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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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A B S T R A C T

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 overridden 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