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Why have southern pine beetle outbreaks declined in the southeastern U.S. with the expansion of intensive pine silviculture? A brief review of hypotheses

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ABSTRACT

The southern pine beetle has shown a dramatic decline in outbreak activity over much of the southeastern United States since the turn of the 21st century compared to previous decades. Concurrently, from the 1950s through the present day, a twenty-fold increase in pine plantation area has occurred across the region while trends in genetic tree improvement and pine silvicultural advances have seen a marked increase in application towards the end of the 20th century. We examine southern pine beetle outbreaks in the Piedmont and Coastal Plain physiographic provinces of the southeastern U.S. relative to this increase in pine plantation area and intensive management. While climate and natural enemy hypotheses are discussed, the substantial changes to the management and condition of the southern pine resource in the form of plantations that are genetically improved, younger, faster growing, less overstocked or more fragmented may provide a more robust explanation for regional declines in SPB outbreak activity.

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Contents

1. Introduction: Southern pine beetle in the 21st century

As a native forest insect pest, the southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, has long been considered the most economically important and destructive in the Southeastern United States. This is due primarily to the prevalence of its major pine hosts, the economic importance of pine plantation culture across the region, as well as the ability of SPB to mass attack and overwhelm healthy host trees when their populations grow exponentially following invasion of weakened hosts. Thus, aggregations of SPB-infested and killed trees, known as 'spots' (Fig. 1), once initiated, often will multiply and expand rapidly into regional

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Fig. 1. Southern pine beetle 'spot' from above and within.

'outbreaks' that can envelope forest landscapes and encompass multiple counties and states, often over successive years (Birt, 2011b; Hain et al., 2011). Such expansive outbreaks in southern pine forests every 5–7 years used to be the norm for the better part of the 1960s through the 1990s, according to the best available records on outbreak activity (Clarke et al., 2016). Several major works, including hundreds of scientific papers on SPB population dynamics were published based on this approximately 40-year period of outbreak activity (Coulson and Klepzig, 2011).

Most SPB outbreaks during the latter half of the 20th century impacted southern pine plantations, particularly loblolly (*Pinus taeda* Linnaeus), shortleaf (*Pinus echinata* Miller) and Virginia pine (*Pinus virginiana* Miller), as well as natural pine stands. These outbreaks often enveloped hundreds of counties across multiple states during any given year. By the late 1980s, 15% of the gross annual growth of southern pine was lost to mortality, much of which was attributed to pine bark beetles (USDA, 1988). Over the last 15–20 years (1996–2016), however, major SPB outbreaks spanning more than a county or two and persisting for longer than a year have largely failed to materialize across most of the Piedmont and Coastal Plain regions of the Southeast where intensive pine plantation culture is most common. With each passing year, it becomes more apparent that something is different about SPB outbreak dynamics. While still a significant threat to the resource, SPB is not currently the widespread and regularly cyclical pest that it used to be in the southeastern U.S. Although 20 years is not a long time within an ecological context, it is a notable gap given the continuing expansion of intensively managed, even-aged, single-species (monoculture) pine plantations across the region.

Although notable multi-year outbreaks of SPB have occurred since the turn of the 21st century and continue to this day, examples are less common in southern pine stands that are managed intensively in the Piedmont and Coastal Plain physiographic provinces of the Southeast. Indeed, the vast majority of SPB activity in the last two decades has been in forests that are largely unmanaged, overstocked, on less than ideal sites, or are approaching natural senescence (Nowak et al., 2016, 2015). In more northern areas, many afflicted stands are natural and consist of species such as shortleaf, Virginia, white (*Pinus strobus* Linnaeus), Table Mountain (*Pinus pungens* Lambert) or pitch (*Pinus rigida* Miller) pine (Nowak et al., 2016). Intensively managed pine stands, on the other hand, typically involve genetically improved loblolly pine or, less commonly, slash pine (*Pinus elliottii* Engelmann) and some combination of wider seedling spacing, herbicide site preparation and/or release from hardwood competition, mechanical site preparation, fertilizer application, pre-commercial and commercial thinning, and other methods (Allen et al., 2005). Genetic tree improvement programs have been transformative to southern pine plantation culture, resulting in high quality loblolly and slash pine seedlings bred for superior growth rate, stem form, adaptability and disease resistance (Byram et al., 2005). The use of some of the above intensive practices in combination with the rapid growth and yield potential of genetically improved trees have additive effects on tree growth and therefore, when used in tandem, greatly improve productivity and profit margins for growers (Cumbie et al., 2012; Fox et al., 2007a; Jokela et al., 2010).

The last widespread SPB outbreak in the Southeast (1999–2002) occurred primarily in the Southern Appalachians and Cumberland Plateau physiographic regions and impacted multiple pine species (loblolly, shortleaf, Virginia, white, pitch, Table Mountain) that were generally growing as natural stands, unmanaged plantations or in mixed pine/hardwood stands (Nowak et al., 2016). While this outbreak did impact some intensively managed loblolly plantations, these were primarily areas outside of the natural range of loblolly pine and which now have mostly reverted back to hardwood stands. Other more recent and notable areas of SPB outbreak include Atlantic coastal areas from Virginia Beach north through Chincoteague/Assateague Islands off the Delmarva Peninsula (Asaro, 2013–14; Chamberlin, 2015), the New Jersey Pine Barrens (http://www.state.nj.us/dep/parksandforests/forest/njfs_spb.html), and Long Island, New York (http://www.dec.ny.gov/animals/99331.html). Many of these areas contain older (50 + years), unmanaged pines growing on poor soils and exposed to occasional high winds, saltwater intrusion and salt spray from major storms like Hurricanes Irene (2011) and Sandy (2012). While southern pine beetle is relatively new to some of the more northern locations due to milder winters, it is none-the-less no surprise that, with these stand conditions, SPB has reached outbreak levels. In the South, several recent outbreaks were mostly limited to National Forests such as the Oconee in Georgia (2007) and the Homochitto (2012), Tombigbee (2014) and Bienville (2015) in Mississippi in higher-risk stands. These outbreaks spread very little beyond the National Forest boundaries and were short-lived. In the last 10 years, there have been far fewer reported hectares of beetle-killed pine across 13 states in the Southeastern U.S. (<2025 ha) compared to the Pine Barrens of southern New Jersey alone (>12,000 ha) (Schlossberg, 2016).

To date, the widespread expansion of genetically improved trees and associated silvicultural practices across the southern pine growing region have received little mention as a potential explanation for SPBs decreased abundance at the regional level (Clarke et al., 2016). This is surprising given the importance of the southern pine resource to the regional economy and its importance to forest product output nationally. The southeastern U.S. is considered the 'wood basket' of the United States and currently supports one of the healthiest, most sustainable and most productive landscapes of native pine species in the world (Fox et al., 2007a). While widespread and intensively managed pine monocultures are often criticized on environmental grounds (Rousseau et al., 2005; Williams, 2000), plantations that exhibit genetic and age-class diversity and are grown within a patch-work mosaic of hardwood, mixed-pine hardwood, and agricultural uses can, at the landscape level, provide a sound balance between productive economic output and essential ecosystem services (Rousseau et al., 2005). In addition, while monocultures are generally considered less stable and more vulnerable to pest problems than natural and/or mixed plant populations, this is not necessarily always true of plantation forests (de Groot and Turgeon, 1998). Tree breeders must continue to maintain genetically heterogeneous populations of pines across the landscape to minimize potential losses from unforeseen vulnerabilities (McKeand et al., 2003; Wheeler et al., 2015). Yet, so far, great strides have been made in limiting the impacts of major threats to southern pine plantations such as the southern pine beetle via wider tree-spacing and thinning, pales weevil (*Hylobius pales* Herbst) via delayed planting or chemically treated seedlings (Lynch, 1984) and fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) via resistance breeding (Schmidt, 2003).

2. Southern pine beetle hazard rating

The U.S. Forest Service has constructed a hazard map for the southern pine beetle (http://www.fs.fed.us/foresthealth/technology/nidrm_spb.shtml) (Fig. 2). The parameters used in the model for which this map is based include host basal area (all pines species), SDI (Stand Density Index) and outbreak history (Fig. 3).

High stand density is a well-known risk factor for southern pine beetle (Guldin, 2011). Yet many high-density stands remain across the South without precipitating major outbreaks of the southern pine beetle in recent history. For example, several states such as Texas, Louisiana and Arkansas that used to be routinely decimated by SPB outbreaks prior to the mid-1990s have witnessed virtually undetectable levels of the insect for the last two decades and counting, even though recent droughts have triggered widespread infestations of secondary *Ips* bark beetles (Clarke et al., 2016). In addition, between 1952 to the turn of the 21st century, pine plantations in the South increased from approximately 730,000 ha to 13 million ha (Fox et al., 2007a), with almost 16 million ha of plantations by 2012 (Huggett et al., 2013; Oswalt et al., 2014). Yet, while southern pine plantation area has increased dramatically across the Southeast and currently exceeds the area of natural southern pine (South and Harper, 2016), this trend has been associated with a decline in SPB outbreak activity. Our goal is to introduce some potential hypotheses which may explain this apparent paradox.

3. SPB outbreak history (1960–2016) in the piedmont and coastal plain of the U.S. south

To address why SPB outbreaks have declined so dramatically in recent years within the southern pine growing region of the Piedmont and Coastal Plain, we first need to present an outbreak history of SPB and explain how outbreaks have been defined and quantified. Forest entomologists in the southern states have been keeping records of SPB activity since about 1960 (Birt, 2011a,b), although a rigorous definition for an SPB 'outbreak', until the late 1970s, was not always applied consistently among the state and federal government entomologists who collected these data (Duehl et al., 2011; Price et al., 1998; Pye et al., 2004). The definition of an outbreak is one SPB spot (a minimum of 2–10 infested trees) per 405 ha (1000 acres) of susceptible host type (all stands designated as loblolly/shortleaf and oak-pine forest type) per county or parish. For example, if a particular county has 50,000 acres (20,243 ha) of pine and pine-hardwood forest type, 50 distinct spots are required before that county can be considered to be in outbreak status. Forest type designation and susceptible host

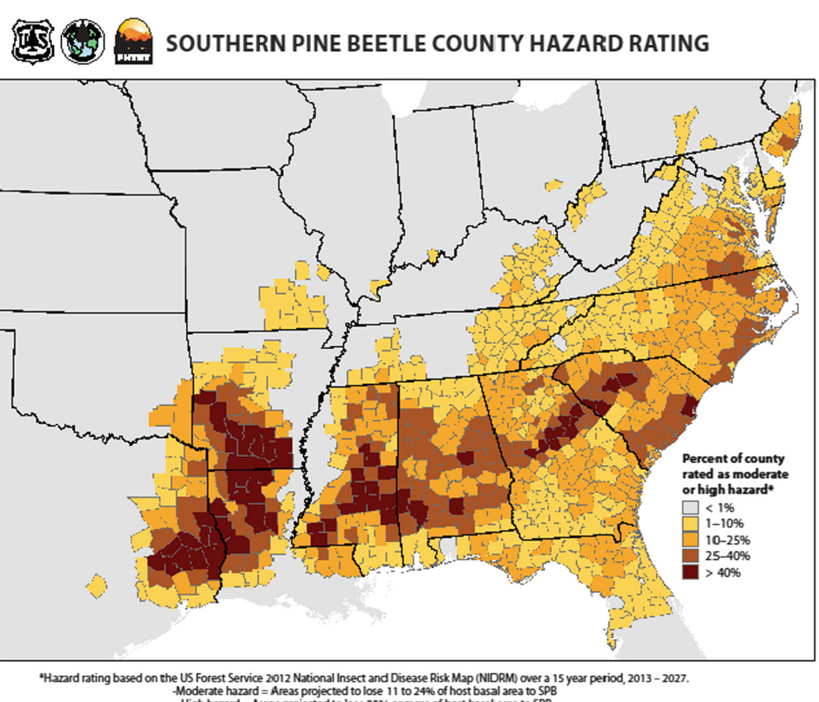

Fig. 2. Southern pine beetle county hazard rating map.

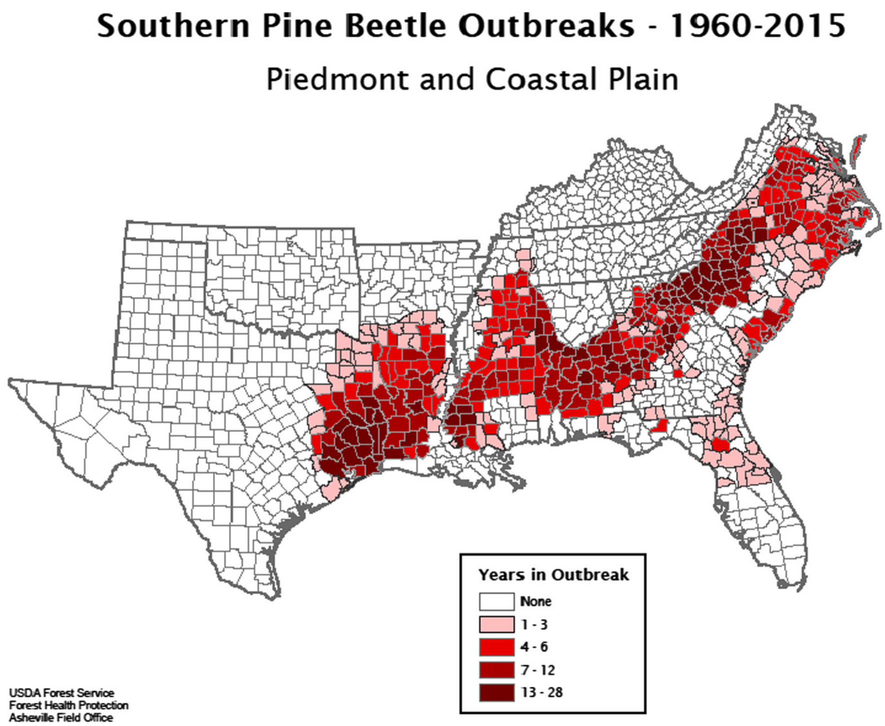

Fig. 3. Outbreak history of the southern pine beetle in the Piedmont and Coastal Plain physiographic provinces of the Southeastern U.S. (13 states).

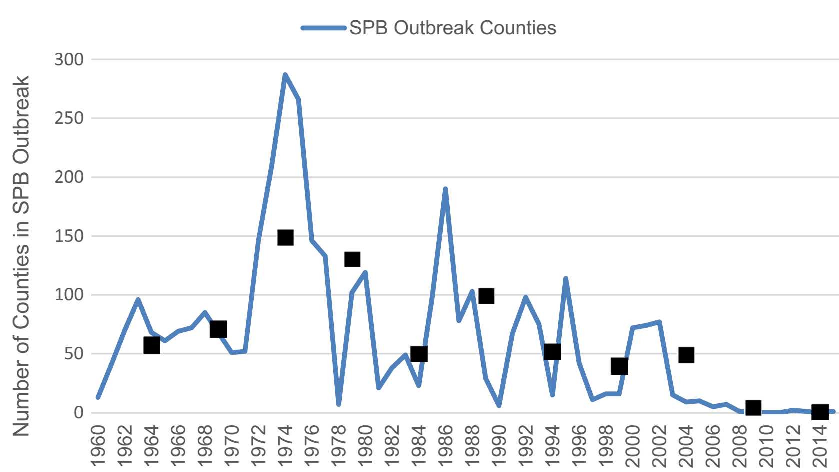

Fig. 4a. Annual number of southern pine beetle counties in outbreak status across the Piedmont and Coastal Plain physiographic provinces of the southeastern U.S. (1960–2015). Black squares represent the 5-year average for number of outbreak counties.

acreage per county is estimated using Forest Inventory and Analysis (FIA) data provided by the USDA Forest Service. One major limitation with this definition is that spot size is not considered, so spots are counted whether they consist of ten trees or cover one hectare, for example. Additionally, smaller spots over time can coalesce into one large spot if they form in the same plantation or otherwise in close proximity, so the time of year when spots are counted can influence whether they are counted as multiple spots or as one. Furthermore, other methods by which host acreage can be estimated per county, such as using satellite imagery combined with statistical modeling techniques (Krist et al., 2007), can produce different host acreage estimates. Despite these limitations, this definition of outbreak has served as a robust measure of SPB activity across a 13-state region for over 50 years, and thus provides some consistency when comparing different periods of time. Counties across these states, while variable in size, provide a convenient local unit of measure of SPB impact. In addition, if volume of timber killed by SPB across the U.S. South is used as a measure of activity instead of outbreak counties, a similar cyclic pattern of SPB activity is observed over several decades, followed by a recent decline (Clarke et al., 2016).

We calculated the number of annual outbreak counties across the primary southern pine growing regions of the Piedmont and Coastal Plain physiographic provinces (Bailey, 2004) of AL, AR, GA, FL, LA, MS, NC, SC, TN, TX, and VA that were considered to be in outbreak status from 1960–2015 based on state and federal reports (Figs. 4a–4c). In addition to a steady decline in peak activity since the mid-1970s, a fairly sudden and dramatic decline in activity since approximately the mid-1990s is apparent in many states. Between 1960 and 2004, each successive five-year average of the annual number of outbreak counties was at least 50 across the area in question, and has steadily declined over successive decades.

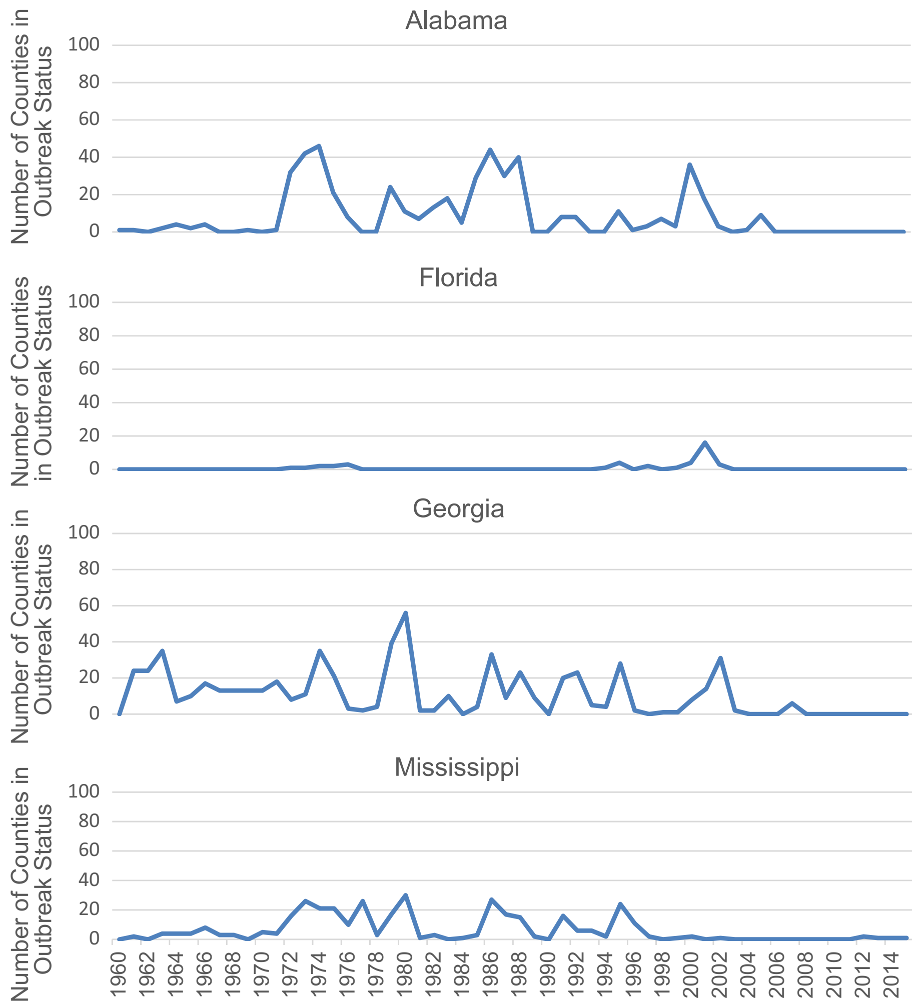

Fig. 4b. Annual number of southern pine beetle counties in outbreak status across 4 southern U.S. states (Alabama, Florida, Georgia, Mississippi) (1960–2015).

Over the last ten years, that average has dropped to virtually zero (Fig. 4a). Only 18 outbreak counties have been declared over the last ten years across the region, or less than two counties per year on average. This is historically unprecedented since such records have been kept. The drop-off in activity over the last twenty years has been so dramatic in several states such as Texas, Louisiana and Arkansas that SPB levels are practically undetectable, with pheromone traps deployed during annual spring surveys failing to produce even a single trapped beetle in many years (Clarke et al., 2016). In addition, the extreme levels of SPB activity that were witnessed in plantations during the early to mid-1970s have never since been repeated on such a scale (Fig. 4a), despite the fact that loblolly pine plantation acreage has seen a 20-fold increase since the 1950s (Fox et al., 2007a). In the following section, we compare this SPB outbreak history with other trends in pine silviculture, some of which are very well documented and quantified in the forestry literature.

4. Why has SPB activity declined across the southeastern U.S.? A review of hypotheses

Our goal is to expand the discourse on this important question and to stimulate potential new avenues of research. However, it is not our intention to thoroughly review or analyze SPB population dynamics literature; a recent compendium of decades of SPB literature covers this topic in significant detail at the tree (Stephen, 2011), stand (Ayres et al., 2011), landscape (Birt, 2011a) and regional (Birt, 2011b) scales. When studying the factors that influence insect population ecology, three broad sets of categorical variables are typically examined for their influence: (1) weather and climate, (2) natural enemies, inter- and intra-specific competition and predator-prey dynamics (top-down controls), and (3) plant host condition and pest-host interactions (bottom up controls). To date, many SPB population studies have considered the influence of climate/weather or natural enemy/competitor variables as primary explanations for regional outbreak dynamics, but have fallen short of demonstrating strong or consistent correlations. On the other hand, the potential influences of host physiology, genetics, stand structure and distribution across the landscape have received comparatively little detailed study, at least as they relate to the regional expansion and influence of plantation silviculture. Placing a greater emphasis on the study of host-related variables that influence SPB dynamics could allow for manipulation using forest management practices (Fettig et al., 2007). In contrast, weather cannot be controlled or accurately predicted beyond a limited time frame, and biological factors (natural enemies, competitors, pheromones) can only be influenced to a very limited and localized extent. Most likely, all the above variables are significant and interact in complex ways to influence SPB outbreak dynamics. However, it is often most practical to study these variables separately to examine their respective influence. Below we present a brief discussion of the climate/weather and natural enemy/competitor hypotheses and why

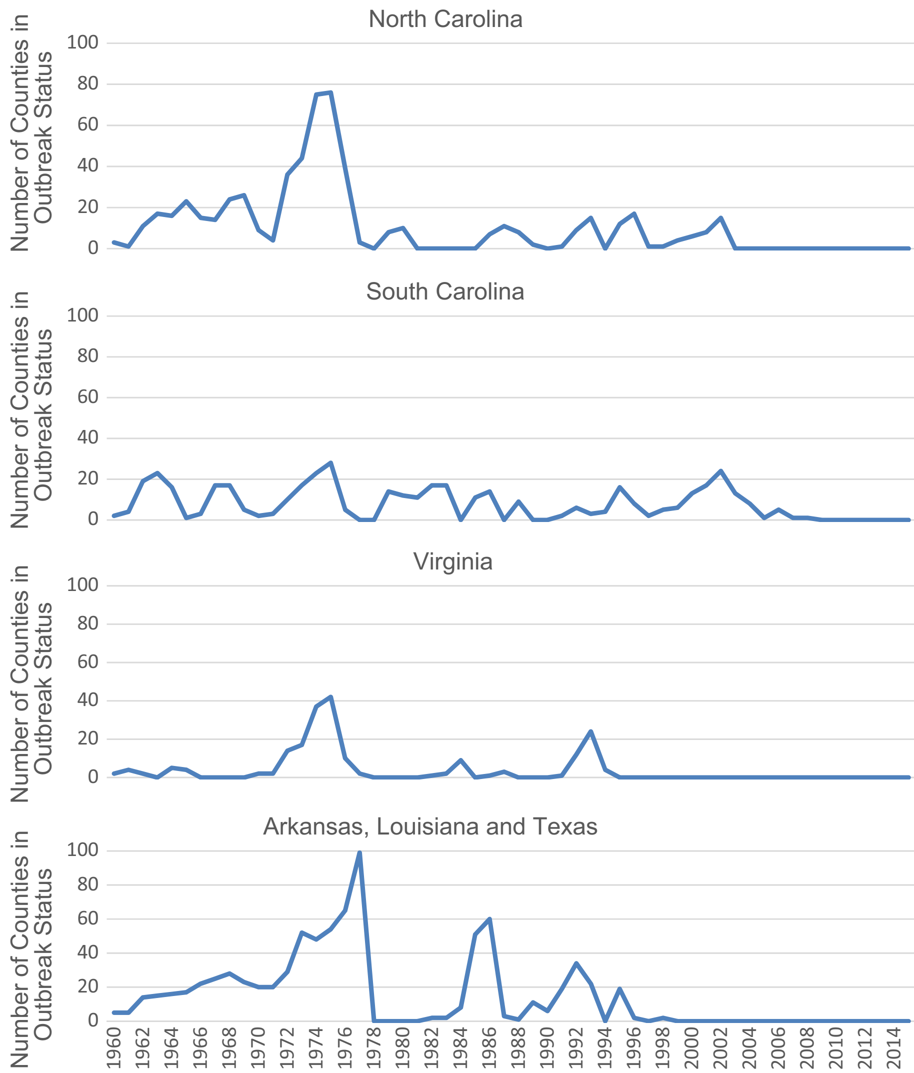

Fig. 4c. Annual number of southern pine beetle counties in outbreak status across 6 southern U.S. states (North Carolina, South Carolina, Virginia, Arkansas, Louisiana, Texas) (1960–2015).

we think they do an incomplete job at explaining the SPB outbreak patterns presented in Figs. 4a–4c. We then discuss 3 host-oriented hypotheses (genetics, intensive silviculture and stand fragmentation) that we think should receive more attention and study as they relate to SPB regional outbreak dynamics. None of these hypotheses are mutually exclusive but all are potentially additive or interactive. There may also be other potential hypotheses that could affect SPB populations that are not considered here. For example, we do not consider possible regional changes to the population genetic structure of southern pine beetle populations because there has been almost no research in this area and thus there is little basis for forming a cogent hypothesis.

4.1. Climate/weather hypothesis

It is logical to seek a meteorological explanation for changes in SPB population dynamics, particularly considering the compelling evidence of the role of climate warming and drought influencing the devastating bark beetle outbreaks in Western North America (Hicke et al., 2016; Kolb et al., 2016). However, climate and weather data to date have fallen short at explaining SPB regional outbreak dynamics in the Southeastern U.S. While measurable differences in climate between 1960–1995 and 1995–2016 are evident, for example, it is also true that the inherent climatic diversity across states such as Virginia, Georgia, and Texas is of far greater magnitude, and yet SPB declines have been observed across these and other southern states. Further, many states in the South over the last 15 years have seen extremes of weather from year to year, including exceptional periods of flooding and drought, unusually warm and cold winters, relatively mild to extremely hot summers, damaging ice storms and hurricanes (Southeast Regional Climate Center, www.sercc.com/). Yet, during this time, no regional SPB outbreaks have materialized. For example, an exceptional drought that impacted Texas and parts of Louisiana and Arkansas during 2011 resulted in widespread tree mortality (Moore et al., 2016), but no southern pine beetle activity was documented in that region during or after the event (Fig. 4c). Friedenberg et al. (2008) could determine no clear role for climate as an explanation for the recent cessation of SPB outbreaks in East Texas, but they suggested that forest management efforts may have contributed. While we are not discounting the influence of climate or weather variables at smaller scales, it seems that any correlations to be found with SPB outbreaks are weak and difficult to tease out at the broader regional scale (Birt, 2011a,b; Duehl et al., 2011).

A gradation towards warmer winter seasons in the northeastern U.S. may indeed be partly responsible for the recent SPB outbreaks observed in areas such as the Pine Barrens in New Jersey and Long

Island, NY where such phenomena have never been documented until the 21st century (Weed et al., 2016). However, SPB was detected attacking high-elevation red spruce stands in West Virginia in the late 19th century (Hopkins, 1899), which is in a colder climatic zone than the coastal plain of New Jersey up through Long Island, Connecticut and eastern Massachusetts (http://planthardiness.ars.usda.gov/PHZMWeb/), so these more northern locations have probably been climatically favorable for SPB before, even in its absence. Regardless of when and how SPB reached the northeastern U.S., significant impacts to a pine resource that is largely mature, overstocked, unmanaged, occasionally battered by coastal storms, and in an area lacking mill capacity to support spot harvests, are an inevitable outcome.

4.2. Natural enemy hypothesis

The major predator of SPB thought to have the most influence on population dynamics is the clerid beetle, *Thanasimus dubius*. Delayed-density dependence driven by insect predators is currently the most well-tested explanation for the pattern of SPB population cycles (Birt, 2011b). Turchin et al. (1991, 1999), for example, demonstrated that East Texas SPB population growth or decline rates in a given year are inversely related to the population size of the previous year or two, while SPB brood survival was significantly higher in trees protected from predators than in control trees. However, as Birt (2011b) points out, the model by Turchin et al. (1991) is not spatially explicit, so it remains unclear whether the delayed-density dependence hypothesis would be strengthened or weakened by adding a spatial component to the model. In addition, it's not clear what the virtual disappearance of SPB in Texas and adjacent states for the last 20 years means, but the predator-prey dynamic models may need to be revisited in light of these more recent trends. Indeed, many important natural enemies of southern pine beetle, such as *T. dubius*, also feed on other bark beetle species and thus are still able to thrive in SPBs absence. Delayed-density dependence may also be driven by other factors, such as the interaction between SPB, their parasitic *Tarsonemus* mites, and the blue-stain fungus *Ophiostoma minus*. Blue-stain fungus infects the phloem of SPB-infested trees, inhibiting SPB brood development and survival. The parasitic mites appear to facilitate the spread of the blue-stain fungus. Hofstetter et al. (2005) concluded that SPB population regulation by blue-stain fungi was greater than that measured for clerid beetles.

While there is no question that natural enemies play a major role in SPB population dynamics at the tree, stand and perhaps even landscape level (Berisford, 2011; Reeve, 2011; Birt, 2011a, b), there seems to be no evidence that the same top-down controls operating 20–50 years ago are not still operating today. Weed et al. (2016) examined the spatio-temporal dynamics of this predator-prey system and concluded that the effect of *T. dubius* on long-term SPB dynamics is highly variable across the southern U.S. and generally uncorrelated beyond approximately 18 miles (30 km). Therefore, predator-prey dynamics alone are unlikely to be an effective measure for understanding South-wide SPB outbreak trends.

4.3. Genetic resistance hypothesis

Planting of genetically unimproved loblolly in the Southeast U.S. came to a virtual halt in the early 1980s, with nearly all subsequent plantations consisting of first-generation, open –pollinated improved trees. Standing volume of first-generation, open-pollinated improved loblolly pine across the Southeast has exceeded unimproved volume since around 1990, while second-generation improved trees began to exceed unimproved volume by 2000 (Aspinwall et al., 2012) (Fig. 5). There is currently little compelling evidence that genetic tree improvement to increase growth rates and improve form has inadvertently produced SPB-resistant trees per se, although this hypothesis has been poorly tested. Only one study we are aware of near Aiken, South Carolina showed that SPB had a strong preference for pines from specific seed sources compared with others (Powers et al., 1992). In fact, this study was originally set up in randomized blocks to evaluate fusiform rust resistance and growth rates of disease-resistant versus susceptible seed sources, with the SPB outbreak that spread through the 7-acre (2.83 ha) study site being pure happenstance. Interestingly, blocks containing trees from local seed sources were disproportionately attacked by SPB over seed sources from the western gulf region (Arkansas, Louisiana, and Texas). There was

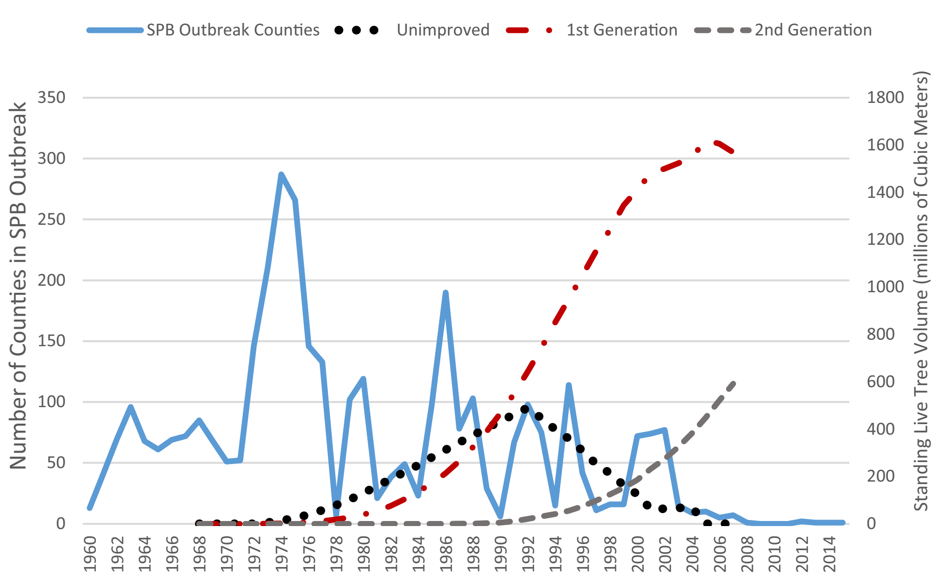

Fig. 5. Annual number of Piedmont/Coastal Plain counties in SPB outbreak status (blue, solid line) (1960–2015) compared to annual standing live tree volume of genetically unimproved loblolly pine (black, dotted line), 1st generation open pollinated, improved loblolly (red, dash-dot line) and 2nd generation open pollinated, improved loblolly (gray, dashed line) (1968–2007). Genetic tree improvement graphs were adapted from Aspinwall et al. (2012) with their permission using data they provided.

no relationship between stand characteristics or rust infection patterns and SPB damage (Powers et al., 1992).

The link between pine tree oleoresin production and resistance to SPB has been well-documented (Cook and Hain, 1987; Coyne and Lott, 1976; Reeve et al., 1995). Additionally, oleoresin flow has been shown to vary by pine species (Hodges et al., 1979) and genetic families (Nebeker et al., 1992). Furthermore, Strom et al. (2002) found that first-generation progeny from trees that were not attacked by SPB (in a stand with adjacent attacked trees) had higher resin flow when compared to trees from the general population. Finally, Roberds et al. (2003) showed a positive link between genetic growth characteristics and resin properties associated with tree defense. In their study, they concluded that selecting genetic traits for faster growing loblolly pine would also lead to increases in resin flow. If there has indeed been a change in resin flow due to attempts to improve growth characteristics, it is plausible that the extraordinary efforts to plant 2nd generation improved seedling across the landscape could have large scale impact on SPB colonization success (Fig. 5).

On the other hand, multiple accounts exist of progeny tests being ravaged by expanding SPB infestations, although these anecdotes have not been quantified or scaled up to the regional level in any meaningful way. Martinson et al. (2007) found no evidence that longleaf pine are physiologically more resistant to SPB than loblolly pine due to higher resin flow, despite the fact that longleaf pine stands are attacked much less frequently. Indeed, they argued that both loblolly and longleaf pine are equally likely to be killed when growing together in front of expanding SPB infestations despite the landscape level pattern of low mortality in longleaf pine. They suggested that greater behavioral avoidance of longleaf by SPB may be a product of coevolutionary processes, along with the fact that longleaf pine stands tend to exhibit a more open-grown, low-density structure (see below).

4.4. Intensive silviculture hypothesis

After witnessing the steady increase of SPB destruction among the increasingly expanding, overstocked pine plantations of East Texas between the mid-1950s and mid-1970s, Hedden (1978) suggested that intensive forest management was the only method available to land managers to reduce further timber losses. The 1990s was a period of transition between more frequent, widespread, multi-year SPB outbreaks and more minor, localized, single-year outbreaks among southern plantations (mainly loblolly and slash pines) (Figs. 4a–4c). During the same time period, there was a dramatic increases in pine plantation acreage and a rapid expansion of various intensive silvicultural practices. For example:

- Between 1970 and 1990, annual acres of forest land fertilized in the southeastern U.S. increased from less than 100,000 acres (40,486 ha) to approximately 200,000 acres (80,972 ha). Between 1990 and 2000, the area of plantations fertilized in the Southeast increased from approximately 200,000 acres (80,972 ha) to over 1.4 million acres (566,802 ha) per year (Fox et al., 2007b; Albaugh et al., 2007). The vast majority of this land was planted with loblolly and slash pine. In addition, between 1970 and 1990, changes in acreage fertilized with phosphorous across the southeast was negligible. Between 1990 and 2000, acres of phosphorous fertilization increased from less than 100,000 acres (40,486 ha) to over 1 million acres (404,858 ha) per year (Albaugh et al., 2007, 2012) (Fig. 6).
- Average planting density for commercial pine plantations in the South was estimated to be about 750 seedlings per acre (1852 per ha) in 1952 (South and Harper, 2016), 650 trees per acre (1605 per ha) in 1990 (Dubois et al., 1991), and 510 trees per acre (1260 per ha) based in more recent surveys (Dooley and Barlow, 2013). Wider tree-spacing is less likely to produce overstocked, stagnant stands at younger tree ages, especially if precommercial and/or commercial thinning is delayed or not employed.
- The use of herbicides for site preparation to control hardwood sprouting began to replace intensive mechanical site prep in the 1970s and 1980s. In addition, herbicide use for herbaceous weed control and release of pines from hardwood competition ramped up significantly during the 1980s with the development of several newer herbicide formulations such as glyphosate, hexazinone, imazapyr, metsulfuron methyl, and triclopyr. These newer compounds were cheaper and more environmentally benign, replacing herbicides such as 2,4,5-T and rapidly becoming standard silvicultural tools in intensively managed pine stands (Fox et al., 2007a). For example, approximately 600,000 acres (242,915 ha) per year of imazapyr was used on commercial forestland in the U.S. during the late 1980s and early 1990s. During the last ten years (2005–2015), average annual

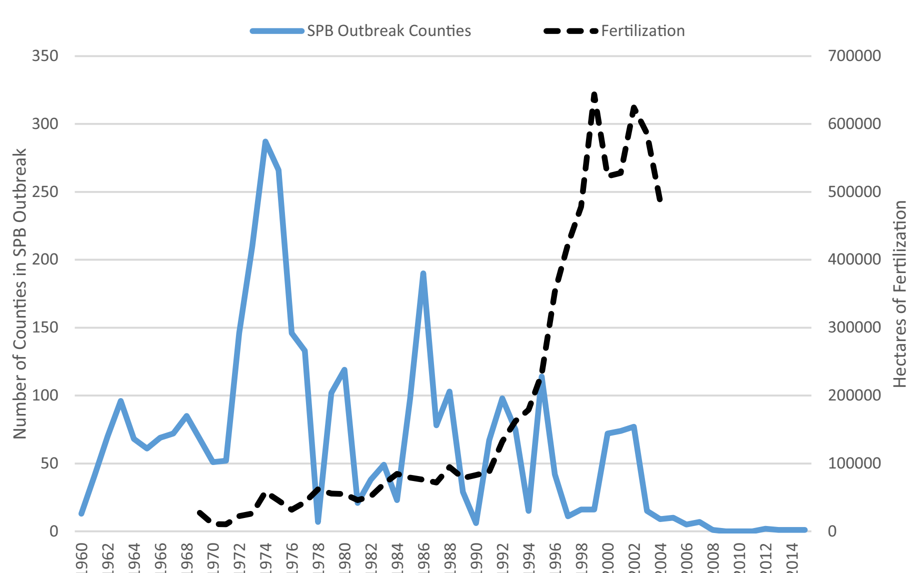

Fig. 6. Annual number of Piedmont/Coastal Plain counties in SPB outbreak status (blue, solid line) (1960–2015) compared to annual number of pine plantation acres fertilized (black, dashed line) (1969–2004) across the southeastern U.S. Fertilization rate graph was adapted from Albaugh et al. (2007) with their permission using data they provided.

use of imazapyr was 1.5–2 million acres (607,000–810,000 ha) per year (Dow AgroSciences Marketing Research Team via Gordon Forster, Crop Production Services, personal communication, May 25th, 2016). Significantly large growth responses of pine stands exposed to herbaceous and hardwood competition control are widely documented (Fox et al., 2007a).

- Pre-commercial and commercial thinning practices have become more routine today compared to earlier decades, although this remains anecdotal as quantifying these trends for an entire region is difficult and problematic. However, thinning is recognized as a key silvicultural practice that enhances growth potential of genetically improved pine trees, in concert with other practices like herbicide and fertilizer applications. Thinning is also generally considered one of the most effective practices for preventing or mitigating impacts from bark beetles by improving tree condition and creating barriers to beetle population growth and spread (Clarke, 2012; Guldin, 2011; Nowak et al., 2015). The U.S. Forest Service Southern Pine Beetle Prevention Program, which was initiated in 2003, has so far helped support thinning and other treatments on over 1.2 million acres (486,000 ha) of private, state, and federal lands (Nowak et al., 2008), although this most likely represents just a fraction of such treatments across the Southeastern U.S.

To be clear, we are not implying that there is a direct link between any of the aforementioned trends and reduced SPB activity at the local level. For example, we do not suggest that a direct physiological mechanism exists for increased tree resistance to bark beetles when fertilizer or herbicide is applied. Interestingly, multiple lines of evidence suggest fertilized pines are less resistant to bark beetles (Reeve et al., 1995; Warren et al., 1999; Wilkins et al., 1997). Nonetheless, a strong correlation exists between an increase in intensive practices and a decline in SPB epidemics at the regional level, and trends for each management practice discussed above suggests significantly more pine acreage where growth rates are faster, stagnation of growth within stands is absent or less pronounced, rotations are shorter, and there is less inter- and intra-specific competition among potential crop trees. Such stand characteristics are well known to prevent or diminish the impacts of the southern pine beetle (Clarke, 2012; Guldin, 2011; Nowak et al., 2015). Where spots do materialize, the relative availability of mills and markets in the Southeast, although depressed in recent years, enables spot disruption via cut-and-remove or cut-and-leave harvesting that is more often not practical or economical in other regions.

4.5. Forest fragmentation hypothesis

A decline across the landscape of vulnerable pine stands that are overstocked, have unimproved or poor genetics and low growth rates may help disrupt SPB population growth and expansion of outbreaks over large areas. SPB spots commonly become disrupted when they run out of host material and come to a stand edge that transitions to hardwoods or an abrupt gap in forest contiguity such as a highway, road, farm, development, etc. (Ayres et al., 2011; Birt, 2011a). Fragmentation of pine plantations into smaller parcels due to more widespread urbanization and development over the last 50 years may also help disrupt the contiguity of pine plantations, a subset of which may be high-risk stands. Nowak et al. (2015) found that larger stands were more likely to contain an SPB spot. Adjacency of large stands may have been more common in decades past when a larger proportion of the landscape was owned by timber and paper companies or private landowners with large properties, although this is speculative. Today, SPB spots still materialize where resources are vulnerable and concentrated, but perhaps it is more difficult for these populations to grow, expand, and build enough momentum to envelope the larger landscape in many areas of the Southeast than it used to be.

Some of the most notable instances of localized SPB outbreaks in the Southeast over the last ten years have occurred on state and federal lands such as the Oconee National Forest in Georgia (2007), Pocahontas State Park in Virginia (2007), parts of the Kerr Reservoir shoreline, managed by the Army Corps of Engineers in Virginia (2008), the Homochitto National Forest in Mississippi (2012) and the Bienville National Forest in Mississippi (2014). What these occurrences have in common is that they represent areas with higher risk pine forest, less intensive management, longer rotations, and less genetically improved stands, within a larger landscape of lower risk pine stands, hardwood and mixed pine / hardwood forest, or other land uses. This may explain why each of these outbreaks failed to expand much beyond the state or federal forest boundaries and/or persist for more than a year or two, although it should be pointed out that active suppression efforts via cut-and-remove and cut-and-leave tactics also likely played a role and have been shown to be effective (Clarke and Billings, 2003). So far, only a few of these more recent outbreaks have resulted in a county or counties reaching outbreak status, and this mainly occurred with counties dominated by federal land.

Forest fragmentation across the southern United States has increased over the last several decades in association with increased development and urbanization (Griffith et al., 2003; Ritters, 2016). However, linking these broad trends to changes in SPB population dynamics would require complex analysis, and there may be insufficient or easily obtainable data for running predictive models. For example, forest fragmentation patterns alone would not be very informative without additional data regarding fragmentation patterns across vulnerable pine stands. Across large landscapes containing preferred forest types (loblolly-shortleaf, oak-pine, longleaf-slash, etc.), southern pine beetle dynamics would be influenced by the interaction of fragmentation patterns and age-class diversity, stand structure and pine basal area, among other variables. Quantifying such forest landscape patterns even at the scale of a county would be difficult, to say nothing of scaling up to a state or physiographic province. Yet, an analysis that relates historical SPB outbreak data to temporal changes in fragmentation patterns among vulnerable stands at the county level would be one way to begin addressing this question.

5. Conclusions

An association is evident between a decrease in the frequency and severity of southern pine beetle outbreaks in the Piedmont and Coastal Plain physiographic provinces of the southeastern U. S. and an increase among several variables associated with intensive pine silviculture and genetic tree improvement efforts. While direct cause-and-effect relationships are unproven, the temporal overlap of these shifting trends towards the end of the 20th century is compelling. Yet, despite a 50+ year record of SPB outbreak dynamics in the Southeastern U.S., recent dramatic declines in outbreak frequency indicate that this is perhaps not a long enough time sequence to be certain which variables most influence regional fluctuations. Much more data and analysis is required on all of the above hypotheses before a better understanding of SPB outbreak dynamics can be achieved. Even if fragmentation patterns and recent changes to forest susceptibility do explain some of the decline in SPB outbreak activity, we are not suggesting that this change is permanent. Reversion back to more SPB-susceptible landscapes is possible if economic trends steer management away from certain practices, particularly thinning and tree improvement. The last two decades have seen large scale ownership conversion from traditional forest industry to timber investment management organizations (TIMOs) and real estate investment trusts (REITS) and a rising interest in the use of pine plantations for biomass production. It remains to be seen whether these developments will lead to more or less application of various silvicultural practices, although they will likely lead to shorter rotations in many instances. A reverse trend towards unthinned, overdense plantations over a significant part of the landscape could increase SPB risk significantly. Even on short rotations of 10–15 years, young stands that are overstocked can be vulnerable to SPB infestation and spread (Cameron and Billings, 1988). The prevalence of genetically unimproved, overstocked, unthinned stands established in the 1950s, when major pine reforestation efforts in the South escalated, was quite possibly what led to the massive and unprecedented outbreak years of the 1970s, when these plantations were approaching maturity (Hedden, 1978). Further, outbreaks on several National Forests in the South over the last couple of decades reveal that overstocked, under-managed pine stands remain a significant problem on some federal lands (Nowak et al., 2015; Clarke et al., 2016).

Although pine plantation acreage has expanded dramatically since the 1950s, major problems from the southern pine beetle have gradually declined in these systems. In addition to the Southeast becoming the 'wood basket' of the U.S. and boosting the economy of many states, current pine silvicultural practices, when utilized, have evolved to become a paragon of good forest management that generate essential ecosystem services across a large region and in a sustainable manner. Active forest management, therefore, can simultaneously provide economic output and environmental benefits while also keeping problems with major insect pests and diseases to a minimum. However, simply increasing the acreage of intensively managed pine plantations is not the only approach or even the best approach to reducing the impacts of the southern pine beetle and other pests on the forest landscape.

Across the Southern U.S., there are important efforts underway to restore many pine-dominated landscapes to a more natural condition (Nowak et al., 2016). Longleaf pine restoration involves returning this species to appropriate sites where it is maintained in open stands among a variety of native grasses and herbs, a system that is largely maintained by regular prescribed burns. Longleaf pine stands have historically been less vulnerable to southern pine beetle outbreaks than loblolly and other southern pine species, and restoration of longleaf has been supported under the SPB Prevention Program since its beginnings in 2003 (Nowak et al., 2008). Shortleaf pine restoration is another emerging effort, although currently shortleaf pine and other natural stands of southern yellow pine species continue to decline in acreage (South and Harper, 2016). While shortleaf pine is vulnerable to SPB, restoration efforts that emphasize wide-spacing in pure stands or mixed pine/hardwood stands on appropriate sites will likely mitigate this risk. Efforts that aim to restore less abundant pine species to ideal sites and return selected areas to a more natural condition can help maximize biodiversity, ecosystem health, and recreational opportunities. Natural regeneration of loblolly pines following harvest of intensively managed plantations is occurring as well (South and Harper, 2016). Naturally regenerated and mixed pine/hardwood forests can be economically productive, albeit less so than intensively managed stands on shorter rotations, while simultaneously being more resistant to attack by the southern pine beetle. Maintaining or increasing practices such as thinning, prescribed burning, spot-harvests (cut-and-remove or cut-and-leave), genetic tree improvement, matching tree species and genotypes to appropriate sites, promoting diverse forest types, age-class diversity and markets, and restoring native pine forest habitat will likely go a long way towards minimizing the impact of the southern pine beetle.

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