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Old pests in new places: Effects of stand structure and forest type on susceptibility to a bark beetle on the edge of its native range

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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 rapidly assess local impacts, while utilizing familiar metrics so that the wheel need not be re-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. 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 with higher probability than mixed pine/hardwood stands, regardless of whether the stands were upland or wetland habitats. The effects of stand type (wetland or upland) were over-ridden by the effect of stand composition. Research from the south has found that wet or waterlogged stands tend to be more susceptible to SPB, potentially due to lower tree defenses. Our finding that wetland/upland status is less important than stand composition suggests that defenses were not the primary determinant of stand susceptibility. 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 stands with high percentage pine and high pine basal area were more susceptible. Stands composed of smaller, closer together, shorter, and younger trees, with lower percent live crown, were also more susceptible. Discriminant analyses found that a simple model including DBH, pine basal area, and percent live crown could be used to successfully separate and prioritize stands more likely to be infested in the future. Our results suggest that thinning is an appropriate management strategy for forest managers seeking to build resilience, and that all else being equal, conifer stands should receive priority for management attention over mixed stands.

1. Introduction

Outbreaks of forest insect pests can kill thousands of hectares of trees and pose persistent challenges to forest management. Even native insects whose hosts are adapted to their presence can 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. In this case, it is challenging to determine appropriate management responses because research specific to the new zone of infestation has not yet been conducted. For example, managers must decide whether to invest in suppression or prevention tactics that were designed for the insect's historic range.

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The 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. SPB outbreaks have been regularly documented throughout the south since the beetle was officially recognized in 1868 (Clarke et al., 2016). Historical documents suggest that similar widespread outbreaks occurred during the 18th and 19th 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 to 2002 resulted in over 1 billion dollars just in the direct costs of lost timber (Clarke and Nowak, 2009). Since 2002, however, SPB has remained at non-outbreak levels across much of the south (Asaro et al., 2017; Clarke et al., 2016), with the exception of Mississippi, which experienced an upturn in SPB infestations over the last several years, escalating to outbreak status in 2016–2017 (United States Forest Service-Forest Health Protection, 2017a). While the US Forest Service's Southern Pine Beetle prevention program reported no major outbreaks across the south between the program's inception in 2003 and the recent activity in Mississippi (United States Forest Service-Forest Health Protection, 2017b), an outbreak began in southern New Jersey, beginning in approximately 2002 (Dodds et al., 2018). 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), more damage than had previously been recorded. In 2014 and 2015 respectively, SPB was detected for the first time in trees on Long Island, New York (Schlossberg, 2014) and in Connecticut (Dodds et al., 2018). These detections were followed by extensive tree mortality on Long Island, and smaller mortality events in Connecticut. Since then, small numbers have also been trapped in Rhode Island and Massachusetts (Dodds et al., 2018). Although these latter states have yet to detect tree mortality due to SPB, the mortality events in New York and Connecticut suggest that SPB's range is continuing to expand. Northern distribution limits of SPB are constrained by the beetle's ability to survive beneath the bark during the winter months, emerging the following spring. Minimum annual temperature–the coldest night of the year–at a given latitude thus plays a key role in the northern range expansion of SPB (Trần et al., 2007). The minimum winter temperature in New Jersey has increased by > 4 °C over the last 50 years (Weed et al., 2013). 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).

Southern New Jersey is home to over 1 million acres of federally protected pine and mixed pine-oak forest (New Jersey Pinelands National Reserve). As SPB expands its range northward to the Pinelands and beyond, the potential host species change. Traditional host species in the south include the four primary species of southern yellow pines (Clarke et al., 2016; Hopkins, 1909; Payne, 1980)–loblolly, longleaf, shortleaf, and slash pine (*Pinus taeda, P. palustris, P. echinata, P. elliottii*) (United States Forest Service Forest Products Laboratory, 1936). However, 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). The vast majority of previous research on SPB in the southeastern U.S. has focused on loblolly and longleaf pines,while pitch pine has received little attention (Fig. 1). An early investigation looked at the effects of winter temperatures on SPB survival in pitch and shortleaf pines (Beal, 1933). At the level of the stand, there has been some work on the interaction of fire and SPB, and their effects on Table Mountain pine (*Pinus pungens*)/pitch pine forests in the southern Appalachians (Knebel and Wentworth, 2007; Lafon and Kutac, 2003; Williams, 1998). Within the Southern Appalachians, stands with a high percentage of pitch pine have been identified as more susceptible to

SPB (Belanger and Malac, 1980). Variation among pitch pine stands, and the contribution of that variation to SPB susceptibility, has not previously been investigated.

A similar range expansion is taking place in mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins), a related bark beetle species that killed millions of hectares of trees in the western U.S. and Canada during the 1990–2000s. There has been range expansion of MPB from lodgepole pine (*P. contorta*), its historical host, into jack pine (*P. banksiana*), a novel host (Cullingham et al., 2011; de la Giroday et al., 2012). Examples of research in this system include studies on: chemical similarities between the two host species (Burke and Carroll, 2016; Erbilgin et al., 2014), beetle reproductive success in the novel host (Cudmore et al., 2010), effects of landscape factors on dispersal into the novel environment (de la Giroday et al., 2011), and differential responses of historical and novel host defenses to beetle fungal associates (Arango-Velez et al., 2016). Differences in host stand-level characteristics that may affect susceptibility to the beetle, however, have not yet been explored in jack pine, the novel host of mountain pine beetle, nor in mid-Atlantic and northeastern pitch pine, a system whose climate was previously unsuitable for southern pine beetle.

A population-based risk assessment procedure for SPB has been in place since 1986 across the southern states, utilizing spring beetle trapping numbers (Billings and Upton, 2010). 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 can be difficult to implement standardized trapping procedures across multiple jurisdictions within states, and across state lines, such that landscape-scale risk of infestation can be assessed on a region-wide scale. Here, then, we focus on risk assessment related to host susceptibility rather than beetle population levels determined by trapping. Stand-level host susceptibility 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, 1980, Coster and Searcy, 1981). Although there was some regional variation, these southwide data show that some stand characteristics are correlated with infestation by SPB. Each of these characteristics is related to the biology of SPB aggregation behavior and the progression of an infestation through a stand (Table 1). Unlike some bark beetle species, SPB attack healthy pines, forming discrete infestations of tens to thousands of trees, 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 damaged 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). This mass attack strategy overcomes 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. Spot growth is facilitated by both the re-emergence of attacking adults as well as the progeny from earlier attacks. Thus, stand characteristics that promote spot formation and spot growth increase the risk of infestations arising and persisting. Table 1 summarizes previous research on the relationship between measured stand/tree variables and the mechanisms through which
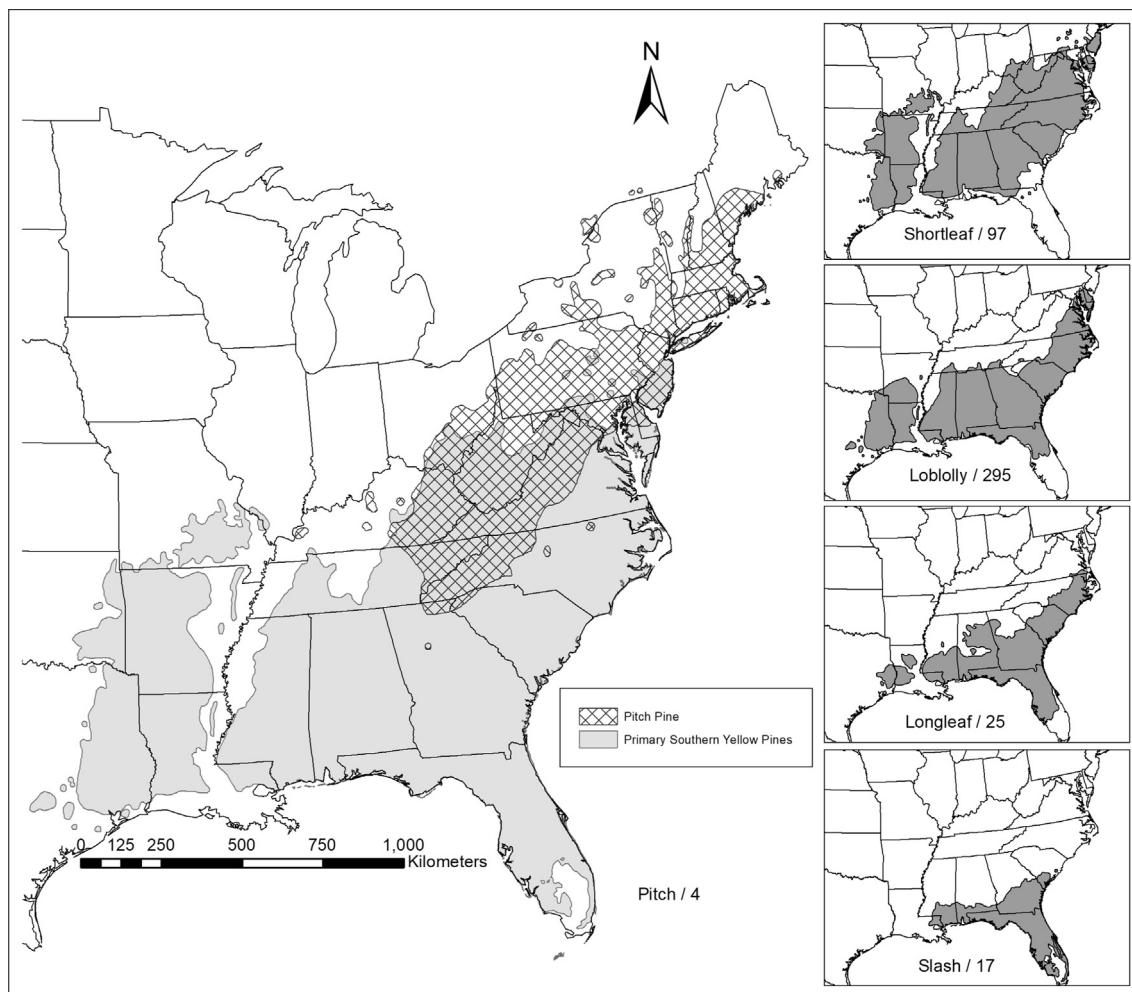
Fig. 1. Distributions of SPB host pine species across the eastern U.S. Main figure shows combined distributions of the four primary southern yellow pines that have historically been the focus of studies concerning SPB and pines. The four species are shown individually at right. Number following species name indicates number of articles returned when searching Web of Science for "*Dendroctonus frontalis*" and "*Pinus [species name].*"

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

Tree/Stand Characteristic	Known or proposed mechanism of influence on stand susceptibility	References
Inter-tree distance[a]	*Resource availability (among trees)–tree vigor and/or tree defenses*; trees with more resources (whether due to less competition/lower density or to seasonal changes in precipitation) may be less well-defended	Lorio (1986) and Reeve et al. (1995)
	Distance between hosts–beetle flight; the vulnerability of adjacent trees to attack from already-infested trees appears to depend on proximity to the infested trees	Gara and Coster (1968) and Johnson and Coster (1978)
Basal area[a]	*Resource availability (among trees)–tree vigor and/or tree defenses;* see above	Lorio (1986)
	Distance between hosts–beetle flight; see above. Basal area—in cases where thinned stands meant lower basal area—was shown to indicate a lower probability of infestation growth	Showalter and Turchin (1993)
Percent pine	*Distance between hosts–beetle flight*; in addition to basal area, stand composition—i.e., having pure pine vs. mixed pine composition—also significantly affected infestation growth	Gara and Coster (1968) and Showalter and Turchin (1993)
Site moisture/Site index	*Resource availability (within stand)–tree vigor and/or tree defenses*; see above	Lorio (1986)
Percent canopy cover	*Stability and concentration of pheromone plume*	Thistle et al. (2011) and Vite (1970)
DBH/Height	*Stand age/size*	Lorio (1978)
Age	*Distance between hosts–beetle flight*; inter-tree distance may increase as a stand ages, and susceptibility has been shown to have a parabolic relationship with stand age	Ylioja et al. (2005)
	Stand age/size	Lorio (1978)

[a] Stand density (trees/ha) and basal area (m^2/ha) are sometimes conflated in the literature. However, high basal area can arise from high densities of small trees, or lower densities of larger trees. Because distance between trees has been shown to be specifically significant in infestation growth, we describe tree or stem density in terms of distances among trees (inter-tree distance), as distinct from basal area.

these variables may influence host susceptibility; the majority of the prior research was conducted in an operational context, and so focused on predictors more than mechanisms.

Here 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 whether susceptibility to infestation is related to one or more of the four forest types that includes pitch pine; (3) to determine the stand structure variables that have the strongest influence on susceptibility; and (4) to calculate a hazard rating for pitch pine infestation based on stand structure characteristics.

2. Methods

2.1. 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 includes 56 municipalities and nearly 500,000 residents. Although most 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. 2).

Aerial detection surveys conducted by New Jersey Forest Service between 2002 and 2013 show a northward spread over time of localized infestations by SPB (spots) (Weed et al., 2013, New Jersey DEP, unpublished data). To cover the entire range of the current outbreak, our study included Atlantic, Burlington, Camden, Cape May, Cumberland, Gloucester, and Salem Counties (Fig. 3). 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 (Fig. 3). New Jersey Forest Service aggressively suppressed SPB activity north of the river, due to the high concentration of pine-dominated stands in the area. Consequently, there were fewer and smaller spots in the northern region. We sampled uninfested stands north of the Mullica River to characterize their stand structure, but we restricted our sampling of spots (both from the aerial data and for our field sampling plots) to those south of the river.

2.2. Forest type

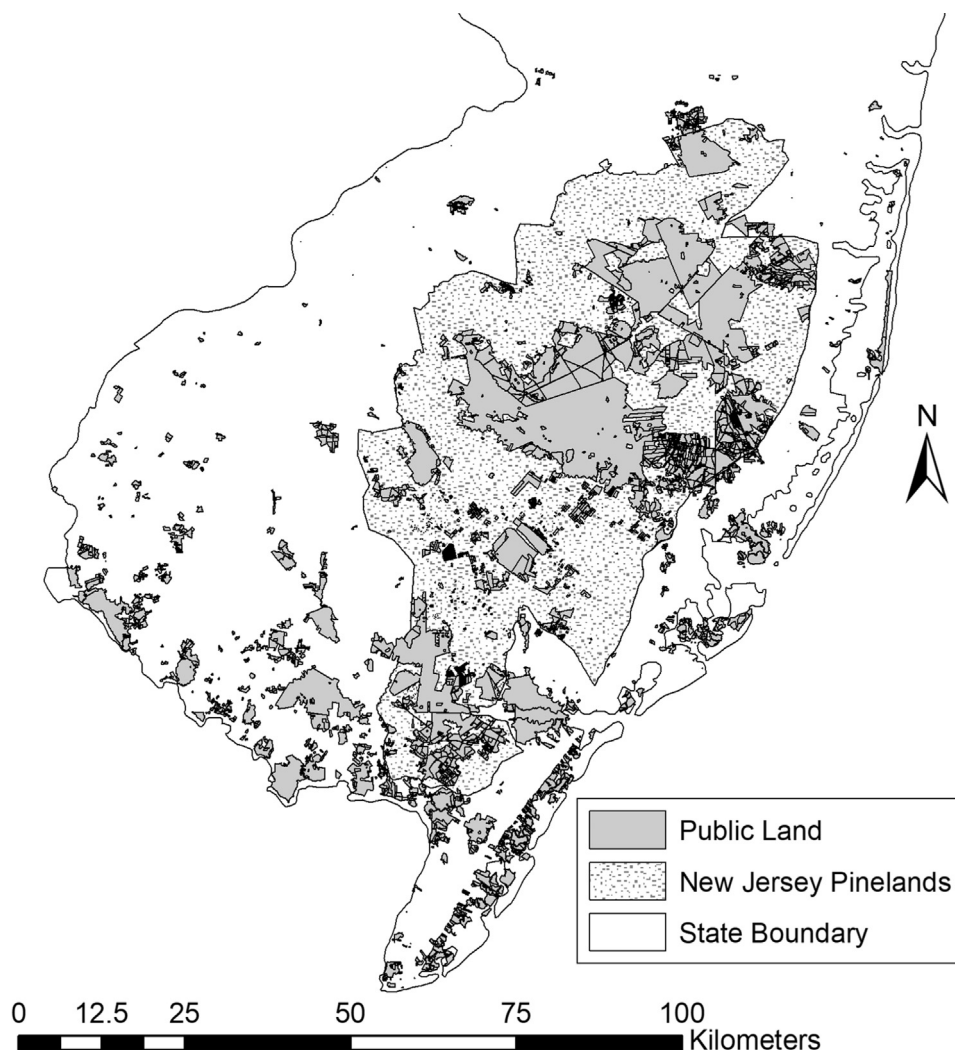The majority of the forested land within the Pinelands is comprised

Fig. 2. Map of southern New Jersey, showing land in public ownership against the boundary of the federally demarcated Pinelands.
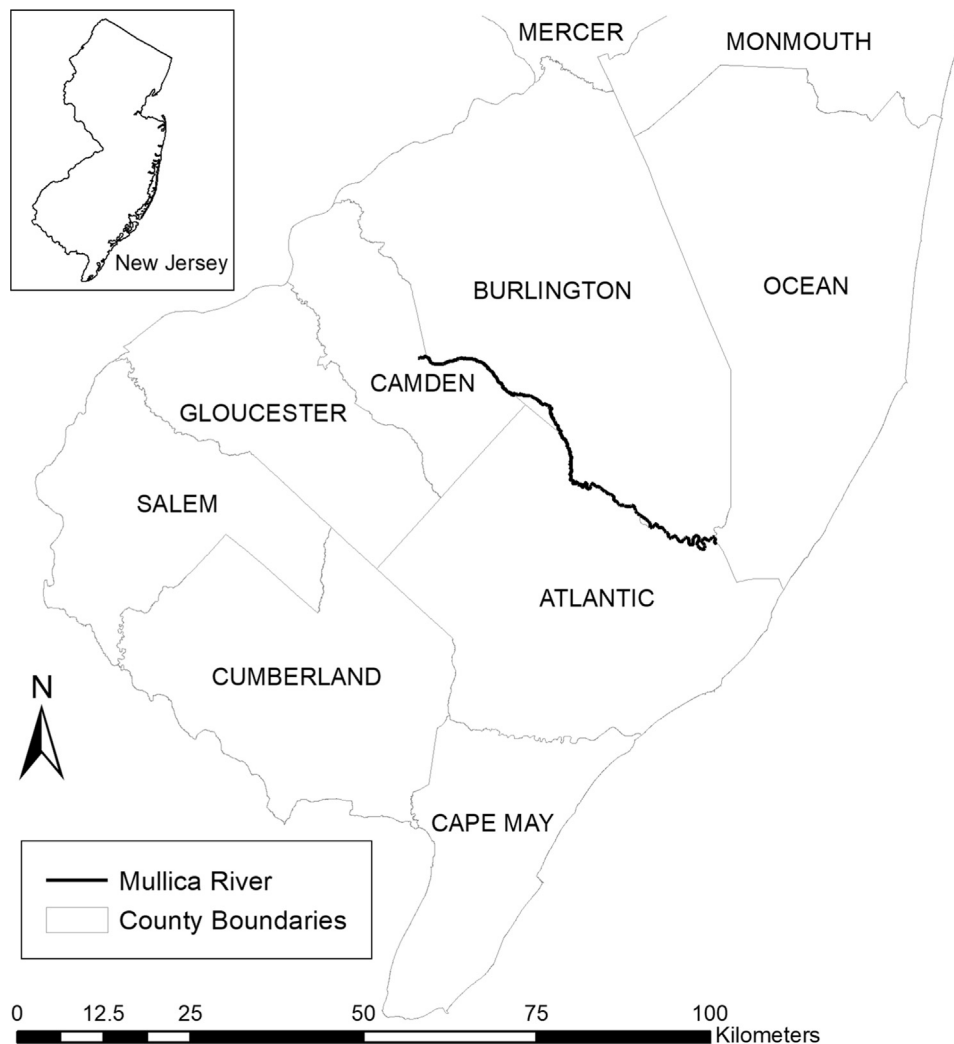
Fig. 3. Counties in southern New Jersey, with Mullica River shown.

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). 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, 2010a). Classifications are based on a modified Anderson system developed by NJDEP (New Jersey Department of Environmental Protection, 2010b). We selected all forest types including a conifer component. Although aerial data does not distinguish among the pine species, the vast majority of conifers in the Pinelands are pitch pine. To simplify analyses to categories that would be meaningful for management, some cover classifications were merged. For example, "coniferous forest" was divided into "10–50% crown closure" and " > 50% crown closure" types in the original data, and we merged these into a single category. 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. 4). Deciduous forest types and shrub/scrub forest types were not included in the analysisbecause 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 comprised 217 ground-truthed infestations. These were initially identified in aerial detection surveys (Fig. 5), and subsequently re-drawn by walking infestation perimeters with a GPS unit for better resolution than the air-drawn shapefile. 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, we restricted this analysis to state-owned land in counties south of the Mullica. Due to the dynamic nature of spots that continue to grow throughout the summer, and the static nature of sampling that takes place at a single point in time, we did not attempt to analyze spot size against forest type.

2.3. Forest structure

2.3.1. Plot sampling

Using the NJDEP LULC data described above, we used ArcGIS (Environmental Systems Research Institute (ESRI), 2012) to randomly select control (uninfested) plots across the four forest types described,
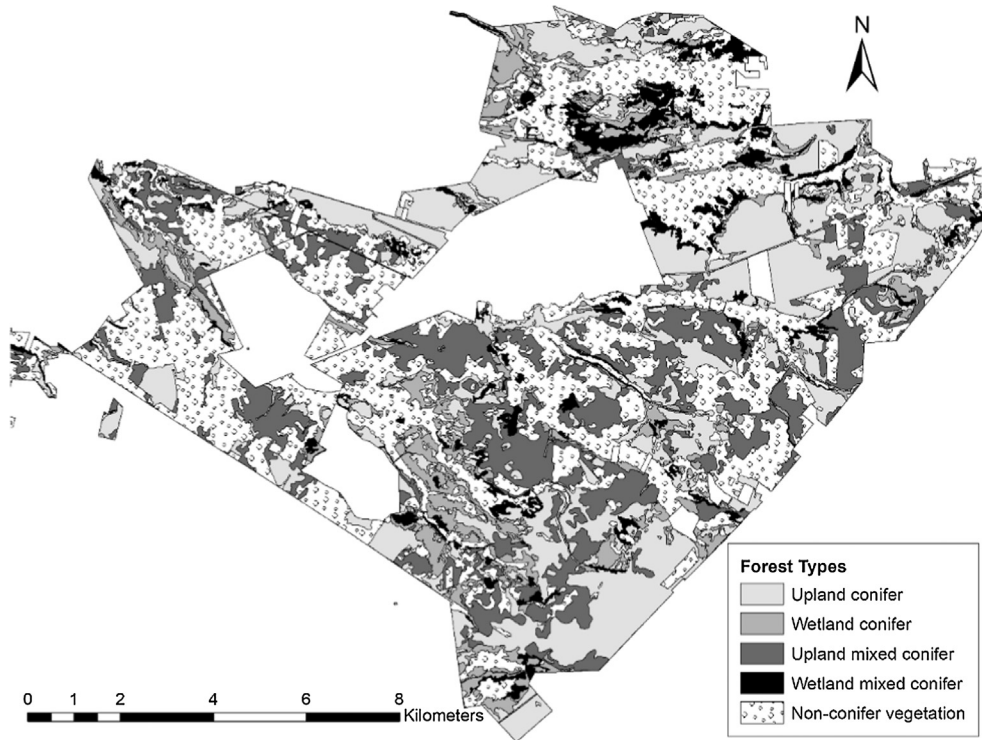
Fig. 4. Sample land use land cover forest type map, showing the boundary of Brendan Byrne State Forest and the four forest types used in the analysis.
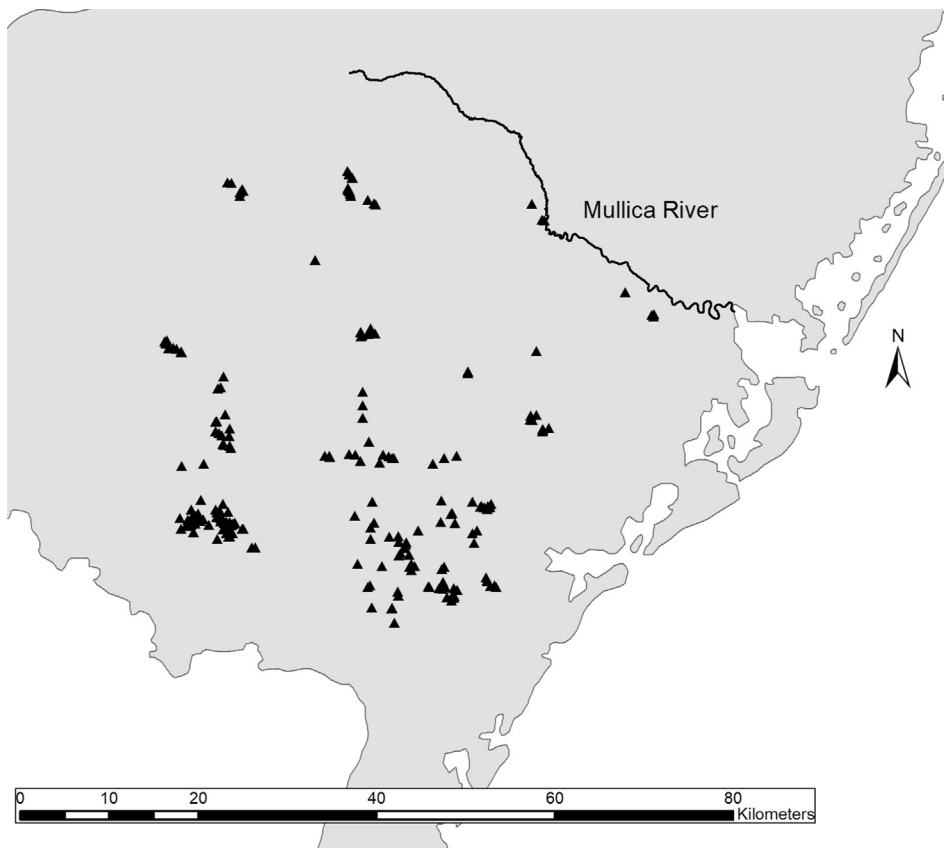

Fig. 5. Spot locations for forest type analysis, aerially detected and ground-truthed by NJDEP 2011–2013. NJDEP conducted aggressive suppression activities in the region north of the Mullica River, resulting in many fewer and smaller spots, so this region was not appropriate for spot analysis. However, general forest type characterization was done both north and south of the river.

with buffers appropriate for efficiency of plot access. We established 12 control (uninfested) plots each in the northern and southern regions (Fig. 6). We then selected 24 plots situated within recent SPB infestations identified by NJDEP ground-truth surveys from aerial detection data (hereafter referred to as spot plots; Fig. 6). As in the forest type analysis, we restricted our spot plot sampling to the southern region due to management activity in the northern region. Many of these spots had been managed for SPB suppression, i.e., the infested trees had been
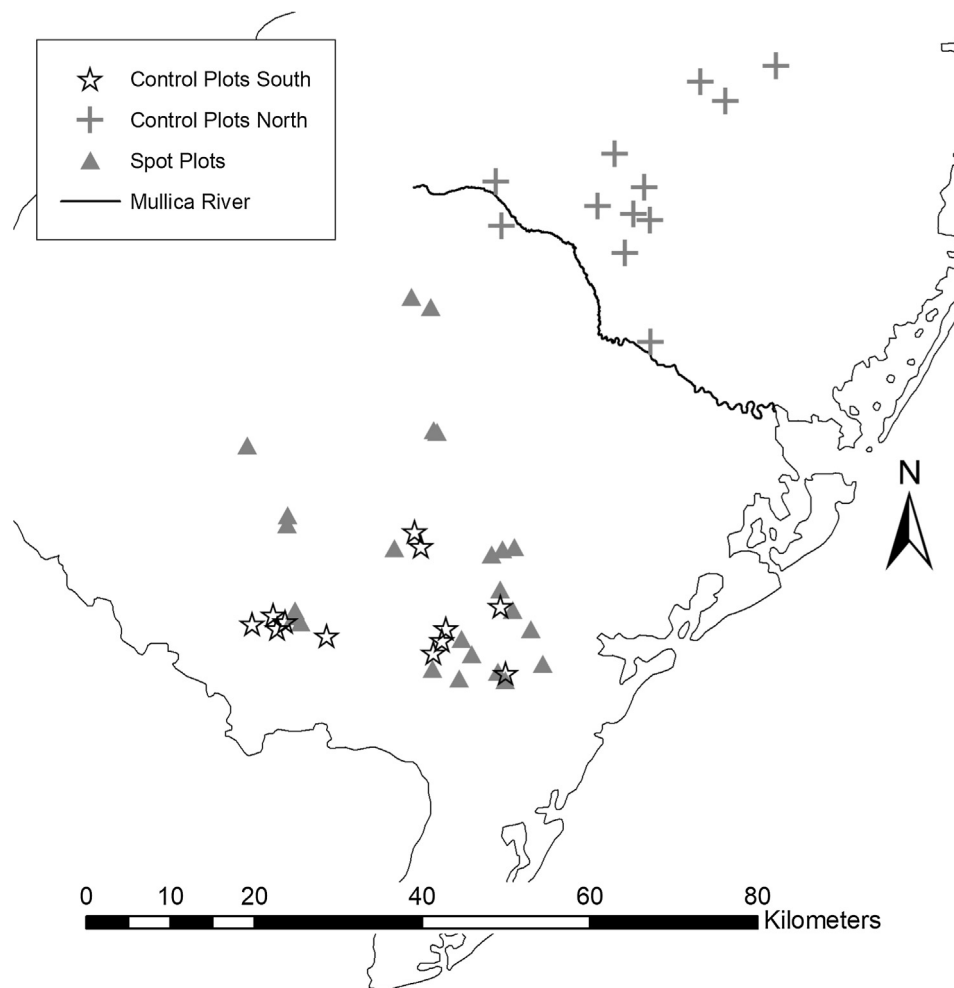
Fig. 6. Locations of control and spot plots where forest structure data was collected. As in the forest type analysis, the landscape was characterized both north and south of the Mullica River (control plots), but due to management activity north of the river, spot activity was only sampled south of the river.

cut down along with a small buffer zone. 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.

In each plot we sampled three 50-meter transects with sampling points every ten meters. At each of the 15 sampling points per plot, we located the nearest pine tree (> 15 cm diameter at breast height), measured its age, diameter at breast height (DBH), and height, and then from this focal tree, we recorded basal area of pine, basal area of hardwoods, distance to nearest and second nearest pine > 15 cm DBH, and percent canopy cover. (Surveys of SPB-infested stands in the southern U.S. have typically only considered trees of larger size classes (e.g., > 5 in. (12.7 cm), with infested stands averaging ∼ 13 in. (33.0 cm) diameter in loblolly and shortleaf pines (Coster and Searcy, 1981).) Hemispherical photography was used, in conjunction with the program ImageJ (Schneider et al., 2012) to estimate percent canopy cover. To calculate site indices, 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 set of site index equations, which we then used to calculate site index for each tree. These were then averaged into a single site index for each plot. Analyses were performed on plot-level means of each variable. Prior to taking the means, inter-tree distances and second inter-tree distances were log-transformed, and hardwood basal area was square-root transformed to improve normality.

2.3.2. Principal components analysis

Because the forest stand structure variables were highly correlated with one another (Table 2), and it was not possible to use multiple regression due to non-independence of the variables, we used principal components analysis (PCA) to reduce the dimensionality of the data, to compare infested versus uninfested plots, and to determine the contributions of the forest structure variables to risk of infestation. PCA is an unconstrained ordination method, using only the variation of the variables in question, without respect to group membership (McGarigal et al., 2000). It thus retains more variance from the original data than do similar constrained ordination methods (McCune and Grace, 2002). Here we conducted the PCA on all plots in the southern region (12 uninfested and 24 infested plots). Because there were fewer infestations in the northern region—due to management actions, as well as the timing of our sampling (SPB appeared first in the southern region)—we then sought to test how susceptible the northern uninfested plots were to (future) SPB infestation relative to the southern stands. To do this we used the eigenvectors obtained from the southern region PCA to calculate principal component scores for the northern plots. We then examined their relationship in multivariate space with respect to the direction of increasing risk along each component axis.

2.3.3. Discriminant analysis

Discriminant analysis (DA) is a constrained eigenanalysis method that finds the maximal separation between groups that can be obtained from the variables of interest (McCune and Grace, 2002). Because it can be used to find variable coefficients that maximize the distance between

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

	1	2	3	4	5	6	7	8	9	10	11	12	13
(a)													
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. Inter-tree distance I	0.76	−0.77	0.57	−0.33	−0.77	0.30	0.23	1.00					
9. Inter-tree distance II	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. Site index	−0.30	0.27	0.00	0.28	0.09	0.17	−0.18	−0.17	−0.17	−0.61	0.08	1.00	
13. Percent canopy	−0.04	−0.06	0.25	0.14	−0.23	0.07	−0.16	−0.05	−0.04	0.08	−0.01	−0.14	1.00
(b)													
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. Inter-tree distance I	0.86	−0.48	0.54	−0.34	−0.64	0.29	0.17	1.00					
9. Inter-tree distance II	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. Site index	−0.26	−0.08	0.15	−0.06	−0.04	0.04	0.01	−0.07	0.03	−0.40	0.09	1.00	
13. Percent canopy	−0.19	0.11	0.16	0.23	−0.14	−0.03	−0.15	−0.46	−0.41	−0.31	−0.33	−0.27	1.00

infested and uninfested stands, previous work attempting to determine stand hazard ratings for SPB have often employed this method (Birt, 2011; Hicks et al., 1979; Ku et al., 1980; Kushmaul et al., 1979). Here there are only two groups, infested and uninfested, so there can be only one ($k − 1$) resultant canonical axis, as opposed to PCA, which can produce two or more important axes. Because this analysis can only produce ($k − 1$) canonical components, more variation is lost in the analysis than in a PCA (McCune and Grace, 2002). To obtain this simplified result, as well as to compare our results with past attempts at hazard rating analysis, we additionally performed discriminant analysis, again using the infested and uninfested plots from the southern region. We used the quadratic method to account for unequal variance between groups, with prior probabilities based on the actual proportion of infested and uninfested plots. We performed a logistic regression on the canonical variable to obtain a probability of infestation curve. A canonical variable for the northern uninfested plots was obtained by multiplying the variables by the coefficients from the analysis of the southern plots (i.e., parallel to the method used in the PCA).

We performed further discriminant analyses to find the most parsimonious model for use in the field. We tested several combinations of variables to find the best fitting model that would enable managers to obtain a risk index for their stands. As in the prior analyses, these models were tested using the southern region plots only, both infested and uninfested. We then used the coefficients obtained from these analyses to determine model performance on the northern region sites.

All statistical analyses were performed using JMP Pro 12.1.0 (SAS Institute Inc., 2015) and R 3.2x (R Core Team, 2017).

3. Results

3.1. Forest type

Forests north of the Mullica River were overwhelmingly comprised of the upland conifer type, totaling nearly 45,000 ha (Fig. 7). Forests south of the Mullica, by contrast, were dominated by the mixed conifer type, both in upland and wetland areas (Fig. 7), comprising over 65% of
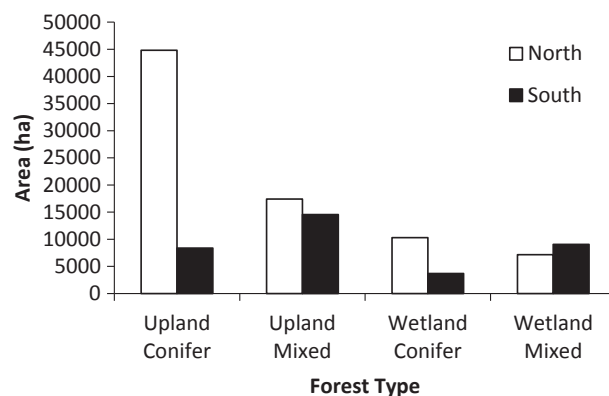

Fig. 7. Regional distribution of area in hectares of each forest type.

the forested landscape (Fig. 8a). Forty percent of spots in the southern region were in the upland conifer type, though this type covered less than 25% of the landscape. A further 27% of spots were 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. 8a). Median spot size was 0.77 ha, with minimum size 0.001 ha, and maximum size 36 ha. The ten next largest spots below the maximum were between 5 and 12 ha in size.

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. 8b).

3.2. Forest structure

3.2.1. Principal components analysis

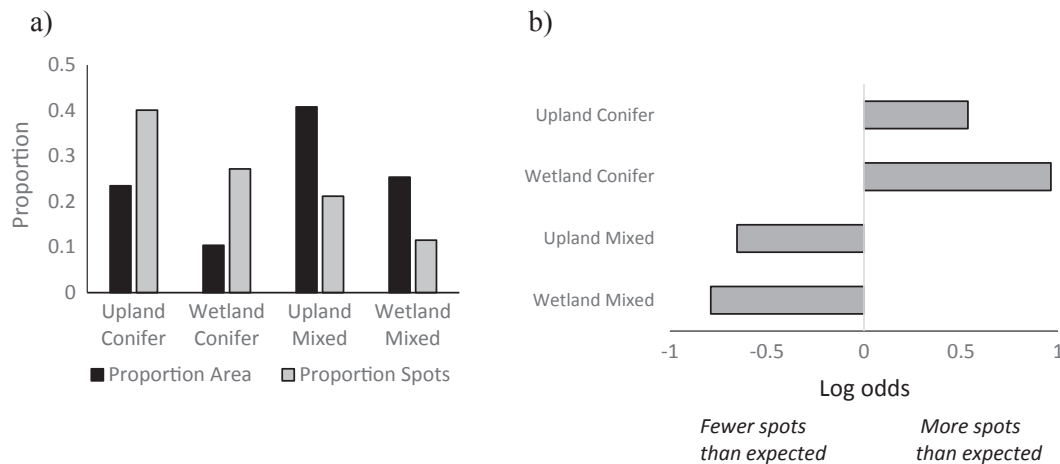Many features of stand structure varied between infested and

Fig. 8. (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.

Table 3
Means and standard deviations for measured forest structure variables by region and status.

	Southern Infested	Southern Uninfested	Northern Uninfested
DBH (diameter at breast height, cm)	28.9 ± 6.0	32.4 ± 6.0	26.2 ± 4.4
Pine basal area (m²/ha)	21.8 ± 7.5	14.9 ± 7.1	24.0 ± 5.5
Hardwood basal area (m²/ha)	11.1 ± 6.2	12.5 ± 6.4	2.6 ± 2.1
Total basal area (m²/ha)	32.9 ± 7.5	27.4 ± 6.8	26.7 ± 4.7
Percent pine	65.9 ± 15.3	54.9 ± 21.1	89.3 ± 7.9
Crown base height (m)	10.6 ± 2.6	9.9 ± 3.0	7.7 ± 2.3
Percent live crown	34.9 ± 7.7	43.4 ± 9.5	47.3 ± 10.3
Inter-tree distance I (m)	3.7 ± 1.2	5.2 ± 1.9	3.2 ± 0.8
Inter-tree distance II (m)	5.4 ± 1.8	7.5 ± 2.4	4.7 ± 1.1
Age (yrs)	69.9 ± 23.5	84.9 ± 24.2	82.4 ± 22.8
Height of codominant trees (m)	16.5 ± 3.1	17.4 ± 3.3	14.5 ± 2.5
Site index	14.0 ± 3.0	12.6 ± 2.8	9.6 ± 1.9
Percent canopy closure	74.2 ± 4.2	77.7 ± 7.8	68.5 ± 6.2

uninfested stands in the southern region (Table 3).

Principal components analysis resulted in two component axes, representing 70.4% of the variation in the data (Table 4). On principal component one (PC1), diameter at breast height, inter-tree distances, age, and height varied closely with one another, and in opposition to percent pine. Each of these variables had > |80%| loading values; on PC2, only two variables, basal area and percent live crown, had > |80%| loading values (Table 4). Infested and uninfested stands separated on both axes of the PCA (Fig. 9; PC1: $p = 0.054$, PC2: $p = 0.027$).

Based on the PCA, stands in the northern region (as yet uninfested), will be at higher risk than the southern region in terms of PC1 but lower risk in terms of PC2. That is, risks in the northern region are increased by the preponderance of nearly monospecific pine stands (high percent pine in PC1) but attenuated by a tendency for lower total basal area and higher percent live crown (PC2; Fig. 10).

3.2.2. Discriminant analysis

The PCA showed that diameter at breast height, inter-tree distances, age, and height tended to vary with one another. To minimize multicollinearity, we selected just one of these variables—inter-tree distance—to include in the list of variables used for the discriminant analysis. Univariate analysis of the variables by group membership showed that inter-tree distance I had the largest F-value, and thus most appropriate for inclusion in the analysis (McGarigal et al., 2000); inter-tree distance II was not considered, as this is not a value often measured
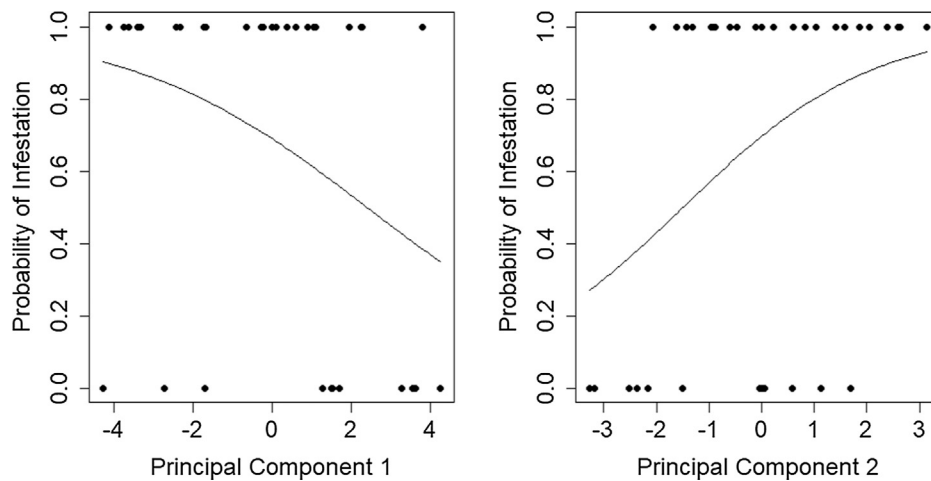
Table 4
Loadings and eigenvectors for principal components 1 and 2, which together accounted for 70.4% of the total variance. The loadings represent each variable's contribution to the total variance (product of the eigenvector and the square root of the eigenvalue). Variables with loadings > |0.80| shown in bold. The eigenvectors represent the coefficients to calculate the principal component scores for a measurement stand.

	PC1			PC2	
	Loading	Eigenvector		Loading	Eigenvector
Diameter at breast height (DBH)	**0.89**	0.36	Total basal area	**0.89**	0.51
Inter-tree distance I (NND)	**0.88**	0.36	Crown base height	0.75	0.43
Inter-tree distance II (SNND)	**0.87**	0.35	Pine basal area	0.51	0.29
Age	**0.81**	0.33	Hardwood basal area	0.45	0.26
Height	**0.81**	0.33	Site index	0.40	0.23
Hardwood basal area	0.80	0.32	Height	0.37	0.21
Crown base height	0.60	0.24	% Canopy closure	0.17	0.10
% Canopy closure	0.09	0.04	DBH	−0.03	−0.02
% Live crown	−0.05	−0.02	% Pine	−0.08	−0.05
Total basal area	−0.14	−0.06	Age	−0.09	−0.05
Site index	−0.24	−0.10	Inter−tree distance I	−0.28	−0.16
Pine basal area	−0.75	−0.30	Inter−tree distance II	−0.33	−0.19
% Pine	**−0.89**	−0.36	% Live crown	**−0.85**	−0.49
Variance Explained	**46.7%**			**23.7%**	

Fig. 9. Stands that were infested or not tended to differ in their characteristics both in terms of PC1 and PC2 (from logistic regressions, *p* = 0.054 and *p* = 0.027, respectively).

in the field. Discriminant analysis clearly distinguished between infested and uninfested stands in the southern region (Fig. 11). Two out of 36 plots were misclassified.

Along the canonical variable axis, infested stands were those located in the more positive direction, and uninfested stands in the more negative direction. Canonical variables for the northern uninfested stands calculated using the coefficients from the southern stand analysis resulted in a mean value and confidence interval that were more positive (higher risk) than the southern uninfested stands, but not as positive as the infested stands (Fig. 11).

Correlations of the original stand variables with the canonical variable axis, or loadings, showed that pine basal area, inter-tree distance I, and percent live crown had the highest values, with inter-tree distance I and percent live crown varying closely with one another (Table 5). To find the most parsimonious model for use in a hazard rating, we tested several combinations of smaller variable sets, intended to maximize ease of data collection for forest managers with varying financial and personnel resources. DBH, basal area (pine, hardwood, and total), and percent pine were included because these are commonly

measured by foresters and do not require lab processing or other time-consuming methods; inter-tree distance and percent live crown were also included, although these are less commonly measured, due to their importance in both the principal component analysis and discriminant analysis.

The two models with the lowest Wilks' Lambda (least percentage of variation unexplained), highest p-values, and lowest number of uninfested plots incorrectly predicted were (Table 1, Supp. Material):

Model 1: (DBH · 0.0449) − (pine basal area · 0.0626) + (percent live crown · 0.0878)

Model 2: − (pine basal area · 0.0342) + (percent live crown · 0.0815) + (inter-tree distance · 1.4341).

These models had very similar p-values and number of incorrectly predicted plots (Table 1, Supplementary Material). After centering the data for the northern region plots, we multiplied their values by these coefficients to find the index value for each plot; mean values for infested versus uninfested plots in each model provide convenient break
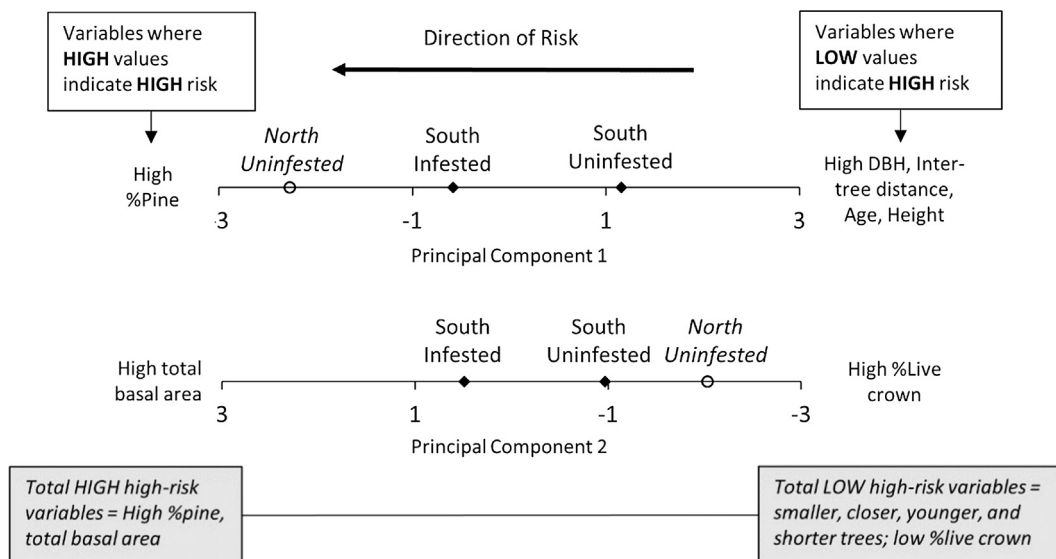

Fig. 10. Group means for each principal component. The numerical order of PC2 is displayed in reverse order, so that the direction of risk is the same in both plots. The location of the still largely uninfested northern Pinelands in this multivariate space of stand structure was calculated using the eigenvectors of the PCA of southern stands. Variables shown represent those > |0.80| in the PCA loading matrix. Variable labels at the ends of each plot indicate the direction of higher values. For example, in PC2, stands with high total basal area are at higher risk, as are stands with lower %live crown. Note that the northern stands are at higher risk along PC1, but lower risk along PC2. Trees smaller than 15 cm DBH were not included in our sampling.
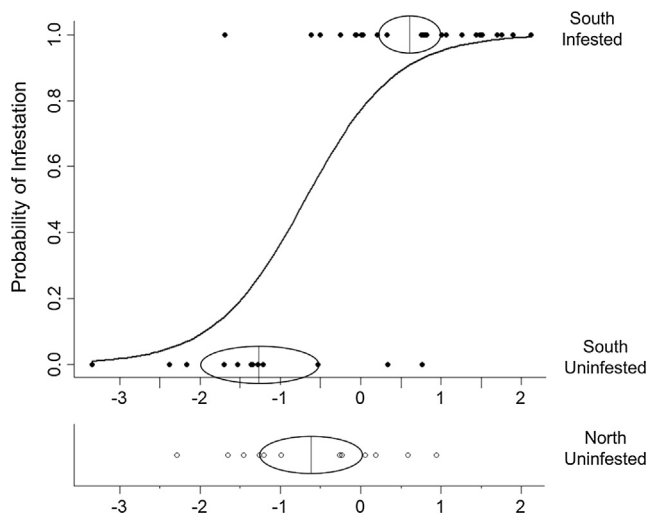
Fig. 11. Probability of infestation among southern plots across the canonical variable derived from discriminant analysis (top). Dots represent individual infested or uninfested plots. Line represents logistic regression of the canonical axis values (chi-square = 23.38, *p*-value < 0.0001). Ellipses and vertical lines show 95% confidence limits and group means. Canonical variable for "North Uninfested" plots (bottom), calculated using coefficients derived from "South" group analysis.

Table 5
Unstandardized coefficients used to calculate the canonical variable for each stand structure variable (left). Loadings, or correlations between each stand structure variable and the canonical variable (right).

	Coefficients		Loadings
Hardwood basal area (HWBA; m2/ha)	1.99	Pine basal area	0.59
Pine basal area (m2/ha)	0.11	Total basal area	0.49
Percent pine	0.07	Percent pine	0.43
Site index	0.04	Site index	0.31
Percent live crown	−0.11	Crown base height	0.18
Percent canopy closure	−0.12	HWBA	−0.11
Total basal area (m2/ha)	−0.13	Percent canopy closure	−0.42
Crown base height (m)	−0.22	Inter-tree distance I	−0.61
Inter-tree distance I (m)	−0.69	Percent live crown	−0.64

points for low-, medium- and high-risk values in both versions of the model (Fig. 1, Supplementary Material). Mean values were very similar between the two models, with break points as follows: Model 1—Low risk: −3 to −0.44; Medium risk: −0.45 to 0.89; High risk: 0.90–3.00; Model 2—Low risk: −3 to −0.45; Medium risk: −0.46 to 0.92; High risk: 0.93–3.00.

4. 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. This suggests that the percent conifer component of a stand overrides any effect of whether or not the stand is dry/upland or wetland. Previous work in the southern United States has shown strong evidence for high site moisture contributing to stand susceptibility (Hicks, 1980; Lorio, 1968, 1978; Reeve et al., 1995; Warren et al., 1999). This is as predicted based on the growth differentiation hypothesis of environmental effects on plant defenses (GDBH; Herms and Mattson, 1992; Loomis, 1932; Lorio, 1986). The GDBH 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. Predictions that follow from the hypothesis are 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, being less well-defended, than dry stands. In the Pinelands, the effects of high percentages of pine trees apparently overwhelms effects related to whether a stand is a dry or wet one.

The disproportionate number of spots in wetland conifer sites of our study region could additionally be related to factors that we did not measure, such as tree stress from root mortality, decreased respiration of soil and roots due to flooding, or effects of the typically dense understory on the pheromone plume that enables mass attack by beetles. Pitch pine grows under a wide variety of moisture conditions, from relatively dry sites to nearly waterlogged sites (Little and Garrett, 1990; McCormick, 1979). 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 of aggregation pheromones 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.

Our SPB risk assessment for the New Jersey Pinelands combined analyses of the full landscape of interest (Figs. 4, 5, 7, 8) with intensive measurements of replicated stands drawn from within this landscape (Figs. 6, 9–11). 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 containing intermediate levels of conifers (25–75%). A comparison of PCA and discriminant analysis methods showed that the former provides a more nuanced result, while the latter gives adequate results in cases where a single index result is desired, or resources for data collection are low. The PCA showed that stands at highest risk—high percent pine—were on average those with low tree size, inter-tree distance, age, and height. Stands composed mostly of pine and at highest risk, therefore, were those that tended to be smaller, closer together, shorter, and younger. In addition, stands with high total basal area and low percent live crown were at higher risk. When introducing new data, our analysis showed that the new stands were at higher risk along the first component axis, but at lower risk along the second.

The discriminant analysis similarly showed that inter-tree distance and percent live crown have a strong influence on the separation of the infested versus the uninfested stands. Low values of these two variables were in the direction of higher risk on the canonical axis, along with high pine basal area (pine basal area and percent pine were highly correlated in both the northern and southern stands). Discriminant analysis has the benefit of producing a set of coefficients that yield a numerical estimate of susceptibility (Birt, 2011), but in the case of the northern region stands in the Pinelands, the single value means that we can only see that they are intermediate in susceptibility between the

southern infested and uninfested stands. The PCA provides the more detailed information that they are more at risk in terms of the variables on PC1 (the new stands average higher percent pine and lower age/height/DBH/inter-tree distances), but less at risk in terms of the variables on PC2 (averaging lower total basal area and higher percent live crown) (Fig. 10). The single value is most efficient for prioritizing stands for preventative treatment such as thinning, but the PCA provides more information about which variables contribute most to higher susceptibility.

Our analysis of the most parsimonious models found that separation between potentially infested versus uninfested stands can be determined using just a handful of easily measured variables, such as those in Model 1: DBH, pine basal area, and percent live crown. Using the formula described, a risk index can be calculated using centered values from an individual resource manager's stand data. Priorities for stand management can subsequently be determined. For managers with access to more resources for field data collection, the PCA method can provide more nuanced information about which stand properties are contributing most to susceptibility.

Our results support 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 (Nowak et al., 2015; Clarke et al., 2016). While suppression tactics are presently being actively utilized in both New Jersey and New York, they are not yet relevant for the New England states where SPB trap catches have been recorded, but no tree mortality has taken place (Dodds et al., 2018). Thinning, however, may be undertaken as a preventative measure in advance of mortality events occurring in the more northern states. Our data support the use of these measures because it shows that higher basal area stands are at higher risk.

One notable finding among our results was that inter-tree distances vary positively with age, height, and DBH in New Jersey pitch pine forests. In other words, as stands age, the distance between trees tends to increase, and thus stands with the oldest and maximally spaced trees were at lower risk. This supports thinning in general as a management tactic, but provides further good news for managers who worry that thinning to decrease susceptibility leaves old, large trees in place and thus may place these valuable trees at risk. Stands containing these trees were shown to be at less risk in our study. Increased distance is known to decrease the odds that adjacent trees will become infested (Gara and Coster, 1968; Johnson and Coster, 1978). Our results suggest that self-thinning with increasing age occurs naturally within pitch pine stands, and supports previous work showing that susceptibility increases with age to a point, but then decreases beyond it (Lorio, 1978; Ylioja et al., 2005). The lack of infestations at young ages has been attributed to the limited phloem to sustain brood populations (Belanger et al., 1993). Previous studies in southern pine systems showed conflicting evidence with regard to basal area versus stem density. 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, while analyses of data from ESPBRAP (Coster and Searcy, 1981; Hicks, 1980) emphasized instead the importance of basal area, sometimes with density showing little effect. Effects of background beetle population size may have affected 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 this suppression program draws to a close due to funding constraints, 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. 7, Table 3)—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.

We stress that all stand structure-based risk assessments are limited by their lack of consideration of localized SPB population levels, which can have a strong influence on risk. Paine et al. (1983) suggested a response surface method resulting in a three-dimensional figure with one axis representing tree/stand/site hazard, one axis representing both distance to next nearest infestation and estimated population size, and the third axis showing overall risk. This would be the ideal risk assessment method, but the amount of data required for such an analysis is impractical for most forest managers, particularly in the Northeast, where most stands are not being managed for commercial purposes.

An important general question that can be asked of invasions or range expansions of any forest pest is whether old pests in new places will have a *disproportionate* impact on forests in their new habitat. Tree-killing species that cause mortality on the scale of bark beetle events have not been previously well-established in the mid-Atlantic and New England states, so comparisons with similar species are not possible. Future work on this question could consider the relative size of SPB infestations, and their proximity to one another at both local and regional scales. Comparisons with infestation occurrence in the south will also need to consider differences in landscape heterogeneity between the southern and northern states, including both grain size and land use. Evaluating the potential for disproportionate impact in newly occupied ecosystems will become increasingly important as climate change, land-use, and trade continue to affect the ranges of both native insects and their host species.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.009.

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