Northward expansion of southern pine beetle generates significant alterations to forest structure and composition of globally rare *Pinus rigida* forests

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ABSTRACT

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman), a native insect that has historically affected pine (*Pinus* spp.) ecosystems in the southeastern U.S., has recently expanded northward causing extensive tree mortality in pitch pine (*P. rigida*) and pitch pine-oak (*Quercus* spp.) forests of eastern Long Island, NY. Given the historic lack of SPB within this region, little is known regarding its potential impacts. This study examined the immediate effects of SPB-induced tree mortality and management (i.e., cut-and leave suppression) on the structure and composition of affected forest communities to inform management recommendations and projections of future forest conditions. Overstory pine basal area declined significantly following SPB infestation and management (67–100% mortality), although management partly mitigated these effects. There was no immediate impact of SPB or management on seedling and sapling density or composition, with hardwood species making up the majority of this layer and pine representing < 6% of stems regardless of mortality agent. Pitch pine was less likely to be browsed by ungulates than white oak and scarlet oak. SPB infestation significantly increased snag basal area, whereas downed woody debris volumes were greatest following management. Understory community composition in pitch pine stands that had SPB or were managed had greater understory plant diversity largely through a higher abundance of disturbance-adapted species. There was less between-site variation in understory species assemblages in pine-oak forests experiencing pitch pine mortality and an increase in regeneration of pitch pine and scarlet oak in these areas. Collectively, the short-term results suggest SPB could functionally eliminate pitch pine from infested stands in the absence of additional management, and that management in pine-oak stands may exacerbate this trend, leading to increasing dominance of hardwoods species in pine barren communities. Based on our results, fuels reduction treatments combined with site-specific restoration of barrens structure and composition may be useful in maintaining stands with lower fire hazard and greater resilience to this new threat.

1. Introduction

Climate change has been associated with expansion of forest insects into areas with naïve hosts that have not adapted to this disturbance, as well as marginal habitats that rarely experienced damage, resulting in greater impacts relative to those observed in historically affected forests (Carroll et al., 2003; Hickling et al., 2006). This is especially worrisome where insects expand into rare or threatened ecosystems with geographically limited ranges, such as mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in high elevation five-needle pine forests of western North America and southern pine beetle (*Dendroctonus frontalis* Zimmermann; SPB) threatening new areas of pitch pine (*Pinus rigida*) barrens in the northeastern U.S. (Bentz et al., 2011; Weed et al., 2013; Lesk et al., 2017; Dodds et al., 2018). These novel dynamics represent significant challenges to forest managers given the lack of knowledge on their ecological impacts and associated management strategies for sustaining core ecosystem functions following outbreaks.

The genus *Dendroctonus* has several North American species that can cause widespread tree mortality in coniferous forests. One of the most damaging, SPB, is a primary tree killer associated with hard, or 2–3 needle, pine (*Pinus* spp.) mortality in the southeastern U.S. Outbreaks in the southeastern U.S. historically caused dramatic financial losses,

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primarily due to market flooding of salvaged forest products (Pye et al., 2011). Southern pine beetle-caused tree mortality often results in dramatic changes in forest composition (Coleman et al., 2008a), nutrient cycling, understory species composition, and wildlife habitat values (Leuschner et al., 1976; Maine et al., 1980; Kulhavy and Ross, 1988). Outbreaks can rapidly kill large numbers of trees over vast areas and alter long-term management plans.

For more than a decade, SPB has expanded its range into the northeastern United States and is now found further north than previously recorded (Dodds et al., 2018). This range expansion has resulted in extensive pitch pine mortality due to epidemic SPB populations in New Jersey beginning in 2001 (Trần et al., 2007) and more recently on Long Island, NY, where it was first detected in 2014 (Lesk et al., 2017; Dodds et al., 2018). Further range expansion inland and to the north through other forested areas with suitable host species may be expected in future years (Ungerer et al., 1999). In particular, projections of SPB survival under future climate change scenarios (Lesk et al., 2017) suggest winter temperatures by 2040 will be warm enough to allow SPB to exist across the entire northeastern United States, creating a need for improved understanding of potential impacts of SPB on pitch pine forests across this region.

The Central Pine Barrens region of Long Island, NY, where SPB has been found, is one of the largest contiguous extant pine barrens in the northeast and is representative of other pitch pine forests across the broader northeast in terms of both ecological conditions (DeGraaf et al., 2006) and ownership patterns (U.S. Census Bureau, 2009; King et al., 2011). Pitch pine barrens are a globally unique ecosystem that serve as habitat for several rare and endangered species, such as the pine barren tree frog (*Hyla andersonii)* (NJFAC, 2006) and Karner blue butterfly (*Lycaeides melissa samuelis*) (USFWS, 1997). Pine barrens have historically been perpetuated by disturbance, primarily frequent fires (Little, 1979; NJFAC, 2006) that may have occurred on a return interval as frequent as 20 years or less (Forman and Boerner, 1981; Lorimer and White, 2003). Fire is an important part of the regeneration ecology of pitch pine and it drives local levels of serotiny (Givnish, 1981), while creating the mineral soil exposure and direct sun necessary for regeneration establishment (Burns and Honkala, 1990). However, wildfire suppression and land-use changes in the last century (Dombeck et al., 2004; Troy and Kennedy, 2007) have allowed many barrens to be converted (Jordan et al., 2003), succeeding often into mature, closed canopy forests (Trani et al., 2001) dominated by more shade-tolerant species (Little, 1979; Lorimer and White, 2003; Nowacki and Abrams, 2008) such as oak species (*Quercus* spp.) and red maple (*Acer rubrum*). Stands that contain pitch pine are often overstocked and in conditions conducive to SPB outbreak.

Populations of SPB are considered pulse eruptive (Berryman, 1986), with endemic populations colonizing weakened trees (Hain et al., 2011) and epidemic (=outbreak) populations growing rapidly and killing healthy trees. Through mass attack guided by pheromones, SPB can overwhelm pine host defenses and kill healthy trees. The beetle does particularly well in overstocked stands where trees are stressed (Coulson et al., 1974). Multiple generations per year, as many as nine in some portions of its traditional range (Hain et al., 2011), and likely nearer to three in the northeast based off of other northern phloem-inhabiting bark beetles (Schenk and Benjamin, 1969), allow for almost constant growth in terms of trees killed in an infestation. Infestations start by impacting only a few trees and can quickly build to thousands killed over a single growing season. Emerging beetles from successive generations disperse to adjacent trees and expand the infestation away from previously infested trees.

SPB impacts to forest structure and stand dynamics have been extensively studied in the southeastern U.S. (Duncan and Linhoss, 2005; Coleman et al., 2008a, 2008b) and more recently in New Jersey (Clark et al., 2017). In the overstory, southeastern stands that were affected by SPB had lower levels of overstory pine, with future stand development predicted to move from pine to mixed hardwood dominance, due in

large part to the presence of more shade-tolerant hardwood species in the understories of these stands (Coleman et al., 2008a). Stands that had been infested by SPB in North Carolina had lower basal areas of pine and some variation in pine species composition (Knebel and Wentworth, 2007). In New Jersey, an average of 95% of pine basal area was killed in infested stands (Clark et al., 2017). Understory communities can also be affected, with lower abundance of regeneration reported in loblolly pine stands (Coleman et al., 2008a), but a more complex relationship found for Virginia pine (*Pinus virginiana*) that involved gap size and soil exposure (Duncan and Linhoss, 2005). Pine basal area of saplings were also very low in areas where SPB had occurred and were treated in New Jersey (Clark et al., 2017).

Little information is available to determine how SPB will affect pitch pine forests in the northeastern US where many stands have gone unmanaged and fire has been excluded for long periods of time. These forests have been free of aggressive bark beetles and it is unknown how the introduction of SPB will alter these systems. In its natural condition, pitch pine barrens in this region were subject to frequent fires (Olsvig et al., 1998), but the current suite of stressors affecting these forests are different and include urbanization, a long history of fire suppression, an influx of invasives, and elevated levels of herbivory, generating the potential for novel and unexpected dynamics following pitch pine mortality. Fire suppression in pitch pine can lead to overstocked stands with high basal area resulting in conditions at particular risk to SPB infestation (Coulson et al., 1974). Lack of fire and soil disturbance observed in these forests provides little opportunity for regeneration of pitch pine, a situation noted previously for the species (Groeschl et al., 1993; Jordan et al., 2003).

Various tools have been developed to assist natural resource managers who are concerned about local or regional SPB populations. Preemptive stand treatments are commonly prescribed to reduce the susceptibility of at risk stands (Nowak et al., 2015), and direct suppression can be undertaken in actively infested stands (Billings, 2011). Most direct suppression for limiting SPB-caused mortality in infested stands has taken place in the southeastern U.S., but these methods are now being implemented in infested northeastern U.S. pitch pine forests as well. It is unclear how these suppression treatments, combined with SPB activity in a stand, influence residual forest structure in northeastern pitch pine forests. The two suppression methods, cut-and-leave (CAL) and cut-and-remove (CAR), involve felling infested and uninfested living buffer trees to suppress active infestations and have a history of success (Swain and Remion, 1981). All cut trees are left on site during CAL treatments and removed during CAR treatments. While CAL treatments may kill some brood in the downed trees (Hodges and Thatcher, 1976), the primary mechanism stopping spot expansion is the disruption of the aggregation pheromones that guide emerging beetles to adjacent trees to attack. During summer months, SPB has low fat reserves (Coppedge et al., 1994) that restrict dispersal ability and consequently beetles emerging from cut trees on the ground are unlikely to disperse far and find or initiate new infestations.

Southern pine beetle is one of the most aggressive tree killing bark beetles in North America and represents a significant new disturbance in globally rare inland and coastal pitch pine forests of the northeastern United States. The goal of this study was to evaluate the immediate effects of SPB-caused forest disturbances and associated management on stand structure and composition in the Central Pine Barrens of New York. Specifically, we aimed to identify SPB impacts in infested, managed, and control stands including (1) overstory forest structure and composition, (2) regeneration patterns, including associated deer browse impacts and understory species composition within affected forests, and (3) standing and downed woody debris.

2. Materials and methods

2.1. Study area and design

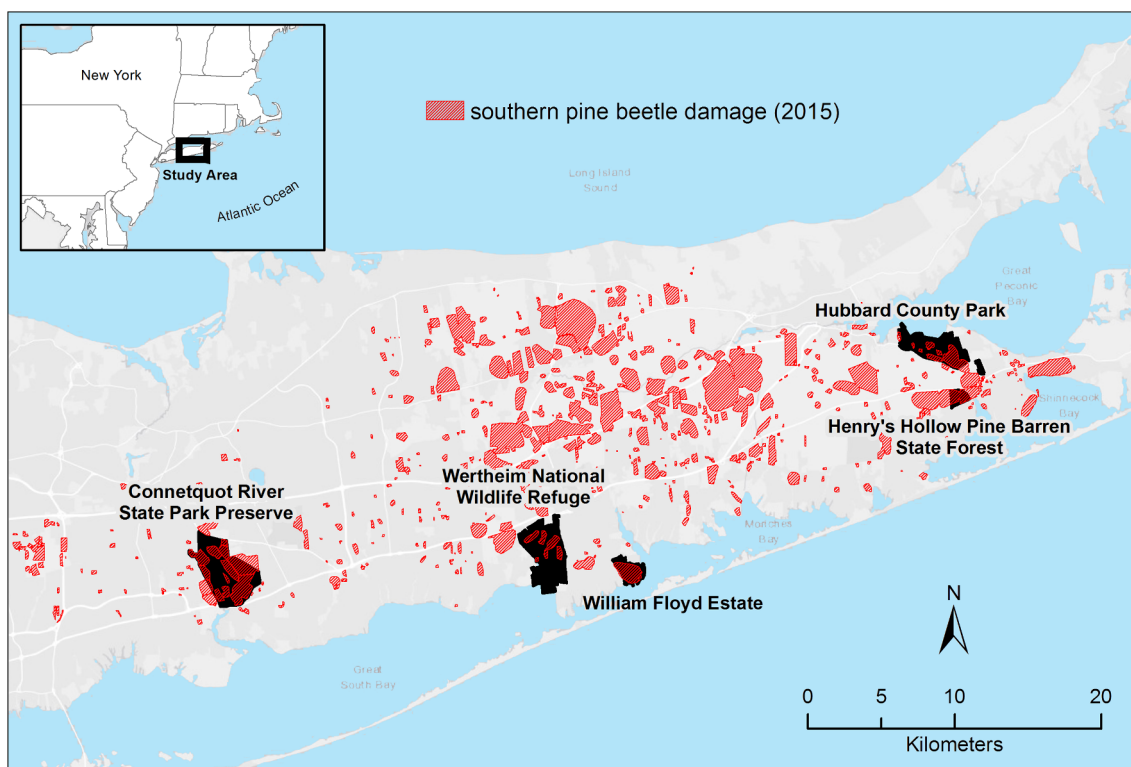Study sites were selected based on discussions with New York State

Fig. 1. Study area on Long Island, New York. Southern pine beetle damage was mapped during aerial insect and disease surveys, with suspect areas ground surveyed to confirm presence of the beetle. Properties containing study sites are shaded black.

Department of Environmental Conservation staff members and other local stakeholders, aerial detection surveys from 2015 that recorded the presence and size of SPB infestations on Long Island, and subsequent ground-truthing efforts of these infestations. From the available sites, the infestations that covered the most area and supported multiple generations of SPB were selected in order to assess the potential effects of SPB at the stand level. Twenty-six stands from five sites were ultimately selected across the south shore of Suffolk County (Fig. 1) and were evenly distributed between the two forest types of interest: (1) pitch pine-dominated (n = 13), and (2) mixed pitch pine-oak (n = 13). Stands were selected to represent three possible treatments within each cover type: (1) stands subject to SPB infestation and subsequent cut-and-leave management (n = 10, hereafter referred to as "managed"), (2) stands infested by SPB with no subsequent management (n = 10, hereafter referred to as "unmanaged"), and (3) stands with no SPB or management impacts (n = 6, hereafter referred to as "control"). Care was taken to ensure that control stands had similar stand structure and composition to infested stands (i.e., managed and unmanaged treatments) prior to SPB infestation. Whenever possible, control stands were selected from forests adjacent to managed or unmanaged treatments that were not impacted by SPB.

2.2. Field methods

In order to assess the impacts of SPB and management on forest structure and composition, three to four 400 m² circular plots were located in each stand. Plots were established following random distances and azimuths through representative portions of each stand with a minimum distance of 40 m between plot centers. Plots in infested stands (i.e., managed and unmanaged stands) were repositioned as necessary in order to contain at least one SPB host tree, as we sought to accurately describe the effects of SPB-induced mortality on forest conditions. Species, diameter at breast height (DBH; 1.37 m), and canopy class were recorded for each tree and snag (DBH ≥ 7.6 cm) centrally rooted within the 400 m² plot.

All pines were investigated for signs of SPB, including serpentine galleries, pitch tubes, and emergence holes (Clarke and Novak, 2009). Tree saplings (2.5–7.5 cm DBH) and seedlings (< 2.5 cm DBH) were tallied by species in nested 25 and 10 m² plots, respectively, located 5.5 m from the overstory plot center at azimuths of 120° and 240°. Seedlings with clipped or torn leaders indicative of mammalian browsing were tallied separately by species to assess the level of browse damage. Percent cover of understory vegetation was tallied by species in nested 1 m² plots, located 5 m and 10 m from the overstory plot center at azimuths of 0°, 120°, and 240°.

Downed coarse woody debris (CWD) and fine woody debris (FWD) were sampled using the line-intercept method to assess the volumes of each within treatments. Three 20 m CWD transects originated from plot center at magnetic bearings of 0°, 120°, and 240°. The diameter at intersection, species, and decay class was recorded for all CWD (≥ 7.6 cm diameter and ≥ 1 m long) intersected by a transect (Brown, 1974). Standing dead trees leaning at more than 45° from vertical were considered downed CWD. Fine woody debris (< 7.6 cm diameter) of size classes < 0.6 cm, 0.7–2.4 cm, and 2.5–7.5 cm was tallied along the outer 1 m, 2 m, and 4 m, respectively, of the 0° CWD transect.

2.3. Statistical analyses

The influence of SPB, management, forest cover type, and their interaction on overstory density and species composition, sapling and seedling densities, deer browse likelihood, downed woody debris (DWD) volumes, and snag basal area were examined using mixed model analysis of variance (ANOVA) through generalized linear models (GLM) in R (R Team, 2015). Overstory and understory data were averaged by site. Negative binomial distributions were specified for overstory and sapling data to correct for non-normal, right-skewed distributions. Presence or absence of seedling browse ("1" where browsing occurred, "0" where browsing was not observed) was analyzed using a generalized linear model (GLM) with a binomial distribution specified. This

model was compared to a null model using the "lmtest" package (Zeileis and Hothorn, 2002) to test for an overall effect of species on browse likelihood. The model was then used to test the effects of cover type, treatment, and species composition (pitch pine or pine-oak) on browse likelihood. Downed woody debris data was rank-transformed to partly correct for unequal variances between treatment combinations and was analyzed using a GLM with a normal distribution assumed (no distribution specified). In cases where a significant main effect was detected, post-hoc Tukey's honestly significant difference (Tukey HSD) pairwise analysis was used to identify differences between individual treatment combinations. An alpha level of 0.05 was used for all tests.

In order to identify the effects of SPB and management on understory plant community composition, percent cover data was examined for each cover type through multivariate statistical analyses. First, gradients in understory composition across treatments were evaluated using non-metric multidimensional scaling (NMS). A primary matrix of species based on percent cover was constructed for each cover type and species occurring in < 1/3 of stands were removed to limit the influence of rare species on results. A general relativization was used to equalize the contribution of the remaining species to the ordination results. The "slow and thorough" autopilot mode for the NMS analysis was performed to determine the appropriate number of axes containing the solution with the lowest amount of stress (the difference between the original rank order of scores and those from each randomly regrouped dataset), which was selected as the appropriate dimensionality. The resulting NMS ordinations were graphed to show the two axes explaining the highest percentage of variance in the data and resulting axis scores were compared to species percent cover values using Kendall's tau in R to identify significant correlations between axes and species abundance. Second, multi-response permutation procedures (MRPP) were run using Sørensen's index to assess the significance of effects of SPB and management on species composition. MRPP tests an average within-group distance for each "group" of response data (treatment in this study) against many weighted average within-group distances calculated using random permutations of response data. Significant p-values (< 0.05) demonstrate that groups significantly influence the response variable in comparison to random chance, so that groups are more similar than we would expect if no effect was present (Peck, 2010). Finally, indicator species analysis (ISA) was used to identify species particularly associated with each treatment based on Dufrêne and Legendre (1997). Indicator species analysis measures the level to which a given species is associated with each treatment based on frequency and abundance and compares the resulting indicator values to those of many iterations of randomly regrouped data. Indicator species analysis then calculates the proportion of iterations resulting in indicator values greater than or equal to the observed values. All multivariate analyses were run using PC-ORD version 6 (McCune and Mefford, 2011).

3. Results

Post-treatment pitch pine basal area (BA) was directly impacted by SPB and management (Table 1). Pitch pine mortality resulting from SPB and management varied significantly by forest cover type ($P = 0.03$) and treatment type ($P < 0.05$), but not their interaction ($P > 0.05$) and ranged from losses of $0.1 \pm 0.1\,\mathrm{m^2/ha}$ to $14.8 \pm 3.4\,\mathrm{m^2/ha}$. Mortality of pitch pine was significantly higher in unmanaged stands than uninfested controls ($P < 0.0001$) and significantly lower in managed stands than those that were unmanaged ($P = 0.033$). Mortality was also significantly greater in pitch pine forests than in pine-oak forests ($P = 0.03$).

The diameter distributions of the average forest in each treatment category demonstrates a marked loss of pitch pine from SPB-infested (both unmanaged and managed) pine forests (Fig. 2). This resulted in a narrow, reverse-J-shaped distribution in aftermath forests, decreased overall stand densities, and removed a majority of pitch pines from the

Table 1
Basal area (mean $\pm$ SE, $\mathrm{m^2\,ha^{-1}}$) change of pitch pine by treatment combination. Values with different letters were significantly different within a cover type based on Tukey's HSD alpha = 0.05. "Unmanaged" stands were impacted by southern pine-beetle (SPB) but received no suppression treatments; "Managed" stands were impacted by SPB and subsequently treated with cut-and-leave suppression strategies; "Control" stands had no SPB impact or associated treatments.

Variable	N	Change in pitch pine basal area
Treatment		
Control	6	-0.4 ± 0.1[a]
Unmanaged	10	-12.6 ± 1.1[c]
Managed	10	-10.5 ± 2.3[b]
Cover type		
Pine	13	-10.8 ± 2.2[a]
Pine-oak	13	-7.1 ± 1.5[b]

overstory, which also dominated the largest size-classes. In pine-oak forests all pitch pine is removed from unmanaged sites while a small component in managed sites remain, representing many different size classes. Basal area for all species in unmanaged and managed stands was significantly lower than controls ($P < 0.0001$) after SPB infestations, but not significantly different from each other (Fig. 3). In contrast, there was no significant difference in basal area between treatments in pine-oak forests following infestation (Fig. 3). Similar patterns were observed for total stem density in stands after SPB infestations with unmanaged and managed stands having significantly lower numbers of trees per hectare than control pine forests ($P = 0.017$ and 0.027, respectively), but no differences after infestation in pine-oak stands (Fig. 3). Quadratic mean diameter (QMD) across species was the only stand condition that was significantly different in pre-infestation pine stands with control stands having greater QMD than unmanaged and managed stands ($P < 0.0001$). Following SPB infestation, there was no difference in QMD between treatments in pine stands (Fig. 3). There was no pre-infestation or post-infestation differences in QMD for pine-oak stands (Fig. 3).

Total seedling and sapling densities were not significantly affected by cover type, treatment, or their interaction ($P > 0.05$), both when tested as a group and when each species was tested individually. Pitch pine, which made up 5.8% of seedlings and 5.6% of saplings counted across all stands, was less frequently tallied in the understory of pine-oak stands than under pitch pine cover. Overall seedling and sapling densities were lowest in managed pitch pine forests (5272 ± 1859 and 169 ± 50 stems/ha for seedlings and saplings, respectively), where pitch pine seedlings occurred at the highest densities (1678 ± 1227 stems/ha). No pitch pine saplings were observed in pine-oak stands (Fig. 4).

The probability of a seedling having browse damage (found on 34% of all species) was partly a function of species, based on a null model comparison ($P = 0.001$). According to GLM results, pitch pine was significantly less likely to be browsed than white oak (*Quercus alba*) ($P = 0.004$), scarlet oak ($P = 0.001$), black gum (*Nyssa sylvatica*) ($P = 0.030$), scrub oak (*Q. ilicifolia*) ($P > 0.006$), and other hardwood species with < 10 occurrences ($P = 0.029$), but was not less likely to be browsed than red maple (*Acer rubrum*) ($P = 0.102$) (Fig. 5). However, only scarlet oak and white oak were more likely to be browsed than pitch pine ($P = 0.017$ and $P = 0.049$), according to post-hoc Tukey's pairwise comparison. Likelihood of browse impact was significantly higher in pine-oak managed stands versus pine-oak controls (80 ± 6.9 vs. $37.5 \pm 12.5\%$ for managed and control, respectively; $P = 0.02$), whereas management treatment did not affect overall browse likelihood in pitch pine stands ($P > 0.05$). The likelihood of browse damage was not influenced by treatment combination for pitch pine or hardwood species, although the low densities of pitch pine seedlings may have influenced these results. There was a significantly lower likelihood of browse among pines in pine-oak forests
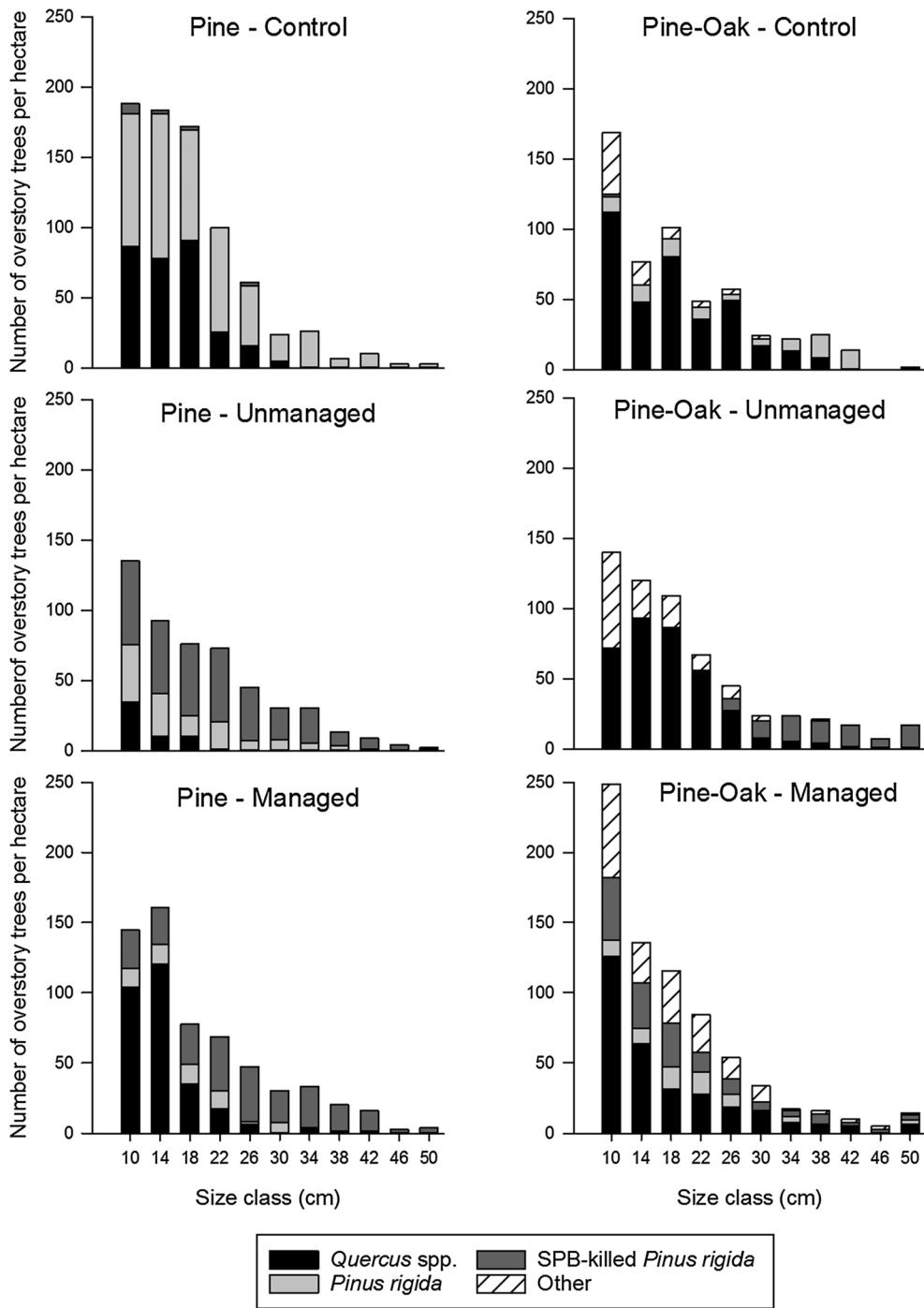
Fig. 2. Size class distributions of trees in study sites, by treatment. Distributions represent the treatment average. See Table 1 for treatment definitions.

(22 ± 15%) than hardwoods in pine-oak (78 ± 6%; $P = 0.002$) and pitch pine (73 ± 7%; $P = 0.01$) forests. Browse likelihood of pitch pine seedlings in managed stands (20 ± 20%) was significantly lower than that of hardwood species in both managed (77 ± 6%; $P < 0.05$) and unmanaged stands (82 ± 7%; $P = 0.03$).

Downed woody debris volume was influenced by treatment, cover type, and their interaction ($P < 0.05$, see Figs. 6 and 7). DWD volume was not significantly influenced by treatment in pine-oak forests ($P = 0.28$), but was significantly increased by management ($P < 0.001$) in pitch pine forests relative to pitch pine controls. DWD volume was also significantly higher in managed pitch pine versus unmanaged pitch pine stands ($P < 0.001$). Basal area of snags was affected by treatment and was significantly higher in unmanaged, SPB-impacted stands relative to control and managed stands

($P < 0.001$). There was no difference in snag basal area between control and managed areas for pine-oak forests, whereas pitch pine forest control stands had significantly higher snag basal areas than managed stands in this same forest type.

Non-metric multidimensional scaling (NMS) analysis produced a three-axis solution for pine-oak forests ($P = 0.04$, final stress = 8.08, instability = 0) and accounted for 78% of the variation in understory data (Fig. 8). Stress values for this solution (< 20) indicate that the resulting three-axis solution adequately reflected the ecological distance among samples (Clarke, 1993). The two axes explaining the greatest amount of variation were Axes 1 and 2. The gradient represented by Axis 1 was not significantly associated with any species. Axis 2 had a negative correlation with scarlet oak ("SO", $\tau = -0.53$)
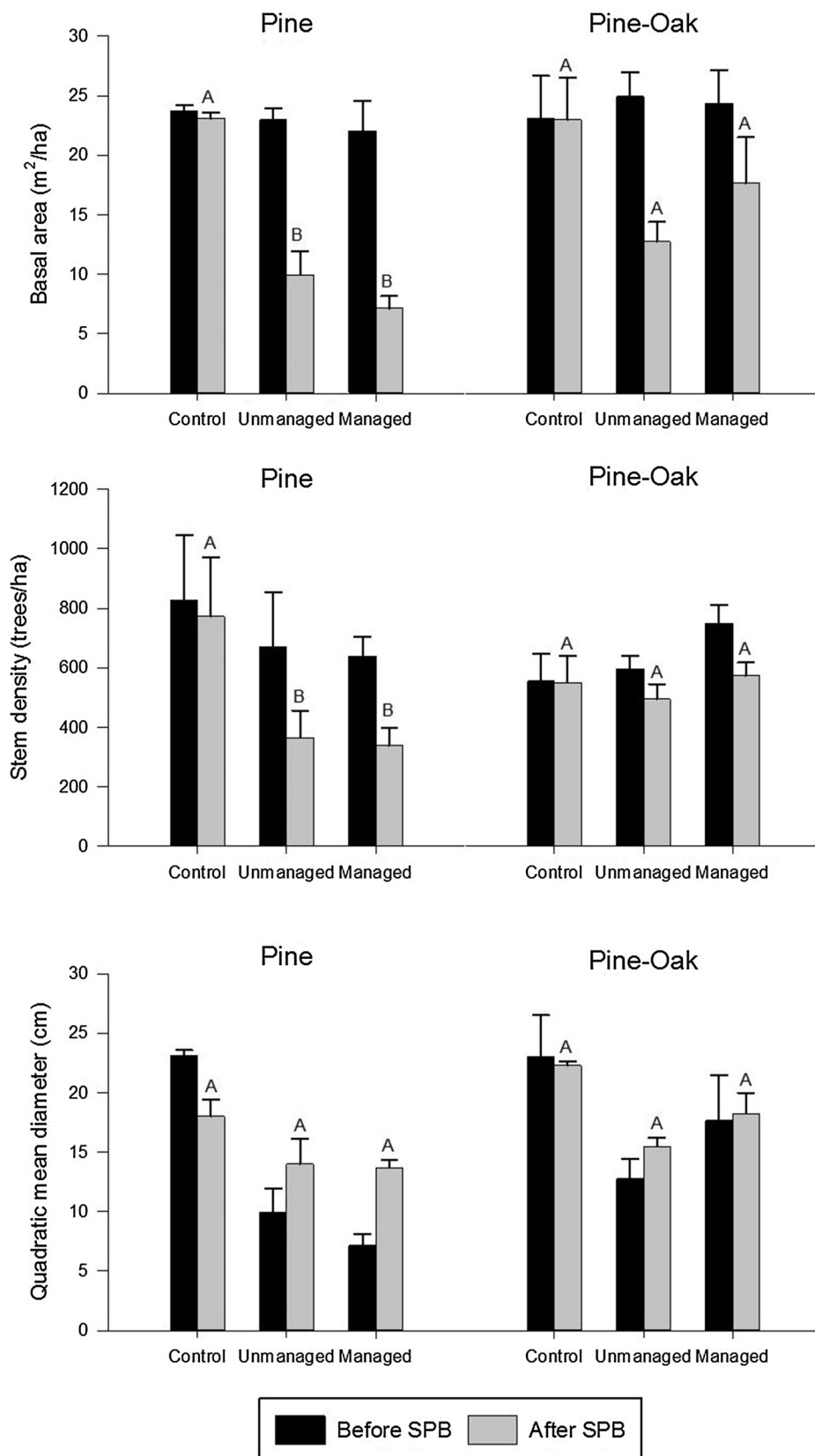
Fig. 3. Total basal area, stem density, and quadratic mean diameter (QMD) for all species combined in pine and pine-oak stands by treatment. Post-treatment values with different letters were significantly different at alpha = 0.05. There were no pre-treatment differences in structural conditions, except for QMD in pine stands, which was significantly higher than unmanaged and managed stands.
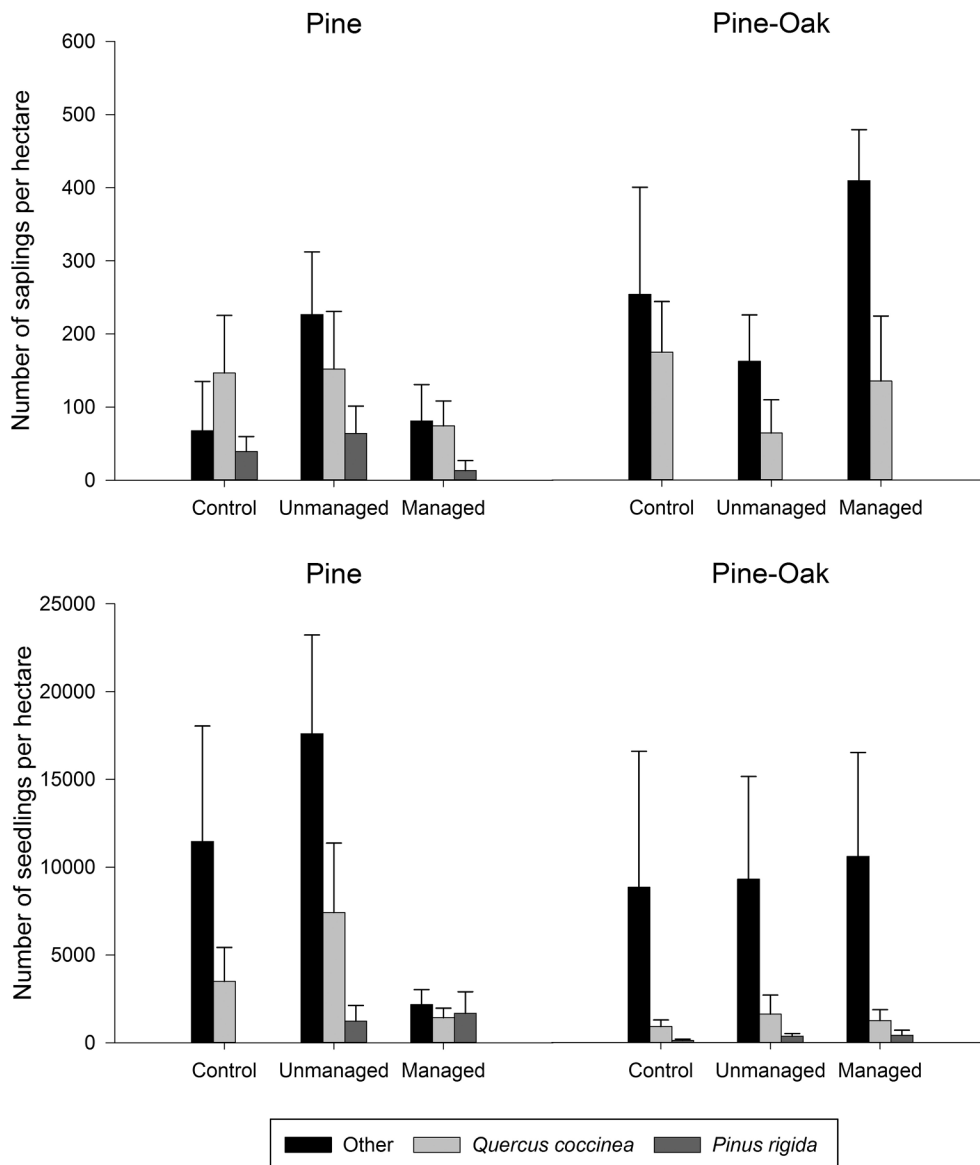
Fig. 4. Mean species composition of saplings and seedlings by cover type and treatment. Other category includes *Q. alba, Q. ilicifolia, Acer rubrum*, and *Nyssa sylvatica*. See Table 1 for treatment definitions.

and pitch pine ("PP", $\tau = -0.51$) and a positive correlation with red maple ("RM", $\tau = 0.04$; see Table 2). The understory composition of pine-oak forests did not vary significantly by treatment ($A = 0.01$, $P > 0.05$). Within-treatment variation in understory percent cover data was greatest in control plots dominated by shrubs (Fig. 9), intermediate in managed plots, and lowest in unmanaged plots (average Sørenson distance = 0.64, 0.55, and 0.36, respectively). Management was indicated by greenbriar (*Smilax rotundifolia*; see Table 3) and managed plots had the lowest average density of understory vegetation (Fig. 9).

NMS analysis produced a two-axis solution for pitch pine forests ($P = 0.04$, final stress = 15.93, instability = 0) and accounted for 67% of the variation in understory data (Fig. 10). The gradient represented by Axis 1 was negatively associated with black huckleberry ("BH," *Gaylussacia baccata*, $\tau = -0.64$) and early lowbush blueberry ("EL," *Vaccinium pallidum*, $\tau = -0.77$), and positively associated with star-flower ("SF," *Trientalis borealis*, $\tau = 0.81$), cowwheat ("CW," *Melampyrum lineare*, $\tau = 0.36$), grasses ("GR," $\tau = 0.82$), and mosses ("MO," $\tau = 0.40$; see Table 2). Axis 2 had a negative correlation with dangleberry ("DB," *Gaylussacia frondosa*, $\tau = -0.67$) and positive

correlation with scrub oak ("SR," $\tau = 0.61$) and common highbush blueberry ("CB," *Vaccinium corymbosum*, $\tau = 0.57$). The understory composition of pitch pine forests did not vary significantly by treatment ($A = 0.08$, $P > 0.05$). Within-treatment variation in understory percent cover data was greatest in managed stands, intermediate in unmanaged stands, and lowest in controls (average distance = 0.54, 0.50, and 0.28 respectively). Control stands were indicated by late lowbush blueberry (*Vaccinium angustifolium*, "LL"; see Table 3) but no other indicator species were identified for pitch pine forests.

4. Discussion

Southern pine beetle infestations and subsequent management cause significant changes to pine forest overstory and understory communities in the southeastern U.S., and can influence the successional trajectories of stands (Coleman et al., 2008a). We observed similar near-term impacts in northeastern pitch pine forests where SPB and its management are novel disturbances in this region. Even though there are limits to having only one season of data, it does allow us to elucidate immediate impacts and some short-term effects of SPB and
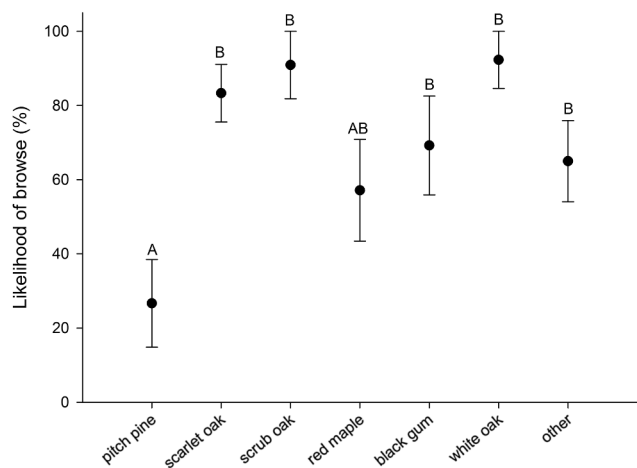
Fig. 5. Likelihood of browse occurring within major species across all treatment combinations (mean ± SE). "Other" represents species with < 10 occurrences. Letters denote significant differences as determined by a binomial GLM with pitch pine as the reference level. Species with the same letters were not significantly different based on alpha = 0.05.
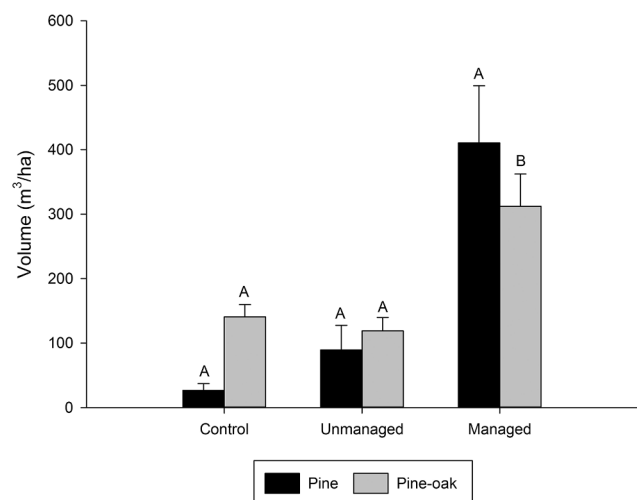

Fig. 7. Basal area (m^2 ha − 1) of snags for all species by treatment combination (mean ± SE). Treatments with the same letters were not significantly different within a forest type based on Tukey's HSD alpha = 0.05. See Table 1 for treatment definitions.

the combination of rapid overstory mortality and limited pine regeneration makes the future of pine in SPB-infested or managed sites unlikely, unless restoration activities are pursued. In particular, given many of these areas have well-developed understory and midstory layers dominated by hardwood species, mortality of overstory pines quickly shifts dominance of these forests towards broadleaf species. The scope of our study was on SPB-infested stands and our results relate to these stand types and may not be transferable to all pitch pine or pitch pine-oak stands on Long Island.

Management actions also increased the likelihood of ungulate browse damage and abundance of downed woody debris (DWD), suggesting management responses may further affect the ecology of pitch pine stands. These findings add to the growing body of literature on the impacts of novel pest dynamics on forest structure and function (Weed et al. 2013) and suggest the compounding impacts of disturbance and management may create more immediate, dramatic effects, particularly in pitch pine stands where the host species is more influential on ecosystem structure and function.

4.1. Overstory impacts

SPB impacts on overstory species composition varied by cover type with significant overstory basal area loss of pitch pine in all treatment combinations, exacerbating the conversion of pitch pine stands to pine-oak cover. Pitch pine was generally the only tree species present in size classes above 34 cm dbh and the loss of these trees will significantly alter stand structure. Elimination of these structural elements could influence wildlife use and live-tree carbon stores in these stands given the unique role of large trees in affecting these ecosystem properties. This loss of pitch pine due to SPB is similar to longer-term successional trends observed due to fire suppression and a lack of other management activities in pitch pine forests on Long Island (McCabe, 2011) and elsewhere (Jordan et al., 2003), albeit with SPB serving to accelerate these successional dynamics toward greater hardwood species abundance.

Findings from this work indicate effects of management may vary between forest cover types. Pine-oak forests experienced a more severe decline in overstory pitch pine BA when SPB outbreaks were not managed, but still lost a significant amount of pitch pine where management took place (Table 1). Pine forests, however, lost slightly higher densities of pitch pine in infested stands following management efforts, perhaps because cutting was more likely to be applied in severely

Fig. 6. Volume (m^3 ha $^{-1}$) of downed woody debris by treatment combination (mean ± SE). Treatment combinations with the same letters were not significantly different within a forest cover type based on Tukey's HSD alpha = 0.05. See Table 1 for treatment definitions.

management within the study system. Specifically, unmanaged and managed SPB-infested stands had fewer overstory pitch pine, especially in larger size classes, a shift towards higher hardwood dominance in the overstory, lower basal area and stem density, distinct understory community composition, and higher levels of dead wood than controls. Most concerning was the relatively low numbers of pine seedlings and saplings found across treatments. Given the seedbed requirements for this species (exposed mineral soil or thin litter layer; Little, 1959; Šrůtek et al., 2008), it is unlikely future recruitment will occur in affected areas without directed management efforts.

Currently, the vast majority of pitch pine and pitch pine-oak forests on Long Island are unmanaged. These stands are mostly overstocked with limited pitch pine regeneration in the understory. Overstocked pine stands such as these are susceptible to SPB infestations (Coster and Searcy, 1981; Aoki et al., 2018). The rapid loss of the overstory pine with few survivors in many stands will cause dramatic changes in stands affected by SPB. If pine regeneration was abundant, and competing hardwood overstory/intermediate trees were limited, this loss of pine overstory could be seen as beneficial for opening stands and returning them to a more natural state for pitch pine barrens. However,
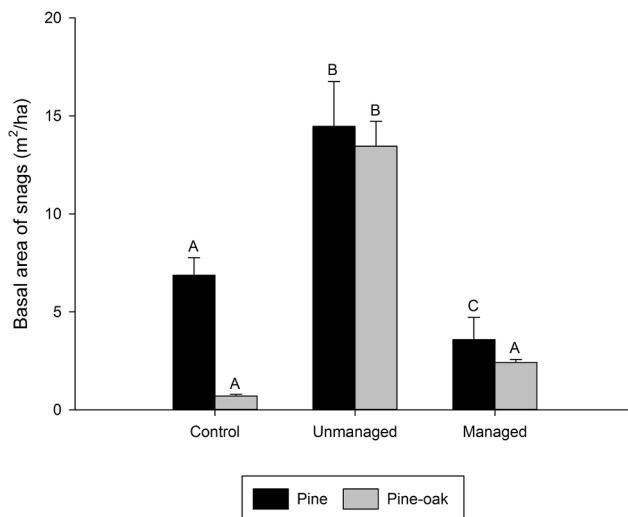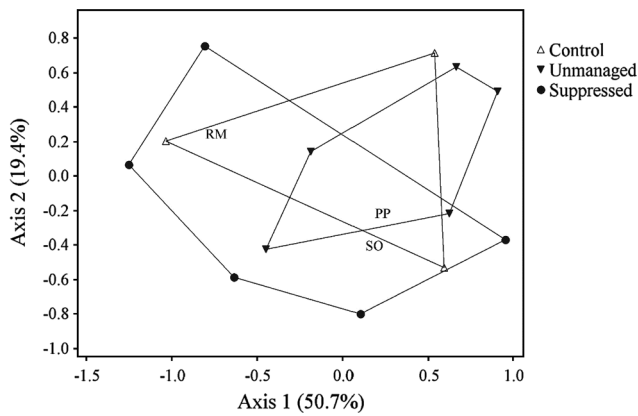
Fig. 8. Non-metric multidimensional scaling (NMS) ordination of understory plant composition in pine-oak forests across treatments. The two axes explaining the highest percentage of variation are presented. Species with significant correlations with either axis are indicated with two-letter abbreviations (RM = *Acer rubrum*, PP = *Pinus rigida*, SO = *Quercus coccinea*), with locations based on weighted average species scores. See Table 1 for treatment definitions.

infested stands rather than those with small infestations. Note that impacts of management were assessed at the plot level and although suppression in pitch pine forests had greater localized impacts, suppression actions at this scale have proven effective at limiting wider, landscape-scale SPB impacts in southeastern pine forests (Fettig et al., 2007). Further study evaluating the expansion of unmanaged infestations and the incidence of outbreaks in the forest matrix surrounding managed treatments may be more informative in evaluating wider-scale impacts.

4.2. Regeneration impacts

Few if any pitch pine seedlings or saplings were observed following overstory mortality. SPB is a markedly different mortality agent in comparison to wildfire or other stand-replacing disturbances that have historically favored natural regeneration of pitch pine (Fowells, 1965; Lorimer, 1984). Canopy gaps caused by SPB and management efforts

increased levels of light in the understory in pitch pine stands; however, unlike fire disturbance, SPB did not create mineral soil exposure or remove competing understory (or overstory hardwood) vegetation. The legacy of fire suppression on Long Island may have also limited the ability of pitch pine to regenerate in areas affected by SPB; understory hardwood species have increased in these forests relative to historic conditions over the past several decades due to the absence of fire (Olsvig et al., 1998; Harrod et al., 2000) and will likely continue to dominate in gaps created by SPB, based on our results.

Deer heavily browsed tree regeneration in the areas examined, which is consistent with previous work in SPB-impacted areas that suggested deer browse may increase slightly following SPB-mediated disturbance with feeding most frequently on preferred broadleaved species (Maine et al., 1980; Horsley et al., 2003; Rozman et al., 2015). Browse likelihood varied by species, with pitch pine less likely to be browsed than most other species according to GLM results, suggesting that deer browse may not be a significant barrier to reestablishing or promoting pitch pine in these areas. In contrast, Little et al. (1958) reported significant browse damage of pitch pines in New Jersey and an associated increase in likelihood of mortality.

4.3. Fuels density and structure

Pitch pine snag basal area increased significantly in unmanaged sites and will ultimately contribute to and increase the DWD component of unmanaged stands in the long term (Schmid et al., 1985), although DWD levels were not immediately elevated. This is consistent with patterns following SPB infestation in the southeastern U.S., where it may take several years before DWD components increase after an infestation (Leuschner et al., 1976; Leuschner, 1981; Evans, 2012). Management reduced overall snag densities relative to control stands, with much of this material transferred to DWD pools. These changes in dead wood density and structure between unmanaged and managed stands may indirectly influence future forest composition with accumulations of downed fuels in unmanaged stands potentially delayed compared to managed stands. SPB may increase forest fire hazard and severity by creating dead woody material (Brown, 1974; Evans, 2012) and alter the availability of habitat for deadwood-dependent organisms.

Table 2
Species correlated with NMS axes. Significant correlations and associated significance based on Kendall's tau are denoted: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

| Species	Common name	Code	Pine-oak			Pitch pine	
			Axis 1	Axis 2	Axis 3	Axis 1	Axis 2
Gaylussacia baccata	Black huckleberry	BH	0.15	0.31	0.08	−0.54*	0.08
Vaccinium pallidum	Hillside blueberry	EL	0.25	0.27	0.04	−0.74***	−0.04
Quercus coccinea	Scarlet oak	SO	−0.01	−0.48*	−0.20	0.28	0.23
Quercus ilicifolia	Scrub oak	SR	–	–	–	−0.01	0.48*
Gaylussacia frondosa	Blue huckleberry	DB	−0.06	0.29	0.00	−0.30	−0.64**
Gaultheria procumbens	Wintergreen	WG	0.16	0.37	0.03	−0.41	−0.44
Quercus alba	White oak	WO	−0.01	−0.40	−0.04	0.03	0.35
Vaccinium angustifolium	Lowbush blueberry	LL	−0.04	0.07	0.07	−0.31	0.24
Pinus rigida	Pitch pine	PP	−0.10	−0.51	0.29	0.32	0.29
Vaccinium corymbosum	Highbush blueberry	CB	−0.13	0.39	−0.26	0.00	0.49*
Trientalis borealis	Star flower	SF	−0.19	−0.26	0.10	0.54*	0.32
Melampyrum lineare	Cow wheat	CW	–	–	–	0.47*	0.18
Myrica spp.	Sweet gale	SB	–	–	–	−0.31	0.01
Grasses		GR	–	–	–	0.70**	0.13
Mosses		MO	−0.10	−0.36	0.36	0.61**	0.03
Smilax rotundifolia	Green cat briar	GB	−0.16	0.13	0.21	–	–
Clethra alnifolia	Sweet pepper bush	SP	−0.03	0.13	−0.19	–	–
Sassafras albidum	Sassafras	SA	−0.13	0.13	0.13	–	–
Acer rubrum	Red maple	RM	−0.11	0.55*	−0.08	–	–
Nyssa sylvatica	Black gum	BG	−0.24	0.21	0.01	–	–
Amelanchier spp.	Serviceberry	AM	−0.35	0.45	−0.06	–	–
Vaccinium fuscatum	Black highbush blueberry	BB	−0.39	−0.30*	−0.07	–	–
Maianthemum canadense	Canada mayflower	CM	−0.15	0.00	0.33	–	–
Toxicodendron radicans	Poison ivy	PI	0.15	0.18	0.05	–	–
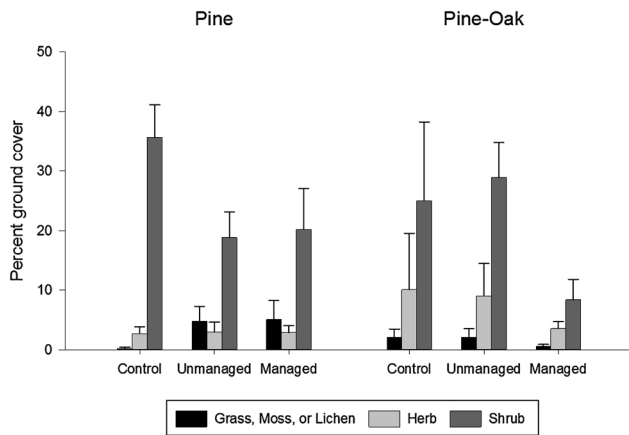
Fig. 9. Mean percent cover of shrubs, herbaceous vegetation, and ground cover (grasses, mosses, and lichens) by treatment combination. See Table 1 for treatment definitions.

Table 3
Indicator species by treatment within each cover type. Significance level denoted: *0.05.

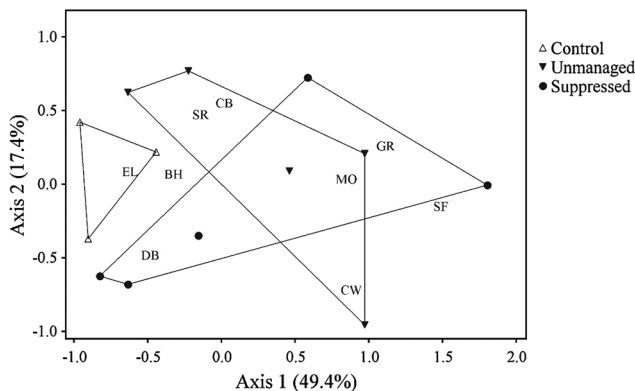| Treatment	Pine-oak	Pitch pine
Control	–	*Vaccinium angustifolium*[*]
Unmanaged	–	–
Managed	*Smilax rotundifolia*[*]	–

Fig. 10. Non-metric multidimensional scaling (NMS) ordination of understory plant composition in pitch pine forests across treatments. Species with significant correlations with either axis are indicated with two-letter abbreviations (EL = *Vaccinium pallidum*, SF = *Trientalis borealis*, CW = *Melampyrum lineare*, GR = grasses, MO = mosses, DB = *Gaylussacia frondosa*, SR = *Quercus ilicifolia*, CB = *Vaccinium corymbosum*), with locations based on weighted average species scores. See Table 1 for treatment definitions.

Management in particular may influence wildlife habitat values (i.e., by felling potential cavity nest sites (Connor and Rudolph, 1995)) and may influence carbon storage as standing materials often become case hardened (Reynolds et al., 1985) and resist decay longer than downed logs (Vanderwel et al., 2006).

4.4. Understory species composition

SPB does not appear to immediately influence understory plant communities in mixed pine-oak forests, but understory assemblages in pitch pine forests where other impacts (e.g. DWD volume and snag basal area) were more extensive were found to differ. Pine-oak stands were more homogenous in areas affected by SPB and understory density declined, but no noticeable differences in species composition were

detected. This finding is not surprising given the short duration of the study and care taken to select areas with similar pre-treatment conditions. Given we lacked pre-SPB measurements in these areas, it is difficult to determine the nature of change in these communities following pitch pine mortality. Nevertheless, the immediate impacts of management were apparent in the greater heterogeneity in understory communities in areas experiencing these treatments. This reflected both the recolonization of these areas through harvesting-induced sprouting of hardwood species, as well as the displacement of lianas previously attached to the branches of felled trees. In particular, the increase in green catbriar in the understory of managed areas likely resulted from the displacement of this liana from the midstory to the forest floor when trees were felled in infested areas. In contrast, understory communities in pitch pine forests became more complex with increased disturbance. In particular, based on our ordination analyses, pitch pine control stands had understories dominated by ericaceous shrubs and scrub oak, whereas moss, grass, and herbaceous species increased with greater overstory disturbance by both SPB and associated management. These species groups often increase in response to greater disturbance severities (Matiu et al., 2017) and higher disturbance frequency (Glitzenstein and Streng, 2003) and may remain an important part of these areas over the near term, particularly following the compounded disturbance of SPB and subsequent management (Ton and Krawchuk, 2016; Carlson et al., 2017). The greater overall impacts of SPB on pitch pine stands likely reflect the greater functional role of pitch pine in affecting understory environmental conditions (and potentially future forest composition) relative to hardwood species in these communities, due in part to their overstory dominance. Longer-term studies would provide more insight into the impact of SPB on understory communities.

5. Conclusions and management implications

This study provides the first evaluation of the effects of SPB and subsequent management on pitch pine forest structure, composition, regeneration, and fuel loading on the northern edge of recent range expansions in Long Island, New York. Results collectively show impacts on composition and structure of affected Central Pine Barrens forests with the potential to dramatically reduce pitch pine from these areas unless mitigation occurs. Pine regeneration was minimal following SPB and management, and the high rates of browse damage on hardwood species (mostly oak) indicate there may be regeneration challenges across species in these areas if protective precautions are not taken. An increase in DWD volume in pitch pine stands following management might also create more fire-prone conditions for several years, a potential benefit to pitch pine but a detriment to nearby urban or suburban developments and less fire-adapted species.

Based on these results, a dramatic decline in importance of pitch pine in any SPB-impacted stand that supported an infestation (i.e., multiple SPB generations) on Long Island is anticipated, further advancing successional trends toward hardwood (predominantly oak) dominance, and greatly shifting forest communities away from barren conditions. As SPB populations disperse through the Central Pine Barrens, more stands will be negatively affected and pitch pine importance will likely decline across a wider area. SPB also initiates infestations that do not grow into larger events, and these stands will see little change in overall vegetation characteristics. Greater species homogeneity could decrease forest resilience (Tilman et al., 1996) by increasing the likelihood of severe pest and disease outbreaks (Thompson et al., 2009), potentially causing more dramatic and sudden shifts in forest composition and structure. These sudden changes could alter nutrient cycling patterns and influence water quality of the underlying aquifer.

As SPB likely continues expanding northward and inland, maintaining host pine cover may require more active preemptive thinning and/or prescribed burning to increase host tree vigor (Belanger, 1980;

Knebel and Wentworth, 2007) and decrease pheromone communication capabilities of SPB (Thistle et al., 2004). Pine stands in New Jersey that were at risk to SPB had higher basal areas, and trees with low inter-tree distances, diameters, and live crowns (Aoki et al., 2018) and these variables can be used to guide management decisions. Active management may prove an even more important consideration for maintaining rare northeastern pine barrens ecosystems and its obligate wildlife species. Moreover, developing strategies for restoring pitch pine to areas where fire suppression has shifted understory dominance towards hardwood species will become increasingly important as SPB impacts these ecosystems.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.12.015.

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