REVIEW ARTICLE

J. For. 116(2):178–191
doi: 10.1093/jofore/fvx009
Published by Oxford University Press on behalf of the Society of American Foresters 2018.

forest threats

Expansion of Southern Pine Beetle into Northeastern Forests: Management and Impact of a Primary Bark Beetle in a New Region

Kevin J. Dodds, Carissa F. Aoki, Adriana Arango-Velez, Jessica Cancelliere, Anthony W. D'Amato, Marc F. DiGirolomo, and Robert J. Rabaglia

After more than a decade of damage in pitch pine forests of New Jersey, an unprecedented range expansion of southern pine beetle (SPB), *Dendroctonus frontalis*, has recently occurred with populations established or detected in parts of the northeastern United States. Widespread tree mortality in pitch pine stands has occurred on Long Island, New York, an area previously free of SPB. Tree mortality has also been documented in several small pine stands in Connecticut. Trapping surveys have detected SPB farther north than it had previously been known to exist, with positive trap catches in Connecticut, Massachusetts, and Rhode Island. Integrated pest management plans that consist of preventative silvicultural treatments, landscape prioritization, detection and monitoring, and direct control provide the best opportunity to reduce the effects of SPB in northeastern US pine ecosystems. Most hard pine species present in the region are at risk to SPB, but less is known about white pine susceptibility. Unmanaged pine barrens are a particular concern, as they provide stand conditions conducive to SPB outbreaks. Infestation suppression implementing cut-and-leave tactics has been used in some areas of Long Island and will continue to be the primary management tool to limit damage from SPB.

Keywords: *Dendroctonus*, climate, pine barrens, integrated pest management, tree mortality

In the fall of 2014, several reports of dying pitch pine (*Pinus rigida* Mill.) on Long Island, New York, prompted natural resource managers to investigate the cause of this mortality. Tree mortality was noted in these stands, and some living trees were actively producing resin along the length of the tree bole. Upon further inspection, attack sites were noted, and live and dead bark beetles were collected from within resin (i.e., pitch tubes) oozing from these wounds. The host tree species, characteristics of attack (i.e., living trees under attack, heavy resin flow on tree bole, dried resin pitch tubes), and sinuous gallery pattern under the bark suggested that the southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, was the causal agent of tree mortality in these stands. Suspect beetles were confirmed as SPB in October 2014. During the winter of 2015, SPB-infested trees were also found in several

Received April 19, 2017; accepted November 11, 2017.

Affiliation: *Kevin J. Dodds (kdodds@fs.fed.us), Marc F. DiGirolomo (mfdigirolomo@fs.fed.us), US Forest Service, Northeastern Area, State and Private Forestry, 271 Mast Rd, Durham, NH 03824 USA; Carissa F. Aoki (Carissa.F.Aoki.GR@dartmouth.edu), Ecology, Evolution, Ecosystems, and Society, Dartmouth College, Hanover, NH 03755 USA; Adriana Arango-Velez (adriana.arangovelez@ct.gov), Connecticut Agricultural Experiment Station, 123 Huntington St, New Haven, CT 06504 USA; Jessica Cancelliere (jessica.cancelliere@dec.ny.gov), New York State Department of Environmental Conservation, Forest Health, 625 Broadway, Albany, NY 12233 USA; Anthony W. D'Amato (awdamato@uvm.edu), Rubenstein School of Environment and Natural Resources, University of Vermont, 204E Aiken Center, Burlington, VT 05405 USA; Robert J. Rabaglia (brabaglia@fs.fed.us), US Forest Service, State and Private Forestry, Forest Health Protection, Washington Office, 201 14th St., SW, FHP 3CE, Washington, DC 20250.*

Acknowledgments: *The authors wish to acknowledge the efforts of state and federal partners who have led much of the response to SPB in the northeastern United States: Claire Rutledge (Connecticut); Charlene Donahue (Maine); Ken Gooch, Felicia Andre, and Rebecca DiGirolomo (Massachusetts); Jen Weimer (New Hampshire); Ann Carter, Rob Cole, Dan Gilrein, Jordan Raphael, John Wernet, and Monica Williams (New York); and Lisa Tewksbury (Rhode Island). Many other individuals surveyed and collected traps as part of SPB detection efforts. Tom Luther and Ann Steketee (US Forest Service, Northeastern Area State and Private Forestry) helped with acquisition of spatial data and map creation. Mike Simmons (University of New Hampshire) helped sample the SPB-infested stand on Wertheim National Wildlife Refuge. Funding for portions of information provided in this manuscript came from US Forest Service Domestic Cooperative Agreement 14-CA-11330110-107, Forest Health Monitoring Agreement 16-DG-11420004-222, and Department of Interior Northeast Climate Science Center.*

locations in Connecticut. Based on previous range maps (Clarke and Nowak 2009), these finds represented the farthest north SPB had ever been reported in North America.

Southern pine beetle is an economically and ecologically important bark beetle that, under outbreak conditions, is capable of causing extensive mortality in pine forests. Before detection in the northeastern United States, SPB's range had been confined primarily to pine forests of the southeastern United States. Historically, SPB outbreaks have occurred from Texas in the southwest and Florida in the southeast, north to southern New Jersey across to southern Missouri (Payne 1980). Southern pine beetle has been historically recorded from Delaware, Maryland, Ohio, Pennsylvania, and West Virginia, but has only occasionally caused outbreaks in these states (Anonymous 1996, 1994, 1978, 1972, Hopkins 1909, 1899, Knull 1934). Populations have also been reported from Arizona, Mexico, and Central America (Fairweather et al. 2006, Payne 1980, Billings et al. 2004, Anonymous 2013).

It is believed that spread throughout New Jersey in the 2000s represented an initial SPB range expansion (Weed et al. 2013), or at least an expansion of outbreak populations. Although the southern tip of New Jersey has traditionally been included in SPB range maps, the last known outbreak occurred in 1939, and infestations were not known to occur regularly here (St. George and Beal 1929, Wilent 2005), suggesting that this area represented the margins of its habitat. It is minimum winter temperatures and not the lack of suitable hosts that restrict the range of SPB (Ungerer et al. 1999, Trân et al. 2007). However, the area suitable for SPB establishment is gradually increasing with predicted warming climates (Lesk et al. 2017).

Southern pine beetles, like most insects, are freeze intolerant. At their lower lethal temperature (3.2° F), their body fluids crystallize, resulting in death after just a few minutes of exposure (Sømme 1982, Ungerer et al. 1999). Increases in minimum temperatures across geographical ranges appear to have allowed the beetle to expand northward across New Jersey and into New York and New England. Previous simulation modeling has shown that an increase of 5.4° F in minimum winter temperature decreases the probability of SPB experiencing its lower lethal temperature in a given location by up to 27% (Ungerer et al. 1999, Ayres and Lombardero 2000). Put another way, the geographic isoline delineating the 50% probability of lower lethal temperature moves northward from 35.4° N to 37.0° N (Ungerer et al. 1999, Ayres and Lombardero 2000). The 50% line coincides with an area just south of historical records of SPB outbreak occurrence (Ungerer et al. 1999, Price et al. 2006, Clarke et al. 2016). While average annual temperatures have not increased very much across New Jersey in the 50 years between 1960 and 2010, minimum winter temperatures have increased approximately 7.6° F over this time period (Weed et al. 2013). Extrapolating from the same model, an increase of 7.6° F predicts that the 50% line will move northward by about 140 miles. Historical information shows that the previous northern limit of regular SPB outbreaks occurs somewhere in the latitudes including Maryland and Delaware. From the northern boundaries of these states, a 140-mile northward trajectory places the new 50% isoline in approximately central Connecticut. Small pockets of tree mortality were first reported in Connecticut in 2015, so it would appear that the model represents the relationship between warming winter temperatures and the occurrence of tree mortality with relative accuracy.

It is possible that the recent outbreak and detection of SPB in the northeastern United States is the result of a population that was present at low, undetectable levels in part of the area for many years. Very little is known about SPB at non-outbreak levels (Birt 2011), and it is possible that populations may have persisted at the northern edge of the species distribution for some time and only now experienced climatic conditions conducive to outbreaks. At very low population levels, SPB does not form spots (= discrete infestations) and may act as a secondary species co-occurring in dead trees with other beetle species (Hain 1980, Bryant et al. 2006), therefore detection would be difficult. However, annual aerial detection surveys have been conducted since the 1980s, and in some cases earlier (Roberts 1994), over much of the northeastern United States, and SPB has never been detected in New York or New England. In addition, over the past 20+ years, hard pine stands throughout this area have been extensively surveyed at different times for various pests, including pine shoot beetle (*Tomicus piniperda* [L.]) and Sirex woodwasp (*Sirex noctilio* F.) (Haack and Poland 2001, Dodds and de Groot 2012), with no signs of SPB attack noted. Many of these stands were ground surveyed for tree damage and also trapped using host volatiles, but no SPB were captured or noted in stands. Lack of evidence of previous infestations, and circumstantial evidence, such as warming northeastern climates (Horton et al. 2014), would suggest range expansion is the likely factor resulting in SPB detections in new environments.

Range expansion of phytophagous insects has been documented on several continents and is a concern as global temperatures continue to rise (Jepsen et al. 2008, Battisti and Larsson 2015, Carroll et al. 2003). As climates warm, many insects will be released from temperature constraints that previously limited them to southern latitudes or lower elevation environments (Vanhanen et al. 2007, Neuvonen et al. 1999, Battisti et al. 2006, Regniere et al. 2012, Sambaraju et al. 2012). Forest pests, including defoliators and bark beetles, will

Management and Policy Implications

The presence of southern pine beetle in northeastern US pine forests will dramatically alter management in some pine habitats. Questions related to SPB biology, associated organisms, and susceptibility of northeastern US forests need to be addressed, but its ability to quickly kill large numbers of healthy trees makes it an imminent threat to regional pine forests. Pine barrens ecosystems, especially those that have gone unmanaged, are at particular risk to SPB infestation. The combination of restricted species distributions, SPB's ability to quickly kill overstory trees, and lack of pine regeneration in many of these stands makes the future of these forests uncertain. Natural resource managers responsible for hard pine stands should consider SPB as a near-term threat when developing management plans. Stand structure objectives of maintaining pine barren habitats are generally in line with reducing SPB hazard and include thinning and prescribed fire to open canopies and reduce understory competition. The southern pine beetle's behavior in white pine will define its impact in the northeastern United States, given the prevalence of this potential host, and it is currently unknown how susceptible this tree or stands are to the beetle. Aggressive management of SPB is needed, and should include suppression efforts and proactive stand management where appropriate.

likely expand ranges and establish in areas where no history of infestation has occurred, and in some cases will encounter native trees for which they share no evolutionary history. These range expansions can have wide-ranging effects on local ecosystems (Niemela et al. 2001, Jepsen et al. 2013, Raffa et al. 2013, Pureswaran et al. 2015).

Bark beetle (Coleoptera: Curculionidae: Scolytinae) range expansions are a particular concern because some species in North America, especially from the genus *Dendroctonus* Erichson, have the ability to kill large numbers of trees over a short period of time. Climate change has been implicated in the expansion, intensity, and duration of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak occurring for more than a decade in western North America (Carroll et al. 2003, Logan and Powell 2009). Mountain pine beetle has been more common in high elevation white bark pine ecosystems (Logan et al. 2010), as well as extending its range across the Canadian Rockies into Alberta (de la Giroday et al. 2012). The expansion of SPB into northeastern US forests represents another potential example of climate-driven range expansion of a phytophagous insect in a new environment.

In the following sections, we discuss existing knowledge on the biology and management of SPB within the context of newly invaded regions of the northeastern United States that contain threatened and rare ecosystems such as pitch pine barrens. We provide information on integrated pest management approaches for reducing the impacts of SPB infestations on the structure and functioning of pine-dominated ecosystems in the northeast, including prevention, landscape prioritization and hazard models, detection and monitoring, and evaluation and direct control, and examples of how these approaches were implemented in the newly invaded region. Collectively, our goal is to establish a baseline understanding of SPB in the northeastern United States to inform forest conservation and management decisions in the face of this novel threat to northeastern pine forests.

Southern Pine Beetle Biology

Two characteristics that make SPB particularly damaging are its ability to attack and kill healthy trees and relatively quick development time that results in multiple generations within an infestation killing trees and expanding the area impacted by beetles. Pioneer beetles, or those first dispersing in the spring, locate a tree, bore into it, and release aggregation pheromones (Borden 1974). The combination of host volatiles and pheromones attracts conspecifics (Sullivan 2011), and if enough beetles respond and attack a tree, the tree's defense system is overwhelmed and beetles can successfully reproduce. Pheromone composition changes as attacks on a tree progress, eventually signaling the tree is no longer suitable for arriving beetles, and attacks shift to adjacent trees (Gara and Coster 1968). This process continues throughout a summer and can result in continual expansion of an infestation if plentiful hosts exist in the stand.

Parents create galleries in the phloem where eggs are laid, and female SPB inoculate phloem with beneficial mycangial fungi (*Entomocorticium* sp A, *Ceratocystiopsis ranaculosus* Perry and Bridges) (Barras and Perry 1972) that are important for successful brood production. A third fungus, *Ophiostoma minus* (Hedgcock) H. and P. Sydow, is often inoculated into the phloem at this time, but unlike the two beneficial mycangial species, this species is carried on the body of adult beetles and associated *Tarsonemus* phoretic mites (Moser 1985, Bridges and Moser 1983). *Ophiostoma minus* is considered antagonistic to developing brood (Hofstetter et al. 2006). Eggs hatch, and larvae mine in the phloem where they feed on fungal spores and phloem tissue for several instars, before entering the bark to pupate. After pupation, brood adults emerge from trees and begin the attack sequence again. Brood adults emerging during summer months typically disperse shorter distances than in the fall (Turchin and Thoeny 1993), and this results in spot expansion over the initiation of new spots. Brood adults that emerge later in the fall may disperse greater distances, searching out weakened trees such as those affected by lightning strikes (Lovelady et al. 1991, Coulson et al. 1983) to attack for the overwintering generation.

Population cycles of SPB have been described as pulse eruptive (Berryman 1986). Outbreaks can occur at irregular intervals when biotic and abiotic conditions favor SPB population buildup. With multiple generations per year (~3 generations in the north of its historical distribution, and as many as nine in the southern limit of its distribution) (Payne 1980), populations can quickly erupt and cause rapid mortality of healthy, vigorous pine trees over large areas. During the non-outbreak phase, low populations are often confined to weakened or dying trees (Hain et al. 2011). During this phase, SPB populations may be hard to detect and go unnoticed until tree mortality becomes evident.

A large community of insects are associated with SPB-infested trees in the southeastern United States (Overgaard 1968, Dixon and Payne 1979). This includes predators, parasitoids, and competitors that can all negatively affect SPB survival (Moore 1972, Coulson et al. 1980, Goyer and Finger 1980). No SPB predator and parasitoid census has been undertaken in the northeast to date, but predators, especially *Thanasimus dubius* F. (Coleoptera: Cleridae), have been observed in large numbers on SPB-attacked trees and in traps during surveys. *Thanasimus dubius* is native to eastern US forests and commonly found associated with other bark beetle species and captured in traps baited with their pheromones (Haberkern and Raffa 2003, Schmitz 1978). The adults feed on SPB adults on the bark surface of trees undergoing mass attack, and their larvae feed on developing brood within host trees (Thatcher and Pickard 1966). *Thanasimus dubius* is the primary predator associated with SPB, but other beetles have also been documented as predators of either adults or larvae (Camors and Payne 1973). A number of Hymenopteran parasitoids, including species of Braconidae, Pteromalidae, Eurytomidae, and Platygastridae, attack SPB within trees in the southeastern United States (Goyer et al. 1980,; Goyer and Finger 1980), and the majority of these are present in the northeastern United States or have been collected in comparable environments (Krombein et al. 1979).

Host Trees in the Northeastern United States

Southern pine beetle is highly polyphagous on North American pine (Payne 1980). In its traditional range, it is known to attack all species of hard pine it encounters and has a strong association with loblolly (*Pinus taeda* L.) and shortleaf pines (*Pinus echinata* Mill.) (Price et al. 2006, Payne 1980). It has also been occasionally reported from Norway spruce (*Picea abies* [L.] H. Karst), red spruce (*Picea rubens* Sarg.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.) (Hain et al. 2011). Southern pine beetle has successfully attacked pitch pine in Mid-Atlantic states, including outbreak populations in New Jersey (Weed et al. 2013), and on Long Island where it has already been responsible for the death of thousands of trees. Much less is known about the susceptibility of other northeastern US pine species to SPB. Red pine (*Pinus resinosa* Ait.) and Scots pine (*Pinus sylvestris* L.) have been documented as SPB hosts in Connecticut, where late-stage brood were observed in trees before they were cut and destroyed (Arango-Velez, pers. obs.). White pine (*Pinus strobus* L.) is also documented as an SPB host (Knull 1934, Hain et al. 2011, Hopkins 1899), but limited observations in New York and Connecticut suggest that successful reproduction in this tree is rare. To our knowledge, SPB has not yet encountered jack pine (*Pinus banksiana* Lamb.) in the northeastern United States. Mountain pine beetle expanded into the jack pine zone in Alberta, Canada, where for the first time it successfully colonized lodgepole x jack hybrids as well as pure jack pine (Cullingham et al. 2011). It is likely that SPB will follow suit and also successfully develop in jack pine if it is encountered in the northeastern United States.

Several new or rare potential SPB hosts have been documented in the northeastern United States. Japanese black pine (*Pinus thunbergii* Parl.) and lacebark pine (*Pinus bungeana* Zucc. ex Endl.) were attacked in Brooklyn, New York, but it is unknown if SPB successfully reproduced in these trees. Southern pine beetle mass attacked these trees, created galleries, and successfully stressed trees to the point where there was advanced canopy fade. Unfortunately, trees were removed and destroyed before any brood success estimates could be recorded. Norway spruce, a known occasional SPB host (Anonymous 2003, Hain et al. 2011), has also been reported to be attacked on Long Island and in Connecticut. No information exists on host suitability of Norway spruce for SPB. One white spruce [*Picea glauca* (Moench) Voss] was heavily attacked by SPB in Connecticut; however, no bark samples could be collected for further analysis of gallery development.

Threatened and Rare Pine Ecosystems at Risk from SPB Range Expansion

If SPB maintains its association with hard pine, suitable hosts will be much more limited in the northeastern United States. (Figure 1). Until SPB invades the core ranges of red (to the west) and jack pine (to the north), most of the hard pines it will encounter in the northeastern United States are found in relatively isolated, small stands. Coastal and interior pine barrens and natural stands of red pine are examples of rare ecosystems that exist in the northeastern United States. Most of the pine barren ecosystems in the northeastern United States are pitch pine dominated (Finton 1998), but jack pine barrens exist at a few sites (Stergas and Adams 1989, Barton and Grenier 2008).

Pitch Pine Barrens

Outside of larger forests in southeastern Massachusetts and Long Island, pitch pine occurs in isolated remnant stands throughout portions of New England and upstate New York (Finton 1998, Bernard and Seischab 1995, Howard et al. 2011, Kurczewski 1999, Seischab and Bernard 1991, 1996). Pitch pine barrens have been substantially reduced in New England, and much of the area representing this forest type currently exists only in small stands (Motzkin et al. 1999, Copenheaver et al. 2000, Finton 1998). On Long Island, the original post-settlement extent of this forest has been fragmented and changed (Kurczewski and Boyle 2000, Cryan 1980), but a large portion is protected from development through state law. However, fire suppression and lack of management put the sustainability of pitch pine barrens in the region in doubt over the long term (Bried et al. 2014, Howard et al. 2011, Milne 1985, Kurczewski 1999).

Southern pine beetle has caused extensive damage to pitch pine forests in New Jersey over the past decade and now is problematic on Long Island. Unmanaged and overstocked pitch pine stands are the norm in the Central Pine Barrens, whereas natural disturbances, including fire, historically maintained open stand conditions that contained mixed oaks (*Quercus*) as well as a diverse understory (Jordan et al. 2003, Bried et al. 2014). As a result, pine barrens management at other sites in the northeastern United States, including Cape Cod National Seashore, New Jersey Pine Barrens, Albany Pine Bush, and Montague Sandplains, often relies on prescribed fire to maintain these conditions. Disturbances are critical for maintaining pitch pine barrens and should be integrated into management plans (Jordan et al. 2003). Potentially, this type of forest structure would be more resistant to SPB than unmanaged stands. Pitch pine barrens often develop dense, close canopy conditions without active management (e.g., stand thinning, prescribed fire), making them highly susceptible to SPB attack and infestation growth.

Data collected from one of the earliest stands found infested in the Central Pine Barrens on Long Island illustrate how quickly SPB can change a forest. Detailed overstory data were collected at the Wertheim National Wildlife Refuge to describe characteristics of attacked trees, as well as tree mortality, and to describe what forest would remain on the site after SPB moved through the stand. This pitch pine–mixed oak stand was approximately 92 ac and was sampled with 47 fixed radius plots established on a systematic grid during the winter of 2015. Southern pine beetle had infested the stand during the summer and fall of 2014. Prior to infestation, the stand was dominated by pitch pine, with oak species also constituting a significant portion of overstory species composition (Table 1). The largest size classes were almost entirely pitch pine, with very few oak trees ≥ 16 inches dbh present in the stand (Figure 2). Unfortunately, at the time of sampling almost all (98%) of the pitch pine in the stand were dead, with SPB responsible for 93% (7,722 trees) of this mortality. The presence of SPB in this stand for one growing season has resulted in a dramatic change in overstory composition. In addition, very few pitch pine seedlings were noted in the understory, highlighting the ability of SPB to dramatically shift stand composition and structural conditions in only one growing season, with potential long-term alterations to ecosystem functioning with the loss of pitch pine from these areas.

Natural Red Pine Stands

Natural red pine stands are rarer than pine barrens in the northeastern United States. Examples of natural red pine stands are present in Maine, Massachusetts, New Hampshire, New York, and Vermont (Cook et al. 1952, Sperduto and Nichols 2011, Swain and Kearsley 2001, Engstrom and Mann 1991, Gawler and Cutko 2010, Edinger et al. 2014) and represent unique regional resources. These stands are generally present on ridge tops and rocky outcrops that are associated with poor soil conditions. The presence of outbreak populations of SPB in natural red pine stands could threaten the persistence of these forest

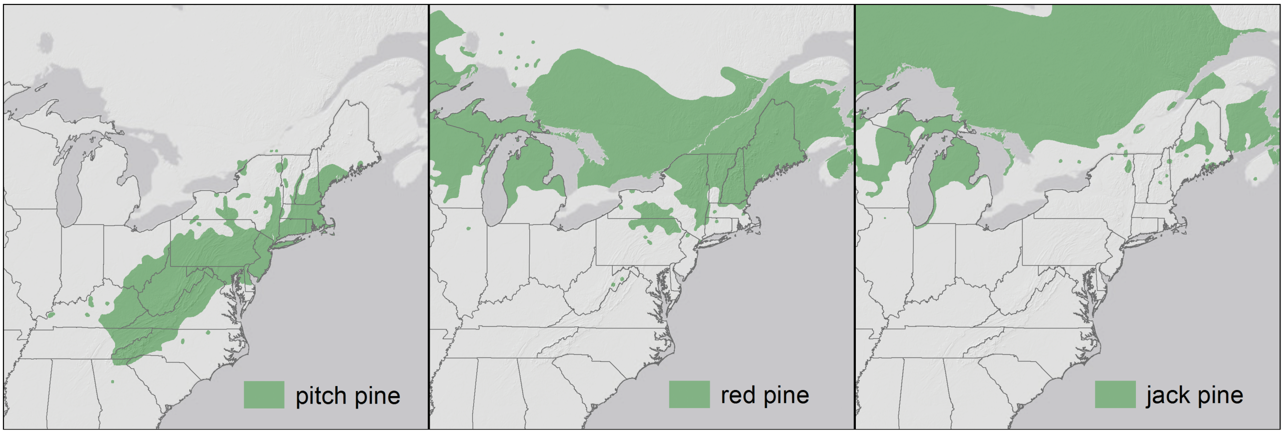

Figure 1. Distribution of pitch pine, red pine, and jack pine.

types in the region and result in the wholesale loss of these stands.

Integrated Pest Management of Southern Pine Beetle

Integrated pest management (IPM) plans for SPB have been developed and involve prevention, prediction, detection, evaluation, and direct control (Clarke 2001). Prevention primarily relies on silvicultural treatments to reduce stand susceptibility (Brown et al. 1987, Nebeker and Hodges 1983) and can be guided by landscape prioritization and hazard models (Hicks et al. 1987). Prediction and detection are conducted with the use of pheromone-baited trapping surveys or from aerial detection surveys. Evaluation of known infestations occurs before any direct control techniques are implemented. These methods can help reduce losses to SPB, but not eliminate damage on a landscape.

Prevention

To address underlying stand and site conditions that are conducive to SPB infestation, preventative silvicultural treatment of high hazard stands should be undertaken (Nebeker and Hodges 1983, Brown et al. 1987). Silvicultural treatments of conifer stands have long been recognized as tools to reduce the impact of bark beetles on forest resources (Fettig et al. 2007). Forest thinning of high hazard stands has been documented as an effective treatment for substantially reducing the likelihood of an SPB infestation in the southeastern United States (Nowak et al. 2015). To help offset the cost of precommercial thinning, the Southern Pine Beetle Prevention Program provides funding to state agencies to help support thinning on state and private lands (Nowak et al. 2008), and this provides additional incentive for landowners to preemptively treat stands.

Prevention in the Northeastern United States To date, silvicultural treatments have not been widely implemented in at-risk areas to reduce stand susceptibility to SPB in the northeastern United States. If undertaken, these treatments should not occur in areas undergoing an SPB outbreak. Areas outside of an SPB outbreak should focus on silvicultural treatments, but significant hurdles exist, including cost associated with treatments. In particular, the lack of local markets and low value of most material harvested during a thinning treatment make these operations a costly undertaking. Public perception of forest thinning in these forest types would also have to be addressed, as early attempts at small-scale thinning operations on Long Island were met with significant opposition.

Stand structure in pitch pine stands in this region vary considerably and range from pure pitch pine to pitch pine mixed with oak and other species (Greller 1977, Olsvig et al. 1998, Bernard and Seischab 1995, Copenheaver et al. 2000, Howard et al. 2011). Management in these stands ranges from non-existent to intensive vegetation treatments that include thinning and prescribed fire with the objective of maintaining pitch pine stands in a more natural state. Fortunately, efforts to restore and maintain pitch pine stands in more natural states (Bried et al. 2014) align with methodology recommended to reduce stand susceptibility to SPB.

Landscape Prioritization and Hazard Models

An important component of prevention is understanding stand susceptibility across large landscapes (Hicks et al. 1987). Various hazard models have been developed and implemented in the southeastern United States for SPB (Hicks et al. 1979, Mason et al. 1985) to assist natural resource managers in prioritizing landscapes for preventative treatments, as well as to provide areas that may need heightened monitoring. Factors such as host species, site quality, age structure, basal area or stem density, growth rates, and proportion of pine in the overstory have all been used to assess SPB susceptibility in southern forests (Coulson et al. 1974, Schowalter and Turchin 1993, Hedden 1978, Belanger and Malac 1980).

Landscape Prioritization and Hazard Models in the Northeastern United States. State-owned lands containing pitch pine on Long Island were rated using an SPB stand hazard model to help prioritize areas where thinning could be undertaken and where infestations found in these areas could be focused on for suppression. If thinning becomes a more prominent tool for SPB management, having strong models developed within these forests will be important for targeting high-risk areas for treatment.

Detection and Monitoring

Aerial detection surveys and pheromone-baited traps are used to detect and monitor SPB populations. Aerial detection surveys are conducted across the United States to track forest health conditions

Table 1. Average diameter, basal area, density and importance value for tree species adjacent to the Black Tupelo trail on the Wertheim National Wildlife Refuge, Long Island, New York.

Species	Avg. dbh (in.)	Total basal area (ft^2)	Density of stems	Relative basal area	Relative density	Importance value*
Pitch pine	11.7	183.3	212	75.4	46.0	60.6
White oak	5.4	13.6	73	5.6	15.8	10.7
Scarlet oak	6.4	26.5	94	10.9	20.4	15.6
Black oak	6.5	17.1	64	7.0	13.9	10.3
Red oak	6.1	0.4	2	0.2	0.4	0.3
Red maple	5.0	1.6	11	0.7	2.4	1.6
Black gum	4.7	0.4	3	0.2	0.7	0.4
Black cherry	4.3	0.2	2	0.1	0.4	0.3
Per acre		105.7	200			

*Importance value = (relative basal area + relative density)/2.

and are used extensively in the southeastern United States for SPB monitoring. Aerial observers map the location of fading crowns that indicate SPB presence in a stand. These flights are conducted several times during the growing season in the southeast, and can also be conducted later in the season to map and estimate acreage killed by SPB.

The combination of beetle-produced pheromones and host volatiles provides strong survey tools for detecting SPB or monitoring populations and are easily deployable. Detection surveys are used in areas outside of where known SPB populations exist with the hopes of locating populations before they become problematic. Monitoring surveys, in comparison, are used within SPB's known range and used to monitor populations from one year to the next. A predictive model exists for estimating SPB activity across the southeastern United States based on pheromone-baited trap catches (Billings and Upton 2010), but this model has not yet been evaluated for use in the northeastern United States. The model operates at larger scales than may be appropriate for the more restricted pine landscapes of the northeastern United States. The standard lure that has been used to monitor SPB populations consists of the pheromone frontalin and host-produced terpenes (Billings and Upton 2010). To increase attractiveness, the pheromone endo-brevicomin can be added to the standard lure combination by placing it adjacent to traps (Sullivan and Mori 2009).

Survey Efforts in New Jersey. Most of the forested land in New Jersey where pine is a dominant or co-dominant component is found in the southern portion of the state. The federally protected New Jersey Pinelands, which contain large holdings of pitch pine, overlaps all but one of the eight counties in southern New Jersey. The New Jersey Department of Environmental Protection began aerial detection surveys for SPB in 2002, concentrating efforts in this area after infested trees were reported from ground-based detections. The first year of aerial detection surveys mapped over 1,411 ac affected by SPB in 227 infestations. Annual acreage affected by SPB varied over the next 15 years, from a low of 350 acres in 2004 to a high of 14,154 acres in 2010 (Figure 3). Over this time period, SPB was only located attacking trees in southern New Jersey.

Southern pine beetle monitoring traps were deployed in Atlantic, Burlington, Cape May, Cumberland, Salem, and Ocean counties in southern New Jersey beginning in 2003, with three separate trapping locations per county. Over time, more intensive sampling was implemented, so that by 2014, there were 22 trapping locations across the six counties. All monitored counties had positive traps in each of the years between 2003 and 2016. Traps in the northern portion of the state have also been positive for SPB over at least the past two years (2015–2016) (Figure 4).

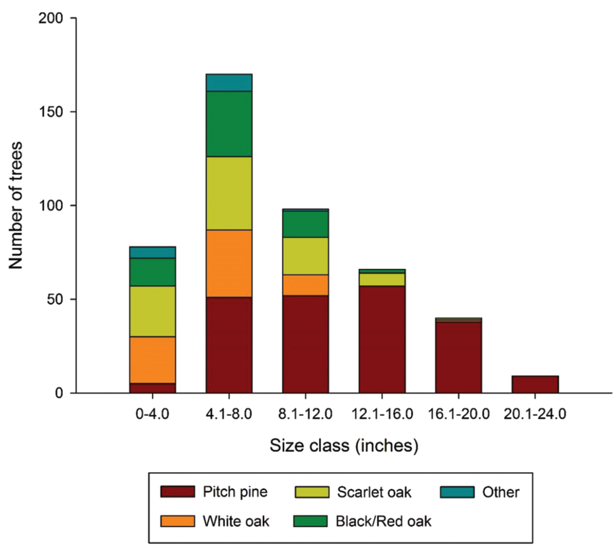

Figure 2. Size class distribution of trees sampled at Wertheim National Wildlife Refuge, Long Island, New York.

Survey Efforts in New York. Quickly after identifying SPB adults from Long Island, a series of site visits were conducted in October and November 2014, to determine the extent of the population. It was apparent that a widespread and well-established SPB population was killing primarily pitch pine throughout eastern Long Island. The initial aerial detection surveys were conducted in December 2014, once leaves had fallen from hardwoods so that detecting stressed

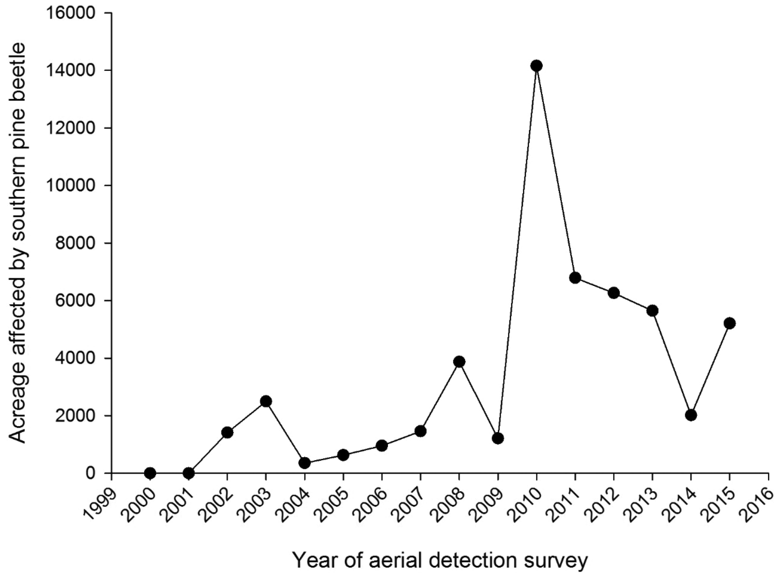

Figure 3. Acreage affected by southern pine beetle in New Jersey from 2000 to 2015.

or dead pines would be easier. The survey, which focused on 197,684 ac of land within the Central Pine Barrens Core Preservation and Compatibility Growth Areas, produced 265 infestations, totaling approximately 14,826 acres. The infestations ranged from lightly damaged (few trees), light moderate (few trees and clusters), and moderate (multiple clusters), to heavy (multiple clusters and classic SPB front pattern). The largest infestations with the heaviest damage were mapped in the southern half of eastern Suffolk County, particularly within the town of Southampton. Several county parks in this area, with large expanses of pitch pine forest, were severely impacted by high tree mortality. Additional aerial detection survey flights from January through August 2015 delineated 38 new infestations, totaling approximately 1,520 ac. In 2016, aerial detection surveys from January through August 2016 mapped 225 infestations, totaling about 6,178 ac. The heaviest damage remained concentrated within the town of Southampton, but another large infestation erupted about 30 km southwest, in the town of Brookhaven.

In the spring of 2015, SPB monitoring and detection surveys were begun in New York. Traps were placed throughout Long Island to monitor populations, while detection traps were placed in areas of New York outside of Long Island. Relatively large numbers of SPB were captured in New York compared to other states (Table 2). The large beetle numbers collected on Long Island were expected given the amount of tree mortality that was found the previous year. However, it was surprising that detection traps in the Hudson Valley, 120 miles north of the nearest infestation, were also positive for SPB (Figure 4). The first SPB was detected in traps in New York sometime between April 19 and May 2, 2015, with captures peaking in mid-June (Figure 5). The earliest catches in 2016 were from the two weeks prior to May 10.

Survey Efforts in Connecticut. The majority of pitch pine forests in Connecticut have been converted for other land uses, but remnant patches exist (Gluck 2015),

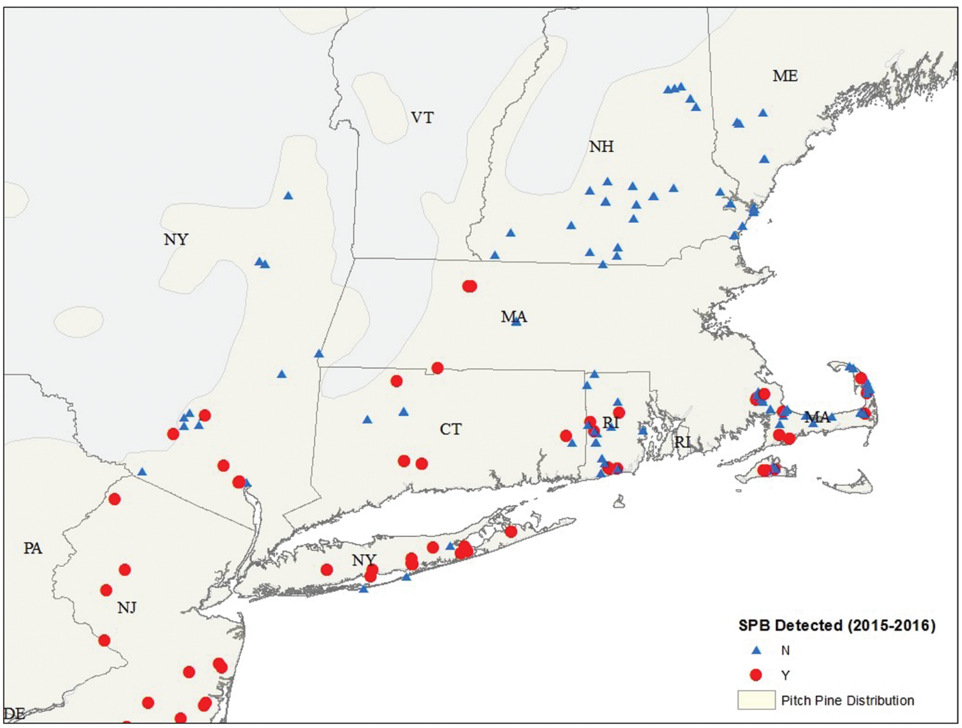

Figure 4. Results from southern pine beetle detection and monitoring traps deployed throughout the northeastern United States in 2015 and 2016.

and are now at risk to SPB. Southern pine beetle was first found infesting red pine in Connecticut in March 2015. Aerial detection surveys were not conducted in Connecticut, and early efforts there relied on ground surveys. Site visits and surveys located individual SPB-infested trees or small infestations across southwestern Connecticut in pitch pine, red pine, white pine, Scots pine, Norway spruce, and white spruce. There was not successful reproduction in Norway and white spruce, but some trees succumbed to attack, likely because SPB-associated fungi were established in these trees.

In Connecticut, monitoring traps were placed in six towns across the state that contained previously SPB-attacked pitch, Scots and red pine. Ten and 22 SPB were captured in survey traps throughout Connecticut in 2015 and 2016, respectively (Table 2, Figure 4; Claire Rutledge, pers. comm.).

Detection Efforts Outside Infested Areas. Northeastern states conduct annual aerial detection surveys over forested lands. While no specific SPB-focused aerial surveys were conducted over forests outside of infested states, pine stands were surveyed during these annual efforts and observers focused more attention on these resources. Several suspect polygons were found in Massachusetts and Rhode Island during annual surveys. However, subsequent ground-based surveys found no SPB-killed trees in these areas.

Detection traps in the northeastern United States used the same base lure as monitoring traps, but the pheromone endo-brevicomin was added to increase attractiveness (Sullivan and Mori 2009) to these traps. Detection surveys were established in Massachusetts, New Hampshire, Rhode Island, and portions of New York outside of Long Island in 2015 and 2016 (Table 2, Figure 4). Maine also surveyed for SPB in 2016. Traps in the northeastern United States were deployed within or near hard pine stands and generally ran for six to eight weeks in the spring.

In addition to detections in the Hudson Valley of New York, SPB was also captured in parts of Massachusetts and Rhode Island (Table 2, Figure 4). Traps were placed in areas of Massachusetts that contained the most pitch pine forests. A total of 32 SPB were captured from 13 traps in 2015, with the majority being found in the north central portion of the state, particularly in Montague Plains Wildlife Management Area, the largest inland pine barrens in the state. This detection represented the farthest north SPB had ever been documented (Figure 4). Southern pine beetle was also detected on Martha's Vineyard. Surveys in Massachusetts in 2016 captured a total of 11 beetles from traps located in southeastern coastal areas and Cape Cod. Only 13 and one SPB were captured in 2015 and 2016, respectively, in Rhode Island during survey efforts (Table 2). Positive traps in Rhode Island occurred in the central and southern portions of the state (Figure 4). While SPB have been detected in traps in Massachusetts and Rhode Island, no infested trees have yet been located in these states. No SPB were detected in traps in New Hampshire (2015, 2016) or Maine (2016) (Table 2, Figure 4).

Evaluation and Direct Control

The best method for stopping an active SPB infestation is by cutting infested trees and a green tree buffer at the active front. Effective suppression methods have seen developed in the southeastern United States (Swain and Remion 1981, Clarke and Billings 2003, Billings 2011) and are being implemented in the northeastern United States. These methods, while previously untested in this region, hold promise for reducing tree losses on local scales. Aerial detection surveys provide locations of SPB infestations that are then ground checked and evaluated for their potential for continued growth. Spots that contain many infested trees and have high hazard stand conditions (e.g., high pine basal area) are often prioritized for suppression activities (Billings and Pase 1979). These treatments can occur during the summer/fall when infestations are active, or during the winter when insects are mostly dormant. Winter suppression activities may be less effective unless high levels of brood mortality occur over the winter, but these have less of an impact on the residual stand because a green tree buffer generally does not need to be cut.

Two methods, cut-and-leave and cut-and-remove, are commonly employed to disrupt spot growth and reduce brood survival in trees (Billings 2011). The two suppression techniques follow the same protocols, with the exception of what occurs after trees are on the ground. Both techniques also involve cutting a green tree buffer at the front of infestations during the growing season to make sure all infested trees are accounted for and further disrupt pheromone signals (Clarke 2012). The length of this buffer is based off the

Table 2. Southern pine beetle captured during detection and monitoring efforts in the northeastern United States. The standard SPB lure contains a terpene mix and frontalin.

State	Survey type	Number of traps	Lure	SPB
2015				
New York	Monitoring	15	SPB lure	2,499
	Detection	8	SPB lure, endo-brevicomin	5
Connecticut	Detection	6	SPB lure	10
Massachusetts	Detection	30	SPB lure, endo-brevicomin	32
Rhode Island	Detection	10	SPB lure, endo-brevicomin	13
New Hampshire	Detection	20	SPB lure	0
2016				
New York	Monitoring	13	SPB lure	11,090
	Detection	21	SPB lure, endo-brevicomin	10
Connecticut	Detection	6	SPB lure, endo-brevicomin	22
Massachusetts	Detection	34	SPB lure, endo-brevicomin	11
Rhode Island	Detection	12	SPB lure, endo-brevicomin	1
New Hampshire	Detection	25	SPB lure, endo-brevicomin	0
Maine	Detection	6	SPB lure, endo-brevicomin	0

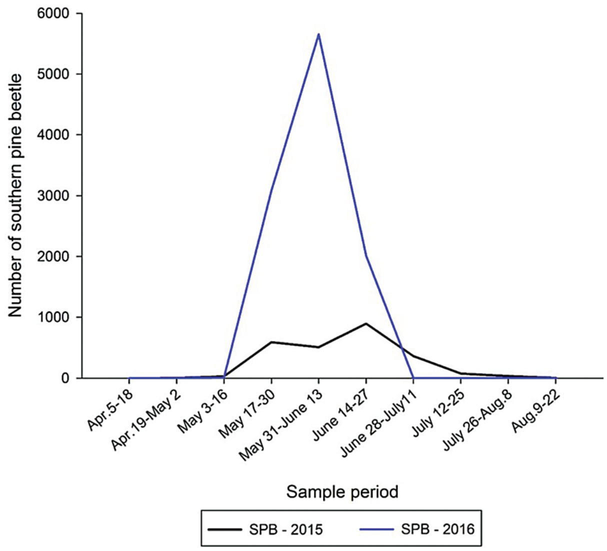

Figure 5. Southern pine beetle flight phenology on Long Island, New York, during 2015 and 2016.

number of actively infested trees at the time of survey (Billings and Pase 1979). In cut-and-leave treatments, all infested and green trees are cut and left on site. Cutting trees containing brood immediately disrupts the infestation and may result in reduced beetle survival in downed trees. Felling the trees and exposing boles to more sunlight and heat does not eliminate brood entirely, however, it can reduce beetle survival (Hodges and Thatcher 1976). Timing of cut-and-leave may be important for increasing brood mortality within trees. Recently attacked trees that were felled in the winter (December) had higher estimates of brood mortality than trees cut during spring, summer, and fall (Hertel and Wallace 1983). Beetles that survive and emerge from downed trees must then disperse and attempt to locate new hosts in an ongoing infestation or initiate a new spot. This does not, however, lead to an increase in proliferation of infestations around treatments (Billings and Pase 1979, Fitzgerald et al. 1994). The increased time dispersing and seeking new hosts likely leads to higher levels of mortality (Pope et al. 1980). Cut-and-remove, the most effective suppression technique (Clarke and Nowak 2009), follows the same procedure as cut-and-leave, but trees are then removed from a site and processed elsewhere. This is ideal because all brood within trees are removed from an active infestation and destroyed. Landowners may also recoup some costs accrued during the suppression effort.

Examples of Evaluation and Direct Control

New Jersey

Spot suppression was conducted throughout the New Jersey Pinelands area beginning in 2011, as well as in additional state-owned land outside the Pinelands boundary. In the following two years, over 250 individual infestations were suppressed on state lands. Particular priority was given to pine-dominated stands north of the Mullica River deemed particularly susceptible; however, most spot occurrences over the course of the outbreak were south of this river. The majority of suppression activities were conducted using cut-and-leave techniques, although a few stands outside the Pinelands Boundary were treated with cut-and-remove or infested material was cut and then chipped on site. Hand crews were used for the cut-and-leave treatments, and mechanized methods were used for cut-and-remove treatments. All suppression activities were conducted during the summer months, with the goal of disrupting spot growth and preventing further tree losses at each active infestation site (Billings 2011). In addition to suppression activities on state-owned land, New Jersey Department of Environmental Protection also received support from the US Forest Service to administer a cooperative program providing suppression cost assistance to private and municipal landowners. A smaller subset of these landowners also participated in preventative thinning activities.

New York

Spot suppression was concentrated in the Central Pine Barrens Core Preservation area, where larger forested blocks and unique habitats occur. After aerial and ground surveys were completed, SPB spots were selected for suppression using a prioritization scheme developed by Billings and Pase (1979) that considers the number of trees containing brood, pine basal area available for infestation to grow into, and whether or not the stand is pulpwood or sawtimber. Only sawtimber stands were surveyed on Long Island.

Due to a limited forest resource industry and no local destination for harvested wood products, only cut-and-leave suppression was implemented on Long Island. Suppression efforts occurred during the summer, fall, and winter. Infested and buffer trees were felled toward the center of an infestation, and left on the ground at the site. All spots were suppressed by hand felling. The objective of fall and winter suppression was to expose beetles to the elements to increase brood mortality. Trees felled were grooved along the top of boles to potentially increase SPB brood exposure to moisture and cold temperatures. Summer suppression aimed to disrupt SPB pheromone plumes (Thistle et al. 2004), making it more difficult for beetles to find and attack trees in high numbers and expand infestations.

Suppression efforts on federal lands including the Wertheim National Wildlife Refuge, William Floyd Estate, and Fire Island National Seashore began in March and April 2015. On Wertheim National Wildlife Refuge, the Forest Health Working Team of the Northeastern Forest Fire Protection Commission (commonly referred to as the Northeast Compact) was used to deploy sawyers from cooperating agencies to carry out suppression efforts. This was the first instance of using this organization to facilitate pest suppression of any kind. Approximately 1,300 infested trees were treated with cut-and-leave on the Wertheim National Wildlife Refuge, and approximately 1,000 total trees were felled on the William Floyd Estate and Fire Island National Seashore. The following year, far fewer attacked trees were located at each site and only low numbers of trees were treated with cut-and-leave. Bark on the top of all trees was grooved to facilitate exposure of the brood to water and cold temperatures.

Concurrent to suppression efforts on federal lands, a large infestation on state land in Henry's Hollow Pine Barrens State Forest was also cut (~2,000 trees) during the early parts of the spring. The next major SPB suppression effort on state land occurred from October 2015 to January 2016, in which 7,564 trees were cut at four infestations in the town of Southampton. The spots selected for suppression were all located on the eastern edge of the Core Preservation Area of the Central Pine Barrens, and were in close proximity to one another. These spots had no clear front, and were coalescing into one very large infestation, containing tens of thousands of trees. Because of limited resources and time, suppression targeted infested trees on the western front in an effort to create a buffer and prevent spread into large stands of uninfested pine to the west. Suppression efforts resumed in the same area from June to August 2016, where 1,923 infested and buffer trees were cut. From October 2016 to January 2017, over 2,000 trees were cut at Southaven County Park in the town of Brookhaven. Suppression was targeted at the northern front to prevent the infestation from spreading into uninfested areas to the north.

Connecticut

Ground surveys in Connecticut found scattered areas where only a few trees were infested by SPB, to spots containing approximately 100 attacked trees. All trees that exhibited signs of SPB attack were cut and chipped on site. In these areas, suppression activities were successful and expansion of SPB to adjacent healthy trees was stopped.

Recommendations

The presence of SPB in the northeastern United States changes immediate- and long-term management of hard pine stands in the region. Southern pine beetle is unlike other insects present in the northeastern United States, whereby infestations of this insect can rapidly and dramatically change local stand conditions in only one season. There has been a strong response from state, federal, and local agencies and organizations to SPB in the northeastern United States, and this will have to continue and expand if damage from SPB populations is to be reduced in the region. The following recommendations should be considered by natural resource managers who are responsible for managing hard pines in SPB's expanded range:

Prevention

- Prioritized preventative treatment of high hazard stands should be undertaken, and whenever possible used to reduce tree losses in these stands. Managing to reduce hazard to SPB is generally in line with restoration goals for natural conditions of healthy natural red pine communities, as well as jack and pitch pine barrens (Jordan et al. 2003). Restoring stands to more natural structural conditions through judicious use of prescribed fire should be considered where appropriate for all hard pine stands of high ecological or social value. Open canopies result in less competition among overstory trees, leading to vigorous trees better able to resist bark beetle attacks (Mitchell et al. 1983). Further, open stand conditions can influence pheromone dispersion (Thistle et al. 2004) and may help disrupt host location by SPB. Finally, these approaches provide opportunities for recruiting younger age classes of pine to replace older cohorts impacted by SPB.
- Current thinning recommendations are based on experiences with loblolly pine in the southeastern United States and provide some guidance for similar efforts in the northeastern United States. Treatments in the northeastern United States will need to consider stand history, pitch pine silvics, site characteristics, restoration efforts, and non-timber resources as silvicultural plans are developed.
- Wherever possible, efforts should be made to incorporate a discussion of forest health and pitch pine stand dynamics in outreach efforts to the general public so that silvicultural treatments and prescribed fire are properly contextualized. Examples where intensive management in pitch pine has been implemented, including the Albany Pine Bush in upstate New York (Albany Pine Bush Preserve Commission 2010) and the Montague Plains in northwestern Massachusetts (Clark and Patterson 2003), should be highlighted.
- The lack of markets for low-grade material is a significant barrier to forest harvesting for much of the northeastern United States, including the areas being impacted by SPB. Development of wood pellet and engineered wood product markets could provide future options for the utilization of materials harvested from stands threatened by SPB. To date, almost all suppression treatments in New Jersey and New York have been cut-and-leave because there is no local destination for cut trees, or the value of the material is too low to make moving it economically feasible.

Landscape Prioritization and Hazard Models

- Hard pine stands should be assessed to determine susceptibility to SPB by considering stand and site characteristics (Mason et al. 1985). Data collected from stands that have been infested by SPB can provide insight to characteristics that make northeastern US pine stands susceptible to the beetle. Landscape scale hazard models that prioritize areas for treatment (Hicks et al. 1979) are recommended for states that have large holdings of pitch pine (e.g., Massachusetts, New Jersey, New York).

Detection and Monitoring

- It is recommended that surveys in hard pine stands in the northeastern United States increase and be incorporated into annual forest insect and disease survey efforts. Annual aerial detection surveys are already conducted over much of the northeastern United States (Roberts 1994), but these may need to be augmented in some areas to increase the number of flights throughout the summer so that growing SPB infestations can be detected in areas where the beetle is a threat. A survey flight in late fall may be helpful for detecting areas where SPB has been active.
- Semiochemical-based monitoring (Billings and Upton 2010) and detection efforts should be continued in known infested areas and adjacent uninfested areas, respectively. Further, high-hazard stands located outside of the known infested area should also be monitored with semiochemical baited traps or annual ground surveys. Endo-brevicomin should be used in conjunction with the standard lure for both monitoring and detection trapping efforts.

Evaluation and Direct Control

- When infestations are found through detection efforts, they should quickly be suppressed to protect as many trees as possible in a stand. Having management plans in place that incorporate SPB could alleviate some of the initial hurdles involved with suppression.

Science

- In addition to recommendations surrounding management of SPB in its currently known range and potential areas where it will likely expand, a better understanding of the beetle's behavior in white pine forests is needed. This would also include studies on the microorganisms carried by SPB and how successful they are on white pine. Early indications are that white pine may be an inferior host compared to hard pines, but studies are needed to adequately assess the potential economic and ecological impact of SPB on northeastern US forests.
- Fire is an important component of pitch pine forests, and the presence of SPB in these ecosystems may influence this disturbance. Suppression activities have the potential to increase fine and coarse fuels, in the near and long term, likely influencing fire behavior in these stands. A more complete understanding of fire behavior and impacts related to SPB would be helpful for management purposes.
- Initial observations of SPB behavior in the northeastern United States suggests that infestations are more diffuse than in the southeast. Southeastern infestations tend to be well defined, with an active front where the most recent attacks occur. Early indications on Long Island suggest that infestations are not forming distinct fronts; instead, tree mortality is more dispersed around the periphery of these infestations. Further, many of these spots, if left unmanaged, continue to grow the following year. Understanding infestation growth patterns in the northeast is important for assessing and developing management plans.

Literature Cited

Albany Pine Bush Preserve Commission. 2010. *Management plan and final environmental impact statement for the Albany Pine Bush Preserve*. Albany Pine Bush Preserve Commission, Albany, New York. 537 p.

Anonymous. 1972. *Forest insect and disease conditions in the United States, 1971*. US Forest Service, Forest Health Protection, Washington, DC. 65 p.

———. 1978. *Forest insect and disease conditions in the United States, 1977*. US Forest Service, Forest Health Protection, Washington, DC. 88 p.

———. 1994. *Forest insect and disease conditions in the United States, 1993*. US Forest Service, Forest Health Protection, Washington, DC. 72 p.

———. 1996. *Forest insect and disease conditions in the United States, 1995*. US Forest Service, Forest Health Protection, Washington, DC. 83 p.

———. 2003. *Forest insect and disease conditions in the United States, 2001*. US Forest Service, Forest Health Protection, Washington, DC. 112 p.

———. 2013. *Major forest insects and disease conditions in the United States, 2012*. US Forest Service, Forest Health Protection, Washington, DC. 44 p.

Ayres, M.P., and M.J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci Total Environ*. 262(3):263–286.

Barras, S., and T. Perry. 1972. Fungal symbionts in the prothoracic mycangium of *Dendroctonus frontalis* (Coleopt.: Scolytidae). *Zeitschrift für Angewandte Entomologie*. 71(1–4):95–104.

Barton, A.M., and D.J. Grenier. 2008. Dynamics of jack pine at the southern range boundary in downeast Maine. *Can J Forest Res*. 38(4):733–743.

Battisti, A., and S. Larsson. 2015. Climate change and insect pest distribution range. In *Climate Change and Insect Pests*, Björkman, C., and P. Niemelä (eds.). CAB International, Boston, MA.

Battisti, A., M. Stastny, E. Buffo, and S. Larsson. 2006. A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Global Change Biol*. 12(4):662–671.

Belanger, R.P., and B.F. Malac. 1980. *Silviculture can reduce losses from the southern pine beetle*. USDA Forest Service, Washington, DC. 17 p.

Bernard, J.M., and F.K. Seischab. 1995. Pitch pine (*Pinus rigida* Mill.) communities in northeastern New York State. *Am Midl Nat*. 134(2):294–306.

Berryman, A.A. 1986. *Forest insects: Principles and practice of population management*. Penum Press, New York.

Billings, R.F. 2011. Mechanical control of southern pine beetle infestations. P. 399–413 in *Southern Pine Beetle II*, Coulson, R.N., and K.D. Klepzig (eds.). Southern Research Station, Asheville, NC.

Billings, R.F., S.R. Clarke, V. Espino Mendoza, et al. 2004. Bark beetle outbreaks and fire: A devastating combination for Central America's pine forests. *Unasylva*. 217:15–21.

Billings, R.F., and H.A. Pase III. 1979. Spot proliferation patterns as a measure of the area-wide effectiveness of southern pine beetle control tactics. P. 86–95 in *Evaluating control tactics for the southern pine beetle*, Coster, J.E. and J.L. Searcy (eds.). USDA Forest Service Technical Bulletin. 1613 p.

Billings, R.F., and H.A.I. Pase. 1979. *A field guide for ground checking southern pine beetle spots*. US Department of Agriculture (ed.). Washington, DC. 19 p.

Billings, R.F., and W.W. Upton. 2010. A methodology for assessing annual risk of southern pine beetle outbreaks across the southern region using pheromone traps. P. 73–86 in *Advances in threat assessment and their application to forest and rangeland management*, Pye, J.M., H.M. Rauscher, Y. Sands, D.C. Lee, and J.S. Beatty (eds.). USDA Forest Service, Pacific Northwest and Southern Research Stations, Portland, OR.

Birt, A. 2011. Population dynamics of southern pine beetle in forest landscapes. P. 91–108 in *Southern Pine Beetle II*, Coulson, R.N., and K.D. Klepzig (eds.). Southern Research Station, Asheville, NC.

Borden, J.H. 1974. Aggregation pheromones in the Scolytidae. P. 135–160 in *Pheromones*, Birch, M.C. (ed.). North-Holland Publishing Company, Amsterdam, Netherlands.

Bridges, J.R., and J.C. Moser. 1983. Role of two phoretic mites in transmission of bluestain fungus, *Ceratocystis minor*. *Ecol Entomol*. 8(1):9–12.

Bried, J.T., W.A. Patterson, and N.A. Gifford. 2014. Why pine barrens restoration should favor barrens over pine. *Restor Ecol*. 22(4):442–446.

Brown, M.W., T.E. Nebeker, and C.R. Honea. 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. *South J Appl For*. 11:28–31.

Bryant, C.M., D.L. Kulhavy, R.F. Billings, and S.R. Clarke. 2006. Characteristics of bark beetle infestations in East Texas during a period of low southern pine beetle activity. *Southwest. Entomol*. 31(3):187–199.

Camors, F.B.J., and T.L. Payne. 1973. Sequence of arrival of entomophagous insects to trees infested with the southern pine beetle. *Environ Entomol*. 2:267–270.

Carroll, A.L., S.W. Taylor, J. Régnière, and L. Safranyik. 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. P. 223–232 in *Mountain Pine Beetle Symposium: Challenges and Solutions*, Shore, T.L., Brooks, J.E., and J.E. Stone (eds.). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre.

Clark, K.H., and W.A. Patterson III. 2003. Fire management plan for Montague Plain Wildlife Management Area. P. 58, *Massachusetts Department of Fisheries, Wildlife, and Environmental Law Enforcement*, Division of Fisheries and Wildlife and Natural Heritage and Endangered Species Program (ed.). Amherst, Massachusetts.

Clarke, S. 2001. Review of the operational IPM program for the southern pine beetle. *Integrated Pest Management Reviews* 6(3):293–301.

———. 2012. Implications of population phases on the integrated pest management of the southern pine beetle, *Dendroctonus frontalis*. *J. Integr. Pest. Manag.* 3(1):F1–F7.

Clarke, S.R., and R.F. Billings. 2003. Analysis of the southern pine beetle suppression program on the National Forests in Texas in the 1990s. *South J Appl For*. 27(2):122–129.

Clarke, S.R., and J.T. Nowak. 2009. *Southern pine beetle*. USDA Forest Service, Pacific Northwest Region, Portland, Oregon. 8 p.

Clarke, S.R., J.J. Riggins, and F.M. Stephen. 2016. Forest management and southern pine beetle outbreaks: A historical perspective. *Forest Sci*. 62(2):166–180.

Cook, D.B., R.H. Smith, and E.L. Stone. 1952. The natural distribution of red pine in New York. *Ecology* 33(4):500–512.

Copenheaver, C.A., A.S. White, and W.A. Patterson. 2000. Vegetation development in a southern Maine pitch pine-scrub oak barren. *J. Torrey Bot. Soc.* 127(1):19–32.

Coulson, R.N., F.P. Hain, and T.L. Payne. 1974. Radial growth characteristics and stand density of loblolly pine in relation to occurrence of southern pine beetle. *Environ Entomol*. 3(3):425–428.

Coulson, R.N., P.B. Hennier, R.O. Flamm, E.J. Rykiel, L.C. Hu, and T.L. Payne. 1983. The role of lightning in the epidemiology of the southern pine beetle. *Z Angew Entomol*. 96(2):182–193.

Coulson, R.N., D.N. Pope, J.A. Gagne, et al. 1980. Impact of foraging by *Monochamus titillator* [Col, Cerambycidae] on within-tree populations of *Dendroctonus frontalis* [Col, Scolytidae]. *Entomophaga*. 25(2):155–170.

Cryan, J.F. 1980. An introduction to the Long Island pine barrens. *The Heath Hen*. 1(1):3–16.

Cullingham, C.I., J.E.K. Cooke, S. Dang, C.S. Davis, B.J. Cooke, and D.W. Coltman. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. *Mol Ecol*. 20(10):2157–2171.

de la Giroday, H.M.C., A.L. Carroll, and B.H. Aukema. 2012. Breach of the northern Rocky Mountain geoclimatic barrier: Initiation of range expansion by the mountain pine beetle. *J. Biogeogr.* 39(6):1112–1123.

Dixon, W.N., and T.L. Payne. 1979. *Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees*. Micsc Publ 1432. College Station, TX: Texas Agricultural Experiment Station. 27 p.

Dodds, K.J., and P. de Groot. 2012. *Sirex*, surveys, and management: Challenges of having *Sirex noctilio* in North America. P. 265–286 in *The Sirex woodwasp and its fungal symbiont: Research and management of a worldwide invasive pest*, Slippers, B., M.J. Wingfield, and P. de Groot (eds.). Springer, Dordrecht.

Edinger, G.J., D.J. Evans, S. Gebauer, T.G. Howard, D.M. Hunt, and M. Olivero. 2014. *Ecological communities of New York State, 2nd ed. A revised and expanded edition of Carol Reschke's Ecological communities of New York*. New York Natural Heritage Program, New York State Department of Environmental Conservation, Albany, NY.

Engstrom, F.B., and D.H. Mann. 1991. Fire ecology of red pine (*Pinus resinosa*) in northern Vermont, USA. *Can J Forest Res*. 21(6):882–889.

Fairweather, M.L., J. McMillin, T. Rogers, D. Conklin, and B. Fitzgibbon. 2006. *Field guide to insects and diseases of Arizona and New Mexico forests*. USDA Forest Service, Southwestern Region. 271 p.

Fettig, C.J., K.D. Klepzig, R.F. Billings, et al. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *For Ecol Manage*. 238(1–3):24–53.

Finton, A.D. 1998. *Succession and plant community development in pitch pine-scrub oak barrens of the glaciated northeast United States*. M.S., University of Massachusetts, Amherst, Amherst, Massachusetts.

Fitzgerald, J.W., R.N. Coulson, P.E. Pulley, et al. 1994. Suppression tactics for *Dendroctonus frontalis* Zimmerman (Coleoptera, Scolytidae): An examination of the occurrence of infestations adjacent to treatment sites. *J Econ Entomol*. 87(2):417–425.

Gara, R.I., and J.E. Coster. 1968. Studies on attack behavior of southern pine beetle. III. Sequence of tree infestation within stands. *Contrib Boyce Thompson Inst*. 24(4):77–86.

Gawler, S., and A. Cutko. 2010. *Natural landscapes of Maine: A guide to natural communities and ecosystems*. Maine Natural Areas Program, Maine Department of Conservation, Augusta, Maine.

Gluck, E. 2015. Connecticut's 13 emperiled ecosystems: Pitch pine-scrub oak barrens. P. 8–11 in *Connecticut Woodlands*. Connecticut Forest & Park Association.

Goyer, R.A., and C.K. Finger. 1980. Relative abundance and seasonal distribution of the major hymenopterous parasites of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera, Scolytidae), on loblolly pine. *Environ Entomol*. 9(1):97–100.

Goyer, R.A., G.J. Lenhard, T.E. Nebeker, and L.D. Jarrard. 1980. *How to identify common insect associates of the southern pine beetle*. US Department of Agriculture, Combined Forest Pest Research and Development Program, Washington, DC.

Greller, A.M. 1977. Classification of mature forests on Long Island, New York. *Bull. Torrey Bot. Club*. 104(4):376–382.

Haack, R.A., and T.M. Poland. 2001. Evolving management strategies for a recently discovered exotic forest pest: The pine shoot beetle, *Tomicus piniperda* (Coleoptera). *Biol Invasions*. 3:307–322.

Haberkern, K.E., and K.F. Raffa. 2003. Phloeophagous and predaceous insects responding to synthetic pheromones of bark beetles inhabiting white spruce stands in the Great Lakes Region. *J Chem Ecol*. 29(7):1651–1663.

Hain, F.P. 1980. Sampling and predicting population trends. P. 107–135 in *The Southern Pine Beetle*, Thatcher, R.C., J.L. Searcy, J.E. Coster, and G.D. Hertel (eds.). USDA Forest Service.

Hain, F.P., A.J. Duehl, M.J. Gardner, and T.L. Payne. 2011. Natural history of the southern pine beetle. P. 13–24 in *Southern Pine Beetle II*, Coulson, R.N., and K.D. Klepzig (eds.). Southern Research Station, Asheville, NC.

Hedden, R.L. 1978. The need for intensive forest management to reduce southern pine beetle activity in East Texas. *South J Appl For*. 2(1):19–22.

Hertel, G.D., and H.N. Wallace. 1983. *Effect of cut-and-leave and cut-and-top control treatments on within-tree southern pine beetle populations*. USDA Forest Service Southern Forest Experiment Station, New Orleans, LA. 4 p.

Hicks, R.R., J.E. Coster, and G.N. Mason. 1987. Forest insect hazard rating—Applying a little understood management tool using the southern pine beetle and the gypsy moth. *J For*. 85(10):20–26.

Hicks, R.R. Jr., J.E. Howard, K.G. Watterston, and J.E. Coster. 1979. Rating forest stand susceptibility to southern pine beetle in East Texas. *For Ecol Manage*. 2:269–283.

Hodges, J.D., and R.C. Thatcher. 1976. Southern pine beetle survival in trees felled by the cut and top-cut and leave method. *Southern Forest Experiment Station Research Note*. SO-219:4.

Hofstetter, R.W., J.T. Cronin, K.D. Klepzig, J.C. Moser, and M.P. Ayres. 2006. Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. *Oecologia*. 147(4):679–691.

Hopkins, A.D. 1899. *Report on investigations to determine the cause of unhealthy conditions of the spruce and pine from 1880–1893. Bulletin 56*. West Virginia Agricultural Experiment Station, Morgantown, West Virginia. 264 p.

———. 1909. *Practical information on the scolytid beetles of North American forests. 1. Bark beetles of the genus Dendroctonus*. US Department of Agriculture, Bureau of Entomology, Government Printing Office, Washington, DC.

Horton, R., G. Yohe, W. Easterling, et al. 2014. Ch. 16: Northeast. P. 371–395 in *Climate Change Impacts in the United States: The Third National Climate Assessment*. Melillo, J.M., T.C. Richmond, and G.W. Yohe (eds.). Global Change Research Program.

Howard, L.F., T.D. Lee, and R.T. Eckert. 2011. Forest community composition and dynamics of the Ossipee Pine Barrens, New Hampshire. *J. Torrey Bot. Soc.* 138(4):434–452.

Jepsen, J.U., M. Biuw, R.A. Ims, et al. 2013. Ecosystem impacts of a range expanding forest defoliator at the forest-tundra ecotone. *Ecosystems* 16(4):561–575.

Jepsen, J.U., S.B. Hagen, R.A. Ims, and N.G. Yoccoz. 2008. Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: Evidence of a recent outbreak range expansion. *J Anim Ecol*. 77(2):257–264.

Jordan, M.J., W.A. Patterson, and A.G. Windisch. 2003. Conceptual ecological models for the Long Island pitch

pine barrens: implications for managing rare plant communities. *For Ecol Manage*. 185(1–2):151–168.
Knull, J.W. 1934. The southern pine beetle in Pennsylvania. *J Econ Entomol*. 27:716–720.
Krombein, K.V., P.D. Hurd Jr., D.R. Smith, and B.D. Burks. 1979. *Catalog of Hymenoptera in America North of Mexico: Volume 1, Symphyta and Apocrita (Parasitica)*. Smithsonian Institution Press, Washington, DC.
Kurczewski, F.E. 1999. Historic and prehistoric changes in the Rome, New York pine barrens. *Northeast Nat*. 6(4):327–340.
Kurczewski, F.E., and H.F. Boyle. 2000. Historical changes in the pine barrens of central Suffolk County, New York. *Northeast Nat*. 7(2):95–112.
Lesk, C., E. Coffel, A.W. Damato, K. Dodds, and R. Horton. 2017. Threats to North American forests from southern pine beetle with warming winters. *Nature Clim Change*, advance online publication.
Logan, J.A., W.W. Macfarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecol. Appl.* 20(4):895–902.
Logan, J.A., and J.A. Powell. 2009. Ecological consequences of forest-insect disturbance altered by climate change. P. 98–109 in *Climate warming in western North America*, Wagner, F.H. (ed.). University of Utah Press, Salt Lake City, Utah.
Lovelady, C.N., P.E. Pulley, R.N. Coulson, and R.O. Flamm. 1991. Relation of lightning to herbivory by the southern pine bark beetle guild (Coleoptera, Scolytidae). *Environ Entomol*. 20(5):1279–1284.
Mason, G.N., P.L. Lorio Jr., R.P. Belanger, and W.A. Nettleton. 1985. *Rating the susceptibility of stands to southern pine beetle attack*. US Department of Agriculture, Forest Service Cooperative State Research Service, Washington, DC. 31 p.
Milne, B.T. 1985. Upland vegetational gradients and post-fire succession in the Albany Pine Bush, New York. *Bull. Torrey Bot. Club*. 112(1):21–34.
Mitchell, R.G., R.H. Waring, and G.B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Sci.* 29(1):204–211.
Moore, G.E. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. *Environ Entomol*. 1:58–65.
Moser, J.C. 1985. Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. *Trans Br Mycol Soc*. 84(Jun):750–753.
Motzkin, G., W.A. Patterson, and D.R. Foster. 1999. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. *Ecosystems* 2(3):255–273.
Nebeker, T.E., and J.D. Hodges. 1983. Influence of forestry practices on host-susceptibility to bark beetles. *J Appl Entomol*. 96:194–208.
Neuvonen, S., P. Niemelä, and T. Virtanen. 1999. Climatic change and insect outbreaks in boreal forests: The role of winter temperatures. *Ecol Bull.* (47):63–67.
Niemela, P., F.S. Chapin, K. Danell, and J.P. Bryant. 2001. Herbivory-mediated responses of selected boreal forests to climatic change. *Clim Change*. 48(2–3):427–440.
Nowak, J., C. Asaro, K. Klepzig, and R. Billings. 2008. The southern pine beetle prevention initiative: Working for healthier forests. *J For*. 106(5):261–267.
Nowak, J.T., J.R. Meeker, D.R. Coyle, C.A. Steiner, and C. Brownie. 2015. Southern pine beetle infestations in relation to forest stand conditions, previous thinning, and prescribed burning: Evaluation of the southern pine beetle prevention program. *J For*. 113(5):454–462.
Olsvig, L.S., J.F. Cryan, and R.H. Whittaker. 1998. Vegetational gradients of the pine plains and barrens of Long Island, New York. P. 265–282 in *Pine Barrens: Ecosystem and landscape*. Forman, R.T.T. (ed.). Rutgers University Press, New Brunswick, New Jersey.
Overgaard, N.A. 1968. Insects associated with the southern pine beetle in Texas, Louisiana, and Mississippi. *J Econ Entomol*. 61:1197–1201.
Payne, T.L. 1980. Life history and habits. in *The Southern Pine Beetle*, Thatcher, R.C., J.L. Searcy, J.E. Coster, and G.D. Hertel (eds.). US Department of Agriculture, Expanded Southern Pine Beetle Research and Application Program.
Pope, D.N., R.N. Coulson, W.S. Fargo, J.A. Gagne, and C.W. Kelly. 1980. The allocation process and between-tree survival probabilities in *Dendroctonus frontalis* infestations. *Res Popul Ecol*. 22(2):197–210.
Price, T.S., C. Doggett, J.M. Pye, and B. Smith. 2006. *A history of southern pine beetle outbreaks in the southeastern United States*. Georgia Forestry Commission, Macon, GA. 65 p.
Pureswaran, D.S., L. De Grandpre, D. Pare, et al. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. *Ecology*. 96(6):1480–1491.
Raffa, K.F., E.N. Powell, and P.A. Townsend. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *P Natl Acad Sci USA*. 110(6):2193–2198.
Regniere, J., R. St-Amant, and P. Duval. 2012. Predicting insect distributions under climate change from physiological responses: Spruce budworm as an example. *Biol. Invasions.* 14(8):1571–1586.
Roberts, M.A. 1994. Aerial detection surveys in the Northeastern Area. P. 15–16 in *Aerial Pest Detection and Monitoring Workshop*. McConnell, T.J. (ed.). USDA Forest Service, Northern Region Forest Pest Management.
Sambaraju, K.R., A.L. Carroll, J. Zhu, K. Stahl, R.D. Moore, and B.H. Aukema. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography* 35(3):211–223.
Schmitz, R.F. 1978. *Taxonomy and bionomics of the North American species of Thanasimus Latreille (Coleoptera: Cleridae)*. Ph.D., University of Idaho, Moscow, ID. 86 p.
Schowalter, T.D., and P. Turchin. 1993. Southern pine beetle infestation development: Interaction between pine and hardwood basal areas. *Forest Sci*. 39(2):201–210.
Seischab, F.K., and J.M. Bernard. 1991. Pitch pine (*Pinus rigida* Mill.) communities in central and western New York. *Bull. Torrey Bot. Club*. 118(4):412–423.
———. 1996. Pitch pine (*Pinus rigida* Mill.) communities in the Hudson Valley region of New York. *Am Midl Nat*. 136(1):42–56.
Sømme, L. 1982. Supercooling and winter survival in terrestrial arthropods. *Comp. Biochem. Physiol. A.* 73(4):519–543.
Sperduto, D.D., and W.F. Nichols. 2011. *Natural communities of New Hampshire*, 2nd ed. New Hampshire Natural Heritage Bureau, Concord, NH.
St. George, R.A., and J.A. Beal. 1929. *The southern pine beetle: A serious enemy of pines in the south*. USDA Farmer's Bulletin, Washington, DC. 21 p.
Stergas, R.L., and K.B. Adams. 1989. Jack pine barrens in northeastern New York: Postfire macronutrient concentrations, heat content, and understory biomass. *Can J Forest Res*. 19(7):904–910.
Sullivan, B.T. 2011. Southern pine beetle behavior and semiochemistry. P. 25–50 in *Southern Pine Beetle II*, Coulson, R.N., and K.D. Klepzig (eds.). Southern Research Station, Asheville, NC.
Sullivan, B.T., and K. Mori. 2009. Spatial displacement of release point can enhance activity of an attractant pheromone synergist of a bark beetle. *J Chem Ecol*. 35:1222–1233.
Swain, K.M., and M.C. Remion. 1981. *Direct control methods for the southern pine beetle*. US Department of Agriculture, Washington, DC. 15 p.
Swain, P.C., and J.B. Kearsley. 2001. *Classification of the natural communities of Massachusetts*. Natural Heritage & Endangered Species Program, Massachusetts Division of Fisheries and Wildlife, Westborough, MA.
Thatcher, R.C., and L.S. Pickard. 1966. The clerid beetle, *Thanasimus dubius*, a predator of the southern pine beetle. *J Econ Entomol*. 59(4):955–957.
Thistle, H.W., H. Peterson, G. Allwine, et al. 2004. Surrogate pheromone plumes in three forest trunk spaces: Composite statistics and case studies. *Forest Sci*. 50(5): 610–625.
Trân, J.K., T. Ylioja, R.F. Billings, J. Régnière, and M.P. Ayres. 2007. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecological Applications* 17(3):882–899.

Turchin, P., and W.T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecological Applications* 3:187–198.
Ungerer, M.J., M.P. Ayres, and M.J. Lombardero. 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *J. Biogeogr.* 26(6):1133–1145.
Vanhanen, H., T.O. Veleli, S. Paivinen, S. Kellomaki, and P. Niemela. 2007. Climate change and range shifts in two insect defoliators: Gypsy moth and nun moth—A model study. *Silva Fennica*. 41(4):621–638.
Weed, A.S., M.P. Ayres, and J.A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecol Monogr*. 83(4):441–470.
Wilent, S. 2005. Mountain pine beetle threaten Canadian, U.S. forests. *The Forestry Source*. 10(5):1.