing in conspecifics (Borden, 1974; Kinzer et al., 1969; Pureswaran et al., 2006). The large number of beetles overcome the defenses of the tree, enabling thousands of beetles to lay their eggs and successfully reproduce within the phloem. If the initial tree draws in enough beetles, these larger numbers are then able to move on to attack adjacent, healthy trees and the infestation grows. Some spots continue to grow outward from the initially infested trees as the adult progeny from earlier attacks emerge and form a wave of attacks. Spots that continue to grow until winter provide the majority of SPB that disperse across the forest the following spring to form the next year’s population of spots. Thus stand characteristics that promote spot formation and spot growth increase the risk of epidemics arising and persisting.

Table 1 summarizes previous research on the relationship between measured stand/tree variables and the mechanisms through which these variables may influence host susceptibility. We sought to investigate the attributes of pitch pine stand structure relative to the current SPB outbreak in New Jersey. Our objectives were 1) to determine the range of variation in stand characteristics across the Pinelands; 2) to determine the scope of SPB infestation relative to forest type; and 3) to determine the relationship between pitch pine stand characteristics and pitch pine mortality. We used land use/land cover data (New Jersey Department of Environmental Protection, 2010) of conifer forest types in New Jersey in conjunction with forest structure data collected in both infested and uninfested plots across the major outbreak area within the New Jersey Pinelands. The majority of the forested land within the Pinelands is comprised of pitch pine and mixed pitch pine/oak stands. These stands occur within one of two floristic complexes within the Pinelands—upland and lowland. Lowland sites, also referred to as wetland sites, are those where the water table is either near or above the surface during some portion of the year. In upland sites, the water table may be 70 – 90 cm below the surface, and sometimes much deeper than that (McCormick, 1979). Pitch pine occurs on a wide range of soil moisture types, from poorly drained to excessively drained soils (Little and Garrett, 1990). Using the existing cover type classifications in the land use/land cover data, we analyzed the occurrence of the four prominent conifer forest types—upland conifer, wetland conifer, upland mixed conifer, and wetland mixed conifer—and compared them to the occurrence of SPB infestations across these types. Next we collected stand structure data in field plots comprising both infested and uninfested sites, to investigate which variables most influenced stand susceptibility to SPB. Finally we

tested the effect of site index on stand susceptibility. Site indices are a measure of tree growth (typically height of codominant trees at age 50) that combines edaphic and climatic factors in a single parameter representing that tree species on that site (Van Laar and Akça, 2007).

## **Methods**

### *Study site*

The New Jersey Pinelands, spanning forests in the south and central portions of the state, represent a unique state-federal partnership designed to preserve and protect over 1.1 million acres of land, the largest area of open space on the eastern seaboard between Richmond and Boston. Because the area was not designated for protection until 1978, the region is bifurcated by roads and towns, including 56 municipalities and nearly 500,000 residents. Although the majority of the land area is forested, it also includes significant agriculture, as well as the US military's Joint Base McGuire-Dix-Lakehurst. Close to half of the Pinelands area is in public ownership, with the majority of public land being owned by the State of New Jersey (New Jersey Pinelands Commission, 2015). In addition, the state owns a number of forested tracts outside the federally designated Pinelands boundary. Because SPB management efforts fall almost exclusively on the state, we restricted our data collection and analysis to these public lands (Fig. 2a).

Aerial detection surveys conducted by New Jersey Forest Service between 2002 and the present show a northward spread over time of localized infestations by SPB (spots). To cover the entire range of the current outbreak, our study included Cape May, Atlantic, Cumberland, Salem and Burlington Counties. Forest types varied considerably

from north to south across the study area, so we also stratified into two regions, north and south of the Mullica River, hereafter referred to as the northern and southern regions.

### *Forest type*

To analyze the prevalence of SPB spots across the landscape, we combined forest cover type data with spot occurrence data. The Land Use Land Cover (LULC) dataset produced by the New Jersey Department of Environmental Protection (NJDEP) uses color infrared photography to classify land cover types across the state (New Jersey Department of Environmental Protection, 2010). Classifications are based on a modified Anderson system developed by NJDEP (New Jersey Department of Environmental Protection, 2010). We selected all forest types including a conifer component. To simplify analyses to categories that would be meaningful for management, some cover classifications were merged. To clarify the distinction between lowland and upland forests, we renamed the “coniferous forest” and “wetland coniferous forest” types as “upland conifer” and “wetland conifer,” respectively. The final types were: upland conifer, wetland conifer (both >75% pine), and upland mixed, wetland mixed (25%-75% conifer; Fig. 2b). Deciduous forest types and shrub/scrub forest types were not included in the analysis because they are not potential habitat for SPB. We used these data to determine the relative proportion of each forest type across the landscape, and then to determine whether forest types differed in the occurrence of SPB spots per unit area. Spot data were produced by NJDEP, and comprise 217 ground-truthed infestations, initially identified in aerial detection surveys (Fig. 3). Based on the area covered by each forest type, we conducted a chi-square analysis to determine whether any forest types exhibited a higher

or lower occurrence of spots relative to that expected if SPB spots per unit area were equal across forest types. Because the occurrence of spots was largely concentrated south of the Mullica River, and because NJDEP SPB suppression and monitoring efforts are largely restricted to public land, we restricted this analysis to state-owned land in counties south of the Mullica, including state lands outside the federal Pinelands boundary.

### *Forest structure*

Using the NJDEP LULC data described above, we used ArcGIS to select plots approximately at random across the four forest types described, with consideration for efficiency of plot access. We established 12 control (uninfested) plots each in the northern and southern regions (Fig. 4). In each plot we sampled three 50-meter transects with sampling points every ten meters. At each sampling point, we located the nearest pine tree ( $>15$  cm diameter at breast height), measured its age, diameter at breast height (DBH), and height, and then recorded basal area of pine, basal area of hardwoods, distance to nearest and second nearest pine  $>15$  cm, and percent canopy cover.

Hemispherical photography was used, in conjunction with the program ImageJ (Schneider et al., 2012) to estimate percent canopy cover. We implemented the same sampling protocol at 24 plots situated within recent SPB infestations identified by NJDEP ground-truth surveys (hereafter referred to as spot plots; Fig. 4). Due to the distribution of spots on the landscape, coupled with NJDEP's aggressive suppression of infested trees north of the Mullica River, we restricted spot plot sampling to the region south of the Mullica River, although uninfested plots were sampled both north and south of the river. Many of these spots had been managed for SPB suppression, i.e., the trees had been cut down. In these cases, we sampled a matching contiguous area of the stand that had not

been cut. If the adjacent area appeared to be different in stand structure from the cut area, the plot was discarded and a new one selected.

There was correlation among variables so principal components analysis was used to reduce the dimensionality of the data in order to compare infested versus uninfested plots. The analysis was performed on plot-level means of each variable. Prior to taking the means, nearest neighbor distances and second nearest neighbor distances were log-transformed, and hardwood basal area was square-root transformed to improve normality. We evaluated potential relationships between stand structure (as represented by principal components) and the probability of a stand being infested or not with logistic regression applied to each of the first two principal components. These analyses were restricted to the southern region because the vast majority of the infestations to this point had been in the south. To evaluate future susceptibility of northern forests with respect to stand structure, we calculated the first two principal components of the northern plots using the eigenvectors obtained from the southern region PCA. We then examined their relationship in multidimensional space with respect to the direction of increasing risk along each component axis.

#### *Site Index and Infestation*

To evaluate possible relationships between the occurrence of SPB spots and site quality for tree growth, we compared site indices in infested versus uninfested plots. We used the 12 control (uninfested) plots, and 24 spot plots described above. As described above, we measured age and height of five co-dominant trees along each transect, for a total of 15 heights and ages per plot. Using the height vs. age curves for pitch pine (Illick



and Aughanbaugh, 1930), we parameterized a site index equation, which we then used to calculate site index for each tree. To evaluate variation within and across plots, we used a nested ANOVA (trees nested within transects, nested within plots). We used the average site index for each plot to test for relations between site quality and occurrence of spots.

All statistical analyses were performed using R 3.2.1 and JMP Pro 12.1.0 (R Core Team, 2015; SAS Institute Inc., 2015).

## **Results**

### *Forest type*

Forests north of the Mullica River were overwhelmingly comprised of the upland conifer type, totaling nearly 45,000 ha (Fig. 5). Forests south of the Mullica, by contrast, were dominated by the mixed conifer type, both in upland and wetland areas (Fig. 5), comprising over 65% of the forested landscape (Fig. 6a). Forty percent of spots in the southern region were found in the upland conifer type, though this type covered less than 25% of the landscape. A further 27% of spots were found in the wetland conifer type, which comprised just over 10% of the area. Spots in the upland mixed type represented just over 20% of the total, and spots in the wetland mixed type covered approximately 12% of the total (Fig. 6a).

The chi-square analysis indicated that spots / area varied strongly among forest types (chi-square = 121.47, df = 3,  $p < 0.001$ ). The log odds for both wetland and upland conifer forest types were positive (more spots than expected), and the log odds for both wetland and upland mixed forest types were negative (fewer spots than expected) (Fig. 6b).

### *Forest structure*

There was high correlation among the various measurements of stand structure (Table 2): 75% of the variation in 12 variables among 36 stands (infested and uninfested stands south of the Mullica River) was explained by the first two principal components (Table 3). Variables that loaded positively on PC1 included: higher hardwood basal area, taller height, older age, larger dbh, and lower tree density (farther neighbor distances). High pine basal area and high percent pine loaded negatively on PC1. PC2 largely reflected a gradient from high percent live crown (negative values) to high total basal area (positive values) (Fig. 7). Logistic regression indicated significant relationships between status (infested vs. not infested) and both principal component axes. The probability of infestation appeared to be highest in stands that were mainly pines (negative values of PC1) and had high total basal area and small crowns (positive values of PC2) [Fig. 8; PC1:  $p = 0.039$ , PC2:  $p = 0.018$ .]

In comparison with their uninfested control stands, the southern infested stands were more negative along PC1, with higher percent pine and higher pine basal area, as well as higher density (distance between neighboring trees). The uninfested stands were more positive along the same axis, with larger trees in both height and diameter, as well as higher hardwood basal area (Fig. 9). The direction of risk thus increases in the negative direction along PC1, and in the positive direction along PC2. In this multivariate space, then, the northern control stands are at even higher risk than the southern infested stands along PC1, but are at relatively lower risk along PC2, as the northern stands tended to have larger crowns and lower total basal area per stand (Fig. 9).

### *Site index and stand infestation status*

As expected, there was high variation among forest plots in their suitability for growth of pines: 41% of the variance in site index was attributable to plots, compared to only 12% (non-significant) among transects within plots. However, there was no difference in site index between infested and uninfested stands ( $F_{1,34} = 1.84$ ,  $p = 0.18$ ), which was counter to theoretical predictions.

### **Discussion**

SPB infestations were far more likely to occur in pure conifer stands than mixed oak/pine stands. This was true in both wetland and upland areas, but wetland conifer stands were especially affected (modest area of occurrence in the southern Pinelands, but many more spots than expected based on area). Wetland mixed sites, on the other hand, had fewer spots than expected. The growth-differentiation balance hypothesis (GDBH; Herms and Mattson, 1992; Loomis, 1932; Lorio, 1986) proposes that plants utilize carbon preferentially for growth when water and mineral nutrients are sufficient, but use carbon increasingly for secondary metabolism (tree defenses/resin flow), when water or nutrients are scarce. In the southern SPB system, the hypothesis predicts that a) resin flow will be lower in stands where trees are growing well, i.e., have sufficient water and nutrients; and b) that wet stands are more likely to be infested than dry stands. The GDBH has been strongly supported in southern pine systems on both counts. Water and nutrient manipulations of loblolly pine have shown that resin flow is higher in trees with restricted water or nutrient resources (Reeve et al., 1995; Warren et al., 1999). Similarly, field data has shown that moist, wet, and waterlogged sites in the south tend to have a higher

probability of infestation (Hicks Jr, 1980; Lorio, 1978, 1968). Following GDBH, we would predict that wetland sites in the Pinelands would be at higher risk than upland sites. This was true for pure pine stands but not mixed stands (Fig. 6b). In addition, the predicted mechanism involved decreased resin flow when water availability is high. In fact, our previous work found that resin flow from pines in wetland sites was significantly higher than from pines in dry sites (see this volume, chapter 2), yet the current study showed that some wetland sites, those composed primarily of pines, actually experienced more infestation. This combination of results not only runs counter to predictions of GDBH regarding environmental effects on constitutive pine defenses, but also undermines the related hypothesis that tree defenses are a predictor of risk for SPB. In the Pinelands, the effects of high densities of pine trees apparently overwhelms effects from variable tree defenses in influencing risk from SPB. Another result from our study that ran counter to GDBH was that sites with infestations did not tend to be sites that were especially good for growth of pine trees (high site index). On these several counts, then, the GDBH is not a good predictor of SPB risk in mid-Atlantic pitch pine systems, in contrast to its strong predictive value in southern yellow pine systems.

The disproportionate number of spots in wetland conifer sites of our study region could be related to factors that we did not measure, such as tree stress from root mortality, decreased respiration due to flooding, or effects of the typically dense understory on the pheromone plume that enables the beetles to carry out their mass attack strategy. Pitch pine grows under a wide variety of moisture conditions, from relatively dry sites to nearly waterlogged sites (McCormick 1979, Little and Garrett 1990). Flooding usually causes a certain amount of stress to plants, primarily in the deprivation

of oxygen and consequent decrease in respiration (Lambers et al., 2008; Taiz and Zeiger, 2002), which may potentially affect secondary metabolism (Nanjo et al., 2011) or at least stress the trees such that they are weakened and more susceptible to spot initiation. Kalkstein (1976) found a significant relationship between moisture surplus and increased occurrence of SPB infestations, and Lorio and Hodges (1968) demonstrated experimentally that continual flooding reduced resin flow in loblolly pine, and that these trees were particularly susceptible to SPB attack. However they also noted that the trees appeared to be so damaged by the flooding that they would have died even without attack by beetles, whereas pitch pine in New Jersey can grow quite well in flooded sites. Neither our measurements nor our observations suggested physiological maladies in pines growing in wetland forest types. An alternative hypothesis is that the generally denser canopies and understories in wetland sites promote effective aggregation of attacking SPB by stabilizing their pheromone plumes. Previous experimental work has shown that plumes may become less stable as canopies are thinned and understories removed (Thistle et al., 2011). More research is needed to quantify the three-dimensional effects of the canopy and understory on SPB pheromone plumes and the beetles' ability to maintain their attack strategy.

A positive feature of our SPB risk assessment for the New Jersey Pinelands is that we combined analyses of the full landscape of interest (Figs. 2, 3, 5, 6) with intensive measurements of replicated stands drawn approximately at random from within this landscape (Figs. 4, 7-9). Stand structure analysis strongly supported the result from landscape analyses that SPB infestations occur with disproportionate frequency in stands primarily composed of conifers, as opposed to mixed stands. Stand measurements further

revealed that higher risk was associated with high stem density (shorter distance between trees) and smaller size (DBH, height, and age).

These stand structure results were broadly similar to results from past research in southern pines. Lorio (1978) found that infestations tended to occur in stands of moderate age ( $> 30$  yrs), and Ylioja et al. (2005) found a parabolic relationship with age, with a similar lack of infestations at young ages, but an additional lack of infestations in older stands ( $> \sim 60$  yrs). The lack of infestations at young ages can be attributed to the insufficient phloem to sustain brood populations (Belanger et al., 1993), but the mechanism for the lack at older ages is not well understood. Although our data did not include young stands ( $< 26$  yrs), our results among older trees support the downward curve of infestation probability with increasing age (Fig. 9) reported by Ylioja et al. (2005). Previous studies in southern pine systems showed conflicting evidence with regard to distances among trees. Gara and Coster (1968) demonstrated that proximity to nearest neighbor trees influenced the ability of SPB to maintain a progression of attacks that keep including new trees. Analyses of data from ESPBRAP (Coster and Searcy, 1981; Hicks Jr, 1980) emphasized instead the importance of basal area rather than stem density. Effects of background beetle population size may affect attack success on neighboring trees, confounding the results from studies including tree distance.

The New Jersey Department of Environmental Protection has aggressively suppressed SPB north of the Mullica River in New Jersey, resulting in few large infestations in the northern Pinelands. However, as the suppression program draws to a close, the northern Pinelands may be at greater risk of SPB infestation. Stands in the north, on average, are comprised of smaller trees, at a closer distance to one another, and

are more likely to be pure rather than mixed conifer (Fig. 5, Table 4)—all characteristics that place stands at greater risk of infestation. SPB shows no sign of retreating in the near future, and indeed seems likely to continue its northward expansion into New England. The northern Pinelands, and stands in the New England states with similar structural characteristics, are particularly at risk of infestation so long as local SPB populations remain at outbreak levels.

As forest resource managers north of the current SPB range expansion boundary prepare to deal with a potentially new pest insect, it is helpful that risk from SPB in the recently invaded New Jersey Pinelands varies with stand structure in about the same way as the relatively well-studied forests of southern yellow pines. This supports the argument that management tactics that have been effective at limiting SPB impacts in the south could be similarly effective in the newly occupied range. These include monitoring to detect early population increases, rapid active suppression of spots when they are still rare, and silvicultural thinning for prevention (Clarke et al., 2016; Nowak et al., 2015). We found that general ecological principles of insect-tree interactions—and known elements of those interactions in our system in particular—could be readily applied to a forest system that has been newly colonized by a pest that had been studied elsewhere. The majority of the data we collected were variables already well-known to forest managers, and are also among those most easily obtained. Many previous models of risk for SPB, for example, included radial growth increment (Birt, 2011), a time-consuming variable to measure when trying to design a rapid management response to a new pest insect.

There would be value in developing a next generation of forest risk models that combine measurements of beetle abundance with knowledge of forest structure across landscapes. Beetle population numbers have been tracked across the south for many years, and have been successfully used to assist managers in assessing outbreak risk in a given summer season (Billings and Upton, 2010), but these numbers have yet to be successfully combined with forest structure risk models.

An important general question that can be asked of invasions or range expansions of any forest pest is whether old pests in new places are having a *disproportionate* impact on forests in their new habitat. Comparisons of damage with respect to forest structure between the new and historical ranges is one potential means of evaluating this question. The answers will become increasingly important as climate change, land-use, and trade continue to impact the ranges of both native insects and their host species.

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Table 1. Forest stand characteristics and the mechanisms of their influence on host susceptibility.

<b>Tree/Stand Characteristic</b>	<b>Mechanism of influence on stand susceptibility</b>	<b>References</b>
Stem density*	Distance between hosts--beetle flight	Gara and Coster 1968, Johnson and Coster 1978
	Resource availability (among trees)--tree vigor and/or tree defenses	Lorio 1986
Basal area*	Resource availability (among trees)--tree vigor and/or tree defenses	Lorio 1986
	Distance between hosts--beetle flight	Showalter and Turchin 1993
Percent pine	Distance between hosts--beetle flight	Gara and Coster 1968, Showalter and Turchin 1993
Site moisture/Site index	Resource availability (within stand)--tree vigor and/or tree defenses (GDBH)	Lorio 1986
Percent canopy cover	Plume integrity and concentration	Vite 1970
DBH/Height	Stand age/size	Lorio 1978
Age	Distance between hosts--beetle flight (distance increases as stand ages)	Ylioja et al. 2005
	Stand age/size	Lorio 1978

\* Stand density (trees/ha) and basal area (m<sup>2</sup>/ha) are sometimes conflated in the literature, but as a measure of cross-sectional area, high basal area can arise from high densities of small trees, or lower densities of larger trees. Throughout this work, we describe tree or stem density in terms of distances among trees (low nearest neighbor distances = high density), as distinct from basal area.

Table 2. Correlation matrix of measured forest structure variables for a) southern plots (both infested and uninfested) and b) northern plots.

a.

	1	2	3	4	5	6	7	8	9	10	11	12
1. DBH (diameter at breast height)	1.00											
2. Pine basal area	-0.60	1.00										
3. Hardwood basal area	0.60	-0.46	1.00									
4. Total basal area	-0.13	0.68	0.32	1.00								
5. Percent pine	-0.65	0.75	-0.89	0.07	1.00							
6. Crown base height	0.55	-0.06	0.73	0.52	-0.52	1.00						
7. Percent live crown	0.02	-0.28	-0.44	-0.63	0.15	-0.69	1.00					
8. Nearest neighbor distance	0.76	-0.77	0.57	-0.33	-0.77	0.30	0.23	1.00				
9. Second nearest neighbor distance	0.74	-0.81	0.54	-0.40	-0.77	0.27	0.27	0.91	1.00			
10. Age	0.83	-0.49	0.50	-0.11	-0.55	0.45	0.07	0.67	0.61	1.00		
11. Height	0.78	-0.32	0.68	0.21	-0.62	0.84	-0.22	0.60	0.57	0.70	1.00	
12. Percent canopy	-0.04	-0.06	0.25	0.14	-0.23	0.07	-0.16	-0.05	-0.04	0.08	-0.01	1.00

b.

	1	2	3	4	5	6	7	8	9	10	11	12
1. DBH (diameter at breast height)	1.00											
2. Pine basal area	-0.51	1.00										
3. Hardwood basal area	0.61	-0.62	1.00									
4. Total basal area	-0.30	0.93	-0.29	1.00								
5. Percent pine	-0.73	0.69	-0.96	0.39	1.00							
6. Crown base height	0.47	0.17	0.44	0.40	-0.32	1.00						
7. Percent live crown	0.00	-0.59	-0.07	-0.74	-0.07	-0.84	1.00					
8. Nearest neighbor distance	0.86	-0.48	0.54	-0.34	-0.64	0.29	0.17	1.00				
9. Second nearest neighbor distance	0.84	-0.67	0.59	-0.55	-0.71	0.17	0.33	0.93	1.00			
10. Age	0.89	-0.31	0.48	-0.15	-0.54	0.63	-0.23	0.76	0.70	1.00		
11. Height	0.83	-0.35	0.64	-0.14	-0.62	0.76	-0.30	0.73	0.71	0.86	1.00	
12. Percent canopy	-0.19	0.11	0.16	0.23	-0.14	-0.03	-0.15	-0.46	-0.41	-0.31	-0.33	1.00

Table 3. Loading matrix for the two principal component axes shown in Figure 7.

Variable	PC1	PC2
DBH (diameter at breast height)	0.89	-0.15
Height of codominant trees	0.86	0.18
NND (nearest neighbor distance)	0.86	-0.38
SNND (second nearest neighbor distance)	0.85	-0.41
Hardwood basal area	0.84	0.37
Height of the live crown base	0.72	0.61
Age of codominant trees	0.64	-0.27
Percent canopy closure	0.25	0.39
Total basal area	0.03	0.91
Percent live crown	-0.28	-0.85
Pine basal area	-0.71	0.54
Percent pine	-0.90	-0.10
cumulative % explained	50.70	75.30

Table 4. Means and standard deviations for measured forest structure variables.

	Northern Uninvaded	Southern Uninfested	Southern Infested
DBH (diameter at breast height, cm)	26.17 $\pm$ 4.41	32.39 $\pm$ 6	28.87 $\pm$ 5.96
Pine basal area (m <sup>2</sup> /ha)	24.01 $\pm$ 5.49	14.91 $\pm$ 7.1	21.8 $\pm$ 7.49
Hardwood basal area (m <sup>2</sup> /ha)	1.33 $\pm$ 1.76	10.69 $\pm$ 6.71	9.64 $\pm$ 6.47
Total basal area (m <sup>2</sup> /ha)	26.65 $\pm$ 4.66	27.43 $\pm$ 6.84	32.93 $\pm$ 7.53
Percent pine	89.32 $\pm$ 7.91	54.85 $\pm$ 21.06	65.94 $\pm$ 15.32
Crown base height (m)	7.68 $\pm$ 2.28	9.92 $\pm$ 3.03	10.6 $\pm$ 2.55
Percent live crown	47.32 $\pm$ 10.25	43.36 $\pm$ 9.54	34.9 $\pm$ 7.72
Nearest neighbor distance (m)	2.83 $\pm$ 0.1	4.23 $\pm$ 0.12	3.1 $\pm$ 0.12
Second nearest neighbor distance (m)	4.3 $\pm$ 0.06	6.65 $\pm$ 0.07	0.19 $\pm$ 0.09
Age	82.4 $\pm$ 22.83	84.88 $\pm$ 24.19	69.94 $\pm$ 23.52
Height of codominant trees (m)	14.54 $\pm$ 2.48	17.35 $\pm$ 3.31	16.45 $\pm$ 3.11
Percent canopy closure	68.49 $\pm$ 6.17	77.65 $\pm$ 7.82	74.16 $\pm$ 4.18

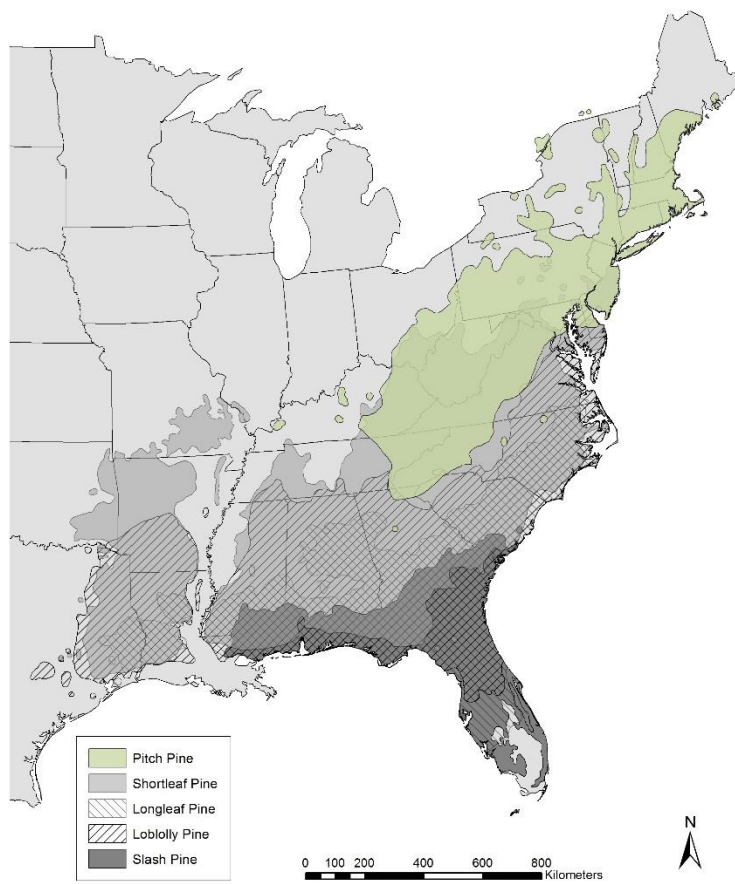
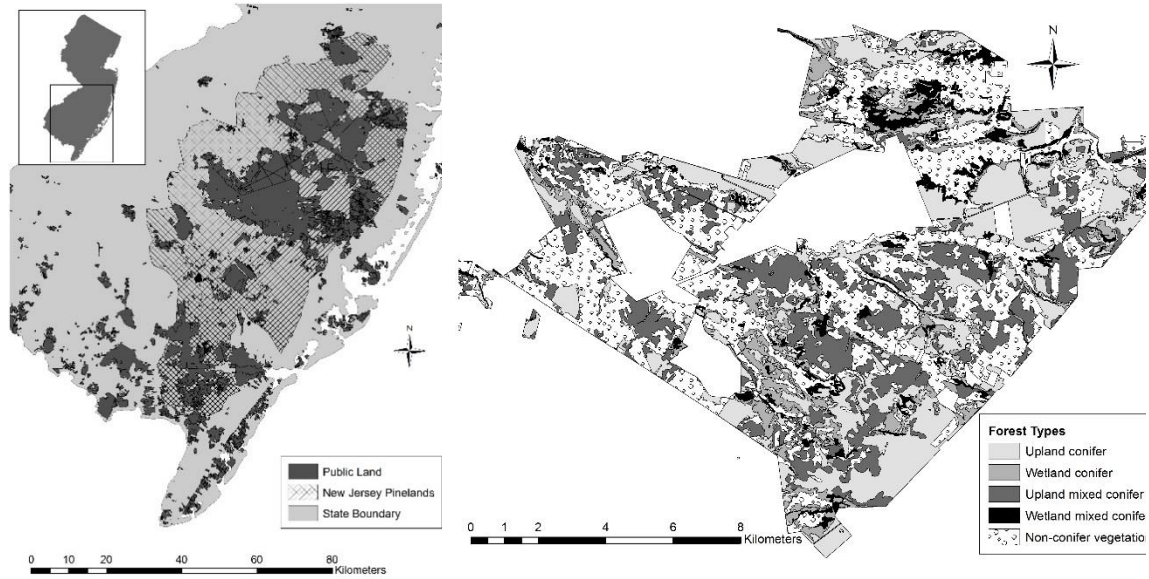


Figure 1. Distributions of primary SPB host species across the eastern U.S.



a)

b)

Figure 2. a) Map of southern New Jersey, showing land in public ownership against the boundary of the federally demarcated Pinelands. b) Sample land use land cover forest type map, showing the boundary of Brendan Byrne State Forest and the four forest types used in the analysis.

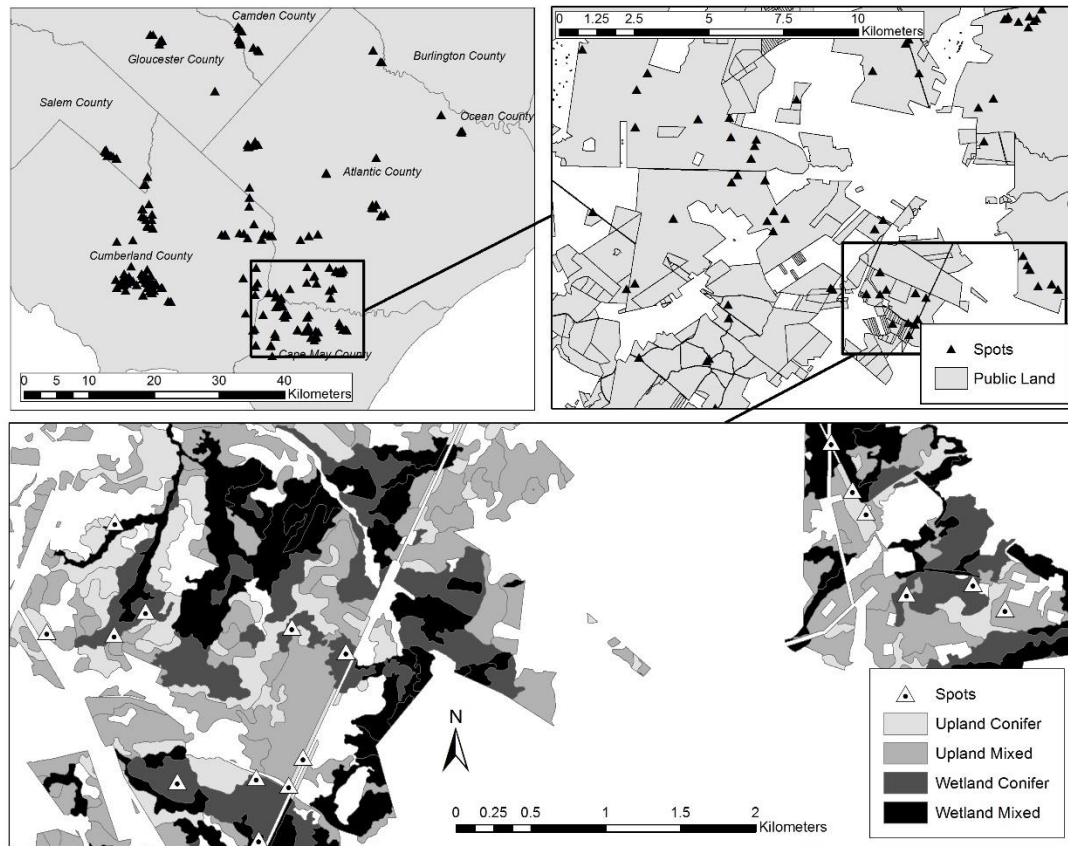


Figure 3. Spot locations for GIS analysis, including all spots aerially detected and ground-truthed by NJFS 2011-2013 (top left), zoomed area shows relationship between spot locations and public land (top right), and selected area shows relationship of spots to forest types (bottom).



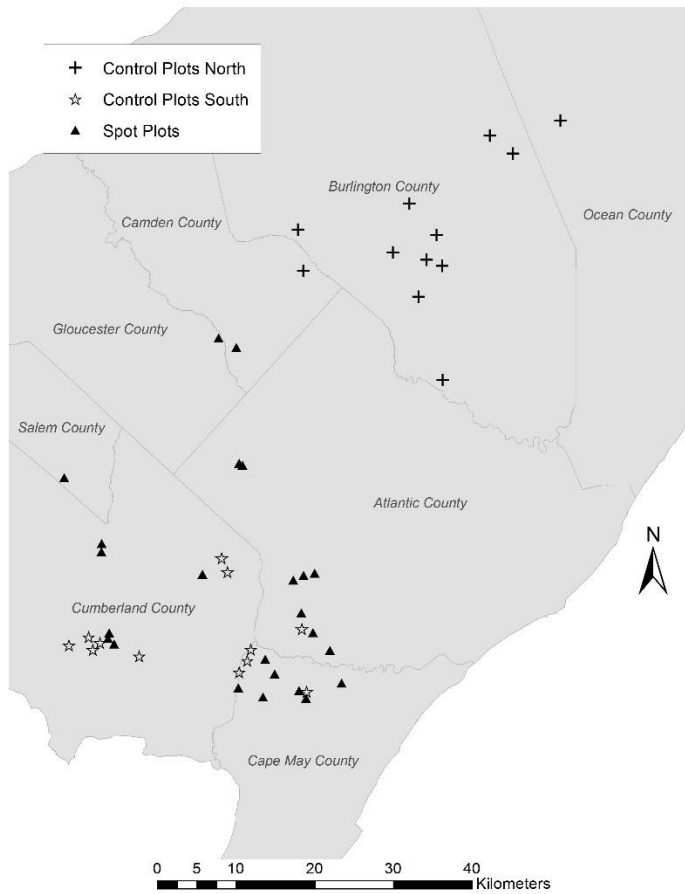


Figure 4. Locations of control and spot plots where forest structure data was collected.

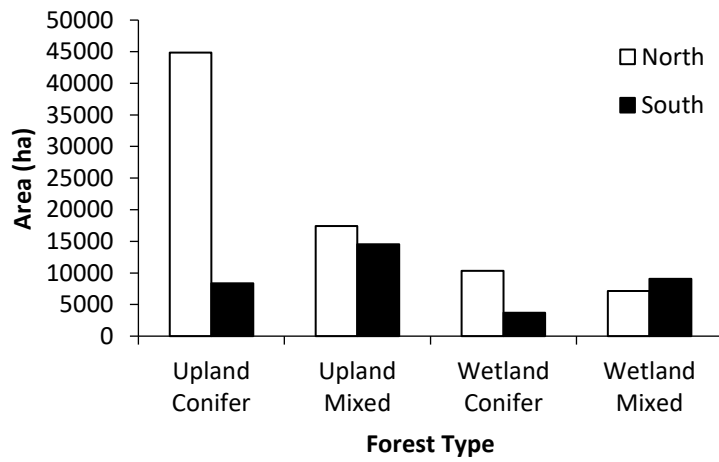


Figure 5. Regional distribution of area in hectares of each forest type.

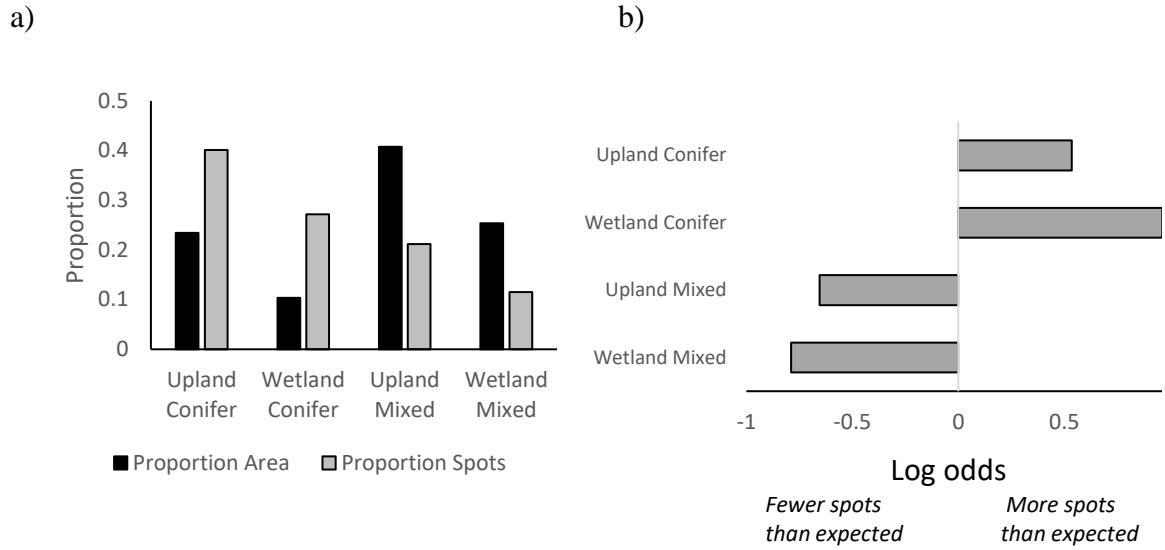


Figure 6. a) Comparison of land area in each forest type with number of spots in each forest type, within the southern region. b) Log odds of number of spots per forest type, based on land area per forest type.

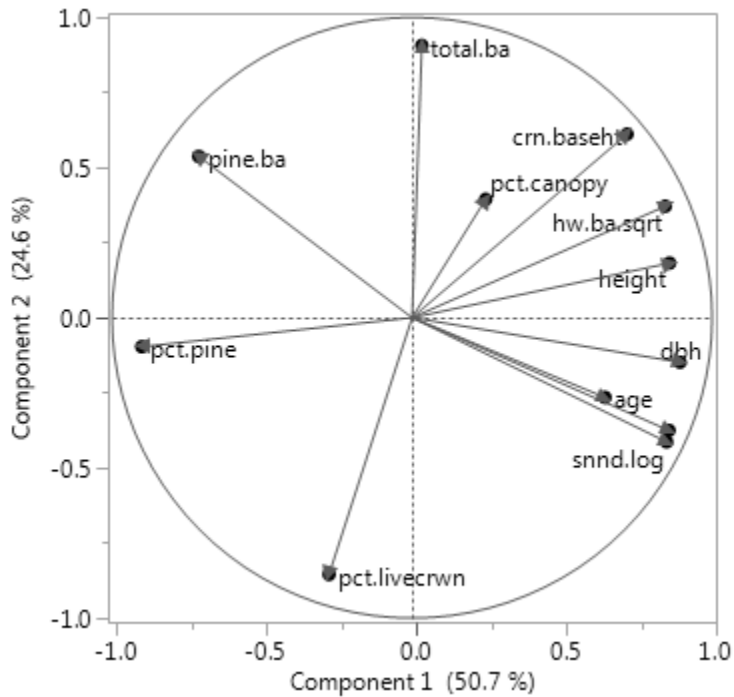


Figure 7. Biplot showing distribution of variables along principal components one and two as measured in 36 forest plots south of the Mullica River.

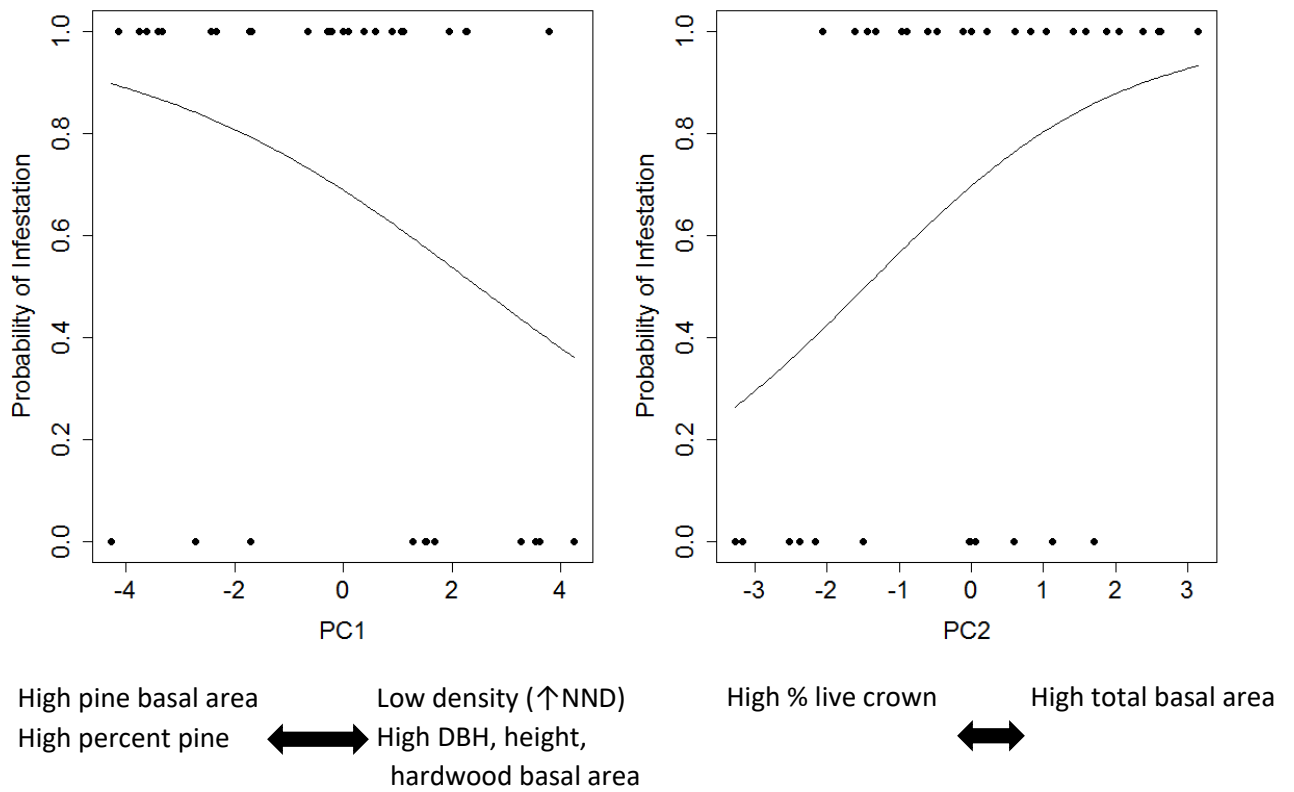


Figure 8. Logistic regression curves of infested vs. not infested status on principal components one (left) and two (right). Descriptors below the x-axis depict variables according to their position on each component, as shown in Figure 7 above.

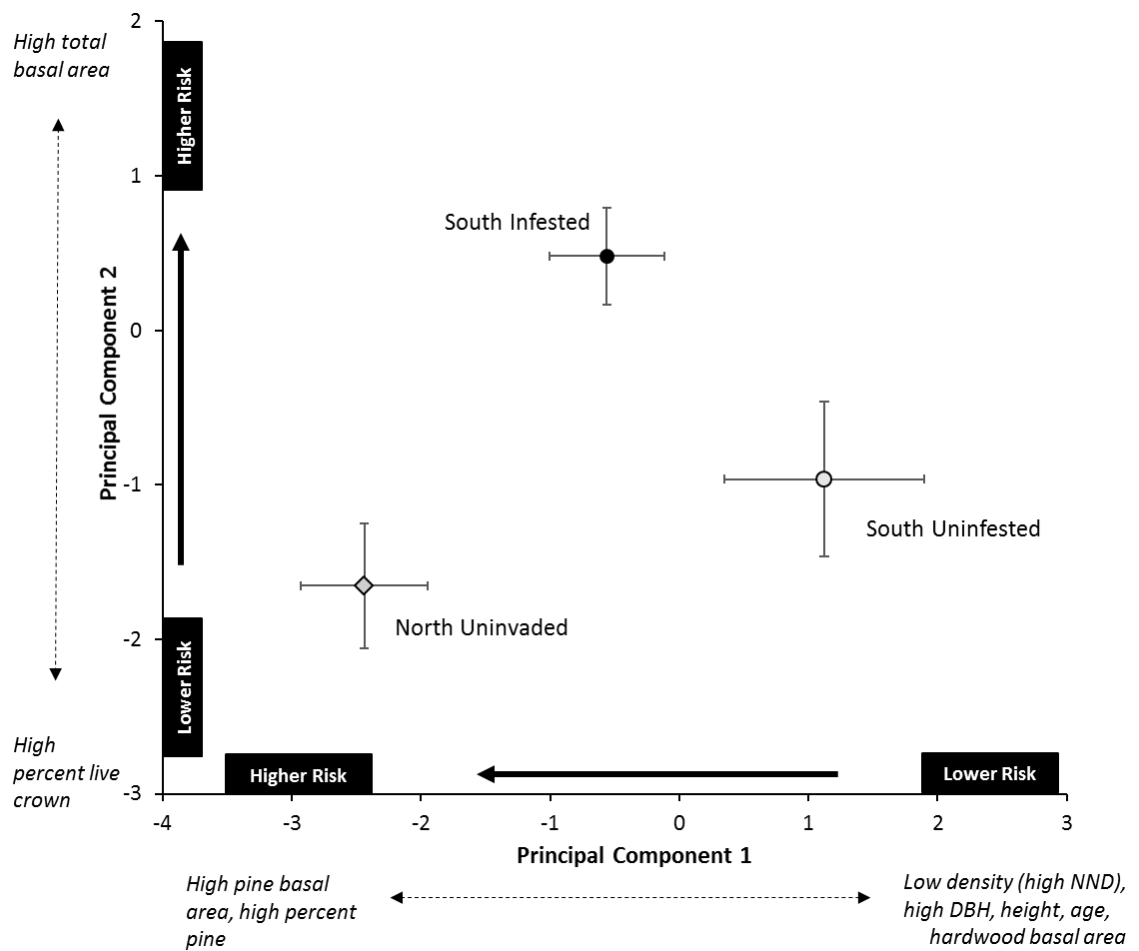


Figure 9. Means and standard errors from PCA of southern region uninfested and infested forest structure plots. The location of the still largely uninvaded northern Pinelands in this multivariate space of stand structure was calculated using the eigenvectors of the PCA of southern stands. In the southern Pinelands, stands infested with SPB tended to be dominated by pine and have high total basal area (negative PC1 and positive PC2 respectively). The northern stands are at comparatively higher risk along PC1, with higher average percent pine and pine basal area, as well as higher density and smaller trees, but they are also at lower risk along PC2, including lower total basal area.

## Chapter Two

### Oleoresin defenses in pines:

#### Finding landscape-scale proxies for risk of bark beetle attack

##### Abstract

Pine trees and their native pest insects have a long co-evolutionary history, of which one major feature is resin production for defense. For insects with irruptive population dynamics that result in widespread tree mortality, managers need to make decisions about which stands should receive priority in terms of risk and possible treatments. Assessing resin defenses in the field, however, has never been readily translatable to stand and landscape scales. Here we use the southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) system to ask whether broader-scale proxies can be found for tree defenses. Plant defense theory provides a framework within which such proxies may be identified via the physiological responses of the plant to environmental conditions such as resource availability. Previous work in the southern U.S. has provided significant evidence that resin flow in loblolly pine (*Pinus taeda*)—a primary SPB host species—tends to conform to the growth-differentiation balance hypothesis. The hypothesis states that moderate drought or nutrient deprivation leads to allocation toward secondary metabolism including resin production, whereas ample resources lead to allocation toward plant growth; severe resource deprivation leads to a decline in both growth and defenses. An alternative hypothesis is the plant stress hypothesis, which predicts that plants with high resource availability and growth also have high defenses. The New Jersey Pinelands recently experienced an SPB outbreak, well north of locations where regular outbreaks previously occurred. The primary pine species in New Jersey, pitch pine (*P. rigida*), is also less well-represented across the south, and has rarely been the

subject of SPB research. We tested several easily measurable features of pitch pine stands against resin flow: soil type, wetland or upland site type, site index, and stand density. Soil type produced differences among stands, but not for reasons supported by either hypothesis; we did not find the predicted relationship between soil drainage and resin flow. Between wetland and upland site types, resin flow was significantly higher in wetland sites, which supports the idea that sites with ample resources encourage both growth and defense. Stand density showed a significant negative correlation with defenses. Although the mechanism for this is not well-understood, this also tends to support the plant stress hypothesis; stands with less competition may have more resources per tree. Site index was not a significant predictor in either New Jersey or in loblolly pine stands in Louisiana. Unlike southern pine species, defenses in mid-Atlantic pitch pine appear to be better predicted by the plant stress hypothesis, with wetland site type and low density of pines as indicators of well-defended stands. We also compared resin flow in pine species that occur across the eastern United States, including northern species that have historically been outside SPB's native range. Loblolly and longleaf pine (*P. palustris*), whose ranges directly overlap with SPB, had by far the highest resin flow of all the species tested. Pitch and white pines (*P. strobus*) were intermediate in resin production, and the most northerly jack and red pines (*P. banksiana*, *P. resinosa*) had the lowest resin flow. It remains to be seen whether SPB's range expansion will take it far enough north to have an impact on these latter species, but if so they are not as well-defended as their southern counterparts.

## Introduction

Bark beetles in the genus *Dendroctonus* (tree-killing), particularly those with eruptive life histories, can cause thousands of hectares of mortality in a single outbreak. The conifers that serve as their host species are long-lived organisms, living tens, hundreds, sometimes even thousands of years. With escape not available as a defensive option, these trees have evolved an array of strategies to combat their natural enemies. Theories of plant defense have tried to elucidate the relationships among plants, herbivores, and the effect that resources available in the environment might have on the relative efficacy of defenses. Because of their basis in plant physiology, testing these theories tends to occur at the level of individual plants or groups of plants. Bark beetle outbreaks, however, occur across scales, from host selection of an individual tree, to region-wide mortality events across many stands of trees (Raffa et al., 2008). How are we to understand the role of tree defenses across these scales? Outbreaks can cause widespread economic (Cohen et al., 2016; Holmes, 1991; Pye et al., 2011) and aesthetic or cultural damage (Boyd et al., 2013), necessitating stand- and landscape-scale tools for resource managers to assess forest risk or susceptibility to bark beetle outbreaks. Here we use the southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) system to explore two questions: 1) Are there landscape-level predictors of resin defenses that can be used to identify stands at risk? and 2) As beetles move beyond their traditional host ranges, will they encounter pine species that are less well defended than southern pines that have a long evolutionary history with the highly aggressive SPB?

SPB is a pine bark beetle native to the southeastern United States, parts of the southwest, and south through Mexico to the mountains of Honduras. Because of its

economic importance, SPB has been intensively managed and studied over the past half-century (Clarke et al., 2016; Price et al., 1992); a Web of Science search for “southern pine beetle” or “*Dendroctonus frontalis*” over the years from 1950 to the present yields over 900 research articles. In recent years, however, SPB has declined across the south (Clarke et al., 2016), while appearing in outbreak numbers across the New Jersey Pinelands (New Jersey Department of Environmental Protection, unpublished data). The Pinelands comprise over a million acres of federally protected forest in central and southern New Jersey, which had not seen an outbreak since the 1930s (Wilent, 2005). In the fall of 2014, SPB was detected for the first time on Long Island, New York (Schlossberg, 2014), and since then small numbers have been trapped in Connecticut, Rhode Island, and Massachusetts (Kevin Dodds, unpublished data). Tree mortality in both New Jersey and Long Island has been severe (Hassett et al. 2015, New Jersey Department of Environmental Protection, unpublished data).

In pine trees, oleoresin exudation provides a first-line defense against bark beetles attempting to make their way into the phloem, where they will make their egg galleries and reproduce. The physical properties of tree resin have long been known to affect bark beetle success in colonizing their host trees (Hodges et al., 1979; Reeve et al., 1995; Webb, 1906). These resin defenses can vary widely among stands, and among individual trees within stands (Mason, 1969). Some of this variation is genetic (Byers, 1995; Strom et al., 2002), but resin flow has also been related to water and nutrient availability (Lombardero et al., 2000; Reeve et al., 1995), as well as other disturbances such as fire (Lombardero and Ayres, 2011). From a management standpoint, it makes sense to assess stand-level tree defenses as part of an overall risk management strategy. Measuring resin



defenses in individual trees, however, is labor-intensive and thus impractical for broader scale risk assessment. We used plant defense theory to test whether there might be easily measurable stand-scale variables that could be utilized to predict variation in defenses across a landscape.

Plant defense theory has a long and storied history (reviewed in Coley et al. 1985, Tuomi 1992, Herms and Mattson 1992, Stamp 2003, Agrawal 2007). One intuitive theory, the plant stress hypothesis (PSH), posits that environmentally stressed host plants lead to better insect performance, or conversely, that more vigorous or faster-growing plants decrease insect performance (Christiansen et al., 1987; Koricheva et al., 1998; Larsson, 1989). The PSH, in its broadest definition, relates all forms of plant stress to all forms of insect performance. Here we consider solely the relationship between environmental stress, the expression of tree defenses, and by implication, bark beetle attack success. In this narrower view, the PSH may be viewed as one among several extensions of the optimal defense hypothesis (Stamp, 2003), which relates the allocation costs of defense to the evolved risk of herbivory experienced by a given plant species. Although there has been extensive discussion in the literature about conflicting tests of the PSH (Huberty and Denno, 2004; Koricheva et al., 1998; Larsson, 1989), the idea that drought-stricken trees lose their capacity for defense persists in modern media coverage of large-scale insect outbreaks (e.g., Rosner, 2015). An alternative hypothesis is the Growth Differentiation Balance Hypothesis (GDBH), which suggests a nonlinear relationship between plant stress and defense capability. Botanists were still elucidating the primary chemistry of plants when Loomis (1932) first posited the theory. Given that plants cells exist in two broad phases: growth (including both cell division and cell

enlargement) and differentiation (including all chemical and morphological changes in mature cells, such as the production of secondary metabolites used in plant defenses), Loomis postulated that growth was largely driven by moisture and nutrients, and that when environmental conditions were favorable, the growth phase would be favored, whereas conditions limiting either moisture or nutrients would shift plant development into the differentiation phase. In other words, moisture or nutrient deficits limit growth, but not photosynthesis, whose products may then be allocated to the secondary metabolites that comprise plant defenses. Lorio (1986) drew upon this work to suggest that the growth-differentiation balance hypothesis might explain seasonal variation in resin defenses produced by pine trees subject to southern pine beetle attack. In this framework, host trees should be more susceptible to beetle attack in the spring, before seasonal water deficits have begun. During this period, trees have ample access to moisture and nutrients required for growth, and photosynthesis produces growth rather than defense compounds. Later in the season, as moisture becomes less available, the carbon produced by photosynthesis is allocated less toward growth and more toward resin defenses, so that host trees become less susceptible to beetle attack. New initiations of SPB infestations decline over the season (Billings 1979), supporting the hypothesis, and extensive research in both the seasonal physiology of southern pines and SPB population dynamics provide further lines of evidence (see Lorio (1986) for details). Reeve et al. (1995) subsequently showed experimentally that greater resources in the form of precipitation can reduce resin defenses in loblolly pine, the most common host of SPB in the southern U.S. Similar results were obtained with the addition of fertilization treatments (Lombardero et al., 2000; Warren et al., 1999). Reeve et al. (1995) also

provided experimental evidence that SPB attack success declines with increased resin flow. The connection between environmental conditions, resin flow, and host susceptibility has thus been widely supported within the southern pine/SPB system. Here we ask whether this work can be extended by determining whether environmental conditions as measured at the stand and landscape level can be used as a proxy for assessing host susceptibility at these broader scales. In addition, little is known about the defensive properties of pitch pine, the primary host species in the recent attacks in New York and New Jersey (but see Kim et al. 2010). As the SPB's range expands farther north and away from its traditional southern pine host species, knowledge of the defenses of pitch pine and other potential host tree species will be essential for forest management.

If the PSH holds true in pitch pine systems, we would expect the highest resin flow on sites with relatively high water availability on which pine trees grow the fastest. On the other hand, the GDBH would be supported if the reverse were true, i.e., if resin flow is highest on slow-growing sites or otherwise resource-poor sites. In either case, if consistent patterns can be found, soil and land cover maps, together with widely collected indicators of tree growth, could be used to predict landscape patterns in pine tree defenses. We tested three possibilities for such measurements in pitch pine stands: soil type, forest/site type, and site index. We additionally tested a fourth possibility, the stocking variables stand density and basal area. Although the GDBH has generally been borne out in southern pine systems, one exception is that thinned stands, which we assume have increased resources per tree in the stand, appear to produce higher resin flows (Mason, 1971; Matson et al., 1987).

Soil types within the New Jersey Pinelands have been intensively mapped in the USDA National Resource Conservation Service's SSURGO database (Soil Survey Staff, 2012), which we used to select study locations with different soil types. Pitch pine occurs on a wide range of soil moisture types, from poorly drained to excessively drained soils (Little and Garrett, 1990), which are reflected in the SSURGO soil type classifications. Each soil type is characterized by a number of different features, among them soil drainage. We assumed that soil drainage would affect the available moisture, and that soil type might therefore serve as a reasonable proxy of average moisture levels within the stand. The second possible stand measurement we tested was forest or site type. The majority of the forested land within the Pinelands is comprised of pitch pine and mixed pitch pine/oak stands. These stands occur within one of two floristic complexes within the Pinelands—upland and lowland. Lowland sites, also referred to as wetland sites, are those where the water table is either near or above the soil surface during some portion of the year. In upland sites, the water table may be 70 – 90 cm below the surface, and sometimes much deeper than that (McCormick, 1979). Soil maps overlap partly with the mapping of wetlands versus uplands, but neither could be used to reconstruct the other. Using New Jersey's land use/land cover data (New Jersey Department of Environmental Protection, 2010), we tested whether wetland versus upland site type might be correlated with resin flow values. We also tested whether traditional forestry measurements of tree growth could be used to predict resin flow. For this we used site index (Van Laar and Akça, 2007), which in the United States is usually defined as the typical height of co-dominant trees for a standard age, e.g., 50 yrs (Husch et al., 2002). Site indices have long been used by foresters because they provide a measure of tree growth and yield that

combines tree physiology, soils, and climate into a single variable that describes the suitability of a given site for a given tree species (Van Laar and Akça, 2007). We would expect site index, as a measurement of growth potential, to be positively correlated with resin defenses if the PSH applies in this study system, and alternatively, if the GDBH is supported, we would expect the correlation to be negative. Lastly, we tested whether stand density might be negatively correlated with resin flow. Although we did not have the opportunity to thin stands as in previous work demonstrating this relationship in southern pines (Mason, 1971; Matson et al., 1987), we used stand density as a proxy. A negative correlation between density and resin flow suggest support for the PSH, as individual trees would have greater access to light, as well as water and nutrient resources.

Because range expansion of SPB has already occurred in New York, and appears to be headed northward into New England, knowledge about how resin defenses vary among *Pinus* species that might be susceptible to SPB will also be an essential component of risk assessment in the northeastern states (Fig. 1; Little, 1971). Previous SPB research has taken place primarily in southern yellow pines, especially loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pines, while the primary SPB host species in New Jersey and New York has been pitch pine (*P. rigida*). Here we compared resin flow among different *Pinus* species that are susceptible to bark beetle attack in various locations within the United States, to determine whether some pines might be more resistant than others to attack by bark beetles. Research on stand-level differences in resin flow have largely been single species studies focused on among-stand variation (e.g., Lombardero et al. 2000, Cook et al. 2015, Hood and Sala 2015), but a recent study by

Arango-Velez et al. (2016) found some support for differing defense responses in lodgepole pine (*P. contorta*) and jack pine (*P. banksiana*) to *Grosmannia clavigera*, a fungal symbiont of mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Differences in resin characteristics, both physical and chemical, have also previously been tested among the four major southern yellow pines (Friedenberg et al., 2007; Hodges et al., 1979, 1977; Martinson et al., 2007), loblolly, longleaf, shortleaf (*P. echinata*) and slash (*P. elliottii*), but not in comparison with pitch pines or the pine species distributed farther north within the U.S.

## **Methods**

### *Study Site*

The New Jersey Pinelands, spanning forests in the south and central portions of the state, represent a unique state-federal partnership designed to preserve and protect over 1.1 million acres of land, the largest area of open space on the eastern seaboard between Richmond and Boston. Because the area was not designated for protection until 1978, the region is bifurcated by roads and towns, including 56 municipalities and nearly 500,000 residents. Although the majority of the land area is forested, it also includes significant agriculture, as well as Joint Base McGuire-Dix-Lakehurst. Close to half of the Pinelands area is in public ownership, with the majority of public land being owned by the State of New Jersey (State of New Jersey Pinelands Commission 2015). In addition, the state owns a number of forested tracts outside the federally designated Pinelands boundary. Because SPB management efforts fall almost exclusively on the state, we restricted our data collection and analysis to these public lands.

### *Soil Type and Resin flow*

We tested the hypothesis that soil type, through its effects on tree physiology, generates predictable spatial patterns in resin defenses that could influence susceptibility to SPB. Using the USDA National Resource Conservation Service's SSURGO database, we selected four study sites within each of the three soil types occurring in highest proportion under coniferous and mixed conifer forests (Soil Survey Staff, 2012). We divided the area north and south of the Mullica River into separate regions, for a total of six soil types, and 24 sites all together. The sites were located within Brendan Byrne State Forest, Peaslee Wildlife Management Area, and Belleplain State Park (Fig. 2). The three soil types in the northern region were: Atsion sand; Lakehurst sand; and Lakewood sand. The soil types in the southern region were: Berryland and Mullica soils; Hammonton sandy loam; and Aura sandy loam. Within their respective regions, the three soil types selected were those covering the largest relative area. At each site, we haphazardly selected 7 co-dominant pitch pines for measurement. We collected two measurements of resin flow per tree per sampling occasion. Measurements followed the methods of Martinson et al. (2007). A .5 inch diameter punch ( $\approx 1.25 \text{ cm}^2$ ) was used to remove the outer bark and phloem without damaging the xylem, and resin flow from the exposed xylem was captured over the next 24 h and weighed. Each site was sampled four times, in late August 2012, early and mid-July 2013, and September 2013; in most cases the same trees were used from year to year. We used a nested general linear mixed model to compare resin flow among plots and soil types, with soil type and date as fixed effects and random effects for trees (within plots and soil types) and plots (within soil types). All resin flow data throughout this study were square root-transformed for normality. At each

site we also measured basal area of pines and hardwoods, diameter at breast height (DBH), height, percent live crown, age, nearest neighbor distance, and density of pines calculated by the point-centered-quarter method (Cottam and Curtis, 1956) using trees >15 cm, i.e., those trees large enough to be susceptible to beetles. In addition, we tested whether the measurements related to stocking—basal area and density—were related to resin flow using linear regression. Basal area was square root-transformed and density was log-transformed to improve normality.

#### *Site type, resin flow, and phloem weight*

We tested a second measure of available moisture within stands, using wetland versus upland types. We used the Land Use Land Cover (LULC) dataset produced by the New Jersey Department of Environmental Protection (NJDEP) to select nine sites each in wetland and upland forest types in the southern region of the Pinelands (Fig. 3); SPB infestations occurred primarily in the southern region. The dataset uses color infrared photography to classify land cover types across the state (New Jersey Department of Environmental Protection, 2010). Resin flow data were collected as described above, and sampling occurred in August 2014. We tested for differences in resin flow between areas classified as wetland vs. upland sites with a nested mixed model that included site type as a fixed effect, and random effects for trees (within plots and site types) and plots (within site types). We also measured the dry weight of the phloem discs removed from each sample while collecting resin measurements, and tested the relationship between phloem weight and site type using the same nested, random effects structure.



### *Site index and resin flow*

In our New Jersey resin flow plots, we tested for relations between tree defenses and site quality for tree growth by measuring site index for pitch pine on each of the 24 sites across six soil types where we measured resin flow. Tree height information was collected by laser hypsometer from each of five co-dominant trees nearest to plot center, and each of five co-dominant trees nearest to a point randomly located at 50m distance from plot center. All ten trees were cored for age. We then estimated site index, or expected height at 50 years, using height vs. age curves for pitch pine (Illick and Aughanbaugh, 1930) to parameterize a site index equation, which we then used to calculate site index for each codominant pitch pine from each plot. We then aggregated these individual site indices to the plot level so that plot-level site indices could be compared with plot-level resin flow averages. A random effects model was used to assess variation in site index among trees within stands and among stands.

In Kisatchie National Forest, Louisiana, we used similar methods to calculate site index, using 6 codominant loblolly pine trees measured for age and height in each of eleven plots. Resin flow measurements were collected as described above, with two measurements on each of six trees per site. Vials were left in place for three hours. Data were collected in August 1997. Resin flow and age/height measurements were collected on the same trees, so a single mixed effects model was used to assess the relationship between site indices and resin flow, as well as the variation among trees and among stands.

### *Comparative resin flow data*

To compare resin flow among pine species, we used previous measurements of resin flow using the same protocol. These data were collected in Kisatchie National Forest, Louisiana (loblolly and longleaf pines; *P. taeda* and *P. palustris*; data collected in 2002 and 2003, with additional loblolly data collected in 1997), Colfax, Wisconsin (red pine; *P. resinosa*; data collected in 1998), Itasca, Minnesota (jack, eastern white, and red pines; *P. banksiana*, *P. strobus*, and *P. resinosa*; data collected in 1997 for jack and white pines, and 1998 for red pine), and Rocky Mountain National Park, Colorado (lodgepole pine; *P. contorta*; data collected in July 2011). Data from 2002 and 2003 in Kisatchie National Forest have been previously published (Martinson et al., 2007) and include five trees in each site, with three measurements taken per tree. Longleaf pine data were collected in nine sites in June and July of 2002, and in 10 additional sites in September of 2003; loblolly pine data were sampled in 10 sites in June and July of 2002, and 10 additional sites in September of 2003. 1997 loblolly pine data from Kisatchie National Forest include six trees in 11 sites, with two measurements per tree. Red pine data from Wisconsin and Minnesota include 10 trees in each of six sites, with two measurements per tree, and have been previously published (Ayres et al., 1999).

## **Results**

### *Soil type and resin flow*

There was a significant fixed effect of soil type ( $F_{5,90} = 10.60$ ,  $p < 0.0001$ ). However, results were contrary to predictions based upon the plant stress and growth-differentiation balance hypotheses: if the GDBH were true, for example, we would have

expected resin flow to be highest in soil types that less-easily retained water, i.e., in the well-drained soils. In fact, the soil type with the lowest average resin flow was a well-drained soil type. The resin flow was approximately similar among the three next lowest soil types, which represented one each of moderately-drained, well-drained, and poorly-drained soils; the soil type with the highest average resin flow was a moderately-drained soil (Fig. 4). There was some variation among seasons and years (resin flow was generally lower in September of 2013 than on other sampling occasions), but the relative position of different soil types and individual trees were quite repeatable across seasons and years. Variance in resin flow among individual trees within a plot was high, representing close to 60% of the total variance (Table 1).

Stand density of pines was significantly related to resin flow (slope =  $-0.18 \pm 0.08$ ,  $p = 0.04$ ,  $R^2 = 0.18$ ; Fig. 5), but basal area was not (slope =  $-0.09 \pm 0.08$ ,  $p = 0.09$ ,  $R^2 = 0.13$ ).

#### *Site type, resin flow, and phloem weight*

Mean resin flow in wetland sites was approximately twice as high as in upland sites ( $F_{1,16} = 6.90$ ,  $p = 0.02$ , Fig. 6). Measurements were highly repeatable. Over 50% of the variance in resin flow was among trees within sites, as opposed to among sites (5%) or within trees (42%). Phloem weight was significantly higher in wetland sites ( $F_{1,16} = 7.31$ ,  $p = 0.02$ ), with 87% of the variation among trees, and 13% among sites. Mean values per tree ranged from .03 - .14 g.

### *Site index and resin flow*

In pitch pine stands in New Jersey there was no effect of site index on resin flow ( $R^2 = 0.01$ ,  $p = 0.70$ , Fig. 7a). Site index was also unrelated to soil type ( $F_{5,13.09} = 0.16$ ,  $p = 0.97$ ). Plot-level site index means ranged from 6.88 – 15.75 m (at 50 yrs). Site indices were calculated from ages and heights per tree before averaging to the plot level; approximately 55% of the variance was explained by among tree variation, and 40% by among stand variation. Ages and heights both within and among stands were not consistently uniform; some stands were relatively even-aged while others were not, with standard deviations ranging from 3.5 – 33.7, and standard deviations among heights within a stand ranged from 1.0 – 5.7 m (SMFig. 1). Heights and ages of individual trees were significantly related, but with considerable variation about the line (SMFig. 2).

In loblolly pine in Kisatchie National Forest, there was also no effect of site index on resin flow ( $F_{1,54.08} = 0.05$ ,  $p = 0.83$ ; Fig. 7b); 72% of the variance was explained by among tree and sample variation, and 28% by among stand variation. We compared both the Kisatchie National Forest and New Jersey Pinelands results to previously published research in red pine in Itasca State Park, Minnesota and west central Wisconsin. Unlike the results from pitch and loblolly pines, the red pine stands showed a significant relationship between site index and resin flow ( $R^2 = 0.50$ ,  $p = 0.01$ ; Fig. 7c).

### *Comparative resin flow*

The two southern pines, longleaf and loblolly, had much higher resin flows than the other pine species in our survey (Fig. 8). The lowest flows were found in the more

northern and western species, red, jack and lodgepole pine, while white and pitch pines exhibited intermediate values.

## **Discussion**

We found that soil type was a significant predictor of resin flow. However, the mechanism of differences among types did not fit either of our hypotheses. If the plant stress hypothesis were true, we would have expected that poorly-drained soils, i.e., stands with better access to water resources, would have higher levels of resin defense, while well-drained soils would have lower levels of defense. If the growth-differentiation balance hypothesis were true, we would have expected the opposite response. In our test of the six most commonly-occurring soil types across both the northern and southern Pinelands, however, we found that the drainage types of each soil type did not correspond to the levels of resin flow, although there were significant differences among soil types. Although soil type may therefore serve as useful predictor of resin defenses for management purposes, the mechanism for these differences remains unknown.

In our test of upland versus wetland sites, we found that resin flow was significantly greater in the wetland sites. This suggests that the plant stress hypothesis is supported in that trees with ample access to water produce higher resin flows. The PSH may also be supported by our finding that trees in stands with lower densities of pines had higher resin flows. Although the mechanism for this is not well understood (Matson et al., 1987), we can assume that individual trees with less conspecific competition within stands may have better growing conditions, and thus better defenses under the PSH. Conversely, these results contradict the growth-differentiation balance hypothesis, which

predicts lower defenses in wetter sites. Site index had no relationship to resin flow on a stand-average basis in either New Jersey pitch pines or Louisiana loblolly pines, although previous work in red pine has shown that such a relationship may exist (Ayres et al., 1999). Although previous work in southern yellow pines over the past forty years has supported the growth-differentiation balance hypothesis on many fronts (Lombardero et al., 2000; Lorio, 1986; Reeve et al., 1995; Warren et al., 1999), the expected relationship between site index and resin flow did not occur in our studies in pitch or loblolly pine.

By using the readily available soil-type data from the Natural Resource Conservation Service's SSURGO database, we sought a stand-scale proxy that would predict stand-level resin flow so that tree defenses could be readily incorporated into a risk assessment strategy. Our study of stand density, forest/site type, and site indices was motivated by the same research goal. We found that mean resin flow does differ among soil types, showing that soil type may in fact serve as a useful proxy for differences in tree defenses among stands. However, the results did not match either of our hypotheses concerning the mechanism behind these differences, demonstrating that further research will be needed to match soil types to levels of resin flow. In both the New Jersey Pinelands and Kisatchie National Forest, site indices were not related to resin flow, again contradicting both the plant stress and the growth differentiation balance hypotheses, which predict a relationship between the level at which sites promote tree growth and the availability of resin defenses.

Wetland sites, however, did exhibit significantly higher resin flow than upland sites, so this simple two-way distinction between wet and dry site types in the Pinelands may form at least one component of a stand-based risk assessment in terms of tree

defenses. This is complicated, however, by our previous work which found that among conifer stands (>75% pine), wetland sites were actually more susceptible to infestation than would be expected given the proportion of that site type occurring on the landscape (chapter 1, this volume). In contrast, among mixed stands, wetland sites were less susceptible to infestation than expected. As a stand- or landscape-scale proxy for susceptibility, stand composition may override site type (and therefore tree defenses) as a predictor of risk. This could translate into a simple two-tier evaluation for stands at risk: pure conifer stands are at higher risk regardless of defenses, but in mixed stands, higher resin flows may provide some protection. In addition, our finding that trees in wetland sites tend to have thicker phloem may further explain increased susceptibility in wetland conifer stands due to improved habitat for beetle larvae. Increased phloem thickness has been shown to improve reproductive success in mountain pine beetle (Amman, 1972), another tree-killing bark beetle. Along with the variation in dry weights, our observation was that low phloem weights included wet widths thinner than the body width of an average beetle.

Unlike southern pine systems, which largely support the growth-differentiation balance hypothesis, our results in pitch pine in New Jersey tend to support the plant stress hypothesis, or the idea that trees with less stressed, better growing conditions may have improved tree defenses. Wetland sites and lower stand densities tend to result in higher resin flows per stand. These are both stand-level measurements that can be easily performed within any forest monitoring and risk assessment program, and thus may serve as good proxies for estimating tree defenses across a landscape. More work is needed to understand the mechanism relating soil type and resin flow, but our finding of significant

differences among types suggests this may also prove to be a useful proxy for tree defenses in the future.

As SPB moves northward beyond its traditional host range into the home ranges of a variety of other *Pinus* species, evolved levels of resin defenses may play an important role in the ability of these relatively naïve species to defend themselves against bark beetle outbreaks. Notably, our comparison of resin flow rates among different host species found that those with native ranges most closely associated with SPB—longleaf and loblolly—had the highest levels of resin defenses. A significant part of SPB life history includes: a) the mass-attack strategy, facilitated by pheromones, that allows beetles to overcome the defenses in live trees (Vité and Renwick, 1968), and b) the requirement that the tree's phloem contain enough moisture to support the symbiotic fungi that feed newly hatched beetle larvae; i.e., the tree must be at just the right edge between living and dead to provide the appropriate reproductive environment (Ayres et al., 2000; Vité and Crozier, 1968), or to put it more bluntly, the beetles must kill the tree to ensure this environment (Callahan, 1966; Raffa and Berryman, 1983). The idea of an evolutionary “arms race” between plant defenses and insect herbivores, in which insects develop tolerances for plant defensive compounds, and plants in turn evolve new mechanisms for defense, each competing for the ability to survive the other (Agrawal, 2007; Dethier, 1954; Ehrlich and Raven, 1964; Fraenkel, 1959), clearly applies to southern pine beetle. The native ranges of pitch and white pine and southern pine beetle do overlap at the southern edges of the former, and the northern edge of the latter, but not as completely as the ranges of loblolly and longleaf pines, which squarely overlap the



range of SPB. More northern species such as red pine and jack pine do not overlap the native range of SPB at all (Fig. 1). A recent re-evaluation of the phylogeny of *Pinus* species (Gernandt et al., 2005) found that the four major southern pines (loblolly, longleaf, shortleaf, and slash) are all found in the same subsection (*Australes*) of subgenus *Pinus*, and loblolly and pitch pine form even more closely related sister groups within their own clade nested within *Australes*. Jack pine and lodgepole pine are similarly closely related, but are found within subsection *Contortae*. All of the aforementioned species fall within section *Trifoliae*. Red pine occurs under section *Pinus*. White pine is yet more distantly related, occurring under subgenus *Strobus*.

Our comparison of resin flow among species found the highest resin flow in loblolly and longleaf pine, intermediate levels in pitch pine, and very low levels in red and white pines, suggesting that perhaps trees in environments with tree-killing, outbreaking species tend to have higher levels of resin defenses. Strom et al. (2002) found that first generation progeny of trees that escaped SPB attack during an outbreak had higher resin flow than a comparison general population, but that most of the chemical constituents of oleoresin did not differ between the populations. This supports the idea that levels of resin flow might be heritable, and also that higher flows may assist trees in escaping from beetle mortality, even in a bark beetle with a mass-attack strategy. The heritability of resin flow rates has also been experimentally shown in loblolly seedlings that were offspring of known parent trees (Roberds et al., 2003). It has further been shown that resin flows and successful SPB reproduction are inversely correlated (Reeve et al., 1995). Thus, the physical component of resin defenses, and their differences among pine species, may prove significant in potential outbreak levels as southern pine beetle

moves northward. The one exception to this general pattern of higher flows in trees where outbreaking bark beetles occur is the exceedingly low flow in lodgepole pine, which overlaps with the occurrence of mountain pine beetle and has experienced millions of hectares of mortality in the U.S. and Canada during the sustained outbreak of the 1990s and 2000s. There are some notable differences, however, between mountain and southern pine beetle. The former is univoltine, and infestations tend to spread across large landscapes, often remaining in one location over several years, while the latter is multivoltine, with infestations occurring in discrete spots that tend to kill all trees in a single location, with spots tending not to continue in subsequent years.

Pitch pine may be intermediate in its defense capabilities between well-adapted southern yellow pines and the more northerly—and potentially more susceptible—pine species. As SPB moves north, both white and red pine will fall increasingly within its range. During the recent outbreak in New Jersey, we observed just one major infestation in one of the many white pine plantations planted throughout the Pinelands by the Civilian Conservation Corps in the 1930s; we noted that the beetles even seemed to prefer the white pine to the surrounding pitch and loblolly pines, though they did not appear to successfully reproduce within the white pines they killed (personal observation). Although the most recent outbreak on Long Island, New York has been concentrated in the extensive pitch pine forests found there, SPB has also been found in the widely-planted non-native species Norway spruce (*Picea abies*) and Japanese black pine (*Pinus thunbergii*) (Hassett et al., 2015). More densely populated than SPB's native southern states, the northeastern U.S. is thus home to not only a different slate of native pines, but also a variety of non-native, planted conifers that are also proving to be

susceptible. In addition to more detailed work on the defenses of individual species, further work will be needed among species to determine relative risk across landscapes containing a mix of species.

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Table 1. Variance components, standard errors, and percent variance explained for random effects in resin flow model. Levels are listed in order of nesting.

Random Effect [nesting structure]	Variance Component	Standard Error	Pct of Total
Tree[Plot,SoilType,Date]	0.3865	0.0289	57.6
Plot[SoilType,Date]	0.0514	0.0204	7.7
SoilType[Date]	-0.0177	0.0067	0.0
Date	0.0439	0.0375	6.5
Residual	0.1888	0.0104	28.2
Total	0.6706	0.0493	100

Fixed effect of soil type:  $F_{5,14.89} = 30.46, p < 0.0001$

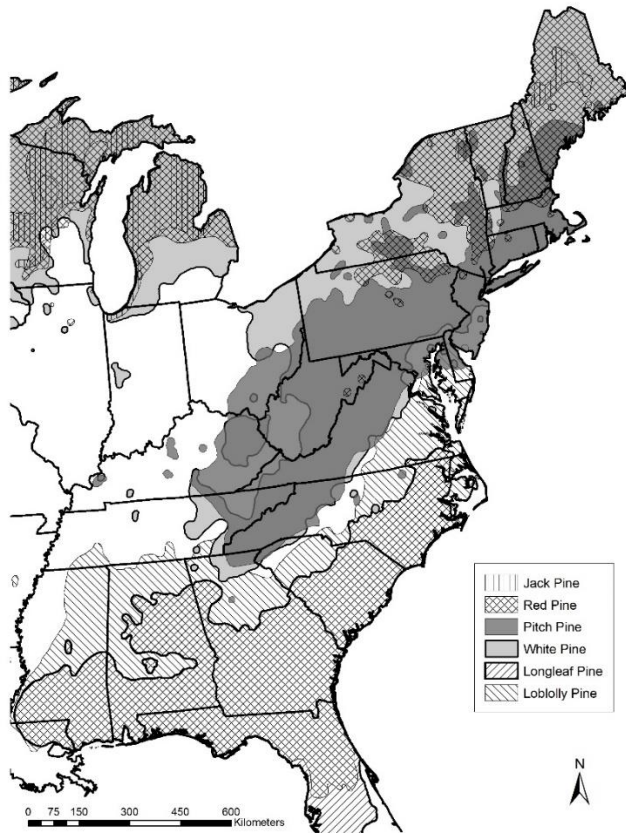


Figure 1. Ranges of pine species in the eastern United States. Data from the United States Geological Survey's Tree Species Range Maps, based on (Little, 1971), available for download at <http://gec.cr.usgs.gov/data/little/>.

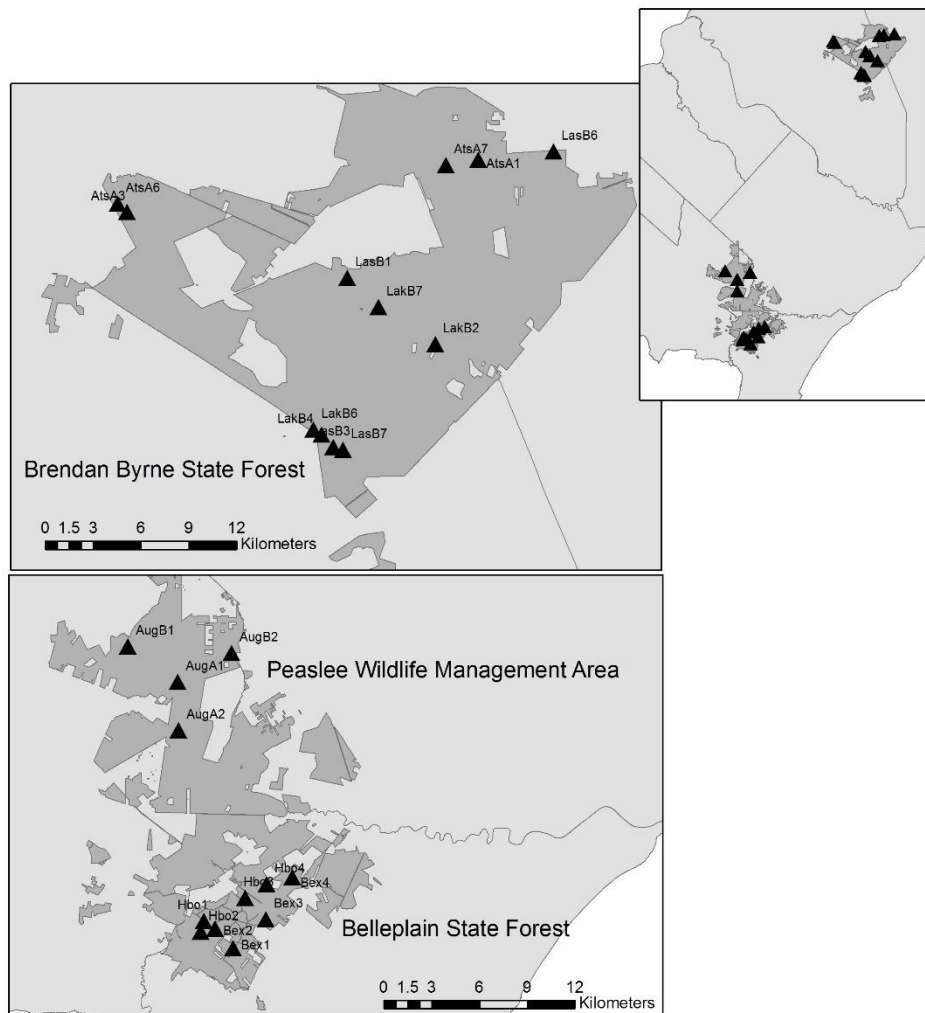


Figure 2. Location of resin sampling plots.

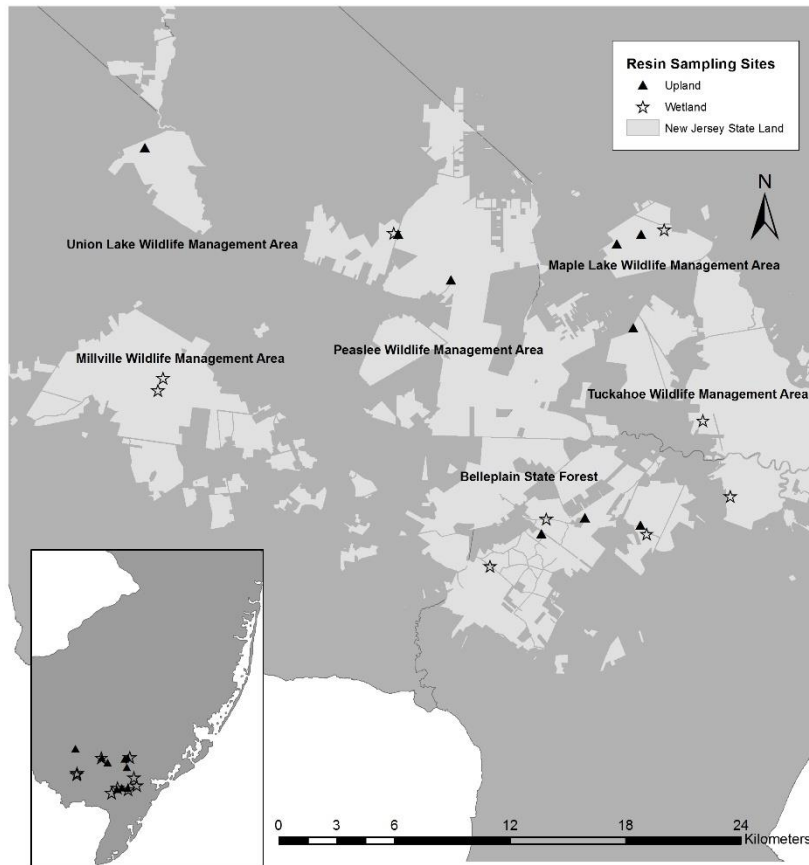


Figure 3. Wetland and upland resin sampling sites.

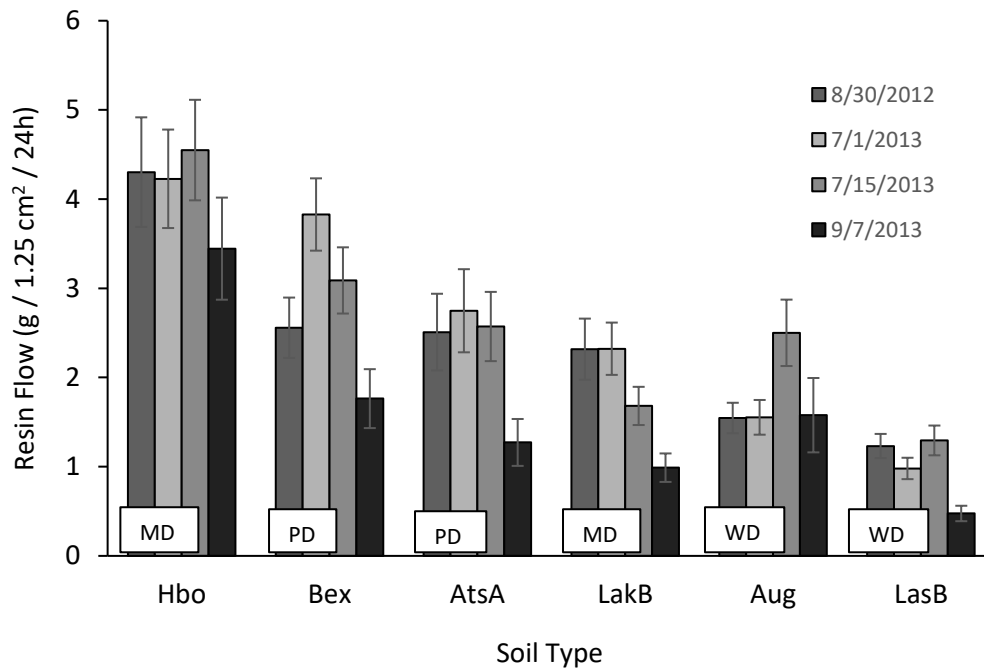


Figure 4. Mean untransformed resin flow with standard error, for six soil types across the Pinelands (MD = moderately-drained, PD = poorly-drained, WD = well-drained)

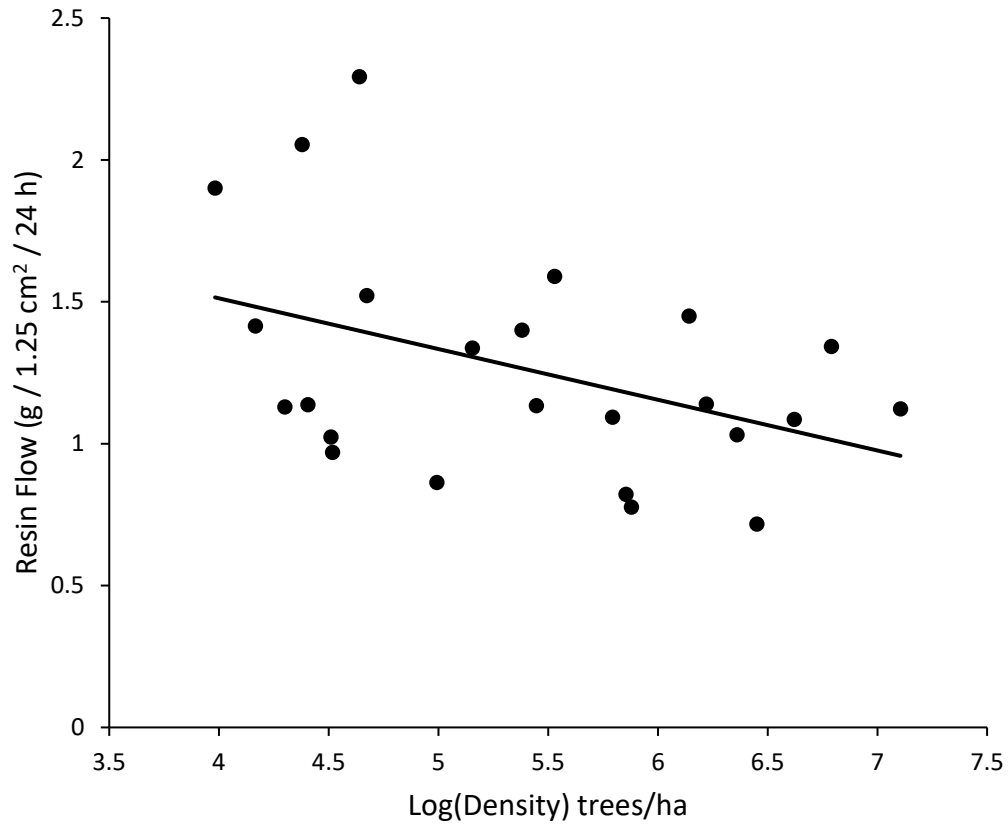


Figure 5. Stand-level resin flow means were significantly related to the number of trees per hectare. Y-axis shows square root-transformed data.

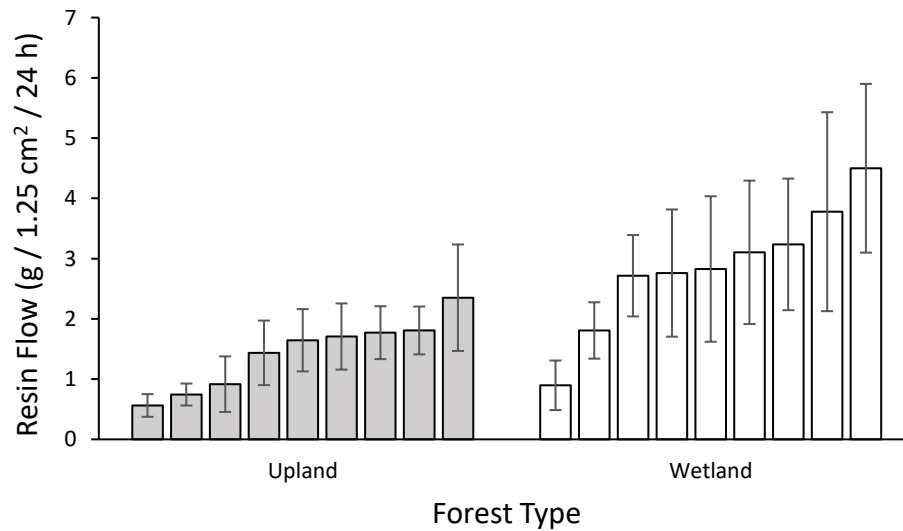


Figure 6. Mean resin flow with standard error in upland and wetland stands. Data shown are untransformed.

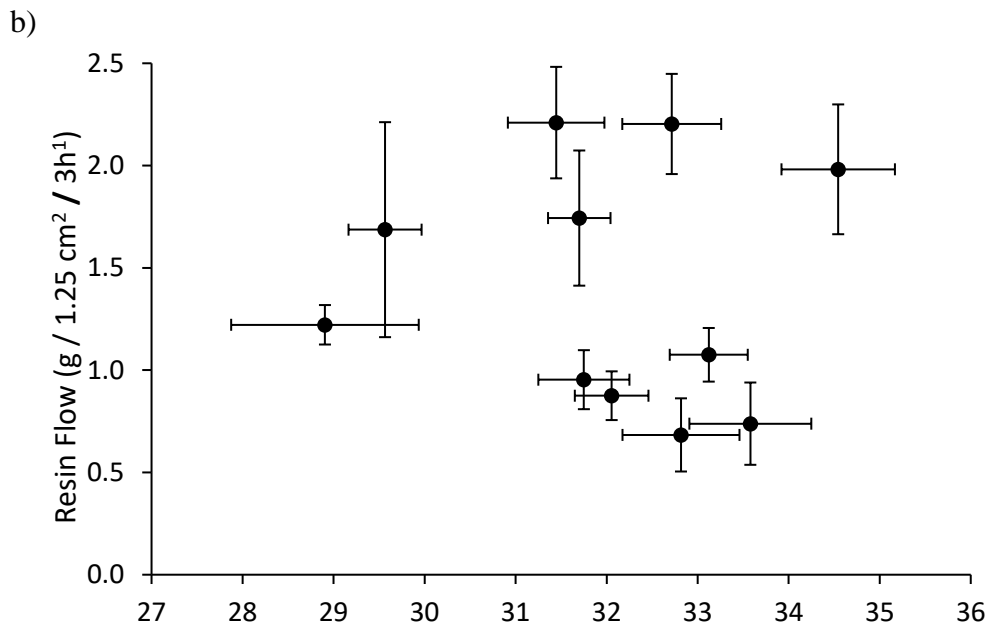
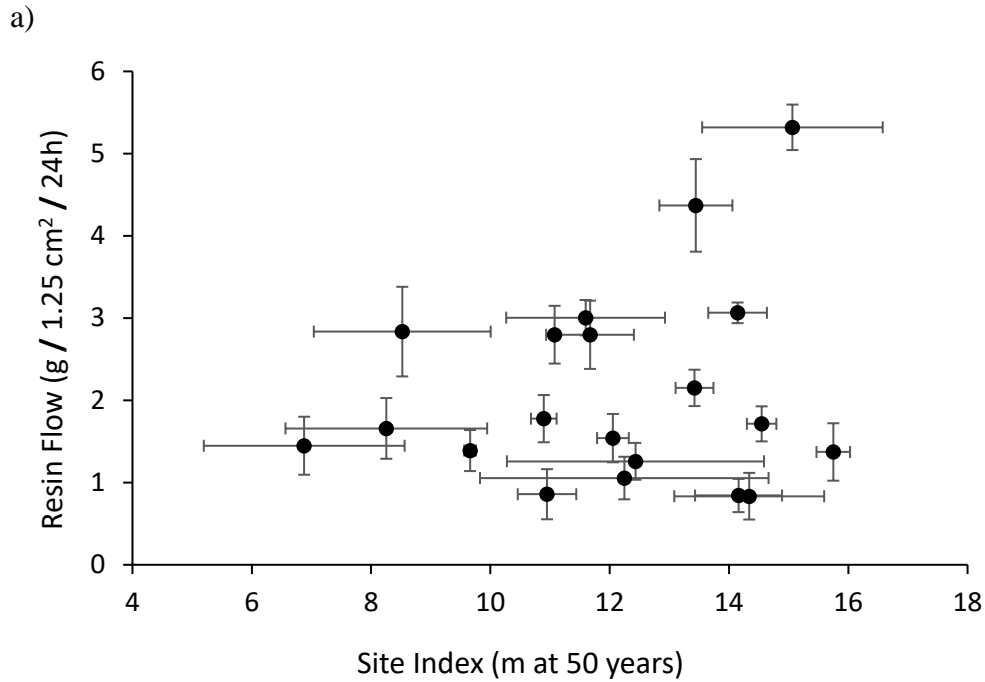


Figure 7. Mean site index and resin flow per plot for the following locations. Error bars indicated standard error, and resin flow values are shown untransformed. a) Pitch pine in the New Jersey Pinelands. The variables were not significantly correlated. b) Loblolly pine in the Kisatchie



National Forest, Louisiana. The variables were not significantly correlated. c) Red pines at Itasca, MN and in west central Wisconsin. The variables were negatively correlated.

c)

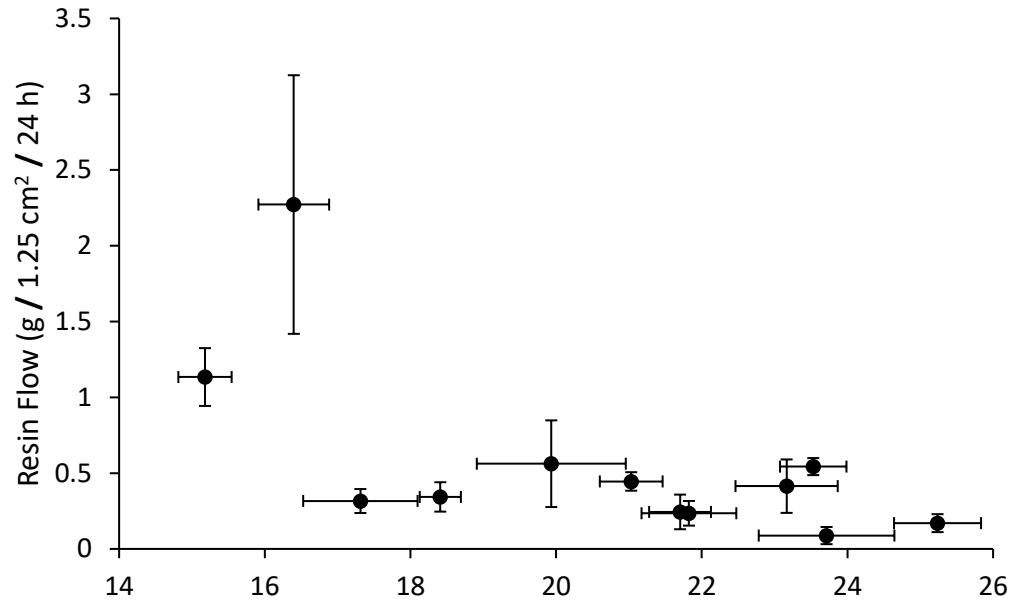


Figure 7, continued.

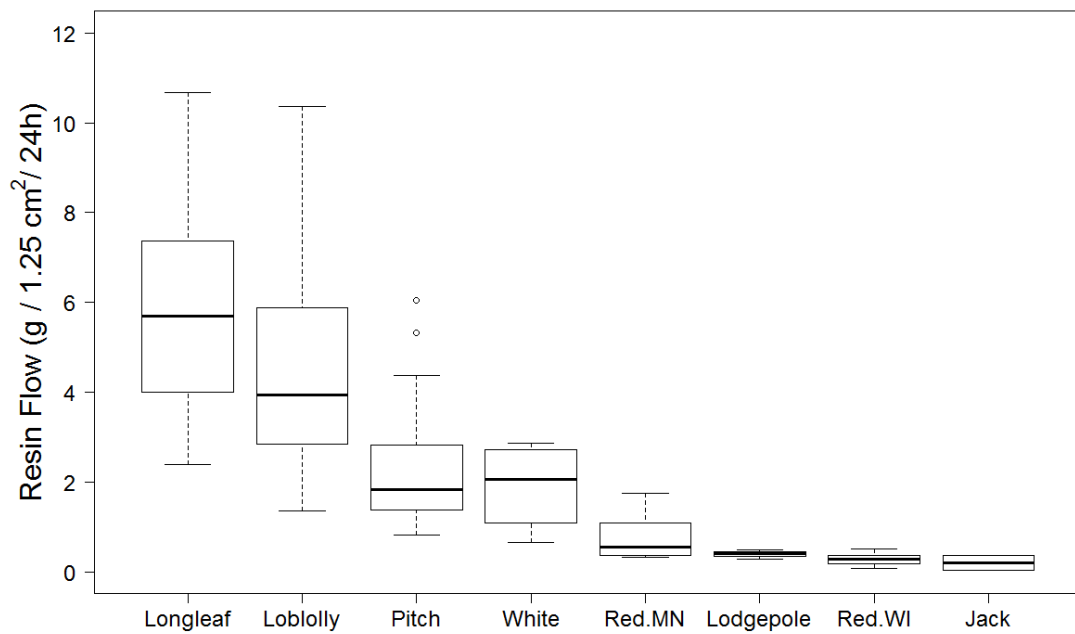


Figure 8. Resin flow comparison among different pine species. Red pine was sampled in two states, so is represented by two separate sets of values.

# Supplementary Material

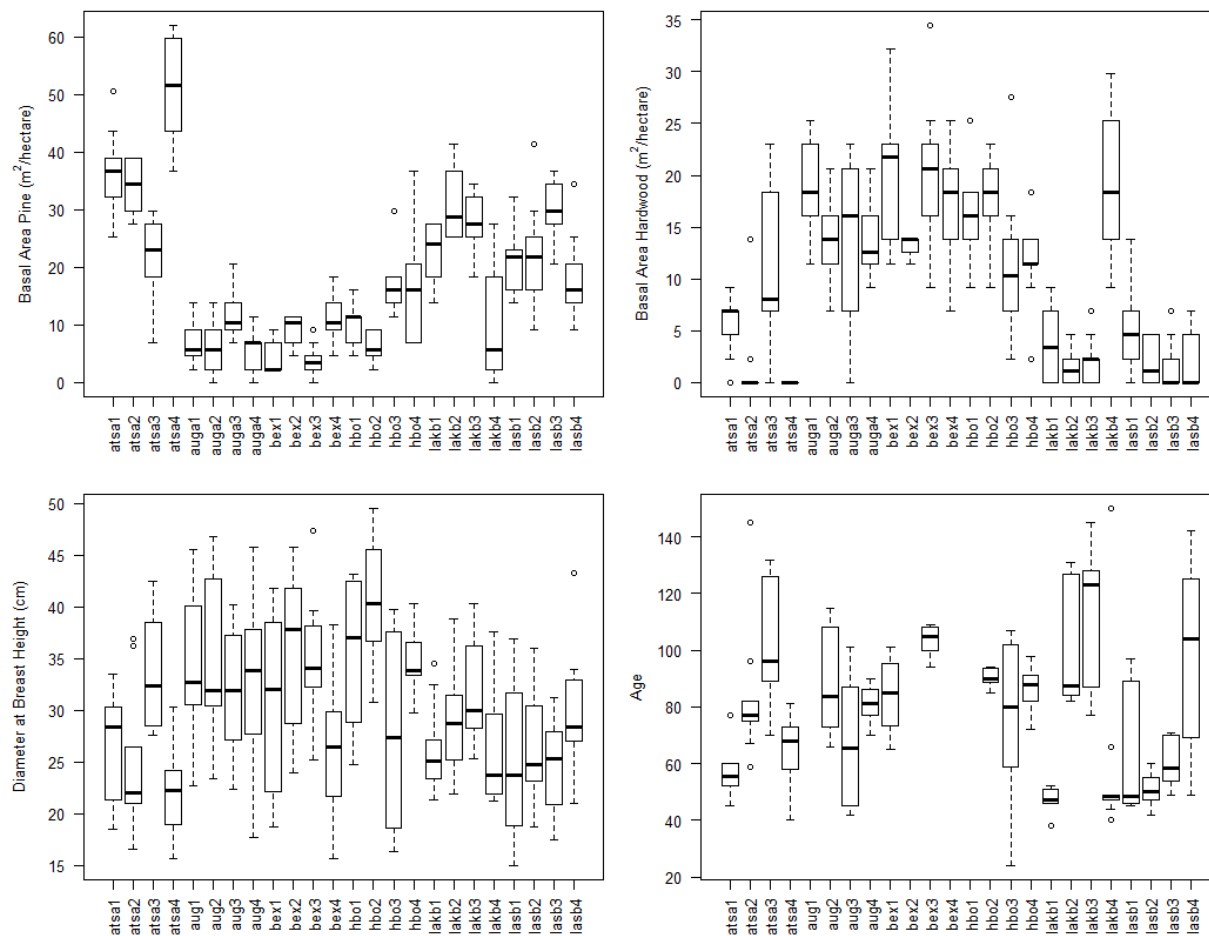
SMTTable 1. Ranges, means, and standard deviations for forest structure variables measured in soil type plots.

Plot Name	Basal Area Pine (m <sup>2</sup> /ha) Range	Basal Area Pine Mean	Basal Area Pine SD	Basal Area Hardwood (m <sup>2</sup> /ha) Range	Basal Area Hardwood Mean	Basal Area Hardwood SD	DBH (cm) Range	DBH Mean	DBH SD	Age (yrs) Range	Age Mean	Age SD
atsa1	25.3 - 50.5	36.7	7.1	0 - 9.2	5.7	2.9	18.5 - 33.5	26.6	5.6	45 - 77	56.4	8.5
atsa2	27.6 - 39	34.0	4.6	0 - 13.8	1.6	4.3	16.6 - 36.9	24.3	7.1	59 - 145	56.4	23.7
atsa3	6.9 - 29.8	21.1	7.7	0 - 23	10.6	7.7	27.6 - 42.5	33.6	5.6	70 - 132	101.4	21.7
atsa4	36.7 - 62	50.5	8.5	0 - 0	0.0	0.0	15.7 - 30.3	22.4	4.4	40 - 81	65.4	12.6
aug1	2.3 - 13.8	6.9	4.2	11.5 - 25.3	18.8	4.3	22.7 - 45.5	34.0	6.8	na	na	na
aug2	0 - 13.8	6.2	4.3	6.9 - 20.7	14.2	4.4	23.4 - 46.8	34.5	7.7	66 - 115	89.0	18.3
aug3	6.9 - 20.7	11.5	4.3	0 - 23	14.2	7.8	22.4 - 40.2	32.5	5.8	42 - 101	66.9	22.4
aug4	0 - 11.5	5.7	3.5	9.2 - 20.7	13.5	3.7	17.7 - 45.8	33.1	8.5	70 - 90	81.0	7.1
bex1	2.3 - 9.2	4.1	3.0	11.5 - 32.1	20.7	6.9	18.7 - 41.8	30.6	8.4	65 - 101	84.3	13.2
bex2	4.6 - 11.5	9.2	3.2	11.5 - 13.8	13.2	1.1	24 - 45.8	35.6	7.7	na	na	na
bex3	0 - 9.2	3.7	2.9	9.2 - 34.4	20.4	6.6	25.2 - 47.3	34.6	6.5	94 - 109	103.2	5.4
bex4	4.6 - 18.4	11.3	4.3	6.9 - 25.3	17.4	5.8	15.7 - 38.3	26.5	6.7	na	na	na
hbo1	4.6 - 11.5	10.1	4.5	9.2 - 25.3	16.5	5.9	24.8 - 43.1	35.8	7.0	na	na	na
hbo2	2.3 - 9.2	6.2	2.4	9.2 - 23	17.4	3.9	30.8 - 49.5	40.3	5.9	85 - 94	90.4	3.5
hbo3	11.5 - 29.8	16.8	5.1	2.3 - 27.6	11.3	7.2	16.3 - 39.7	28.2	8.9	24 - 107	74.3	30.8
hbo4	6.9 - 36.7	16.8	9.6	2.3 - 18.4	11.7	4.1	29.8 - 40.3	34.7	2.9	72 - 98	86.4	8.2
lakb1	13.8 - 27.6	22.7	5.6	0 - 9.2	3.9	3.6	21.3 - 34.5	26.1	4.4	38 - 52	47.4	4.1
lakb2	25.3 - 41.3	31.0	6.1	0 - 4.6	1.6	1.9	21.9 - 38.8	28.9	5.0	82 - 131	99.6	20.9
lakb3	18.4 - 34.4	28.0	4.8	0 - 6.9	2.3	2.2	25.3 - 40.3	31.7	5.4	77 - 145	114.5	24.4
lakb4	0 - 27.6	10.6	10.0	9.2 - 29.8	19.1	6.7	21.2 - 37.6	25.9	5.3	40 - 150	59.0	32.7
lasb1	13.8 - 32.1	21.1	5.6	0 - 13.8	5.3	3.9	15 - 36.9	24.8	7.3	45 - 97	61.0	22.5
lasb2	9.2 - 41.3	21.8	9.3	0 - 4.6	2.1	2.3	18.7 - 36	26.0	5.0	42 - 60	50.3	5.9
lasb3	20.7 - 36.7	29.6	5.1	0 - 6.9	1.6	2.4	17.5 - 31.2	24.9	4.4	49 - 71	60.5	8.8
lasb4	9.2 - 34.4	17.9	7.4	0 - 6.9	2.1	3.0	21 - 43.3	29.9	6.2	49 - 142	100.1	33.7

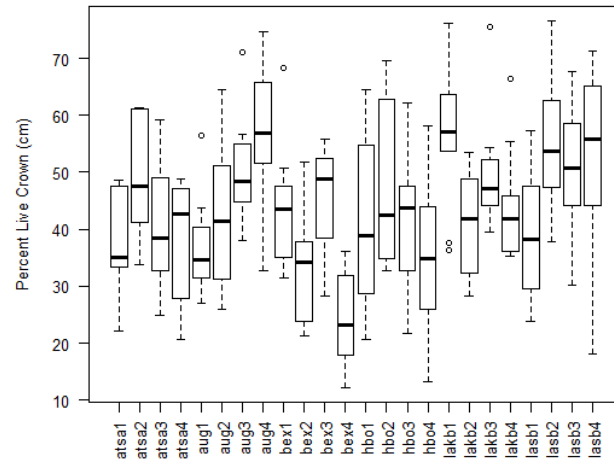
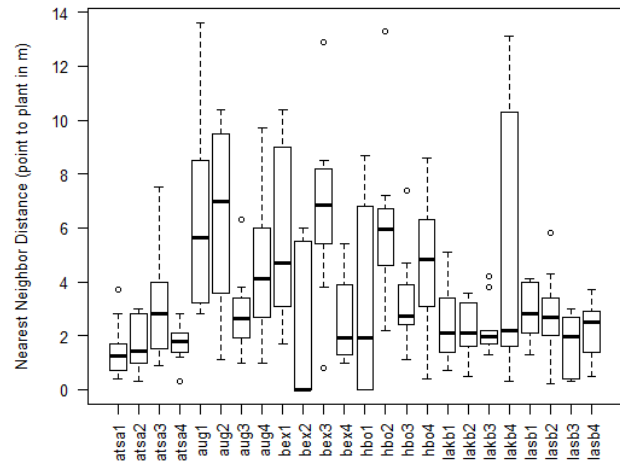
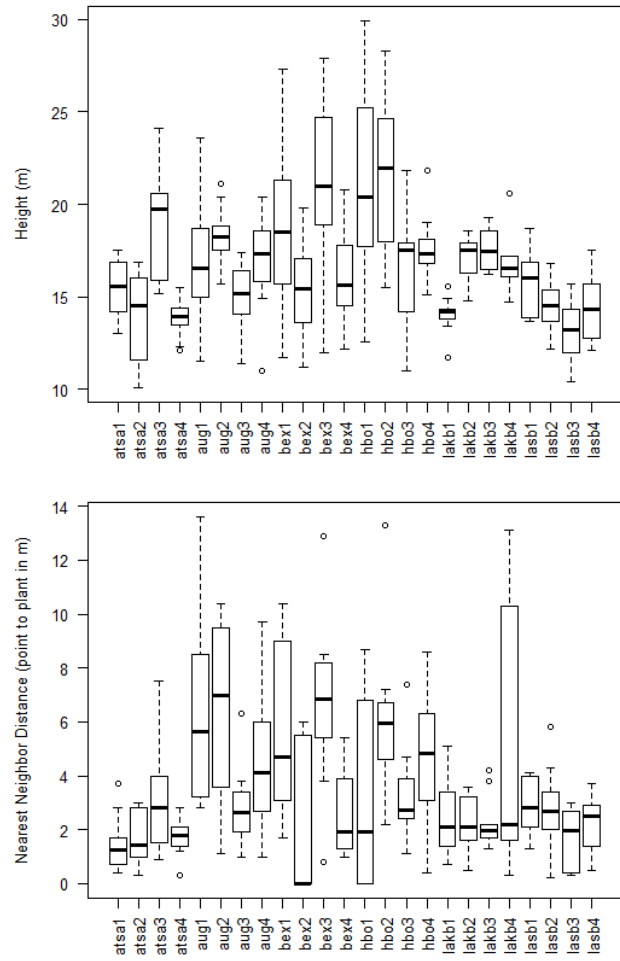
SMTable 1, continued

Plot	Height (m) Range	Height Mean	Height SD	% Live Crown Range	% Live Crown Mean	% Live Crown SD	Nearest Neighbor Distance (m) * Range	Nearest Neighbor Distance Mean	Nearest Neighbor Distance SD
atsa1	13 - 17.5	15.5	1.6	22.1 - 48.7	38.1	8.7	0.4 - 3.7	1.5	1.1
atsa3	10.1 - 16.9	13.9	2.5	33.8 - 61.3	48.7	10.0	0.3 - 3	1.7	0.9
atsa6	15.2 - 24.1	19.3	3.2	24.9 - 59.1	41.4	10.7	0.9 - 7.5	3.4	2.4
atsa7	12.1 - 15.5	13.8	1.0	20.7 - 48.9	38.2	10.8	0.3 - 2.8	1.7	0.7
auga1	11.5 - 23.6	17.0	3.3	27.1 - 56.4	36.8	8.4	2.8 - 13.6	6.3	3.5
auga2	15.7 - 21.1	18.3	1.6	25.9 - 64.6	43.1	13.2	1.1 - 10.4	6.4	3.5
augb1	11.4 - 17.4	15.0	1.7	38.1 - 71.1	50.5	9.1	1 - 6.3	2.9	1.5
augb2	11 - 20.4	17.1	2.7	32.7 - 74.7	57.4	11.9	1 - 9.7	4.6	2.7
bex1	11.7 - 27.3	18.6	4.7	31.4 - 68.4	43.8	10.8	1.7 - 10.4	5.8	3.4
bex2	11.2 - 19.8	15.3	2.5	21.3 - 51.8	33.4	9.2	0 - 6	1.9	2.7
bex3	12 - 27.9	21.0	4.5	28.3 - 55.9	45.5	9.0	0.8 - 12.9	6.7	3.2
bex4	12.2 - 20.8	16.1	2.8	12.2 - 36.2	23.7	8.3	1 - 5.4	2.5	1.5
hbo1	12.6 - 29.9	21.1	5.7	20.6 - 64.5	41.1	14.7	0 - 8.7	3.0	3.5
hbo2	15.5 - 28.3	21.6	4.2	32.7 - 69.6	47.0	14.4	2.2 - 13.3	6.2	2.9
hbo3	11 - 21.8	16.8	3.3	21.8 - 62.1	41.7	11.4	1.1 - 7.4	3.2	1.9
hbo4	15.1 - 21.8	17.7	1.8	13.2 - 58.3	35.9	14.0	0.4 - 8.6	4.7	2.5
lakh2	11.7 - 15.6	14.0	1.0	36.4 - 76.2	56.8	12.6	0.7 - 5.1	2.4	1.4
lakh4	14.8 - 18.6	17.2	1.1	28.3 - 53.4	41.2	8.3	0.5 - 3.6	2.2	0.9
lakh6	16.2 - 19.3	17.6	1.2	39.5 - 75.4	49.5	10.2	1.3 - 4.2	2.2	1.0
lakh7	14.7 - 20.6	16.8	1.5	35.4 - 66.5	43.9	10.0	0.3 - 13.1	5.2	5.0
lasb1	13.7 - 18.7	16.0	1.8	23.9 - 57.2	39.3	11.9	1.3 - 4.1	2.9	1.0
lasb3	12.2 - 16.8	14.4	1.4	37.8 - 76.6	54.7	11.9	0.2 - 5.8	2.8	1.5
lasb6	10.4 - 15.7	13.2	1.6	30.3 - 67.6	50.8	11.8	0.3 - 3	1.7	1.1
lasb7	12.1 - 17.5	14.5	1.9	18.2 - 71.3	53.8	15.7	0.5 - 3.7	2.2	1.1

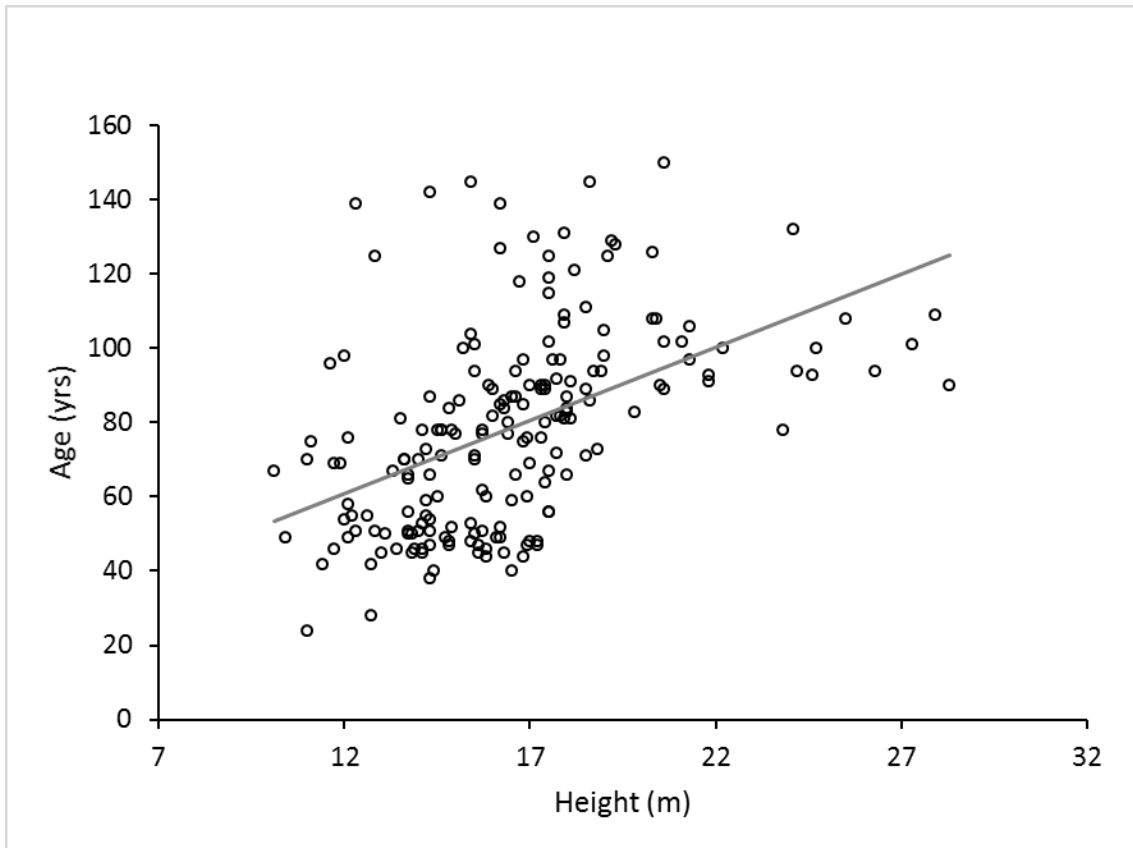
\* Nearest neighbor distances are point to plant measurements.



SMFig. 1: Boxplots for the forest structure variables measured in each sampling plot. Plot names are shown on the x-axis (atsa = Atsion sand, aug = Aura sandy loam, bex = Berryland and Mullica soils, hbo = Hammonton sandy loam, lakb = Lakewood sand, lasb = Lakehurst sand).



SMFig. 1, continued



SMFig. 2: Ages and heights of all individual trees sampled.

## Chapter 3

### Predicting the irregular: Developing models to anticipate outbreaks in a tree-killing bark beetle

#### Abstract

Millions of acres of US forests are affected each year by insect pests, both native and non-native. Of all the insects that cause widespread damage, the ones that exhibit non-cyclical outbreak dynamics are among the most challenging for forest resource managers. Yet these dynamics can be theoretically complex, and models difficult to parameterize. Prediction models are required to help allocate resources for suppression or prevention tactics, but these models must be easily parameterized with data available to managers in the field. Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) is a native insect pest that has caused frequent widespread mortality across its range in the southern United States. Because of its large economic impact, SPB has been intensively studied and monitored for decades. An operational prediction system was developed nearly 30 years ago to predict summer outbreaks based on spring trapping data, using number of SPB and ratio of SPB to its native clerid predator beetle (*Thanasimus dubius* Fabricius) to estimate the likelihood of outbreak. Although it has been in continued use since then by forest managers throughout the southeastern U.S., the system was never developed into a quantitative model. Analytically, one of the challenges produced by outbreak data is that there may be many years and locations where the insect population is effectively zero. This large number of zeros in the dataset produces an extreme case of statistical overdispersion. We utilized mixture models to test the effects of SPB and its predator in current and preceding years on the occurrence of localized SPB infestations—known as

spots—across the landscape. Among several options, a zero-inflated negative binomial distribution provided the best fit to the data. Outbreaks per forest-year were correctly predicted by our models 82% of the time. The independent variables providing the best fit in the final model included: SPB this year and last year, predators this year, ratio of SPB to predators this year and last year, as well as host area per location and number of spots in the previous two years. We also found that a simpler model utilizing only SPB and SPB/predator ratio, although producing a higher AIC than the full model, resulted in nearly identical predicted zero and non-zero counts, as well as similar numbers of correct vs. incorrect predictions of outbreak status. The predator/SPB ratio also appears to be crucial, because models with SPB or clerids alone did not improve performance, and clerids were also not significant in the full best-fitting model. Sensitivity analysis showed that high and low values of the abundance data did not change the shape of the results, suggesting that other unmeasured factors such as local weather or host availability may have a greater impact. Pest species with irregular outbreaks have disproportionate impacts on many natural and managed ecosystems. Their ecological impacts are related to the vexing statistical properties of abundance measurements. The application of zero-inflated mixture models provides a promising new tool for understanding the biology and improving our capacity to predict the irregular.



## Introduction

Millions of acres of United States forests are damaged or killed each year by broad scale disturbances such as fire, insects, and pathogens. 2015 was a record-breaking year for fire, with over 10.1 million acres burned in wildland fires (National Interagency Fire Center, [www.nifc.gov/fireInfo/fireInfo\\_statistics.html](http://www.nifc.gov/fireInfo/fireInfo_statistics.html)), and, for the first time, over 50% of the United States Forest Service budget being spent on fire suppression (United States Forest Service, [www.fs.fed.us/sites/default/files/2015-Fire-Budget-Report.pdf](http://www.fs.fed.us/sites/default/files/2015-Fire-Budget-Report.pdf)). In recent years, US forests sustained equally widespread damage due to insect pests, both native and non-native, with over 10.3 million acres damaged in 2014, 4.6 million of those acres having been killed outright (USDA Forest Service, <http://foresthealth.fs.usda.gov/portal>). For forest managers, understanding the population dynamics of these insects is essential to decision-making about resource allocation and management options. There is a particular need for improved predictions of when and where pest abundance, and therefore tree mortality, will be high.

Insects that produce widespread mortality can be classified into a few categories. Some insect pests persist at high population levels because they are non-native and thus lack native predators, or outcompete local native species (Lockwood et al. 2013). Some of these non-native pests remain at predictably high population levels following arrival—at least while the host populations survive. Examples include hemlock wooly adelgid (*Adelges tsugae* Annand) and emerald ash borer (*Agilus planipennis* Fairmaire), both non-native to North America. Other damaging insects, both native and non-native, display outbreak dynamics over time in which periods when populations are high are interspersed with periods when the insects are rare. Some outbreaks are cyclical—with

recognizable periodicity that usually arises from delayed negative feedback. Others show fluctuations but not cycles. Examples include *Epirrita autumnata* L., a geometrid moth native to Fennoscandia, documented to occur in roughly 10-year outbreak cycles (Tenow 1972, Jepsen et al. 2008), and larch budmoth (*Zeiraphera diniana* Gn.), which exhibits 8-9 year outbreak cycles (Turchin et al. 2003). For forest managers, pest populations that remain consistently high, such as those of non-native species, pose little uncertainty in decision-making and allocation of management resources. Challenges abound in regard to the best practices of suppression or prevention, to be sure, but timing of the insect population is not one of them. Likewise, cyclical outbreaks operating at known intervals present little uncertainty in terms of timing of management activities. The final category—outbreak species with no known periodicity—poses the greatest challenge for resource managers due to the difficulty in developing good predictive models for anticipating when outbreaks will occur.

Oscillations in population numbers have been explained by numerous factors including density dependence, natural enemies, resource availability, and environmental stress (Barbosa and Shultz 1987, Barbosa et al. 2012). Theoretical models of such dynamics range from simple predator-prey models (Volterra 1926, Lotka 1932) to more complex models of alternate stable states or equilibria (Takahashi 1964, Holling 1973, Southwood and Comins 1976, May 1977). While these latter models seem like a good conceptual fit to insects with irruptive dynamics, testing them in nature has proved difficult (but see Ives et al. 2008). Complex models are often difficult to parameterize with empirical data, and as such, are impractical for use by resource managers. Instead, their goal is to develop operational models of outbreak dynamics such that data collection

is straightforward and efficient and predictions of outbreak vs. rare states are relatively reliable.

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann) is a tree-killing bark beetle that is one of the most damaging forest insects in the world (Coulson and Klepzig 2011). When rare, the beetle is nearly undetectable, but during outbreaks, tree mortality can occur over thousands of hectares. The Texas Forest Service has coordinated data collection on SPB and its major predator, the clerid or checkered beetle (*Thanasimus dubius* Fabricius), since 1987. Utilizing a broad network of collaborators across the southern states, these data have been used to predict likely SPB population levels each summer, enabling managers to plan for personnel and budgetary needs in the event of outbreak levels. The number of participating locations has grown throughout the years, but each cooperator records the same information from each trap: number of SPB and number of the clerid beetle predator. Data are collected over a four week period each spring when SPB are dispersing widely, seeking to locate and join aggregations of conspecifics. This seems to coincide with the first flowering of dogwood (*Cornus florida* L.), so cooperators deploy traps when dogwood first flowers in their forest. Using a chart plotting percent SPB against number of SPB trapped per day, managers assess the level and trend of SPB for that summer (Figure S1, supplementary materials. (Billings and Upton 2010)). This method has proved operationally efficient for management purposes, but was developed nearly three decades ago and has not been updated since its development. Here we sought to develop an updated quantitative model that would benefit from the many years of collected data, provide insight into the ecological processes driving the probability of outbreak, and serve as a basis for future modeling

efforts, particularly as SPB expands northward along the Eastern seaboard of the U.S. into previously naïve forests.

Early work in SPB dynamics described cycles of approximately 7-9 years due to delayed density dependence from predator-prey dynamics (Turchin et al. 1999, Reeve and Turchin 2002). The current SPB prediction system mirrors this belief in the importance of predation by employing as one of two predictors the abundance of SPB relative to its predator. Later analyses with additional data found that cycles were not as apparent as initially thought, that various exogenous factors can also play a strong role in dynamics (Hofstetter et al. 2006a, Trần et al. 2007, Friedenber<sup>g</sup> et al. 2008, Weed et al. 2016), and that population dynamics were destabilized by positive feedbacks that could produce quick transitions between very low and very high abundance. Martinson et al. (2013) used both modeling and experimental approaches to show that competitors and predators may provide the necessary drivers at low abundance for a system of population regulation with two approximately stable equilibria (alternate attractors) separated by an unstable equilibrium (escape threshold).

Here our focus was on quantifying an operational model based on outbreak status, so we used infestations per forest-year, or number of spots, as our response variable, with SPB and predator population numbers as predictors. In many locations and in many years, SPB is not in outbreak, so the number of spots is zero. This produces a highly non-normal, overdispersed distribution of the data (Fig. 1). Prior to recent advances in statistical computation, the most straightforward way to deal with such data would have been to perform a transformation. Research has shown, however, that generalized linear models perform better with count data, and in particular, with count data containing a

large number of zeros (Nelder and Wedderburn 1972, McCullagh and Nelder 1989, Bolker 2008). These methods require no transformation, instead utilizing an appropriate discrete probability distribution. (See O’Hara and Kotze (2010) for a detailed discussion of the merits of not transforming count data in ecological research.) In some cases, these methods alone are insufficient to deal with the overdispersion caused by large numbers of zeros. Mixture models, which combine two probability distributions, can then be utilized to separate the zeros from the non-zero counts. In recent years, these models have been employed more frequently in ecological research, involving a variety of data from diverse study systems (Martin et al. 2005, Zuur et al. 2009, Kery 2010).

Here we investigate the applicability of mixture models for understanding, describing, and predicting the dynamics of irregularly irruptive pests. In a mixture model for count data, a binomial distribution is used to model the zeros as in a logistic regression, while another discrete distribution such as the Poisson or negative binomial models the counts. The count process may be handled in one of two ways: modeling the counts to exclude zero (sometimes referred to as a zero-altered, or hurdle model), and modeling the counts to include zero, referred to as a zero-inflated model. In the latter case, zeros may arise in both the binomial and the count process. See Zuur et al. (2009) for a detailed explanation and listing of all the probability functions behind each of the mixture model types. In the case of zero-inflated models, the ecological literature often refers to the zeros from the binomial process as “false zeros,” i.e., zeros due to study design or observer error, and the zeros from the count process as “true zeros,” or zeros stemming from the ecological variables in question (e.g., Martin et al. 2005, Zuur et al. 2009). Others alternatively define the binomial zeros as “site suitability” for the species

in question, and the count process as the variation among suitable sites (Potts and Elith 2006, Kery 2010). However these definitions remain up for debate, and it should be noted that mixture model methods do not provide a way to assign specific lines of data to one type of zero or the other.

## **Methods**

Using SPB, clerid beetle, and infestation/spot data collected by a network of cooperators, and collated and disseminated by the Texas Forest Service between 1987 and 2009 (Martinson et al. 2013), we created a dataset using all forest-years that were complete for six variables (SPB, SPB the year before, clerid beetles, clerid beetles the year before, the ratio of SPB to clerids, and the ratio of SPB to clerids the year before) and the response variable, number of SPB spots that appeared in that forest in that year. In addition, we included spots the year before and spots two years previous among the independent variables to handle possible temporal correlation. All independent variables were centered and scaled prior to analysis. Spots were defined as localized infestations including four or more immediately adjacent beetle-killed trees that were revealed by systematic aerial detection surveys conducted by trained observers in small airplanes. Three outliers for SPB numbers were removed because they seemed to be transcription errors. This resulted in 1774 forest-years across 132 forest ranger districts or state counties, in 13 states (Fig. 2).

### *Distributions of univariate data*

Before beginning the process of selecting the combination of variables that would produce the best-fitting model, we first modeled the univariate spot count data. The most

common distributions for count data are the Poisson and the negative binomial. We tested both these distributions, along with their hurdle and zero-inflated counterparts (Pimentel et al. 2014), using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). All analyses throughout this study were performed in R (R Core Team 2017); zero-inflated models were fit using package *pscl* (Zeileis et al. 2008, Jackman 2015).

### *Model selection*

One characteristic of the southwide dataset is that each forest or ranger district where data were collected presents a different size host area. One way to deal with this issue would be to use density of spots (spots per unit area) instead of count of spots. However, this would necessitate moving into a continuous distribution, which is less commonly used in mixture modeling in ecology, and integer numbers of expected values for both counts and zeros make more sense when communicating with resource managers and other stakeholders. Other methods to account for sampling areas of different sizes include using an offset, taking the natural log of the host area, which does not include a regression parameter, or simply using host area as a standard independent variable. We compared both the latter methods using AIC to see which fit the data better before proceeding with the rest of the model selection.

To the resulting area model, we then added each variable in turn to characterize their influence on the number of spots. Because it is well established that the number of SPB dispersing in spring have an effect on the number of spots that appear in summer per year (Billings and Upton 2010), we first tested the null model (no variables except area) against the model with just SPB abundance in spring as an independent variable. Each

subsequent variable was added, assessed for improvement of fit using AIC, and retained or dropped accordingly. We did this procedure twice, first holding the binomial process constant, adding variables to the count process, and then the same method in reverse. The best fitting models from each process alone were combined for the final best fit of both processes together.

#### *Comparison of best fitting model with simpler models*

Because our interests lay in finding not only the best fitting model, but also one that would be most easily implemented from an operational perspective, we also created a quantitative version of the model currently in use (Fig. S1), which is to say a model including just SPB and %SPB alone (hereafter referred to as the Texas model). We then compared this model to the best-fitting model from the selection process, and to the reduced versions of each, in which we removed variables that were not significant. For completeness, we also tested the simple models of SPB alone, and clerids alone.

In addition to testing these models using AIC, we also compared the expected count values for each model with observed values, as well as the predicted count probabilities. Because of the nature of the model, the most straightforward value obtained from the model is the expected number of zeros, or the expected probability of zero. The predicted non-zero counts or probabilities are then distributed along the range of values in the observed data. In this case, the maximum number of spots was 4767, with the vast majority of counts occurring at much smaller values (Fig. 1). Because the range of values was so wide, many of the counts had extremely small probabilities attached to them, so



we binned these into categories that would be comprehensible and actionable from a management perspective.

Finally, we tested whether the spot predictions were correct in terms of whether or not the system was in outbreak per forest per year. We calculated the expected number of spots across the data, then re-evaluated this number in terms of density, or spots per acre, using each forest location's host area in acres. A widely used definition of outbreak is 1 or more spots/1000 acres (Clarke 2012). We used this density to define each observed and expected spot value as an outbreak or non-outbreak year, and then compared these values for the best-fitting full model and the Texas model to see how well they predicted outbreak status.

#### *Model results among forest locations*

To determine whether the model would perform differently in different locations, we also tested a selected number of the forests for which we had the longest sequence of data (18-22 yrs), using each as a new dataset with which to predict the expected values using the best fitting model.

#### *Sensitivity analysis*

We performed a sensitivity analysis on the final model by varying each of the independent variables in turn, using the 10<sup>th</sup> and 90<sup>th</sup> percentile values to represent low versus high levels for each variable. The remaining variables were held constant at the mean in each test.

## Results

### *Distributions of univariate data*

All three negative binomial models were favored over each of the three Poisson distributions against which we compared them (Table S1; Fig. 3). With both distributions, the hurdle and zero-inflated versions produced identical results, so the hurdle results are not shown in the figure. The mixture models were an improvement over the negative binomial generalized linear model, so we began testing the individual independent variables with both the hurdle and zero-inflated negative binomial models.

### *Model selection*

Testing the offset of  $\log(\text{area})$  method against using area as a simple covariate, we found that the simple covariate method produced a lower AIC (Table S2), so we retained host area as a variable in both the count and the binomial processes for subsequent analyses. The best-fitting model for the count process included SPB this year and last year, clerids this year, %SPB this year and last year, and spots the last two years (Table 1). The best-fitting model for the binomial process included all these variables, with the exception of clerids (Table 2). The AIC value for the model combining the best fit for both processes together was 9907, considerably improved over the fits for each process alone (Tables 1 and 2).

### *Comparison of best fitting model with simpler models*

While our best-fitting model included most of the tested variables, we also wanted to compare several simpler models relevant to the operational question at hand. This

included the Texas Model, a quantified version of the system currently in use across the southern United States (SPB + %SPB), as well as SPB alone and clerids alone. The full model retained its place as best-fitting model, but the Texas model was not far behind with  $\Delta AIC$  of just 4.6. The other simplified versions of the model, including versions removing the non-significant variables from the full and Texas models, did not improve model performance (Tables S3 and 4.).

Although  $\Delta AIC > 2$  is widely accepted as a rule of thumb for distinguishing among models (Burnham and Anderson 2002), we also wanted to see if expected outcomes would be different on a scale useful to managers, regardless of the difference in  $\Delta AIC$  values. Comparing the observed versus the expected counts of both zero and non-zero values, we see that predicted values are very similar across the different models (Table 5). Similarly, expected probabilities are similar between the full and Texas models (Table S4).

When we aggregate the predictions into simple outbreak status numbers, the two models are again nearly indistinguishable (Table 6). Both models correctly predicted outbreak status 82% of the time (it should be noted that they did not predict each row in the data identically, but the overall percentage of correct predictions was the same). Assuming that incorrectly predicting a non-outbreak year is more critical than incorrectly predicting an outbreak year—i.e., not anticipating an outbreak means resources will not be allocated to suppression and other activities on the ground—both models tended to underpredict outbreak years. While both models only produced an incorrect prediction 18% of the time, of that 18%, 81% were in non-outbreak years (Table 6.). Put another way, both models incorrectly predicted non-outbreak years (i.e., a prediction of non-

outbreak when when the observed year was in outbreak) approximately 14% of the time over the entire period of data collection.

#### *Model results among forest locations*

We performed a similar analysis of observed and expected spot counts, this time using data from specific locations to assess the model fit across the landscape. The results were roughly similar to results from the full model, with predictions of zero counts being quite close overall, and predictions of non-zero counts varying by site (Table S5, Fig. 4).

#### *Sensitivity analysis*

We evaluated model response to low versus high values of each of the independent variables in the final full model. In nearly all cases, both low and high values resulted in underprediction of the probability of zero spots and overprediction of the different values of positive counts (Table S6, Fig. 5, top row). Only low spots in the previous year resulted in a predicted probability of zero close to the observed value (Fig. 5, bottom row).

### **Discussion**

We found that zero-inflated, negative binomial models best characterized our data, and that using this distribution, we could correctly predict outbreak status approximately 82% of the time. Poisson models, though traditionally used for count data, did not adequately represent the overabundance of zeros, whether in their standard or zero-inflated form. Because zero-inflated models include zeros from both the binomial and the count processes, it is common in the ecological literature to refer to the zeros

produced by the binomial process as “false zeros” and/or “measurement error” (e.g., Martin et al. 2005, Zuur et al. 2009) or “unsuitable habitat” (e.g., Potts and Elith 2006, Kery 2010). However the model itself does not assign individual samples to one or the other kind of zero, so the statistical outcome actually does not tell us anything about the division in the data between the two kinds of zeros. For this reason we remain agnostic on the narrative convention of assigning biological meaning to each type of zero. In general, however, we find that the zero-inflated model performs well for count data with many zeros, and that it may be particularly useful for analyzing data on non-cyclical outbreaking organisms that are so rare in their low population state that their number is effectively zero.

We also found that conventional model selection measures such as AIC allowed us to distinguish among models, but that from an operational perspective—i.e., keeping in mind that the best model in this case is the one that is most easily implemented and interpreted by resource managers—an Occam’s Razor approach of choosing the simplest possible model seemed to work best. Informative variables in the best-fitting, full final model included SPB, clerids, and %SPB in the current year; SPB, %SPB, and spots in the previous year; spots two years ago; and finally, host area at each sampling location. However the simpler model including just SPB and %SPB for abundance data (along with host area and spots in previous years, which were considered in all models to make them more easily comparable) produced nearly identical accuracy of prediction over the 1774 forest-years. The models also appeared to perform about equally well across forests, although the length of outbreak vs. non-outbreak periods across the sampling period, and

the variable number of years per location for which data were available may somewhat reduce our confidence in per forest predictions with this dataset.

While the evidence for cyclical dynamics caused by predator-prey interactions has diminished over the years (Reeve and Turchin 2002, Friedenbergr et al. 2008, Martinson et al. 2013, Weed et al. 2016), our models show that the ratio of SPB to predators remains in even the simplest of our models, indicating that predators do play a role in outbreak dynamics. Interestingly, the number of predators alone did not perform well as a model, and while they appeared in both the binomial and count processes of the full final model, they were not significant in either case. Clerids in the previous year did not appear in our full final model at all, supporting the finding by Weed et al. (2016), that clerid beetles do not lag SPB in time, and appear to respond instantaneously to SPB dynamics.

Other factors that may drive outbreak dynamics include local weather (Trần et al. 2007), resource availability (Weed et al. 2016), and the antagonist blue-stain fungus that co-colonizes host trees (Klepzig and Wilkens 1997, Hofstetter et al. 2006b). From a management perspective, the first two factors could be incorporated with relative ease into an annual outbreak prediction model at the local scale, but data on the blue-stain fungus and the mites that carry it would be more difficult to collect and analyze. Future work could parameterize models like ours to include the effects of weather and host availability.

Here we showed that a quantitative model for probability of SPB outbreak could be developed using data that are already collected by forest managers across the south, and increasingly, into the mid-Atlantic states. Several next steps follow logically from this work. The first is to better understand the cases in which the model fails, particularly

since incorrect predictions, while not a large proportion of the data, are mostly incorrect in the direction most critical to managers, i.e., predicting non-outbreak when an outbreak occurs. Next a method for operationalizing the model needs to be developed, such that managers can easily work with the model themselves, given their own local data, possibly through a web application or other easily accessible format. Finally, assuming that these data continue to be collected annually, a method of updating the model with each years' new data should be developed, potentially using a Bayesian framework. A similar method has been developed for North American mallards across the breadth of jurisdictions responsible for their management (Nichols et al. 2007).

As of this writing, SPB appears to be extending its reach northward, with an unprecedented outbreak in New Jersey in the early 2000s, the first detection of SPB mortality on Long Island in 2014 (Schlossberg 2014), and the first trap catches of the beetle in Connecticut, Rhode Island and Massachusetts soon thereafter (Kevin Dodds, in preparation), as well as detection of tree mortality in Connecticut in 2015. Because the outcomes of SPB's northern progression is unknown, it is critical to develop and continually update models that can be used for outbreak prediction, using relatively simple monitoring and data collection methods.

SPB are an example of a notable plant pest whose abundances fluctuate dramatically and irregularly. Statistically satisfying prediction systems for such populations have been difficult to develop because of limitations in analytical techniques. Non-normal data were previously transformed, and standard regression techniques applied. With improvements in computational performance and the availability of widely distributed software capable of dealing with the full range of probability distributions, as

well as more complex mixture models, these datasets can now be analyzed using methods more appropriate to their numerical characteristics. This improved availability and efficiency of analytical techniques can only speed the process by which models can be developed and translated back into the field for use in active management. Furthermore, zero-inflated mixture models provide a new framework within which we can analyze the properties of irregularly outbreaking insect pests. Previous work has shown that organisms with irregularly outbreaking dynamics are characterized by endogenous positive feedbacks that drive the population to its upper equilibrium (e.g., Takahashi 1964, Southwood and Comins 1976, Berryman 1987). Data required to parameterize such multiple equilibrium models, however, can be difficult to obtain. Our method of analyzing both infestation and insect abundance data with a zero-inflated mixture model permits the analysis of relatively simple datasets likely to be collected for standard management practices. The regression procedures at the core of both sets of models make possible the inclusion of a wide range of independent variables, which can be selected based on local capacity for data collection. The more complex multiple equilibrium models will undoubtedly continue to drive the development of new hypotheses, while the simpler mixture models provide a framework within which field data can be easily tested for the development of operationally useful prediction models.



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Table 1. AIC values for count models, holding binomial process constant (intercept and host area only). Beginning with the null model, each variable was added in turn. If the additional variable produced an improved AIC greater than two over the previous model ( $\Delta$ AIC), the variable was retained.

	AIC	$\Delta$ AIC	df
SPB + clerids + %SPB + SPB.t-1 + %SPB.t-1 + spots.t-1 + spots.t-2	10673	0	12
SPB + clerids + %SPB + SPB.t-1 + %SPB.t-1 + spots.t-1	10686	13	11
SPB + clerids + %SPB + SPB.t-1 + %SPB.t-1	10745	72	10
SPB + clerids + %SPB + SPB.t-1	10777	104	9
SPB + clerids + %SPB + SPB.t-1 + clerids.t-1	10779	106	10
SPB + clerids + %SPB	10782	109	8
SPB + clerids zero-inflated NB*	10890	217	7
SPB zero-inflated NB	10897	224	6
SPB hurdle NB	10968	296	6
SPB + clerids hurdle NB	10970	298	7
Null model	11177	504	3

\* After the addition of the clerids variable, the zero-inflated models clearly outperformed the hurdle models, so subsequent additional variables above were tested only with the zero-inflated model.

Table 2. AIC values for binomial models, holding count process constant (intercept and host area only).

	AIC	$\Delta$ AIC	df
SPB + %SPB + clerids.t-1 + %SPB.t-1 + spots.t-1 + spots.t-2	10202	0	11
SPB + %SPB + clerids.t-1 + %SPB.t-1 + spots.t-1	10216	13	10
SPB + %SPB + clerids.t-1 + %SPB.t-1	10447	245	9
SPB + %SPB + clerids.t-1	10457	254	8
SPB + %SPB	10461	259	7
SPB + %SPB + SPB.t-1	10463	261	8
SPB + clerids	10471	269	7
SPB	10472	270	6
Null model	11132	929	5

Table 3. Parameter estimates for the final, best-fitting model.

Count model					Zero-inflation model				
	Estimate	Std. Error	Z-value	p-value		Estimate	Std. Error	Z-value	p-value
Intercept	4.14	0.08	49.50	< 0.001	Intercept	-22.00101	5.68276	-3.872	< 0.001
Host Area	0.22	0.10	2.27	0.02	Host Area	-0.03729	0.11138	-0.335	0.74
SPB	0.41	0.09	4.66	< 0.001	SPB	-1.19262	0.49395	-2.414	0.02
Clerids	0.12	0.07	1.60	0.11	Clerids	-	-	-	-
%SPB	0.38	0.10	3.69	< 0.001	%SPB	-0.95223	0.15116	-6.299	< 0.001
SPB.t-1	-0.24	0.07	-3.41	< 0.001	SPB.t-1	-0.2099	0.12939	-1.622	0.10
%SPB.t-1	0.17	0.09	1.85	0.06	%SPB.t-1	-0.11235	0.13283	-0.846	0.40
Spots.t-1	0.48	0.08	5.95	< 0.001	Spots.t-1	-86.24823	21.91155	-3.936	< 0.001
Spots.t-2	0.12	0.05	2.22	0.03	Spots.t-2	-2.06816	1.55773	-1.328	0.18



Table 4. Parameter estimates for the Texas Model.

Count model					Zero-inflation model				
	Estimate	Std. Error	Z-value	p-value		Estimate	Std. Error	Z-value	p-value
Intercept	4.21	0.08	54.68	< 0.001	Intercept	-23.09	6.05	-3.82	< 0.001
Host Area	0.22	0.10	2.31	0.02	Host Area	-0.03	0.11	-0.27	0.79
SPB	0.39	0.07	5.30	< 0.001	SPB	-1.36	0.52	-2.64	0.01
%SPB	0.38	0.08	4.57	< 0.001	%SPB	-0.98	0.14	-7.13	< 0.001
Spots.t-1	0.45	0.08	5.83	< 0.001	Spots.t-1	-88.95	23.18	-3.84	< 0.001
Spots.t-2	0.12	0.05	2.28	0.02	Spots.t-2	-3.65	2.46	-1.48	0.14

Table 5. Comparison of observed and expected counts for each of several models, including the full best-fitting model, the full model with non-significant variables removed, the Texas model, and the Texas model with non-significant variables removed.

Counts	0	1	2	3	4	5	6	7	8	9	10	20	30	40	50	100	200
Observed	1029	33	31	16	16	13	25	15	13	7	14	7	7	4	3	2	0
Full Model	1019	47	31	24	20	17	15	14	12	11	10	6	5	4	3	1	1
Full Model, reduced	1021	46	30	23	19	17	15	13	12	11	10	6	5	4	3	1	1
Texas Model	1019	47	31	24	20	17	15	13	12	11	10	6	5	4	3	1	1
Texas Model, reduced	1022	46	30	23	19	17	15	13	12	11	10	6	5	4	3	1	1

Table 6. Comparison of outbreak status predictions between full best-fitting model and Texas model.

Observed Status	Correct Prediction		Incorrect Prediction	
	Full Model	Texas Model	Full Model	Texas Model
Non-outbreak	1223	1225	256	256
Outbreak	235	233	60	60

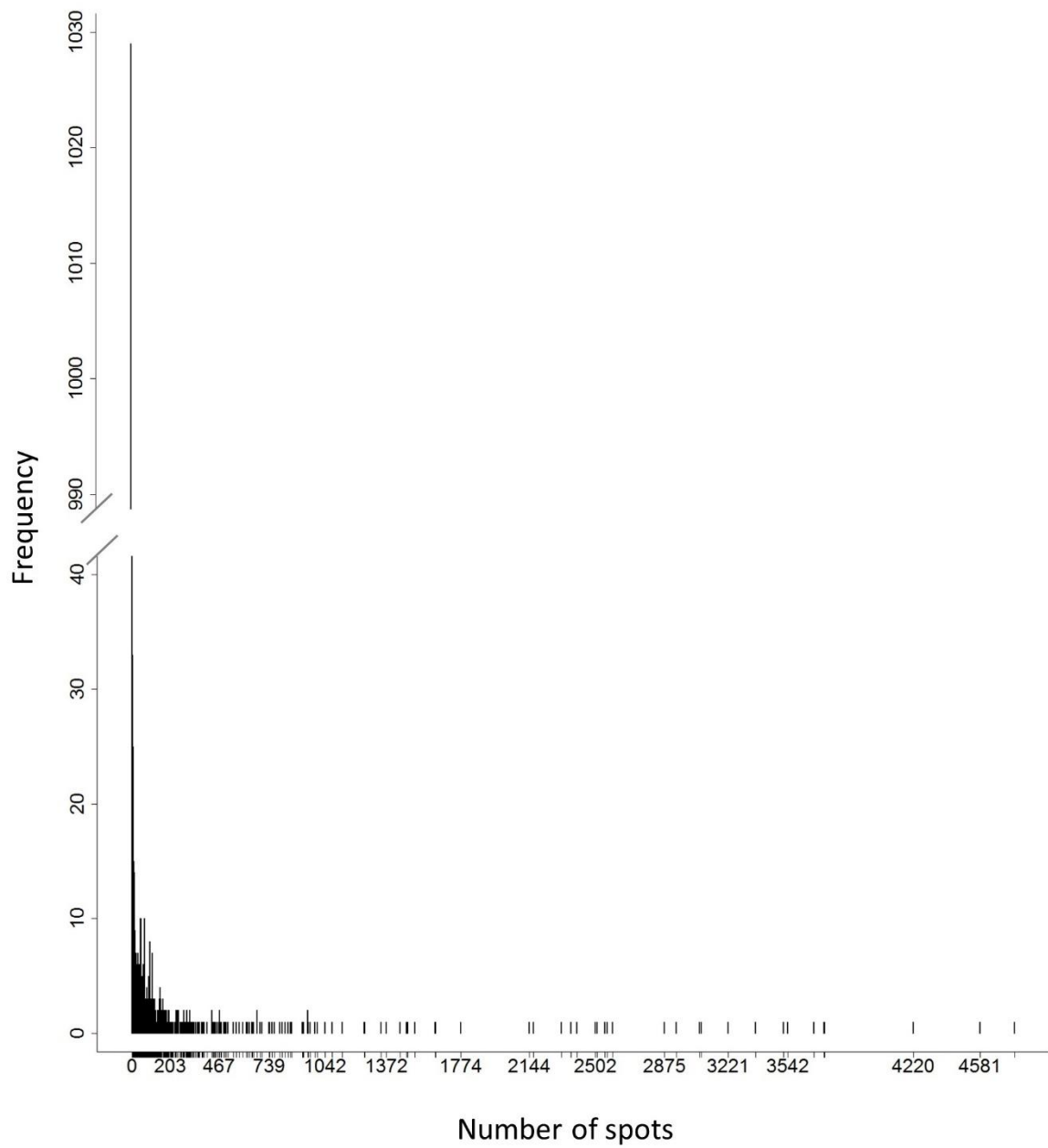


Figure 1. Frequency distribution of numbers of spots per forest per year.

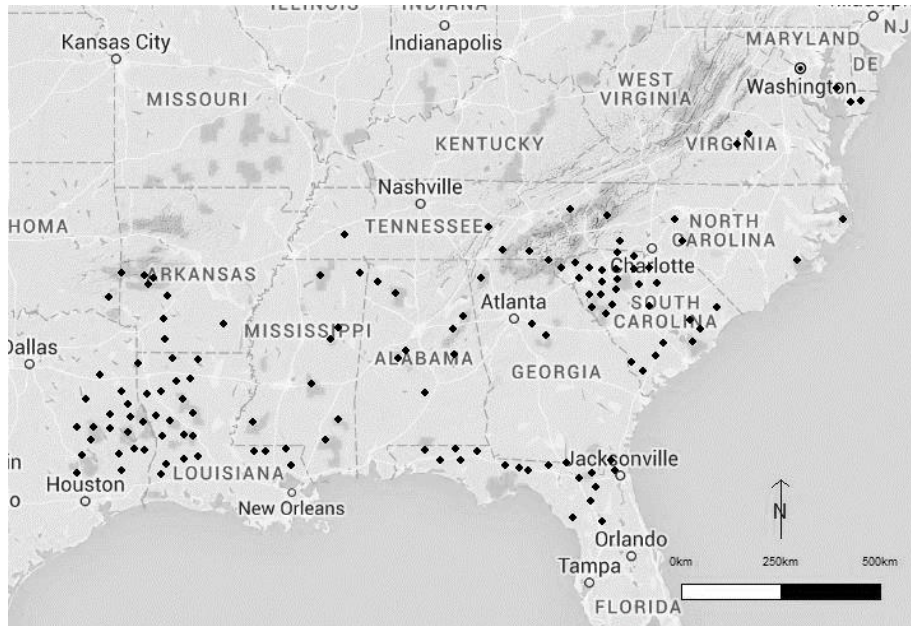


Figure 2: Locations of SPB trapping sites

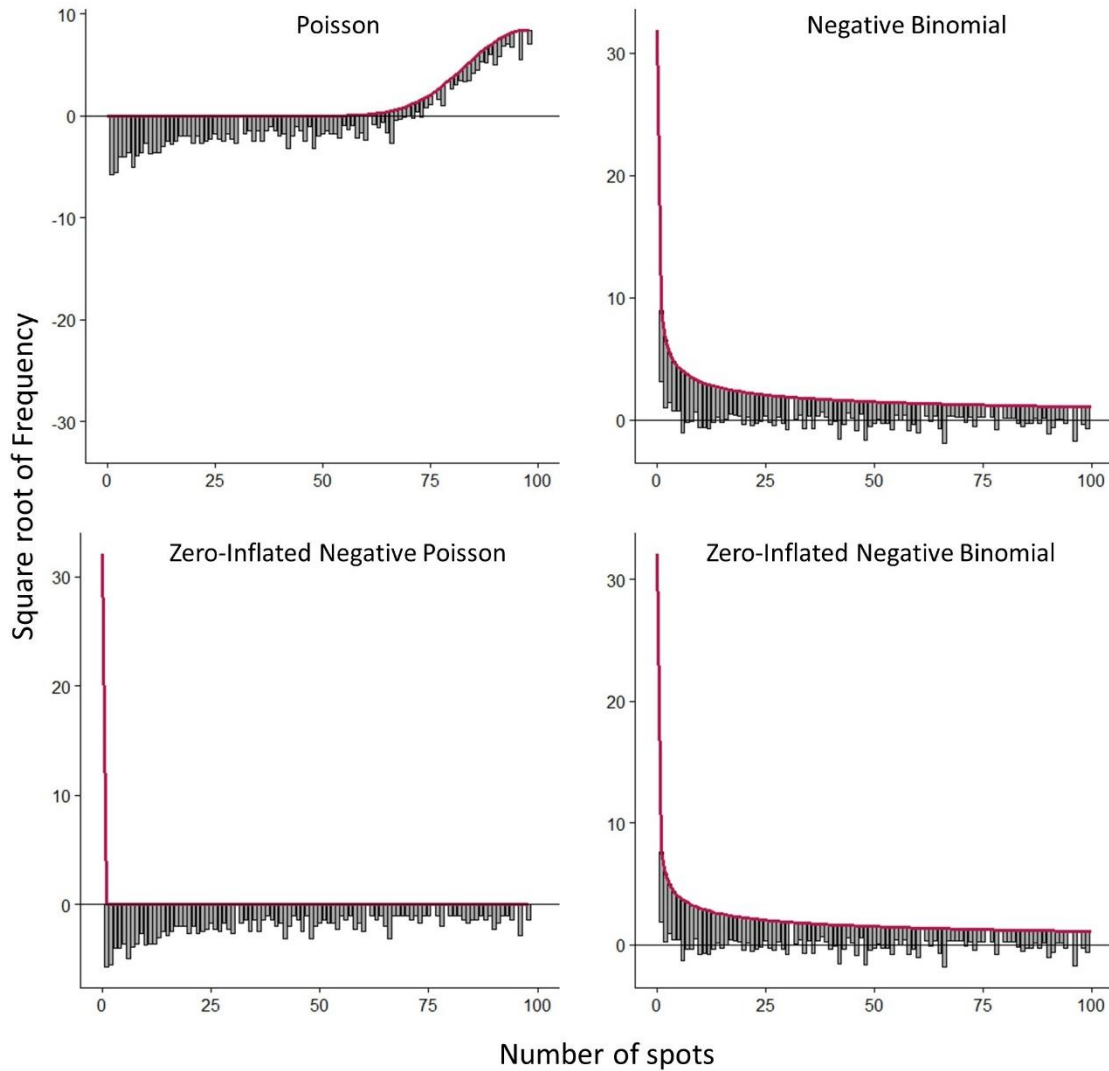


Figure 3. Rootograms (square root of frequency) comparing the univariate distributions of number of spots. The red lines show the expected counts, given each model, and the bars show the observed counts. With the reference line set at zero, and bars shown hanging from the fitted line, a gap between the bar the zero line shows underprediction, and a bar below the zero line shows overprediction. Values greater than 100 are not shown.

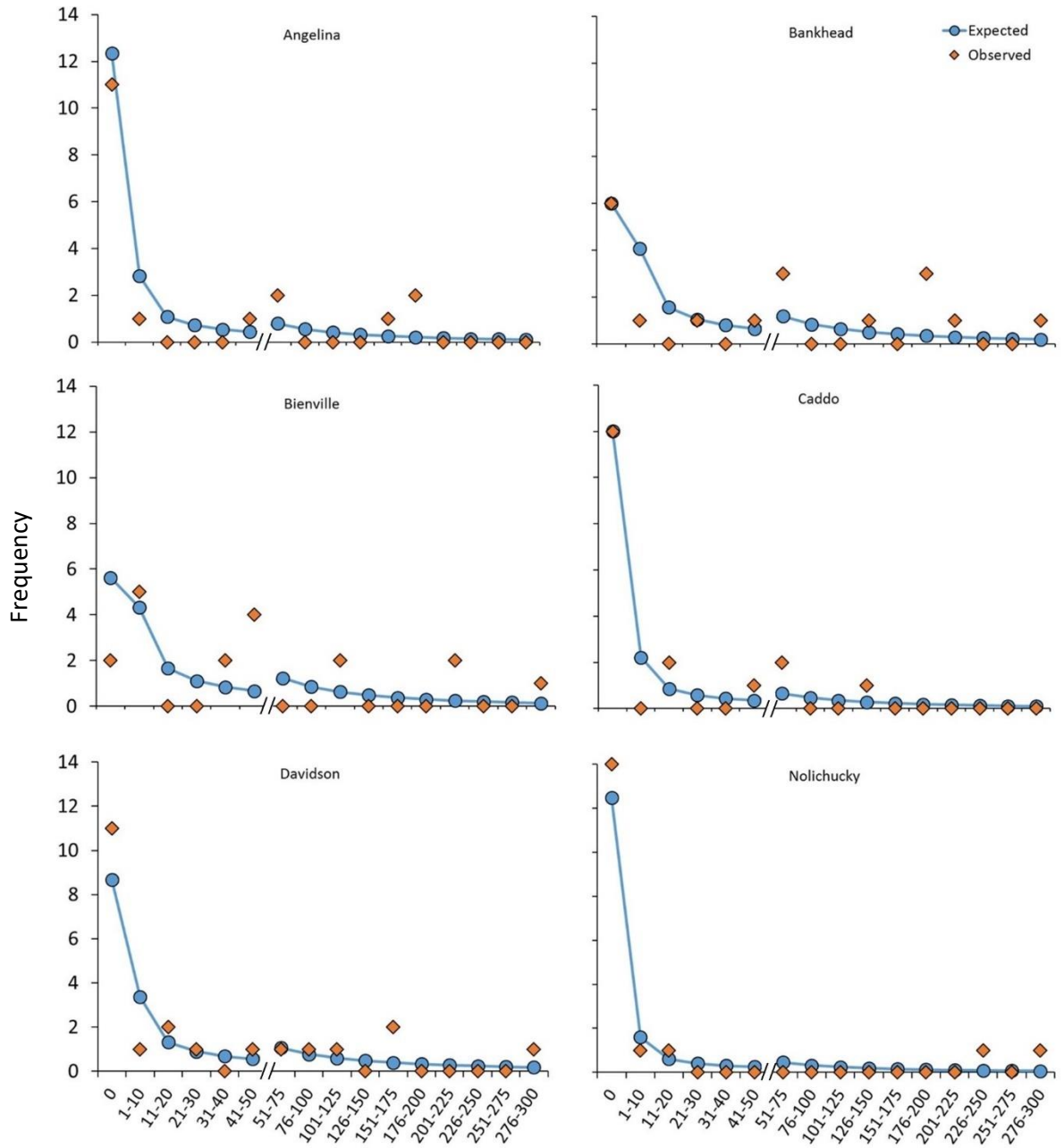


Figure 4. Observed vs. expected frequencies of numbers of spots per range of values for selected forest ranger districts in the dataset. Each forest includes 18-22 yrs of data. Values greater than 300 are not shown as the probability values are close to zero after this point. Note the change in the size of value ranges on the x-axis.

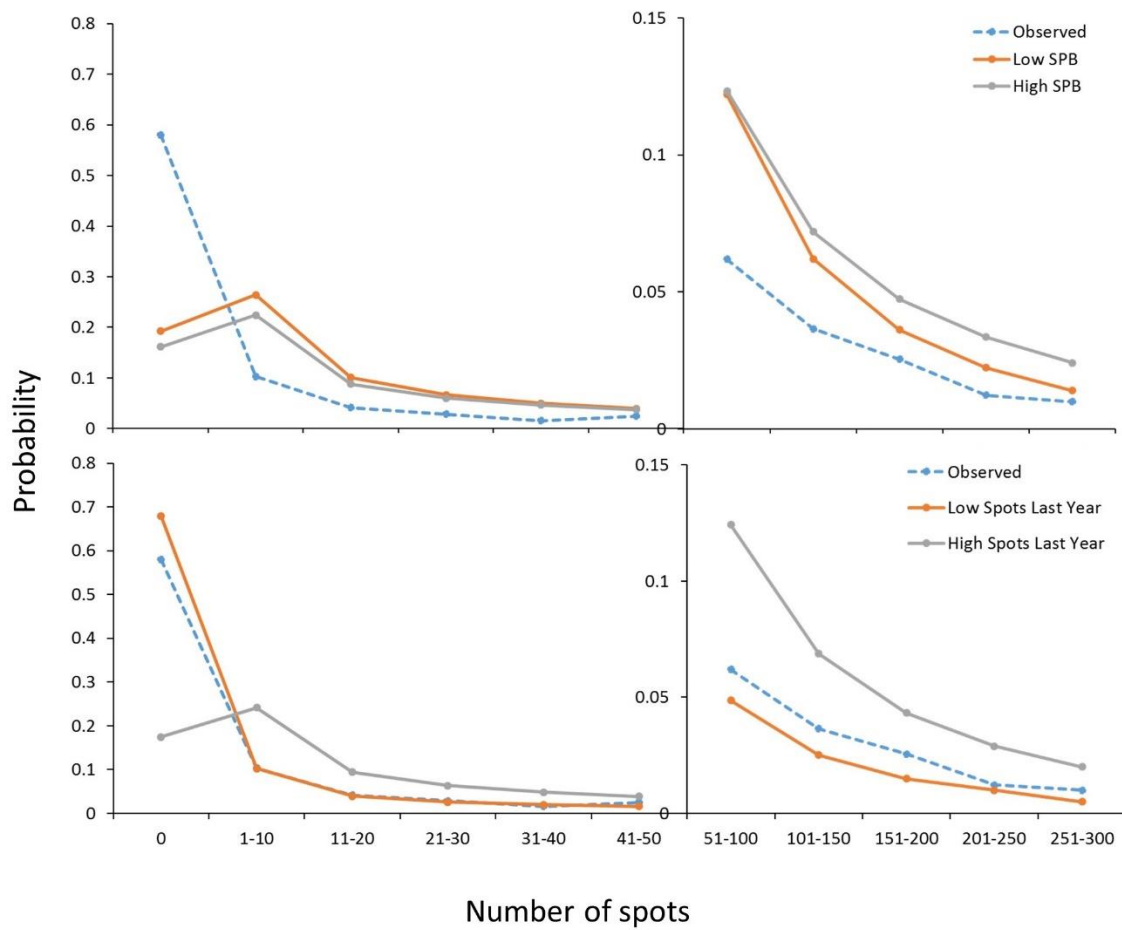


Figure 5. Sensitivity analysis of full best-fitting model. Low vs. high values of SPB did not change the expected probabilities very much (top row), and tended to underpredict the probability of zero. Due to the wide range of spot values, the y-axis and bin size values are modified after 50, to better show the spacing of the different results. Testing low and high values of the other model variables produced similar results. The only tested value that produced a probability of zero close to the observed value was low number of spots in the previous year (bottom row).

## Supplementary Material

SMTTable 1. Comparison of univariate distributions for the dependent variable number of spots.

	AIC	$\Delta$ AIC	df
Zero-inflated negative binomial	11177	0	3
Hurdle negative binomial	11177	0	3
Negative binomial	11193	16	2
Hurdle Poisson	484263	473086	2
Zero-inflated Poisson	484263	473086	2
Poisson	783453	772276	1

SMTTable 2. Comparison between the offset of  $\log(\text{Host Area})$ , which does not produce variable coefficients for area in the resulting model, and using host area in hectares as a regular variable in the model.

	AIC	$\Delta$ AIC	df
Host Area in hectares	11132	0	5
Offset( $\log(\text{Host Area})$ )	11159	27	3
Null Model	11177	46	3

SMTTable 3. AIC comparison among the full best-fitting model, the full model with non-significant variables removed, the Texas model, the Texas model with non-significant variables removed, a clerids-only model, an SPB-only model, and the SPB-only model with non-significant variables removed. In all simpler models, host area and spots in the year and two years prior were retained.

	AIC	$\Delta$ AIC	df
Full Model	9907	0	18
Texas Model	9912	4.6	13
Full Model, reduced	9926	18.3	12
Texas Model, reduced	9929	21.3	11
Clerids Only	9987	79.8	13
SPB Only	9988	80.1	11
SPB Only, reduced	9996	88.2	8

SMTable 4. Predicted probabilities of numbers of spots for the full best fitting model and the simpler Texas model. The range of possible y-values was wide (max = 4767), so two different methods for binning the probability values are shown.

	0	1-10	11-20	21-30	31-40	41-50	91-100
Full Model	0.5745	0.1137	0.0438	0.0294	0.0223	0.0179	0.0085
Texas Model	0.5743	0.1132	0.0435	0.0292	0.0222	0.0179	0.0087

	0	1-100	101-200	300	400
Full Model	0.5745	0.2838	0.0520	0.0248	0.0143
Texas Model	0.5743	0.2831	0.0531	0.0254	0.0146



SMTTable 5. Observed vs. expected spots in selected forests. N per forest ranges from 18-22 years.

No. of Spots		0	1-10	11-20	21-30	31-40	41-50	51-75	76-100
Angelina	Observed	11	1	0	0	0	1	2	0
	Expected	12.34	2.82	1.08	0.72	0.54	0.43	0.80	0.56
Bankhead	Observed	6	1	0	1	0	1	3	0
	Expected	5.99	4.06	1.56	1.04	0.79	0.63	1.18	0.84
Davidson	Observed	11	1	2	1	0	1	1	1
	Expected	8.68	3.36	1.32	0.90	0.69	0.56	1.06	0.77
Mena	Observed	12	5	0	2	0	0	0	0
	Expected	12.89	2.42	0.94	0.64	0.49	0.40	0.75	0.54
Tallulah	Observed	10	0	5	1	0	1	1	1
	Expected	8.58	3.68	1.40	0.93	0.70	0.55	1.02	0.71
Armuchee	Observed	14	3	0	0	0	1	0	0
	Expected	9.95	2.80	1.07	0.71	0.54	0.43	0.79	0.55
Oden	Observed	14	2	0	2	0	0	0	0
	Expected	14.19	1.75	0.68	0.46	0.36	0.29	0.55	0.40
Somerset	Observed	16	3	2	0	0	0	0	0
	Expected	16.14	1.65	0.62	0.41	0.30	0.24	0.42	0.28
Worcester	Observed	14	5	0	0	0	0	0	1
	Expected	15.85	1.67	0.63	0.42	0.31	0.25	0.44	0.30
Bienville	Observed	2	5	0	0	2	4	0	0
	Expected	5.62	4.33	1.67	1.11	0.84	0.67	1.24	0.86
Caddo	Observed	12	0	2	0	0	1	2	0
	Expected	12.03	2.21	0.86	0.58	0.44	0.35	0.66	0.47
Kisatchie	Observed	13	3	0	2	0	1	0	0
	Expected	14.21	2.09	0.78	0.50	0.37	0.29	0.50	0.32
Fairfield	Observed	3	2	2	2	1	1	2	3
	Expected	5.20	3.31	1.30	0.89	0.68	0.55	1.05	0.77
Hardin	Observed	15	1	0	0	0	0	0	1
	Expected	12.25	1.70	0.66	0.45	0.34	0.28	0.53	0.38
Sam Houston	Observed	12	0	2	0	1	0	0	0
	Expected	11.79	2.07	0.80	0.53	0.40	0.32	0.60	0.42
Catahoula	Observed	10	3	1	0	0	2	1	0
	Expected	11.90	1.94	0.74	0.49	0.36	0.29	0.52	0.36
Jasper	Observed	12	3	0	0	0	0	0	0
	Expected	12.80	1.34	0.53	0.36	0.28	0.23	0.43	0.31
Newton	Observed	14	1	0	0	0	2	0	0
	Expected	12.30	1.33	0.52	0.36	0.28	0.23	0.43	0.32
Nolichucky	Observed	14	1	1	0	0	0	0	0
	Expected	12.49	1.60	0.61	0.41	0.31	0.25	0.45	0.32
Oakmulgee	Observed	5	0	2	0	1	1	0	1
	Expected	4.26	3.64	1.41	0.94	0.72	0.58	1.07	0.76
Ocoee	Observed	14	2	0	0	0	0	0	0
	Expected	12.83	1.67	0.63	0.41	0.30	0.24	0.43	0.29
Oconee	Observed	3	1	0	3	0	0	1	1
	Expected	4.59	2.92	1.14	0.78	0.60	0.49	0.93	0.68
Tallapoosa	Observed	2	5	1	0	0	0	2	1
	Expected	5.60	3.17	1.24	0.84	0.65	0.53	0.99	0.72
Uwharrie	Observed	7	5	4	1	1	0	0	0
	Expected	7.33	3.05	1.18	0.80	0.61	0.49	0.91	0.65
Winn	Observed	11	1	1	1	0	0	1	0
	Expected	11.53	2.08	0.79	0.52	0.39	0.31	0.55	0.37

SMTable 6. Sensitivity analysis comparing low versus high values of all variables in the full best-fitting model.

	0	1-10	11-20	21-30	31-40	41-50	51-100	101-150	151-200	201-250	251-300
Observed	0.5800	0.1031	0.0418	0.0287	0.0158	0.0249	0.0619	0.0365	0.0255	0.0123	0.0100
Low SPB	0.1923	0.2644	0.1010	0.0670	0.0502	0.0399	0.1220	0.0620	0.0362	0.0224	0.0140
High SPB	0.1616	0.2244	0.0881	0.0602	0.0465	0.0377	0.1234	0.0720	0.0474	0.0335	0.0241
Low PctSPB	0.2033	0.2778	0.1048	0.0687	0.0509	0.0399	0.1183	0.0569	0.0313	0.0180	0.0111
High PctSPB	0.1490	0.2077	0.0823	0.0567	0.0437	0.0360	0.1205	0.0733	0.0506	0.0368	0.0277
Low Clerids	0.1858	0.2559	0.0985	0.0657	0.0496	0.0249	0.1230	0.0650	0.0388	0.0247	0.0165
High Clerids	0.1733	0.2399	0.0932	0.0632	0.0480	0.0249	0.1243	0.0691	0.0437	0.0294	0.0208
Low SPB Last Year	0.1744	0.2413	0.0939	0.0633	0.0481	0.0249	0.1243	0.0687	0.0432	0.0290	0.0203
High SPB Last Year	0.1938	0.2663	0.1013	0.0674	0.0502	0.0249	0.1215	0.0615	0.0355	0.0217	0.0135
Low PctSPB Last Year	0.1912	0.2629	0.1006	0.0668	0.0502	0.0399	0.1220	0.0627	0.0366	0.0228	0.0145
High PctSPB Last Year	0.1666	0.2310	0.0903	0.0615	0.0469	0.0382	0.1240	0.0708	0.0462	0.0317	0.0226
Low Spots Last Year	0.6789	0.1025	0.0395	0.0261	0.0197	0.0158	0.0486	0.0252	0.0150	0.0100	0.0050
High Spots Last Year	0.1747	0.2416	0.0940	0.0634	0.0482	0.0390	0.1242	0.0687	0.0432	0.0290	0.0201
Low Host Area	0.1947	0.2671	0.1020	0.0674	0.0505	0.0399	0.1212	0.0609	0.0351	0.0214	0.0133
High Host Area	0.1615	0.2244	0.0881	0.0601	0.0465	0.0377	0.1234	0.0721	0.0474	0.0335	0.0241

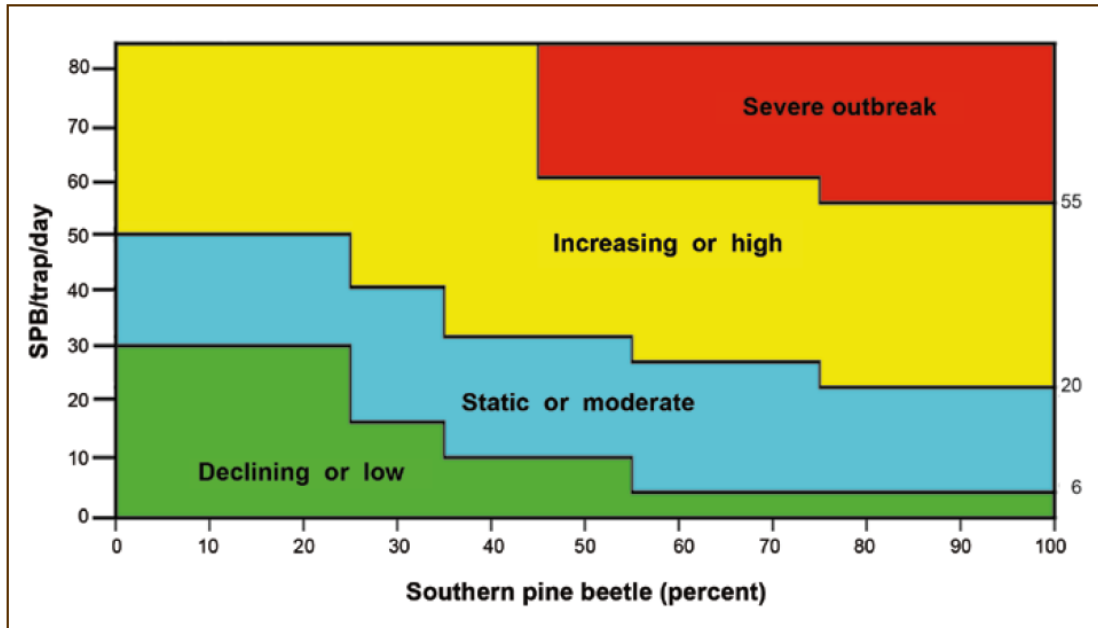


Figure 3—Southern pine beetle prediction chart. The prediction of SPB infestation trend and level for the current year is derived by plotting the mean number of SPB per trap per day and percent SPB for the current year and comparing these data to that for the previous year (if available) for a given locality. Percentage SPB =  $(\text{No. SPB} \times 100) / (\text{No. SPB} + \text{No. Clerids})$ .

SMFigure 1. Prediction chart currently in use for the annual SPB outbreak prediction system (Billings and Upton 2010).

## **Conclusion: Prediction and Known Distributions of Disturbance**

I showed that previous knowledge from southern pine beetle, a well-studied native insect, can be readily applied to assess risk in new forests that are challenged by pest range expansion as the climate warms. Forest risk of insect outbreaks can be thought of in two complementary parts—the susceptibility of the host trees, and the population dynamics of the insect itself. My work investigated both components, showing that risk assessment using available monitoring and measurement tools is possible for managers facing a short time frame to adjust to new pests.

Forest structure data with which forest managers are well familiar, and that can be collected with minimal expense and expenditure of time, can be used both to assess the forest types present and to understand the variables that most affect the probability of infestation. Stand-level forest structure variables appeared to swamp the effects of tree resin defenses. In addition, evidence from New Jersey contradicted evidence from SPB in the south, which had previously supported the Growth Differentiation Balance Hypothesis (Lorio 1986, Reeve et al. 1995). This hypothesis states that as plants come under moderate stress due to lack of resources, they allocate carbon to defenses rather than to growth (Loomis 1932, Herms and Mattson 1992). My results showed that sites well suited to tree growth, by contrast, had higher levels of resin defense. In turn, these wetter sites did not respond uniformly to the probability of infestation. At the stand level, forest structure apparently swamped any effects of defenses. Known relationships between forest structure variables and probability of infestation from southern forests appeared to hold true in New Jersey.

I also demonstrated the efficacy of using zero-inflated models to characterize population fluctuations in non-cyclical pests. These models can be used to assist in annual outbreak predictions in the future. Previous work supported the idea that southern pine beetle population dynamics may be well-characterized by an alternate attractors model (Martinson et al. 2013). That research showed that this model of population dynamics could generate predictions and hypotheses about the shape of the distribution, the role of competitors and predators, and the direction of positive and negative feedback toward or away from the equilibria. The testing of these hypotheses contributed to our understanding of the biology of the insect. From a management perspective, however, a different model was needed, one that could be easily parameterized using the current operational data and used to predict outbreaks in any given year. Zero-inflated models provide a good fit for outbreak data characterized by many zeros from years when the insect was rare. This mixture model framework can be applied in any system of both regularly and irregularly fluctuating population levels.

The general public and popular media often characterize disturbances such as wildfire and insect outbreaks as catastrophic events in the environment. However, for many forested ecosystems that have evolved with these disturbances and indeed rely upon them for maintenance, these occasional events have a probability distribution and contributing independent variables that can be known. No prediction system is perfect, but we can arrive at a relatively strong characterization of the range of variability in a given system, from both the plant and insect perspectives.

As forest managers face a future under climate change, range expansion of native insect pests is among many possible threats (Dukes et al. 2009, Weed et al. 2013). I

showed that previous knowledge of these native insects can be used to develop practical prediction models as insect ranges expand. The next step in thinking about these range-expanding insects will be to characterize the nature of catastrophic, or system-changing events that may take place under a changing climate. Disturbance-adapted systems may be characterized by an alternate attractors model that describes both disturbed and non-disturbed states. Some researchers, however, have used alternate attractors models to describe more extreme system shifts. If we already believe that an alternate attractors model describes our system of *natural* disturbance, how do we additionally describe events that push the system beyond the point of return? What is the probability that one of these outbreaks may be so severe that the forest will never return to its previous state? What factors might contribute to such a probability? The ability to predict extreme events in systems of usually-natural disturbances will be the next step forward in forest risk assessment.

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