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Evaluating The Impacts Of Southern Pine Beetle On Pitch Pine Forest Dynamics In A Newly Invaded Region

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EVALUATING THE IMPACTS OF SOUTHERN PINE BEETLE ON PITCH PINE
FOREST DYNAMICS IN A NEWLY INVADED REGION

A Thesis Presented

by

Molly Heuss

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ABSTRACT

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman), a native insect that has historically affected pine ecosystems in the southeastern U.S., has recently expanded northward causing extensive tree mortality in pitch pine (*Pinus rigida*) and pitch pine-oak (*Quercus* spp.) forests across much of eastern Long Island, NY. Given the historic lack of SPB within these fire-dependent ecosystems, little is known regarding its impacts to forest composition, forest structure, or fuel loading. This study examined the short-term effects of SPB-induced tree mortality on the structure, composition, and fuel loading of pitch pine and pitch pine-oak communities to inform management recommendations and projections of future forest conditions and fire hazard.

Overstory pine basal area declined following SPB infestation and infestation suppression management, particularly in pitch pine forests. These treatments did not impact the density or composition of seedlings and saplings, with hardwood species, including scarlet oak (*Quercus coccinea*), scrub oak (*Quercus ilicifolia*), and black gum (*Nyssa sylvatica*), making up the majority of species in this layer and pine representing <6% of stems. Likelihood of herbivory was influenced partly by species, with pitch pine less likely to be browsed than white oak and scarlet oak. SPB infestation significantly increased the snag component of both forest types, which largely became downed coarse woody debris (CWD) following suppression management. Treatments did not significantly influence understory species assemblages. Understory communities in pitch pine stands were characterized by *Vaccinium angustifolium* prior to SPB or suppression management, with these disturbances leading to an increase in the diversity of understory communities. In contrast, infestation decreased variation in understory species assemblages in pine-oak forests and encouraged regeneration of pitch pine and scarlet oak, while suppression increased diversity largely through increases in disturbance-adapted species, such as *Smilax rotundifolia*. SPB infestation decreased the biomass of live fuels and subsequently increased loading of dead fuels in both forest cover types. Suppression management felled preexisting and SPB-generated snags, especially in pitch pine forests, transforming vertical fuels into horizontal CWD.

Collectively, results indicate SPB could functionally eliminate pitch pine without additional management intervention to maintain this species. Suppression efforts to reduce SPB impacts may accelerate succession towards hardwood dominance, particularly in pine-oak stand, leading to dramatic shifts in forest conditions across the Long Island Pine Barrens. SPB and suppression management significantly increase dead fuel loading and felling of snags during suppression served to decrease the density of ladder fuels effectively decreasing the risk of crowning. However, heavy CWD loading may also promote volatile fire behavior. Therefore, forest managers must weigh the expected potential impacts of SPB relative to changes to fuel structure and composition generated by suppression management activities. Our results demonstrate short-term effects of SPB and suppression management. Given the limited experience with SPB in these forests and the results of this study, further research on fire behavior effects and patterns of stand development over the long-term are needed.

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CHAPTER 1: INTRODUCTION

Native phytophagous insects are one of the primary disturbance agents in North

America's forests (Dale *et al.*, 2001), and recent range expansion of these insects has

generated novel disturbance dynamics in naïve host species and ecosystems (Carroll *et*

al., 2003; Hickling *et al.*, 2006). The moderation of winter low temperatures as a result

of climate change appears to be particularly important in allowing for range expansion

and increased populations of some forest pests limited by winter survival (Weed *et al.*,

2013). For example, such a dynamic has been attributed to the extensive tree mortality

caused by bark beetles in the western U.S. where mountain pine beetle (MPB;

Dendroctonus ponderosae Hopkins) affected an estimated 1.81m ha in 2015 alone

(USDA, 2016). MPB has also begun invading rare forest types like white bark pine

(*Pinus albicaulis*) and novel hosts like jack pine (*Pinus banksiana*) (Logan *et al.*, 2010;

Cullingham *et al.*, 2011). More information is needed to help inform land management

in the wake of these novel pest dynamics, especially as continued range expansion is

anticipated with the progression of climate change (Weed *et al.*, 2013).

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman), a native

phytophagous insect, has recently expanded its range northward, creating concerns

regarding its potential effects on forest ecology and wildfire hazard in the northeastern

United States (Lesk *et al.*, 2017). This species has historically been considered a pest of

pine forests in the southeastern U.S.; however, recent warmer winter weather has

permitted range expansion northward along the Atlantic Coast, a trend that is expected to continue northward and inland over time (Lesk *et al.*, 2017).

SPB was discovered on Long Island, New York for the first time in recorded history in 2014 and has since been impacting forests throughout much of Suffolk County in the Central Pine Barrens, causing extensive pitch pine (*Pinus rigida*) mortality in pitch pine and pitch pine-oak (*Quercus spp.*) forests. Long Island hosts one of the northeast region's largest globally rare Pine Barrens forests, a fire-dependent ecosystem historically maintained by regular fire (Little, 1979; CPBJPPC, 1995; NJFAC, 2006). This ecosystem type hosts an array of rare species (Service, 1997) and Long Island is partly underlain by the sole-source underground aquifer serving >2.8 million people (Smolensky *et al.*, 1990), making the function of overlying forests important to biological diversity and the delivery of key ecosystem services, namely clean drinking water.

Very little information is available regarding SPB impacts on pine barrens of the northeast, as the greatest impacts, and most management responses, have traditionally occurred in southeastern pine forests dominated by loblolly pine (*Pinus taeda*) and other southern hard pines (Duncan and Linhoss, 2005; Coleman *et al.*, 2007; Coleman *et al.*, 2008). Several management tactics have been developed and tested in the southeast, including cut-and-leave (CAL) or cut-and-remove (CAR) infestation suppression (Swain and Remion, 1981), thinning preemptively to improve resistance to SPB colonization (Thatcher *et al.*, 1980; Nowak *et al.*, 2015), and pesticide application of select landscape trees (Swain and Remion, 1981). CAL management has been

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utilized in several locations on Long Island in response to SPB; however, the long-term effects of these treatments on forest structure and composition on Long Island are yet unknown. Therefore, further assessment is needed to identify the immediate impacts of SPB and associated management techniques (i.e., CAL) in this novel host ecosystem and to begin quantifying the effectiveness of management practices designed in the southeastern U.S. within a new region and forest ecosystem.

Given the historic lack of SPB in Pine Barrens of the northeastern U.S., ongoing fire suppression, conversion to urban development, and successional trends toward hardwood dominance, there is concern regarding the persistence of pitch pine as a component of the barrens forests. Pitch pine is variably serotinous (Olsvig, 1980) and generally requires mineral soil exposure and full sun to regenerate (Burns and Honkala, 1990). Historically, these conditions were generated by fire, which allowed pine barrens vegetation to dominate portions of Long Island for thousands of years (Gaffney *et al.*, 1995). However, recent expansion of urban communities adjacent to pine barrens and suppression of wildfires to protect these communities have resulted in the succession of many barrens into mature, closed-canopy forests with a greater component of shade-tolerant and fire-intolerant species (Little, 1979; Trani *et al.*, 2001; Lorimer and White, 2003; Nowacki and Abrams, 2008). Prompt understanding of the impacts of SPB on the structure and function of these forests is critical for informing management recommendations aimed at conserving pitch pine cover now further threatened by range expansion of SPB and anticipating and mitigating long-term effects of global climate change on these forests.

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Many fire-dependent forest ecosystems in North America have recently been subject to extensive bark beetle (*Dendroctonus* spp.) outbreaks, generating concerns about fire hazard and fuel loading following infestations or suppression management (Jenkins *et al.*, 2008; Collins *et al.*, 2012; Evans, 2012). Fire behavior is dependent on a myriad of factors, but fuel loading, composition, and structure are key components responsible for determining the impacts of fire on the surrounding environment (Graham *et al.*, 2004). A review (Black *et al.*, 2013) of the literature suggests bark beetle outbreaks may not significantly alter fire risk, but there are examples (Romme *et al.*, 1986; Lynch *et al.*, 2006; Jenkins *et al.*, 2008) of correlations between fire hazard and bark beetle infestations. Given that many of the areas are being impacted by SPB in the northeastern US exist in the wildland-urban interface, assessments of fuel loading and fire risk are critical for determining appropriate management actions that minimize both SPB and fire risk

This thesis sought to address the abovementioned key information needs regarding SPB impacts by examining the structural, compositional, and fuel loading dynamics following this novel range expansion into the Long Island Pine Barrens. In Chapter 2, we examine the short-term effects of SPB-induced tree mortality on the structure and composition of pitch pine and pitch pine-oak communities to inform management recommendations and projections of future forest conditions. Specifically, we seek to quantify the impacts of these disturbances on overstory structure and species composition, regeneration patterns, deer browse likelihood, understory species composition, and the volume of downed woody debris and snag basal area.

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In Chapter 3, we investigate the effects of SPB and suppression on the structure and composition of fuels. We specifically evaluate fuels loading in the form of 1) live aboveground biomass, 2) dead fuels, including coarse woody debris and snags, and 3) potential ground and ladder fuels to inform future assessments of fire risk following SPB outbreak.

In the final chapter, we present management recommendations, study limitations, and future research directions.

CHAPTER 2: NORTHWARD EXPANSION OF SOUTHERN PINE BEETLE HAS SERIOUS CONSEQUENCES FOR MAINTENANCE OF GLOBALLY RARE PITCH PINE FORESTS

2.1. Abstract

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman), a native insect that has historically affected pine ecosystems in the southeastern U.S., has recently expanded northward causing extensive tree mortality in pitch pine (*Pinus rigida*) and pitch pine-oak (*Quercus* spp.) forests across much of eastern Long Island, NY. Given the historic lack of SPB within these ecosystems, little is known regarding its potential impacts. This study examined the immediate effects of SPB-induced tree mortality and suppression management on the structure and composition of pitch pine and pitch pine-oak communities, two common forest types on Long Island, to inform management recommendations and projections of future forest conditions. Overstory pine basal area declined significantly following SPB infestation and management, particularly in pitch pine forests, whereas lower rates of tree mortality were associated with areas receiving suppression management. There was no impact of SPB or suppression management on the density and composition of seedlings and saplings, with hardwood species, including scarlet oak (*Quercus coccinea*), scrub oak (*Quercus ilicifolia*), and black gum (*Nyssa sylvatica*), making up the majority of species in this layer and pine representing <6% of stems. Likelihood of herbivory was influenced partly by species, with pitch pine less likely to be browsed than white oak and scarlet oak. SPB infestation

significantly increased the snag basal area in both forest types, whereas downed woody debris volumes were greatest following suppression management. Understory species assemblages were not significantly influenced by SPB or suppression, but community composition did shift slightly, particularly on pitch pine sites. Understory communities in unimpacted pitch pine stands were characterized by *Vaccinium angustifolium*, with diversity of understory communities increasing following SPB and suppression management. In contrast, SPB infestation decreased between-site variation in understory species assemblages in pine-oak forests and increased regeneration of pitch pine and scarlet oak. Suppression management increased understory species diversity, largely through increases in disturbance-adapted species, such as *Smilax rotundifolia*. Collectively, results indicate SPB could functionally eliminate pitch pine in the absence of additional management actions, and that suppression 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 active management may be useful in maintaining stands with lower fire hazard and result in more resilient, heterogeneous forested ecosystems.

2.2. Introduction

Phytophagous insects are a major forest disturbance driving forest stand dynamics in many regions of the globe (Dale *et al.*, 2001). For example, western bark beetles have caused tree mortality across 1.81m ha in the western United States in 2015 alone (USDA, 2016). As such, the structure, species composition, and habitat values of

forests over broad areas can shift dramatically in the wake of bark beetle outbreaks (Saab *et al.*, 2014). Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman) is a native primary tree killer associated with pine (*Pinus spp.*) mortality in southeastern forests of the United States. Infestations in the southeast historically caused dramatic financial losses, primarily due to market flooding of salvaged forest products (Pye *et al.*, 2011). SPB-caused mortality has specifically been linked with dramatic changes in forest composition (Coleman *et al.*, 2007), nutrient cycling, understory species composition, and wildlife habitat values (Leuschner *et al.*, 1976; Maine *et al.*, 1980; Kulhavy and Ross, 1988).

Climate change has been associated with expansion of insects into areas with naïve hosts that may not have yet adapted to this disturbance, resulting in greater impacts relative to those observed in historically affected forests (Carroll *et al.*, 2003; Hickling *et al.*, 2006). Climate factors, particularly temperature extremes, are often the primary limitation of insect species' ranges (Neuvonen *et al.*, 1999). Moreover, insect species can often adjust rapidly in response to climate change due to high fecundity and long-distance dispersal potential (Ayres and Lombardero, 2000). In particular, the moderation of winter low temperatures over time may permit range expansion of forest pests limited by winter survival (Weed *et al.*, 2013). Over the past decade, a novel dynamic for SPB has emerged with this species expanding its range into the northeastern United States. This range expansion has resulted in extensive pitch pine (*Pinus rigida*) mortality 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).

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; Lesk *et al.*, 2017). 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 Pine Barrens region of Long Island, NY, where SPB first arrived in 2014, 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 (USCB, 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*) (Service, 1997). These forests generally occur on acidic and nutrient poor sandy outwash soils (Reiners, 1965), with areas containing a greater clay component having higher water holding capacity and a greater component of hardwood species (Tedrow, 1998). Pine barrens have historically been perpetuated by disturbance, primarily frequent fires (Little, 1979; NJFAC, 2006) that occurred on a return interval of <20 years, although little historic fire frequency data is available to confirm these dynamics (Lorimer and White, 2003). Fire is an important part of the regeneration ecology of pitch pine as it is often required to release seeds of the variably serotinous cones and create the mineral soil exposure and direct sun necessary for regeneration establishment (Burns and Honkala, 1990).

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However, wildfire suppression and land-use changes in the last century (Dombeck *et al.*, 2004; Troy and Kennedy, 2007) have allowed many barrens to succeed into mature, closed canopy forests (Trani *et al.*, 2001) dominated by less fire-adapted and 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*).

Unfortunately, SPB is an added stressor in forests like the Long Island Central Pine Barrens that are already impacted by various biotic and abiotic factors. For example, many forests in the northeastern U.S. experience elevated levels of ungulate herbivory relative to historic levels, which is already known to significantly influence forest regeneration and successional trajectories (Côté *et al.*, 2014). Previous research suggests more intensive deer and rabbit browse in response to SPB-created forest openings and edge effects (Maine *et al.*, 1980) may increase selective pressure on preferred broadleaf species (Rozman *et al.*, 2015) and influence future species composition and structure (Matonis *et al.*, 2011; Russell *et al.*, 2016). In addition, many areas on Long Island host dense enough deer populations to significantly influence forest ecosystem succession (USDA, 2014). Given the potential synergistic effects between SPB and deer browse, evaluations of the recent expansion of SPB should consider how deer browse pressure might influence ecosystem response to pine mortality.

Much of our understanding of SPB impacts to forest stand dynamics comes from the loblolly pine (*Pinus taeda*)-dominated forests in the southeastern US (Duncan and Linhoss, 2005; Coleman *et al.*, 2007; Coleman *et al.*, 2008) leaving key knowledge

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gaps regarding how the pitch pine forests currently being affected in the northeastern U.S. will respond to this novel disturbance. Similarly, numerous management options have been developed in the southeastern U.S. for limiting SPB-caused mortality in infested forests and increasing the resistance of uninfested stands, including cut-and-leave (CAL) or cut-and-remove (CAR) infestation suppression (Swain and Remion, 1981), thinning preemptively to improve resistance to SPB colonization (Thatcher *et al.*, 1980; Nowak *et al.*, 2015), and pesticide application of select landscape trees (Swain and Remion, 1981). It is unclear how effective these strategies are in other regions and forest types, particularly in the newly-invaded regions where limited markets for forest products might restrict the range of options available for addressing SPB impacts.

Given the potential influence of SPB on unique pine habitats in the greater northeastern United States, the goal of this study was to fill key knowledge gaps regarding the immediate impacts of SPB damage and associated suppression management. If SPB impacts are similar on Long Island to the southeastern U.S. and in western bark beetle outbreaks, we may expect to find a decline in host species densities (Duncan and Linhoss, 2005; Collins *et al.*, 2011; Kayes and Tinker, 2012), a mild, if any, impact on downed woody debris following infestation alone (Leuschner *et al.*, 1976; Leuschner, 1981), a shift in understory plant communities towards higher densities of mostly shade-intolerant species, particularly in pitch pine stands and larger gaps created by mortality (Maine *et al.*, 1980; Duncan and Linhoss, 2005), and a potential increase in deer browse likelihood (Maine *et al.*, 1980). Therefore, we aimed

to identify impacts of SPB on (1) forest structure, volume of downed woody debris, and species composition, and (2) regeneration patterns, including associated deer browse impacts and understory species composition within affected Long Island forests.

2.3. Methods

2.3.1. Study Area and Design

Study sites were selected to represent six possible combinations of cover type, SPB impacts, and management and were based on discussions with NYSDEC and other local stakeholders, aerial detection surveys, and ground-truthing efforts. Stands containing the highest infested tree density possible were selected in order to assess the potential effects of SPB at the stand level. Twenty-six stands were ultimately selected across the south shore of Suffolk County (see Figure 2.1) and were evenly distributed between the two primary pitch pine forest types being affected by SPB on Long Island (e.g., pitch pine and mixed pitch pine-oak). Stands represented three possible treatments within each cover type: 1) stands subject to SPB infestation and subsequent management (n=10, hereafter referred to as "suppressed"), 2) stands subject to SPB infestation without 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 site conditions, plant communities, and forest structure to infested stands.
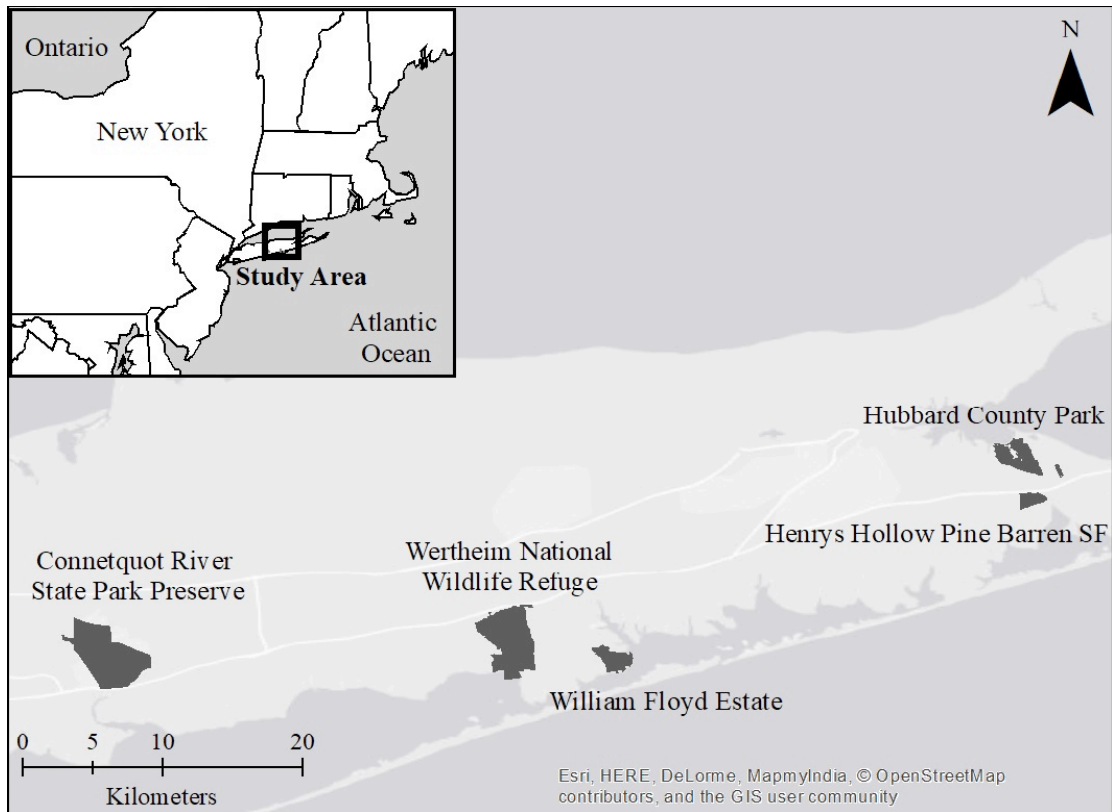
Figure 2.1. Study area on Long Island, New York. Properties containing study sites are shaded gray.

2.3.2. Field Methods

In order to assess the impacts of SPB and management on forest structure and composition, three to four 400 m^2 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 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 $\geq$7.6 cm) rooted within the 400 m^2 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 in 25 and 10 m^2 plots, respectively, located 5.5 m from the overstory plot center at azimuths of 120° and 240°. Seedlings with clipped leaders were tallied separately by species to assess the level of browse damage.

Downed coarse woody debris (CWD) and fine woody debris (FWD) were sampled using the line-intercept method to assess the volume of CWD and FWD within each treatment. 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 ($\geq$7.6 cm diameter and $\geq$1 m long) intersected by a transect (Brown, 1974). Standing dead trees leaning at more than 45° from vertical were considered downed CWD. FWD (<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.

2.3.3. 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 (Team, 2015). 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 (pitch pine or pine-oak) on browse likelihood. DWD 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 suppression on understory plant community composition, percent cover data was assessed separately within each cover type through multivariate statistical analyses. First, gradients in understory composition across treatments were examined using non-metric multidimensional scaling (NMS) in PC-ORD 6 (McCune and Mefford, 2011). 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

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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 densities 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). ISA 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. ISA then calculates the proportion of iterations resulting in indicator values greater than or equal to the observed values.

2.4. Results

The basal area (BA) of the two most abundant overstory species in the forests examined, pitch pine and scarlet oak (*Quercus coccinea*), were directly impacted by SPB and suppression management (Table 2.1). Pitch pine mortality resulting from SPB and suppression varied significantly by forest cover type (m^2/ha basal area, $P=0.03$) and treatment type ($P<0.05$), but not their interaction ($P>0.05$) and ranged from losses of 0.1 ± 0.1 m^2/ha to 14.8 ± 3.4 m^2/ha. Mortality of pitch pine was significantly higher in unmanaged stands than controls ($P<0.0001$) and significantly lower in suppressed stands than those that were unmanaged ($P=0.033$). Mortality was also significantly greater in pitch pine forests than in pine-oak forests ($P=0.03$).

Table 2.1. Basal area (mean± SE, m^2 ha^{-1}) change of pitch pine and scarlet oak by treatment combination. Values with different letters were significantly different within a cover type based on Tukey's HSD alpha=0.05.

Variable	N	Pitch pine
Treatment		
Control	6	-0.4 ± 0.1^a
Unmanaged	10	-12.6 ± 1.1^c
Suppressed	10	-10.5 ± 2.3^b
Cover type		
Pine	13	-10.8 ± 2.2^a
Pine-oak	13	-7.1 ± 1.5^b

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 plots, was less frequently tallied in the understory of pine-oak stands than under pitch pine cover and zero pine saplings were observed in pine-oak stands. On average, we observed the lowest densities of pitch pine seedlings in control stands, but this result was not significant. Overall seedling densities were lowest in suppressed pitch pine forests, where pitch pine seedlings occurred at the highest densities (Table 2.2).

Table 2.2. Seedling densities (mean no. stems ha^{-1} ± SE) of each species by treatment combination. "Other" includes *Sassafrass albidum, Amelanchier spp., Prunus serotina, Quercus stellata,* and *Carya spp.*

Species	Control Pine	Unmanaged Pine	Suppressed Pine	Control Pine-oak	Unmanaged Pine-oak	Suppressed Pine-oak
Pinus rigida	-	1227±897	1801±1237	123±71	360±161	418±290
Quercus coccinea	4680±2685	9258±5018	2530±760	1364±605	2087±1371	1539±629
Quercus ilicifolia	10110±7010	8333±5206	205±167	-	49±49	49±49
Acer rubrum	-	74±74	57±36	1746±1522	6017±4852	426±205
Nyssa sylvatica	-	516±516	25±25	2920±2475	1907±1141	3504±2862
Quercus alba	164±164	4101±3919	262±191	164±164	197±197	1162±191
Other	-	270±157	213±146	246±142	98±60	3045±2364
Total	14953±5645	24050±7013	5460±1806	9878±8046	11280±5762	12320±5941

Likelihood of browse damage (found on 34% of all seedlings) was partly a function of species, based on comparisons with the null model ($P=0.001$). Pitch pine was significantly less likely to be browsed than white oak (*Quercus alba*) ($P<0.05$) and scarlet oak ($P=0.02$), but was not less likely to be browsed than black gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), sassafras (*Sassafras albidum*), or scrub oak (*Quercus ilicifolia*) ($P>0.05$) (Figure 2.2). Likelihood of browse impact was significantly higher in pine-oak suppressed stands versus pine-oak controls (80±6.9 vs. 37.5±12.5% for suppressed and control, respectively; $P=0.02$), but otherwise there was no effect of treatment or cover on overall browse likelihood ($P>0.05$). The likelihood of browse damage was not influenced by treatment combination in 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 (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 suppressed stands (20±20%) was significantly lower than that of hardwood species in both suppressed (77±6%; $P<0.05$) and unmanaged stands (82±7%; $P=0.03$).
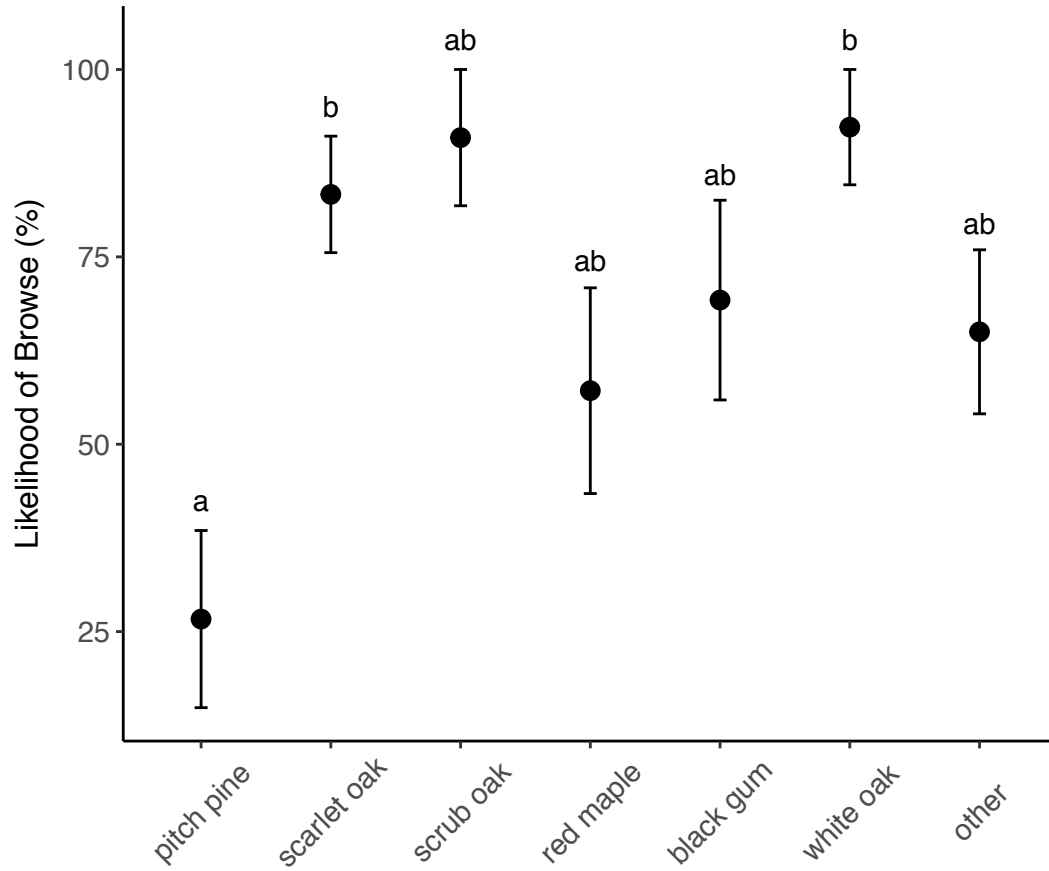
Figure 2.2. Likelihood of browse occurring within major species across all treatment combinations (mean ± SE). "Other" represents species with <10 occurrences.

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DWD volume was influenced by treatment, cover type, and their interaction ($P<0.05$, see Figures 2.3.a & 2.3.b). DWD volume was not significantly influenced by treatment in pine-oak forests ($P=0.28$), but was significantly increased by suppression ($P<0.001$) in pitch pine forests relative to pitch pine controls. DWD volume was also significantly higher in suppressed 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 suppressed stands ($P<0.001$). There was no difference in snag basal area between control and suppressed areas for pine-oak forests, whereas pitch pine forest control stands had significantly higher snag basal areas than suppressed stands in this same forest type.
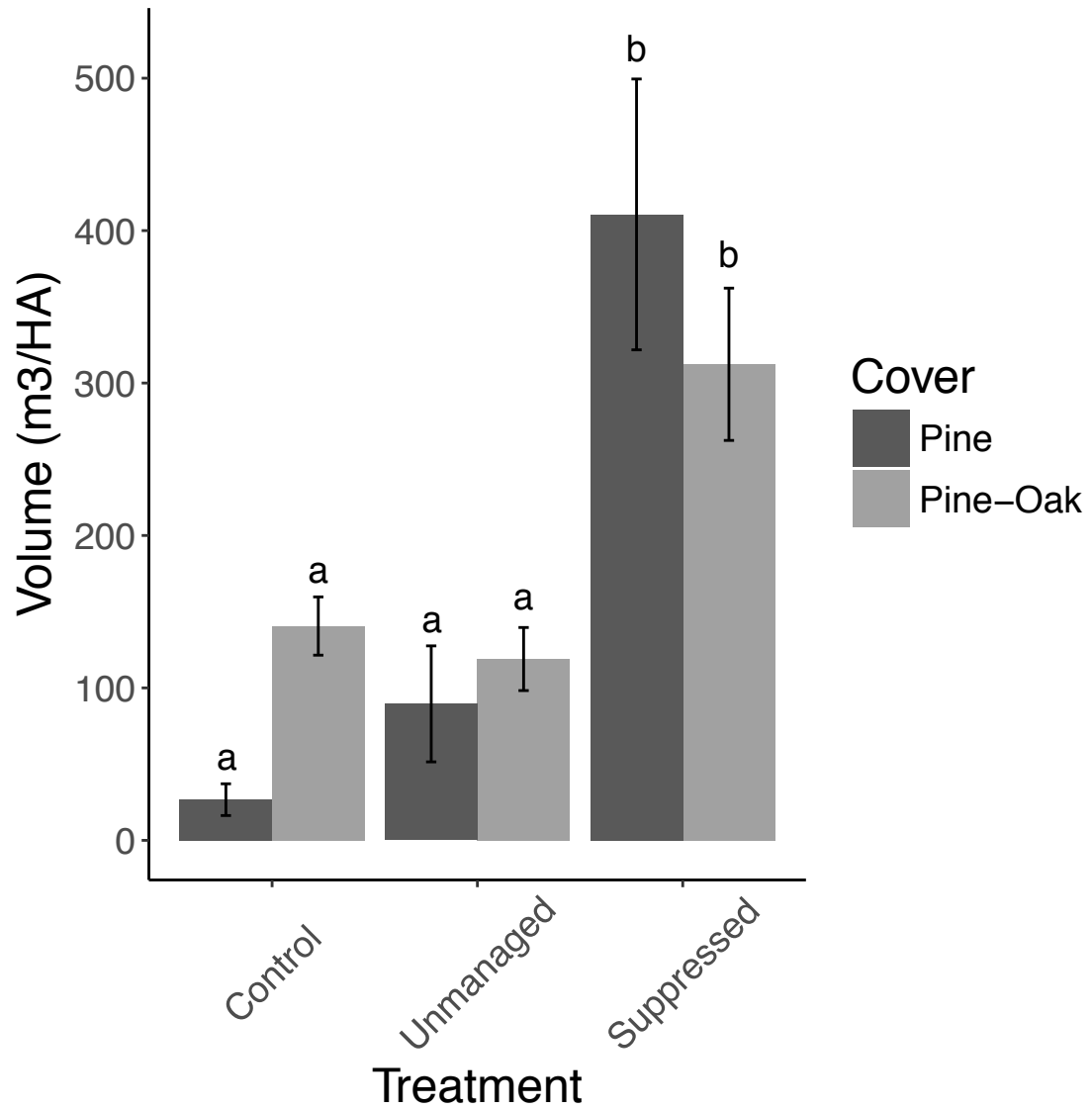
Figure 2.3.a. Volume (m^3 ha^{-1}) of downed woody debris by treatment combination (mean ± SE). Treatment combinations with the same letters were not significantly different within a forest cover type based on Tukey's HSD alpha=0.05.
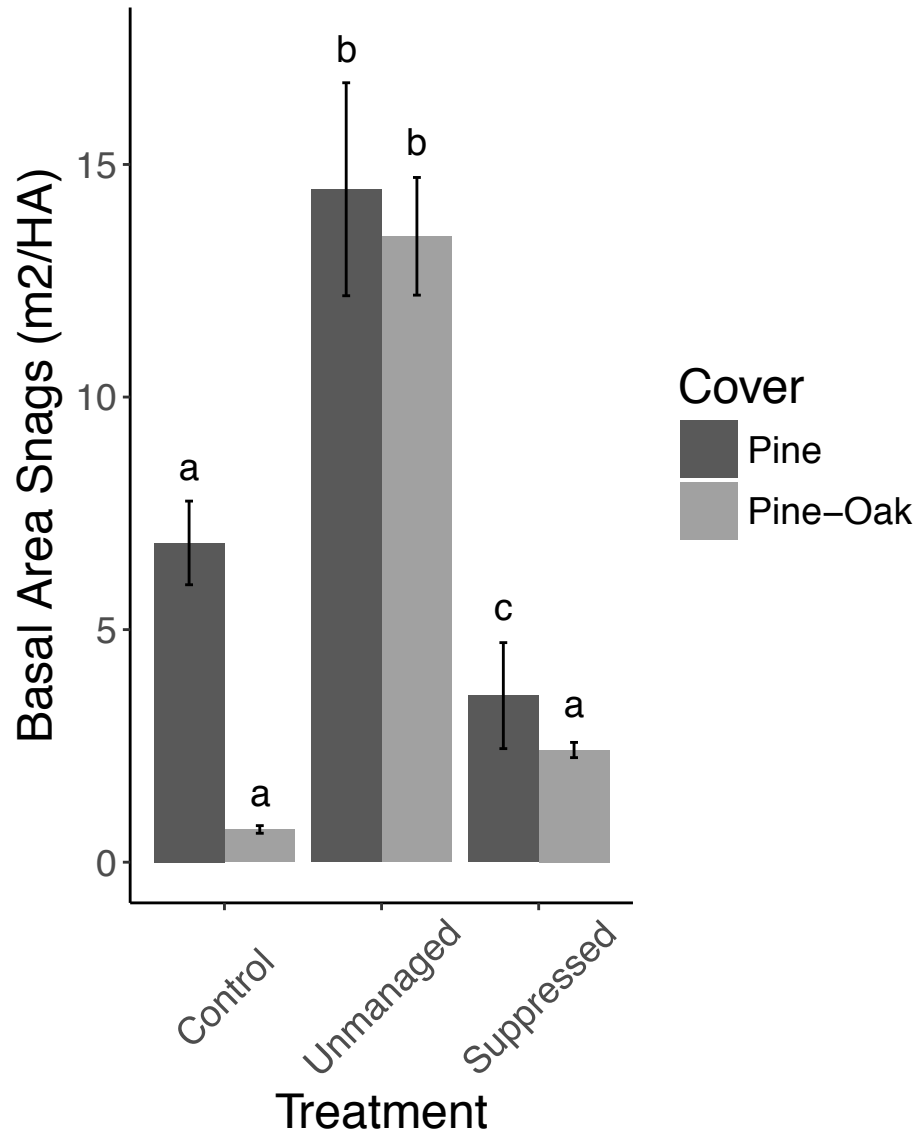
Figure 2.3.b. Basal area (m2 ha-1) of snags by treatment combination (mean ± SE). Treatments with the same letters were not significantly different within a forest type based on Tukey's HSD alpha=0.05.

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 (Figure 2.4.a). 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", τ=-0.53) and pitch pine ("PP", τ=-0.51) and a positive correlation with red maple ("RM", τ=0.04) (see Table 2.3). The understory composition of pitch pine forests did not vary significantly by treatment (A=0.01, P>0.05). Within-treatment variation in understory percent cover data was greatest in controls, intermediate in suppressed plots, and lowest in unmanaged plots (average Sørenson distance=0.64, 0.55, and 0.36, respectively). Suppression management was indicated by greenbriar (*Smilax rotundifolia*; see Table 2.4) but no other significant indicator species were identified.

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 (Figure 2.4.b). The gradient represented by Axis 1 was negatively associated with black huckleberry ("BH," *Gaylussacia baccata*, τ =-0.64) and early lowbush blueberry ("EL," *Vaccinium pallidum*, τ =-0.77), and positively associated with starflower ("SF," *Trientalis borealis*, τ =0.81), cowwheat ("CW," *Melampyrum lineare*, τ =0.36), grasses ("GR," τ =0.82), and mosses ("MO," τ =0.40) (see Table 2.3). Axis 2 had a negative correlation with dangleberry ("DB," *Gaylussacia frondosa*, τ =-0.67) and positive correlation with scrub oak ("SR", τ =0.61) and common highbush blueberry ("CB," *Vaccinium corymbosum*, τ =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 suppressed 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 2.4) but no other indicator species were identified.

Table 2.3. Species correlated with NMS axes. Significant correlations are denoted: *0.05, **0.01, ***0.001.

Species	Code	Pine-oak			Pitch pine	
		Axis 1	Axis 2	Axis 3	Axis 1	Axis 2
Gaylussacia baccata	BH	0.15	0.31	0.08	-0.54 *	0.08
Vaccinium pallidum	EL	0.25	0.27	0.04	-0.74 ***	-0.04
Quercus coccinea	SO	-0.01	-0.48 *	-0.20	0.28	0.23
Quercus ilicifolia	SR	-	-	-	-0.01	0.48 *
Gaylussacia frondosa	DB	-0.06	0.29	0.00	-0.30	-0.64 **
Gaultheria procumbens	WG	0.16	0.37	0.03	-0.41	-0.44
Quercus alba	WO	-0.01	-0.40	-0.04	0.03	0.35
Vaccinium angustifolium	LL	-0.04	0.07	0.07	-0.31	0.24
Pinus rigida	PP	-0.10	-0.51	0.29	0.32	0.29
Vaccinium corymbosum	CB	-0.13	0.39	-0.26	0.00	0.49 *
Trientalis borealis	SF	-0.19	-0.26	0.10	0.54 *	0.32
Melampyrum lineare	CW	-	-	-	0.47 *	0.18
Myrica spp.	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	GB	-0.16	0.13	0.21	-	-
Clethra alnifolia	SP	-0.03	0.13	-0.19	-	-
Sassafras albidum	SA	-0.13	0.13	0.13	-	-
Acer rubrum	RM	-0.11	0.55 *	-0.08	-	-
Nyssa sylvatica	BG	-0.24	0.21	0.01	-	-
Amelanchier spp.	AM	-0.35	0.45	-0.06	-	-
Vaccinium fuscatum	BB	-0.39	-0.30 *	-0.07	-	-
Maianthemum canadense	CM	-0.15	0.00	0.33	-	-
Toxicodendron radicans	PI	0.15	0.18	0.05	-	-
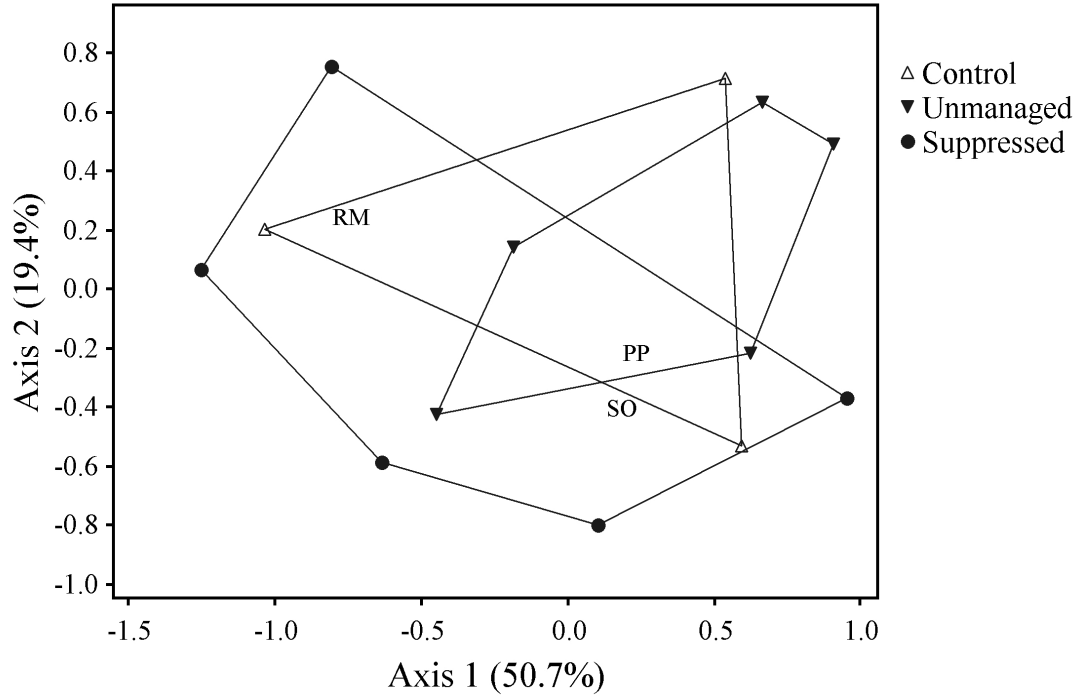
Figure 2.4.a. Non-metric multidimentional scaling (NMS) ordination of understory plant composition in pine-oak forests across treatments. The two axes explaining the highest percentage of variation are presented. Species with significant correlations with either axis are indicated with two-letter abbreviations (RM=*Acer rubrum*, PP=*Pinus rigida*, SO=*Quercus coccinea*), with locations based on weighted average species scores.
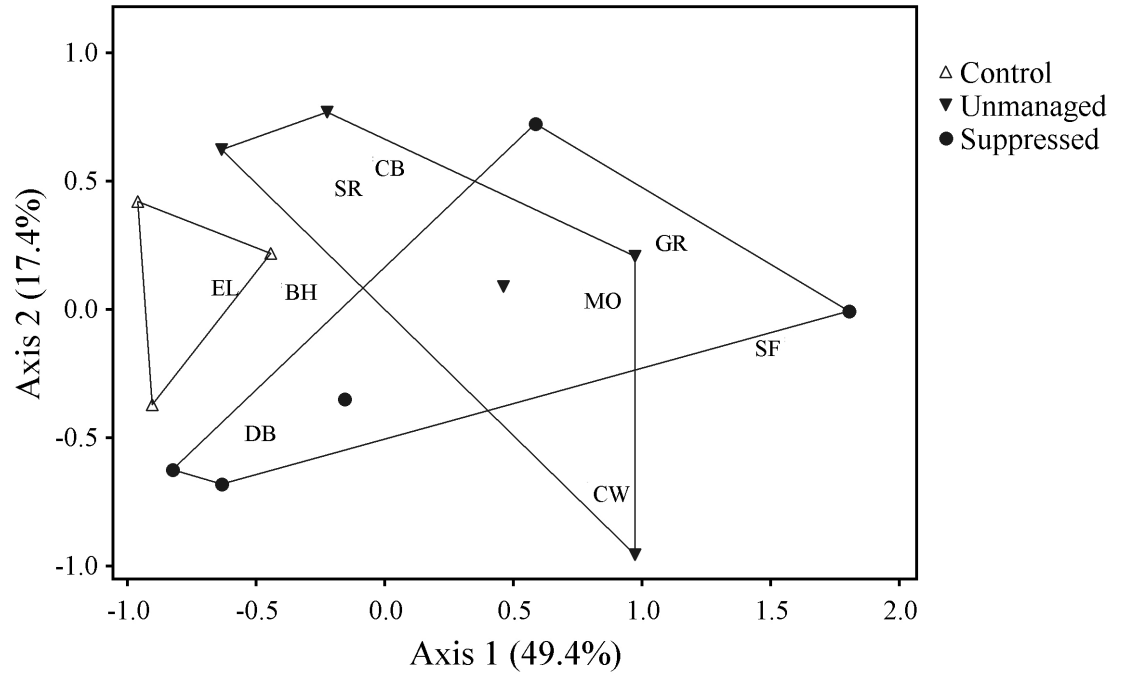
Figure 2.4.b. Non-metric multidimentional scaling (NMS) ordination of understory plant composition in pitch pine forests across treatments. Species with significant correlations with either axis are indicated with two-letter abbreviations (see Table 2.4), with locations based on weighted average species scores.

Table 2.4. Indicator species by treatment within each cover type. Significance level denoted: *0.05, **0.01, ***0.001.

Treatment	Pine-oak	Pitch pine
Control	-	*Vaccinium angustifolium**
Unmanaged	-	-
Suppressed	*Smilax rotundifolia**	-

2.5. Discussion

The immediate impacts we documented suggest the novel expansion of SBP into the northeast may result in significant alterations to pitch pine forest communities across the region. These changes include a decreased overstory pitch pine component with a concomitant shift towards hardwood species and alterations to understory community composition. These overstory effects may be similar to what is already occurring in these forests, but the hastening of pine losses following SPB and suppression could be reducing the opportunity for managers to regenerate pitch pine faster than would be expected otherwise. Management actions associated with suppressing SPB also increased the likelihood of ungulate browse damage (in comparison to control stands) 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 (Lovett *et al.*, 2006) and suggest the compounding impacts of disturbance and suppression management may create more

immediate, dramatic effects, particularly in pitch pine stands where the host species is more influential on ecosystem structure and function.

2.5.1. Overstory Impacts

SPB impacts on overstory species composition varied by cover type with overstory BA loss of pitch pine significant in all treatment combinations, exacerbating the conversion of pitch pine stands to pine-oak cover. This successional trend is similar to those observed due to fire suppression activities in pitch pine forests on Long Island (McCabe, 2011) and elsewhere (Jordan *et al.*, 2003; Coleman *et al.*, 2008), with SPB serving to potentially accelerate these successional dynamics toward greater hardwood species abundance. The functional elimination of pitch pine from the overstory of these forests is similar to dynamics observed following hemlock woolly adelgid (HWA; *Adelges tsugae*), where the dominant overstory conifer (*Tsuga canadensis*) has been functionally removed or pre-emptively salvaged, resulting in hardwood species dominance (Orwig and Foster, 1998; Jenkins *et al.*, 1999).

Findings from this work indicate effects of suppression may vary between forest cover types. Pine-oak forests experienced more severe decline in overstory pitch pine BA when SPB outbreaks were not suppressed, but still lost a significant amount of pitch pine where suppression management took place (Table 2.1). Pine forests, however, lost slightly higher densities of pitch pine in infested stands following suppression efforts, perhaps because management was more likely to be applied in severely infested stands rather than those with small spot infestations. Note that impacts of suppression 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 unsuppressed infestations and the incidence of outbreaks in the forest matrix surrounding suppression treatments may be more informative in evaluating wider-scale impacts.

2.5.2. Regeneration Impacts

Few if any pitch pine seedlings 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). Pitch pine requires mineral soil exposure and low levels of hardwood competition (Fowells, 1965; Burns and Honkala, 1990) to successfully regenerate; a condition often created through wildfire. SPB-caused canopy gaps 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.

Pitch pine may be able to regenerate in low densities in some impacted stands, but appear unlikely to perpetuate as a significant component of the forest based on

initial results, unless other disturbances occur. The densities of pine seedlings found in pitch pine stands following SPB and management, though statistically equal to other treatment combinations, suggests pitch pine may be able to regenerate in these forests if additional measures are taken, such as plantings or prescribed fire. Given the short-term nature of the present study, longer term monitoring of pitch pine regeneration in these areas will be needed to inform the necessity for planting and prescribed fire efforts.

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 two oak species, suggesting that deer browse may not be a significant barrier to reestablishing 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. Although pitch pine demonstrated a fairly low rate of browse in this study (10% of pine seedlings showed damage, found only within 27% of plots containing pine seedlings), this may be reflective of the low density of pitch pine versus other, more preferred species and seasonal ungulate diet variation (Little *et al.*, 1958). Some regions of Long Island host deer densities more than twice that at which foraging and movement begin impacting ecosystems in the long term (USDA, 2014). Given the great potential for herbivory, successful regeneration within the study area may require protective devices to prevent repeated browse damage (Little *et al.*, 1958). This

protection may also be partially provided by the high amounts of DWD in areas impacted by SPB activity and management (see below) (Grisez, 1960; Hunn, 2007).

2.5.3. 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), as has been observed following SPB infestation in the southeastern U.S. (Evans, 2012). Suppression 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 suppressed stands may indirectly influence future forest composition. 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. Suppression 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).

Fuels reduction treatments (Agee and Skinner, 2005) may be pertinent following SPB infestation or suppression to decrease the localized elevated wildfire hazard associated with increased fuel loading and should simultaneously produce conditions more favorable to pitch pine regeneration (discussed further in Chapter 3).

2.5.4. Understory Species Composition

SPB does not appear to immediately heavily influence understory plant communities in mixed pine-oak forests, but does dramatically shift understory assemblages in pitch pine forests where other impacts (e.g. DWD volume and snag basal area) were more extensive. Pine-oak stands became more homogenous in response to SPB, but no noticeable shift in species composition occurred. Greater heterogeneity in understory communities following suppression management relative to unmanaged stands may reflect recolonization of these areas through harvesting-induced sprouting of hardwood species or introduction of species, such as greenbriar, which can be an aggressive colonizer of disturbed forests (Gill and Healy, 1974). 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.

2.5.5. Summary

The future risk and severity of SPB outbreaks has certainly been reduced in affected stands due to the loss of overstory hosts; however, the resulting changes to forest conditions have accelerated the transition of forests to oak-dominated systems that are susceptible to other insects and diseases affecting forests in these areas. For instance, gypsy moth (*Lymantria dispar* Linnaeus), orange-striped oakworm (*Anisota senitoria* Smith), and oak wilt (*Ceratocystis fagacearum* Bretz) are already found on Long Island and have been linked with oak mortality in several areas (NYS, 2012). This greater vulnerability highlights the importance of maintaining pitch pine in these ecosystems using tools such as fuels reductions coupled with prescribed fire that may limit the landscape-level dominance of pine barren communities by oak species while reducing the risk of severe wildfires (discussed further in Chapter 3).

2.5.6. Limitations

Although the findings from this work indicate the potential for significant shifts in forest composition and structure following SPB, our particular results apply to the immediately infested area rather than entire forests . Stands were partly defined by the extent of SPB and management impacts due to our desire to effectively compare treatments, and efforts were taken to prevent sampling of stand edges. Results therefore must be interpreted only as applying to representative pitch pine and pine-oak stands prior to SPB, following SPB infestation, or where suppression management has taken place. Results within oak-pine forests where hosts comprised a much smaller proportion of the overstory may more accurately reflect potential impacts within

broader pitch pine forests where scattered individuals or small pockets of pines are infested

2.6. Conclusion

Results collectively show SPB and suppression management immediately impacted the composition and structure of affected Central Pine Barrens forests with the potential to functionally eliminate pitch pine from these areas unless mitigation occurs. Pine regeneration was minimal following SPB and suppression management and the high rates of browse damage on hardwood species (mostly oak) may further limit regeneration unless proper precautions are taken to protect regeneration. The compound disturbance of SPB followed by suppression stimulated sprouting of competing species and created seedbed conditions favorable for disturbance-adapted species, like greenbriar, creating significant barriers for successful pine recruitment. In pitch pine forests, SPB and suppression may increase diversity of understory communities; however, the lack of pine regeneration in these systems suggests these increases may reflect release and establishment of non-pine species. An increase in DWD volume in pitch pine stands following suppression 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 stands on Long Island is anticipated, further advancing successional trends toward hardwood (predominantly oak) dominance, and greatly shifting the function of these forests.

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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 underlain aquifer.

CHAPTER 3: SHORT-TERM IMPACTS OF SOUTHERN PINE BEETLE AND ASSOCIATED MANAGEMENT ON FUEL LOADING IN NORTHEASTERN PITCH PINE-OAK BARRENS

3.1. Abstract

Many fire-dependent forest ecosystems in North America have recently been subject to extensive bark beetle (*Dendroctonus* spp.) outbreaks, generating concerns about fire hazard and fuel loading following infestations. Southern pine beetle (SPB; *Dendroctonus frontalis*), a native insect historically affecting pine ecosystems in the southeastern U.S., has recently expanded northward causing extensive tree mortality in pitch pine and pitch pine-oak forests across much of the New Jersey pine barrens and the Central Pine Barrens on Long Island, New York. Given the historic lack of SPB within these fire-dependent ecosystems, little is known regarding its potential impacts or those of suppression efforts on fire hazard and fuel loading. This study examined the short-term effects of SPB-induced tree mortality and suppression management on forest fuels in pitch pine and pitch pine-oak forest communities within the Central Pine Barrens. As expected, SPB infestation significantly decreased the biomass of live fuels, with an associated increase in loading of dead fuels, in both forest cover types. Suppression management felled preexisting and SPB-generated snags from pitch pine forests, transforming vertical fuels into primarily horizontal coarse woody debris (CWD). Results indicate that SPB and suppression management significantly increase dead fuel loading of pitch pine and pitch pine-oak forests on Long Island, but suppression in pine-oak forests appears to lessen the effects of SPB on fuel loading.

Overstory mortality and felling of snags decreased the density of ladder fuels and simplified the structure of the forest, effectively decreasing the risk of crown fire. However, heavy CWD loading may promote volatile fire behavior. Therefore, forest managers must consider impacts of SPB relative to changes in fuel structure and composition generated by suppression management activities. Given the limited experience with SPB in these forests, further study is required to determine the resulting fire behavior effects over time.

3.2. Introduction

Bark beetle (especially *Dendroctonus* spp.) outbreaks are occurring at unprecedented levels across many forested regions of North America (Raffa *et al.*, 2008; USDA, 2016) and across the globe (Marini *et al.*, 2012; Hlásny and Turčáni, 2013), influenced in large part by climate change and associated extreme weather events like drought (Anderegg *et al.*, 2015). Many severely affected areas are also fire-dependent plant communities, raising concerns about increased risk of severe wildfire following these outbreaks (Jenkins *et al.*, 2008; Collins *et al.*, 2012; Evans, 2012). Nonetheless, most studies examining *Dendroctonus* spp. outbreaks in the western U.S. suggests fire risk is not significantly altered (Black *et al.*, 2013; Hart *et al.*, 2015), perhaps due to the prolonged period of snag decomposition in unmanaged areas (which prevents immediate, high loads of downed woody debris on the forest floor) and the spatially heterogeneous pattern characteristic of bark beetle outbreaks (Leuschner, 1981). Instead, extremely dry conditions related to changing climate regimes are

believed to be the primary driver of fire risk in these areas (Black *et al.*, 2013). However, there is still uncertainty regarding the effects of bark beetle-caused mortality on fire hazard in different forest types around the globe, particularly in combination with drought, and further research is needed to inform appropriate management responses to these infestations.

Southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman), a native bark beetle historically affecting pine forests in the southeastern U.S., has not been previously correlated with increased occurrence of large-scale fires in its native range. Although several studies and reports detail incidences where fire occurred in recently infested beetle-killed stands (Kulhavy and Ross, 1988; Lynch *et al.*, 2006), the high spatial variability of infestations across the landscape has likely limited the occurrence of large-scale fires following outbreaks. At localized scales in the southeastern U.S., SPB infestations have resulted in increased fuel loading and shifts in overstory structure, with projected risks of increased fire severity (Evans, 2012) or abundant canopy fuels immediately following mortality (Page, 2014). Droughty or dry conditions have also been implicated in increasing fire risk following infestation (Evans, 2012; Black *et al.*, 2013). This previous work and the recent expansion of SPB into the northeastern United States (Weed *et al.*, 2013; Lesk *et al.*, 2017) adjacent to highly urbanized areas has created the need for localized assessments of how SPB infestation in this novel range may influence levels of fuel loading, particularly as periods of drought may create extremely high fire risk even in normally moist regions like the northeast.

Many of the areas impacted by SPB in the northeast are fire-dependent pine barren communities (Little, 1979; NJFAC, 2006) existing along the wildland-urban interface. Wildfire suppression in many such areas over the past century, in concert with recent intensive development (Dombeck *et al.*, 2004; Troy and Kennedy, 2007), have increased the risk of wildfires in and around human population centers (Arno and Allison-Bunnell, 2002). Little is known about how a new disturbance regime, SPB and associated suppression management, will influence wildfire risk in the northeastern United States. As such, an evaluation of the effects of SPB and associated management on fuel loading is of great importance (Little, 1979) to public safety and informed land management.

Data regarding the density, diameter, and vertical structure of fuels, in combination with other factors such as local climate and soils, are used to estimate the hazard and potential behavior or severity of wildfire in a given forest (Anderson, 1982; Riba and Terridas, 1987; Whelan, 1995). Fire spread and increased severity are facilitated by denser fuels (increased fuel loading). Smaller fuels (e.g., twigs, brush, or grass) catch and spread fire more readily, while larger fuels may create more unstable fire conditions where severity and flame height increase rapidly. Low-lying fuels, or ground fuels, are more easily ignited by surface fires, while ladder fuels (those providing a fuel pathway from ground to tree canopy) can influence fire behavior and lead to crown fires (Anderson, 1982). Information regarding these fuels characteristics would be highly informative in estimating the relative change in fire hazard and behavior within SPB-infested stands.

Data detailing fire hazard in pitch pine stands following SPB infestation or management are currently unavailable. Evans (2012) predicted increases in fuel loading and hardwood importance in loblolly stands following SPB infestation, but the most extreme fire risk was only predicted in extremely dry conditions and eight years following SPB outbreak. However, Bried *et al.* (2015) describe the northeastern pine barrens as having higher fire risk and severity associated with fire suppression policies due to recent increases in tree densities in these areas (Dombeck *et al.*, 2004; Troy and Kennedy, 2007). Understanding how SPB infestation will impact fire risk within this context will inform fuels management in the northeast, particularly in areas like Cape Cod and Long Island with a complex wildland-urban interface. This study sought to evaluate the effect of SPB and suppression management on fuel density, structure, and composition in affected Long Island forests in the form of 1) live fuels, 2) dead fuels, including coarse woody debris and snags, and 3) potential ground and ladder fuels. Results are intended to assist land managers in developing strategies to address SPB infestations while mitigating fire hazard and public safety concerns.

3.3. Methods

3.3.1. Study Area and Site Selection

Pitch pine forests represent the primary fire-dependent forest communities in the northeastern United States and often occupy sandy, glacial outwash soils in coastal and interior portions of this region. The Long Island Pine Barrens are one of the larger areas of pitch pine forests comprising 22,000 HA of conserved land and 19,000 HA of

regulated development, and is a fairly representative example of the ecology of, and development issues surrounding, pitch pine forests in the northeast (Tuininga *et al.*, 2002; DeGraaf *et al.*, 2006; USCB, 2009; King *et al.*, 2011). Nutrient poor, sandy soils (Reiners, 1965) and an extensive fire history appear to have maintained pitch pine forest cover across some portion of Long Island for thousands of years (Gaffney *et al.*, 1995), the extent of which expanded greatly in following European settlement (Kurczewski and Boyle, 2000). The arrival of SPB in 2014 has created a novel disturbance dynamic in which trees are added to the fuel pool through beetle-caused tree mortality and/or suppression efforts. This has generated concerns regarding the impacts of this range expansion on fire hazard and the general ecology of the northeastern pine barrens (Lesk *et al.*, 2017).

Study sites were selected as described in Chapter 2 to represent six possible combinations of cover type (pitch pine or pitch pine-oak), SPB impacts (control or infested), and suppression management (unmanaged or suppressed) (n=26). Selected forests were located across the south shore of Suffolk County and were evenly distributed between the two primary pitch pine forest types being affected by SPB on Long Island (e.g. pitch pine and mixed pitch pine-oak).

3.3.2. Field Methods

In order to assess the density of aboveground fuels prior to and following SPB infestation or infestation and suppression management, three to four 400 m^2 plots were located in each stand. An outline of selection and placement methods for plots is in Chapter 2. Species, diameter at breast height (DBH; 1.37 m), and canopy class were

recorded for each tree, and height was recorded for all dead standing trees (DBH ≥ 7.6 cm) rooted within the 400 m^2 plot. Downed coarse woody debris (CWD) and fine woody debris (FWD) fuel loading was sampled at each plot along three transects using the line-intercept method (Brown, 1971). Specific details of the sampling protocol are in Chapter 2. Where available, two dominant or codominant pitch pines were sampled at breast height from each stand using an increment borer to determine age for estimation of site index. Core samples were mounted, sanded, and aged according to standard dendrochronological techniques (Stokes and Smiley, 1996). In suppressed stands where sufficient standing pitch pines were not available two cut pine stumps were aged by counting annual rings.

Aboveground live and dead biomass was calculated following the general protocols used in the Fuels Extension of the Forest Vegetation Simulator, Northeast Variant (FVS FFE). For live tree biomass, tree volume was calculated for each species using species-specific equations (Honer, 1967; Smith and Weist, 1982; Green and Reed, 1985; Clark *et al.*, 1986) and converted to biomass based on the specific gravity for each species. Downed coarse and fine woody debris volumes were estimated from line-intercept diameters based on van Wagner (1968) and converted to biomass using species and decay-class specific wood density values (Harmon *et al.*, 2008). Canopy biomass of living trees was estimated through the use of component ratio equations found in Jenkins *et al.* (2003). Shrub, herb, litter, and duff biomass estimates were based on those provided for pitch pine-oak communities in Rebain (2010). Fuel measurements were compiled into several fuel classifications, including live (i.e., live

tree bole and canopy, shrubs, and herbs), dead (i.e., DWD, snag boles, litter, and duff), and potential ground-fire or ladder fuels (litter, duff, FWD, and overtopped or intermediate snags and live trees) following Bried *et al.* (2015). Dead fuels included fine 1-100-hour fuels (e.g. FWD, litter, and duff), and coarse fuels (e.g. CWD and snags, all 1000+-hour fuels).

3.3.3. Statistical Analyses

The impacts of SPB and suppression management on fire hazard in pitch pine and pine-oak forests of Long Island were examined using mixed model analysis of variance (ANOVA) through generalized linear models (GLM) in R (Team, 2015). Management regime (control, unmanaged infested, or suppressed) was treated as a fixed effect in GLMs and models were run separately for pine-oak and pitch pine forests to develop forest type-specific estimates of management impacts on fuels. In cases where a significant treatment effect was detected, a Tukey's post hoc test was used to identify differences between individual treatments. Negative binomial distributions were specified for green fuels and dead fuels data to correct for non-normal, right-skewed distributions. An alpha level of 0.05 was used for all tests.

3.4. Results

SPB infestation decreased the density of live fuels in both cover types (Table 3.1). For pitch pine forests, control areas had significantly higher live fuel densities than other treatments ($P<0.0001$), whereas suppressed stands were not significantly different from unmanaged stands ($P=0.12$). Control pine-oak stands also had a

significantly higher amount of live fuels ($P=0.02$) than unmanaged stands, whereas there was no difference in biomass of live fuels between suppressed and control stands or suppressed and unmanaged stands ($P>0.10$, see Table 1).

Dead fuel density was significantly higher in suppressed and unmanaged pine stands compared to control plots ($P<0.0001$). In mixed pine-oak forests, unmanaged stands had a significantly greater amount of dead fuels than controls and areas that were suppressed ($P<0.005$). Suppressed stands had a moderate biomass of dead fuels, higher than controls ($P=0.02$), but lower than unmanaged stands ($P=0.005$). The increase in dead fuels in both forest types following suppression management was largely due to an increase in CWD (Figure 3.1).

Ground and ladder fuels were not significantly impacted by treatment ($P>0.1$), although there was a general trend of decreasing fuel densities with increasing disturbance severity in both forest types (see Table 3.1).

Table 3.1. Biomass (megagrams ha^{-1}) of fuels by treatment and cover type (mean ± SE). Treatment combinations with the same letters were not significantly different within the given forest cover type and fuel type based on Tukey's HSD alpha=0.05.

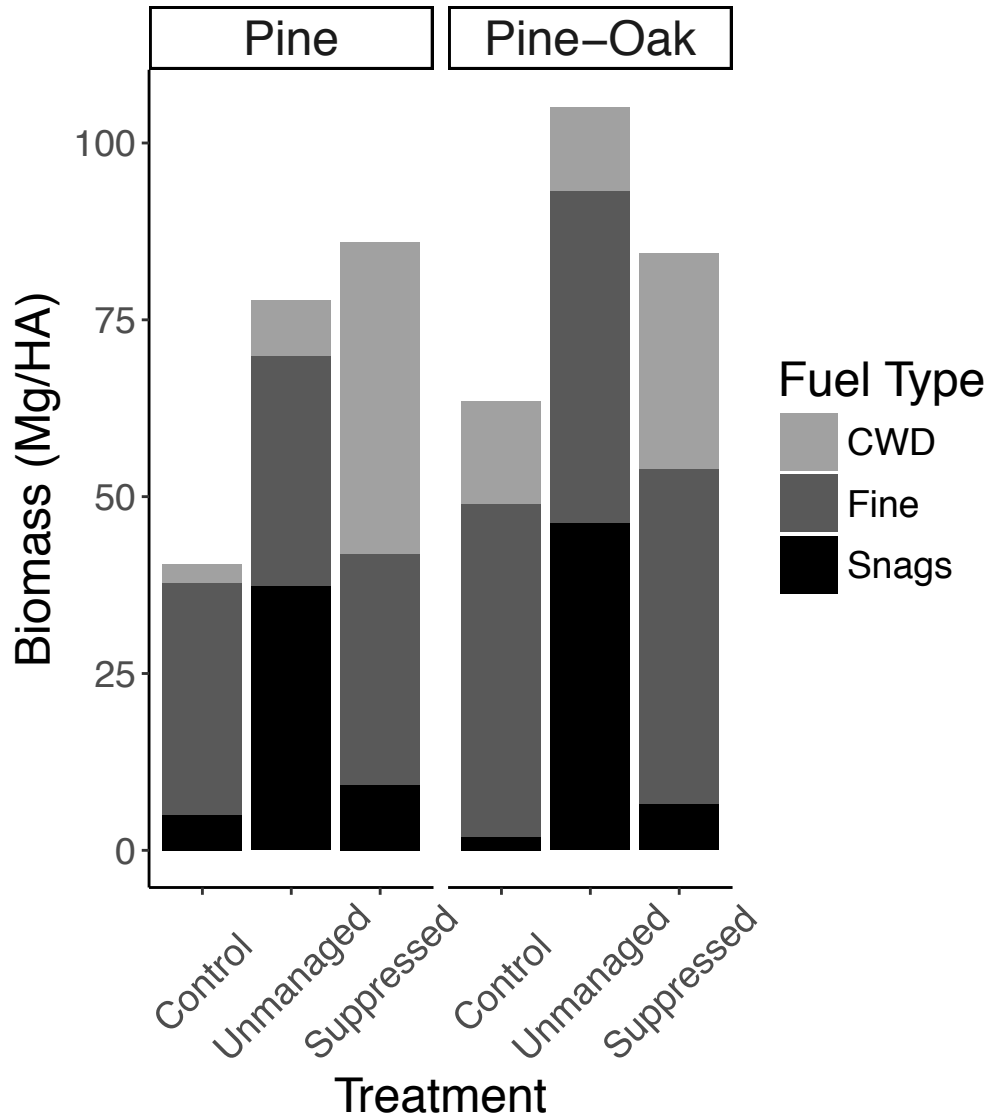| Treatment	Live Fuels		Dead Fuels		Ground and Ladder Fuels	
	Pine-Oak	Pine	Pine-Oak	Pine	Pine-Oak	Pine
Control	112.0±19.5[a]	97.1±6.6[a]	63.5±2.4[c]	40.4±2.5[b]	90.5±14.6[a]	70.7±4.9[a]
Unmanaged	62.0±5.1[b]	47.3±5.7[b]	105.5±5.4[a]	77.8±5.1[a]	81.7±5.7[a]	62.0±4.3[a]
Suppressed	89.8±13.2[ab]	33.2±4.2[b]	84.1±5.3[b]	87.4±6.7[a]	79.4±3.2[a]	58.2±3.4[a]

Figure 3.1. Biomass (megagrams ha⁻¹) of fine fuels, coarse woody debris, and snags in each cover type. Fine fuels include fine woody debris, litter, and duff.

3.5. Discussion

The increased extent and severity of bark beetle outbreaks in fire-dependent

conifer forests across North America has generated concerns regarding subsequent

impacts on wildfire risk. SPB-caused mortality on Long Island increased fuel loading through the creation of snags and suppression management transformed these vertical fuels into primarily ground-level CWD. Results from this study are consistent with other studies of mountain pine beetle and SPB infestations that describe increased fuel loading in affected stands (Collins *et al.*, 2012; Evans, 2012; Saab *et al.*, 2014) and the expectation of increased fuels for several decades due to snag decomposition (Collins *et al.*, 2012). Given the immediate, short-term nature of this study, future work is needed to determine how climate patterns and associated vegetation development in these areas might influence long-term wildfire risk in SPB-impacted pine barrens.

The influence of SPB-caused tree mortality and suppression management on fuel loading varied by forest type. In pitch pine stands, there was no difference in fuel loading between unmanaged and suppressed stands, with both treatments resulting in a decrease in live and increase in dead fuels relative to controls. In contrast, dead fuels in mixed pine-oak stands were significantly greater in unmanaged stands relative to suppressed stands and controls. Live fuels were also lower in unmanaged stands than controls, whereas there was no difference in live fuel loads between suppressed and control stands. This difference in live fuel abundance likely reflects the increase in sprout-origin hardwoods and other disturbance-adapted species following suppression management (Chapter 2). The greater amount of dead fuels in unmanaged pine-oak stands relative to suppressed areas may be due to the higher amounts of SPB-induced mortality in these areas resulting in higher snag biomass (see below).

SPB infestation increased dead fuel levels in both forest types, mostly in the form of snags, whereas suppression management changed the structure of coarse fuels by transforming these snags largely into CWD on the forest floor. The increase in CWD biomass observed following suppression may alter fire fuels dynamics by making large fuels more accessible to ground fires (Anderson, 1982). Nonetheless, CWD is less flammable than small-diameter snags, FWD, brush, and leaf litter, due to a large diameter, low surface-area-to-volume ratio, and increased moisture retention (Knapp *et al.*, 2005). The removal of this vertical structure may serve to decrease crowning risk in these stands (Anderson, 1982; Jenkins *et al.*, 2008). As such, the short-term increases in ground fire severity need to be weighed against the potential for increased dead ladder fuels in unmanaged areas.

While prescribed fire could aid managers in regenerating pitch pine and decreasing the risk of extreme wildfire in the near future, fire of sufficient severity to regenerate pine may not be a viable management tactic in dry forests with a heavy fuel load. Prescribed fires are used in many fire-dependent forests to establish regeneration of fire-tolerant or shade-intolerant species (Arthur *et al.*, 1998; Brose and Waldrop, 2000). Fire not only opens cones of serotinous pines, including pitch pine, it can also decrease vegetative competition, increase sunlight availability, and create mineral soil exposure, all of which are necessary for pitch pine regeneration (Fowells, 1965; Burns and Honkala, 1990). However, prescribed fire in the northeast is generally conducted during the dormant season and is often not of high enough severity to sufficiently reduce hardwood species competition in the long term. In this case fire may be used to

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maintain a component of pitch pine where it already exists (Little and Moore, 1949;

Little, 1979; Arthur *et al.*, 1998; Motzkin *et al.*, 1999) while establishment of pitch pine

regeneration through plantings and/or mechanical site preparation during mast years

may be required in pitch pine-oak stands (Little and Moore, 1952). In addition, high

fuel loading and the presence of ladder fuels (particularly prevalent in our unmanaged

stands) may create unpredictable or severe fire conditions (Anderson, 1982; Jenkins *et

al.*, 2008), suggesting that fuels reduction treatments, such as thinning from below and

reduction of ladder fuels (Brown *et al.*, 2003; Agee and Skinner, 2005; Bried *et al.*,

2015), may be necessary prior to prescribed fire. Our data suggests unmanaged SPB-

infested stands in particular may require ladder fuel reduction treatments, while ground

fuel reduction may be pertinent in suppressed stands to remove the sudden influx of

CWD. Prescribed burns may thereafter be utilized to maintain pitch pine as a

component of the forest throughout its development (Little and Moore, 1949).

More in-depth fire hazard assessment is needed to elucidate the complex and

long-term consequences of SPB infestation and suppression management on fuel

loading and structure and the appropriateness of prescribed fire. Suppression in pitch

pine stands may increase downed fuel loading in the immediate area, but the results

presented do not describe the fuel dynamics of the surrounding forest. The effects of

limiting the spatial extent of SPB infestation via suppression on forest-wide fire hazard

are still uncertain. Fire risk within the surrounding forest may be functionally lowered

by suppressing small-scale infestations and preventing widespread impacts.

Additionally, even greater levels of coarse dead biomass appear in the absence of

management in mixed pine-oak stands in the form of snags, suggesting suppression may be particularly beneficial in these forests to increasing public safety and simultaneously decreasing fire risk. Due to the high variation in forest composition and environmental conditions in the northeast and the unique fire history of the Long Island Pine Barrens (Jordan *et al.*, 2003) these findings must also be applied with caution beyond the study area.

3.6. Conclusion and Management Implications

SPB increased fuel loading relative to control stands, and suppression shifted the vertical structure of fuels, potentially increasing localized fire hazard. Mixed pine-oak stands may benefit from suppression by experiencing slightly decreased overall dead fuel loading. Further study is needed to elucidate the long-term consequences of SPB infestation and suppression management on fuel loading and fire hazard, as fuels decompose and vegetation develops in impacted areas. However, our results may be used in concert with other management considerations to determine the appropriateness of suppression in different forest cover types. Increased fire frequency or severity in Long Island forests would be a concern for adjacent communities, but might provide future opportunities for pitch pine regeneration.

Regular use of low-to-moderate-intensity prescribed fire may be successful in maintaining a component of pitch pine within mixed pitch pine-oak forests and preparing the seedbed for pine regeneration in existing pitch pine forests. Our results suggest that the increased fuel loading in unmanaged and suppressed stands may

require fuels reduction treatments prior to prescribed burns. Fuels reduction treatments in combination with thinning from below may be most useful in preparing pitch pine-oak stands for regeneration of pine. In the absence of fuels reduction, unmanaged and suppressed stands may possess an elevated risk of severe wildfire based on the increased biomass of snags and CWD. Fuels treatments in these stands may be costly and time intensive, but may simultaneously decrease the risk of expensive and hazardous wildfires while promoting regeneration of pitch pine and promoting ecosystem-level heterogeneity. More in-depth fire hazard evaluations may be used to guide stand-specific management plans.

CHAPTER 4: SUMMARY

4.1. Conclusions, Management Implications, and Limitations

This study provided the first evaluation of the effects of SPB and subsequent suppression management on forest structure, composition, regeneration, and fuel loading on Long Island, New York in an attempt to inform future management of southern pine beetle (SPB; *Dendroctonus frontalis* Zimmerman) in the Northeast. SPB shifted overstory tree composition following host tree mortality, decreased the importance of overstory pitch pine relative to preexisting hardwood species, and furthered successional trends toward hardwood dominance. In pine-dominated forests SPB and suppression increased understory diversity and the representation of pitch pine seedlings; however, pine regeneration densities were low suggesting non-pine species are likely to now predominate in these areas. Findings also indicate that heavy deer browsing pressure may also limit regeneration of hardwood species and protection measures for seedlings may be necessary.

Our results indicate that pitch pine regeneration is not likely to establish in SPB-impacted areas without the aid of additional management techniques such as planting and/or prescribed burning, even in stands already dominated by pitch pine. Pitch pines only accounted for 5.7% of seedlings and saplings tallied, averaged across all plots, and no saplings were tallied in pine-oak forests. Pitch pine was observed at the highest densities in suppressed stands, where other species of seedlings were at their lowest densities. This suggests pitch pine may have the greatest opportunity to regenerate in

pitch pine stands that have experienced suppression or some other disturbance in addition to infestation and is consistent with the natural regeneration ecology of this species, including the importance of mineral soil exposure and full sun required for seedling establishment (Burns and Honkala, 1990). Infestation alone is unlikely to create these necessary conditions and previous work examining SPB impacts in the New Jersey Pine Barrens documented a similar low level of immediate regeneration of pine except in stands where felled trees were chipped and soil disturbance occurred (Clark *et al.*, 2017). Based on these results, we may expect to see a dramatic decline in importance of pitch pine in many SPB-impacted stands on Long Island and the legacy effects of SPB may be felt for decades to come.

DWD increased in response to suppression management, while SPB-killed trees remained as snags in the absence of management. In pitch pine stands, suppression decreased snag basal area below its original density. These patterns of fuel development and restructuring following management are fairly consistent with results from other bark beetle infestations (Collins *et al.*, 2012; Evans, 2012; Saab *et al.*, 2014). Differences in DWD loading between treatments within mixed pine-oak forests were insignificant however, further suggesting that impacts of SPB to mixed stands are less dramatic than in host-dominated forests. Pitch pine forests displayed significantly higher DWD volumes in suppressed stands relative to both other treatments.

The fuels conditions in these stands have important implications for localized fire hazard and behavior and can inform the appropriateness of potential management strategies. Forest fuel conditions were impacted by SPB infestation

through increases in snags in unmanaged areas and increases in horizontal ground fuels, namely coarse woody debris, in areas experiencing suppression. Both conditions present different fire hazard conditions than control stands, with suppression stands likely having greater localized fire hazard and flaring likelihood due to grounded snag biomass, but perhaps lower crowning potential due to decreased ladder fuel density relative to unmanaged stands. Of the two forest types examined, mixed pine-oak stands appeared to benefit from suppression through slightly decreased fuel loading relative to SPB-impacted areas. Prescribed fire regimes preceded by initial fuels reduction treatments may successfully regenerate pitch pine in pure stands and maintain pine as a component in mixed pitch pine-oak forests. Additional thinning of pitch pine-oak stands may be required to provide sufficient sun for regeneration, and thinning from below should further reduce the risk of crowning via ladder fuels.

There were several important limitations to this study, including: 1) the limited duration of data collection, 2) a relatively small sample size, 3) plot location procedures, and 4) unstudied potential confounding environmental and historical factors. One season of data allows us to elucidate some short-term effects of SPB and suppression within the study system, but does not permit long-term projection, particularly without the use of modeling. Additionally, at the time of study SPB had severely impacted several large forested areas in the Long Island Pine Barrens, but the majority of infestations identified were not large enough to permit three plots, and therefore stands selection was limited by availability. Control stands were comprised of forests adjacent to, and generally similar in composition and structure to affected forests but with no obvious SPB infestation. Due to

the prevalence of small (i.e. 0-10 trees) infestations, particularly in close proximity to large outbreaks, the potential pool of control stands was limited. Once affected forests were selected, we defined a "stand" as the area impacted by SPB in order to truly assess the effects of SPB within an infestation, to effectively compare treatments, and to prevent sampling of stand edges. This may lead to overestimating the impacts of SPB to the wider forest if findings are applied too broadly. Finally, historical land-use practices and underlying environmental factors such as slight variations in soil type or moisture may have influenced species composition or stand development prior to SPB and further studies should seek to increase the underlying variation in site conditions and the number of replicates, if possible.

Further study is needed to elucidate the long-term consequences of SPB infestation and suppression management on pitch pine cover, forest development, fuel loading, and fire hazard. However, our results may be used in concert with other management considerations to determine the appropriateness of suppression in different forest cover types. 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). Therefore, active management may prove an even more important consideration for maintaining rare northeastern pine barrens ecosystems and dependent biodiversity.

REFERENCES

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211, 83-96.

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, D., Bentz, B., Hood, S., Lichstein, J.W., Macalad, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J.D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist 208, 674-683.

Anderson, H.E., 1982. Aids to determining fuel models for estimating fire behavior. In. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Arno, S.F., Allison-Bunnell, S., 2002. Fire-prone forests: can we adapt to them? In, Flames in our forest: disaster or renewal? Island Press, Washington, DC, USA.

Arthur, M.A., Paratley, R.D., Blankenship, B.A., 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. The Journal of the Torrey Botanical Society 125, 225-236.

Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. The Science of the Total Environment 262, 263-286.

Belanger, R.P., 1980. Silvicultural guidelines for reducing losses to the southern pine beetle. In: Thatcher, R.C., Searcy, J.L., Coster, J.E., Hertel, G.D.E. (Eds.), The southern pine beetle. USDA Forest Service, pp. 165-177.

Black, S.H., Kulakowski, D., Noon, B.R., DellaSala, D.A., 2013. Do bark beetle outbreaks increase wildfire risks in the Central U.S. Rocky Mountains? Implications from recent research. Natural Areas Journal 33, 59-65.

Bried, J.T., Gifford, N.A., Robertson, K.M., 2015. Predicted crown fire risk adds incentive to restore open-canopy pine barrens at the wildland-urban interface. Journal of Sustainable Forestry 34, 147-167.

Brose, P.H., Waldrop, T.A., 2000. Using prescribed fire to regenerate table mountain pine in the Appalachian Mountains. In: Moser, W.K., Moser, C.E. (Eds.), Fire and forest ecology: innovative silviculture and vegetation management. Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida, USA, pp. 191-196.

Brown, J.K., 1971. A planar intersect method for sampling fuel volume and surface area. Forest Science 17, 96-102.

Brown, J.K., 1974. Handbook for inventorying downed woody material. U.S. Forest Service General Technical Report INT-16. In, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Brown, J.K., Reinhardt, E.D., Kramer, K.A., 2003. Coarse woody debris: management benefits and fire hazard in the recovering forest. In. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America: 1. conifers, 2. hardwoods. In, US Forest Service Agriculture Handbook. USDA Forest Service, Washington D. C., USA.

Carlson, A.R., Sibold, J.S., Assal, T.J., Negrón, J.F., 2017. Evidence of compounded disturbance effects on vegetation recovery following high-severity wildfire and spruce beetle outbreak. PLoS ONE 12, e0181778.

Carroll, A.L., Taylor, S.W., Regniere, J., Safranyik, L., 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore, T.L., Brooks, J.E., Stone, J.E. (Eds.), Challenges and solutions: proceedings of the Mountain Pine Beetle Symposium. Information Report BC-X-399. Canadian Forest Service, Pacific Forestry Centre, Kelowna, British Columbia, Canada, pp. 221-330.

Clark, A.I., Phillips, D.R., Frederick, D.J., 1986. Weight, volume, and physical properties of major hardwood species in the Piedmont. In. Southeastern Forest Experiment Station, Asheville, North Clemson, South Carolina, USA.

Clark, K.L., Ayres, M.P., Aoki, C., Wengrowski, E., Peterken, J., 2017. Impact of southern pine beetle on forest structure and fuel loading in a wildfire-prone landscape. In: Potter, K.M., Conkling, B.L. (Eds.), Forest health monitoring: national status, trends, and analysis 2016. General technical report SRS-222. USDA Forest Service, Asheville, North Carolina, USA.

Clarke, S.R., Novak, J.T., 2009. Southern pine beetle. U.S. Forest Service forest insect and disease leaflet 49. In, Pacific Northwest Region, Portland, Oregon, USA.

Coleman, T.W., Clarke, S.R., Meeker, J.R., Rieske, L.K., 2007. Forest composition following overstory mortality from southern pine beetle and associated treatments. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 38, 1406-1418.

Coleman, T.W., Meeker, J.R., Clarke, S.R., Rieske, L.K., 2008. The suppression of *Dendroctonus frontalis* and subsequent wildfire have an impact on forest stand dynamics. Applied Vegetation Science 11, 231-242.

Collins, B.J., Rhoades, C.C., Battaglia, M.A., Hubbard, R.M., 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. Forest Ecology and Management 284, 260-268.

Collins, B.J., Rhoades, C.C., Hubbard, R.M., Battaglia, M.A., 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. Forest Ecology and Management 2011, 2168-2175.

Connor, R.N., Rudolph, D.C., 1995. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. The Wilson Bulletin 107, 81-92.

Côté, S.D., Rooney, T.P., Tremblay, J., Dussault, C., Waller, D.M., 2014. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35, 113-147.

CPBJPPC, Central Pine Barrens Joint Planning and Policy Commission, 1995. Central Pine Barrens Comprehensive Land Use Plan. In, Great River, New York, USA.

Cullingham, C.I., Cooke, J.E.K., Dang, S., Davis, C.S., Cooke, B.J., Coltman, D.W., 2011. Mountain pine beetle host-range expansion threatens the boreal forest. Molecular Ecology 20, 2157-2171.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simerloff, D., Swanson, D.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. BioScience 51, 723-734.

DeGraaf, R.M., Yamasaki, M., Leak, W.B., Lester, A.M., 2006. Technical guide to forest wildlife habitat management in New England. University Press of New England, Hanover, New Hampshire, USA.

Dombeck, M.P., Williams, J.E., Wood, C.A., 2004. Wildfire policy and public lands: integrating scientific understanding with social concerns across landscapes. Conservation Biology 18, 883-889.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345-366.

Duncan, R.S., Linhoss, J.E., 2005. Regeneration of virginia pine (*Pinus virginiana*) following southern pine beetle (*Dendroctonus frontalis*) outbreak in the Sipsey Wilderness, Alabama. Forest Ecology and Management 212, 65-74.

Evans, J., 2012. Fuel dynamics in southern pine beetle-killed stands and their implication to fire behavior. In, Forest Resources. Clemson University, p. 134.

Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetative management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238, 24-53.

Fowells, H.A., 1965. Silvics of forest trees of the United States. In, Agriculture Handbook.

Gaffney, R.J., F. J. Grucci, J., Cannuscio, V., Cowen, R.E., Stark, J.R., 1995. Central Pine Barrens comprehensive land use plan. In. Central Pine Barrens Joint Planning and Policy Commission, Great River, New York, USA.

Gill, J.D., Healy, W.M., 1974. Shrubs and vines for Northeastern wildlife. In, General Technical Report. USDA Forest Service, Northeastern Forest Experiment Station.

Glitzenstein, J.S., Streng, D.R., 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. Natural Areas Journal 23, 22-37.

Graham, R.T., McCaffrey, S., Jain, T.B., 2004. Science basis for changing forest structure to modify wildfire behavior and severity. In. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA, p. 43.

Green, E.J., Reed, D.D., 1985. Compatible tree volume and taper functions for pitch pine. Northern Journal of Applied Forestry 2, 14-16.

Grisez, T.J., 1960. Slash helps protect seedlings from deer browsing. Journal of Forestry 58, 385-387.

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., 2008. Woody detritus density and density reduction factors for tree species in the United States: a synthesis. U.S. Forest Service General Technical Report NRS-29. In, Newtown Square, Pennsylvania, USA.

Harrod, J.C., Harmon, M.E., White, P.S., 2000. Post-fire succession and the 20th century reduction in fire frequency on xeric southern Appalachian sites. Journal of Vegetation Science 11, 465-472.

Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences 112, 4375-4380.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12, 450-455.

Hlásny, T., Turčáni, M., 2013. Persisting bark beetle outbreak indicates the unsustainability of secondary Norway spruce forests: case study from Central Europe. Annals of Forest Science 70, 481-491.

Honer, T.G., 1967. Standard volume tables and merchantable conversion factors for the commercial tree species of Central and Eastern Canada. In. Forest Management Research Services Institute, Ottawa, CA, p. 21p.

Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a Northern Hardwood forest. Ecological Applications 13, 98-118.

Hunn, J.R., 2007. Retention of logging debris to reduce deer browsing and promote forest regeneration. In, College of Agriculture and Life Sciences, Department of Natural Resources. Cornell University.

Jenkins, J.C., Aber, J.D., Canham, C.D., 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 29, 630-645.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. Journal of Forest Science 49, 12-35.

Jenkins, M.J., Hebertson, E., Page, W., Jorgensen, C.A., 2008. Bark beetles, fuels, fires, and implications for forest management in the Intermountain West. Forest Ecology and Management 254, 16-34.

Jordan, M.J., Patterson, W.A., Windisch, A.G., 2003. Conceptual ecological models for the Long Island pitch pine barrens: implications for managing rare plant communities. Forest Ecology and Management 185, 151-168.

Kayes, L.J., Tinker, D.B., 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. Forest Ecology and Management 263, 57-66.

King, D.I., Schlossberg, S., Brooks, R.T., Akresh, M.E., 2011. Effects of fuel reduction on birds in pitch pine-scrub oak barrens of the United States. Forest Ecology and Management 261, 10-18.

Knapp, E.E., Keeley, J.E., Ballanger, E.A., Brennan, T.J., 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. Forest Ecology and Management 208, 383-397.

Knebel, L., Wentworth, T.R., 2007. Influence of fire and southern pine beetle on pine-dominated forests in the Linville Gorge Wilderness, North Carolina. Castanea 72, 214-225.

Kulhavy, D., Ross, W.G., 1988. Southern pine beetle and fire in wilderness areas: the Kisatchie Hills Wilderness, Kisatchie National Forest. Stephen F. Austin State University Faculty Publications.

Kurczewski, F.E., Boyle, H.F., 2000. Historical changes in the pine barrens of central Suffolk County, New York. Northeastern Naturalist 7, 95-112.

Lesk, C., Coffel, E., D'Amato, A.W., Dodds, K., Horton, R., 2017. Threats to North American forests from southern pine beetle with warming winters. Nature Climate Change.

Leuschner, W.A., 1981. Impacts of the southern pine beetle. In: Thatcher, R.C., Searcy, J.L., Coster, J.E., Hertel, G.D. (Eds.), The southern pine beetle.

Leuschner, W.A., Burkhart, H.E., Spittle, G.D., Ragenovich, I.R., Coulson, R.N., 1976. A descriptive study of the host site variables associated with occurrence of *Dendroctonus frontalis* Zimm. in east Texas. Southwestern Entomology 1, 141-149.

Little, S., 1979. Fire and plant succession in the New Jersey Pine Barrens. In: Forman, R.T.T. (Ed.), Pine barrens: Ecosystem and landscape. Rutgers University Press, New Brunswick, New Jersey, USA.

Little, S., Moore, E.B., 1949. The ecological role of prescribed burns in the pine-oak forests of southern New Jersey. Ecology 30, 223-233.

Little, S., Moore, E.B., 1952. Mechanical preparation of seedbeds for converting oak-pine stands to pine. Journal of Forestry 50, 840-844.

Little, S., Moorhead, G.R., Somes, H.A., 1958. Forestry and deer in the Pine Region of New Jersey. In. USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Logan, J.A., Macfarlane, W.W., Willcox, L., 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications 20, 895-902.

Lorimer, C.G., 1984. Methodological considerations in the analysis of forest disturbance history. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 15, 200-213.

Lorimer, C.G., White, A.S., 2003. Scale and frequency of natural disturbances in the northeastern US: Implacations for early successional forest habitat and regional age distributions. Forest Ecology and Management 185, 41-64.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56, 356-405.

Lynch, H.J., Renkin, R.A., Crabtree, R.L., Moorcroft, P.R., 2006. The influence of previous mountain pine beetle *(Dendroctonus ponderosae)* activity on the 1988 Yellowstone Fires. Ecosystems 9, 1318-1327.

Maine, J.D., Leuschner, W.A., Tipton, A.R., 1980. A qualitative analysis of the southern pine beetle's wildlife impact. In. Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

Marini, L., Ayres, M.P., Battisti, A., Faccoli, M., 2012. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. Climate Change 115.

Matiu, M., Bothmann, L., Steinbrecher, R., Menzel, A., 2017. Monitoring succession after a non-cleared windthrow in a Norway spruce mountan forest using webcam, satellite vegetation indices and turbulent CO_2 exchange. Agricultural and Forest Meteorology 244-245, 72-81.

Matonis, M.S., Walters, M.B., Millington, J.D.A., 2011. Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. Forest Ecology and Management 262, 286-298.

McCabe, L., 2011. Analyzing tree regeneration as an indicator of the health of the Long Island Pine Barrens. In, Environmental Protection Division, Pre-Service Teacher Internship Program. Hofstra University, Hempstead, New York, USA.

McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate analysis of ecological data. In. MjM Software Design, Gleneden Beach, Oregon, USA.

Motzkin, G., Patterson, W.A., Foster, D.R., 1999. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. Ecosystems 2, 255-273.

Neuvonen, S., Niemelä, P., Virtanen, T., 1999. Climatic change and insect outbreaks in boreal forests: the role of winter temperatures. Ecological Bulletins 47, 63-67.

NJFAC, Forestry Advisory Committee, State of New Jersey Pinelands Commission, 2006. Recommended forest management practices. In, New Lisbon, New Jersey, USA.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58, 123-138.

Nowak, J.T., Meeker, J.R., Coyle, D.R., Steiner, C.A., Brownie, C., 2015. Southern Pine Beetle Infestations in Relation to Forest Stand Conditions, Previous Thinning, and Prescribed Burning: Evaluation of the Southern Pine Beetle Prevention Program. Journal of Forestry 113, 454-462.

NYS, Department of Environment and Conservation, Division of Lands and Forests, Forest Health Section, 2012. Forest Health Aerial Survey Report. In, Albany, New York, USA.

Olsvig, L.S., 1980. A comparative study of northeastern pine barrens vegetation. In. Cornell University.

Olsvig, L.S., Cryan, J.F., Whittaker, R.H., 1998. Vegetational gradients of the Pine Plains and Barrens of Long Island, New York. In: Forman, R.T.T. (Ed.), Pine Barrens: Ecosystem and Landscape. Rutgers University Press, New Brunswick, New Jersey, USA.

Orwig, D.A., Foster, D.R., 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125, 60-73.

Page, W., 2014. Bark beetle-induced changes to crown fuel flammability and crown fire potential. In, Wildland Resources. Utah State University, Logan, Utah, USA.

Peck, J.E., 2010. Multivariate analysis for community ecologists: step-by-step using PC-ORD. MjM Software Design, Gleneden Beach, Oregon, USA.

Pye, J.M., Holmes, T.P., Prestemon, J.P., Wear, D.N., 2011. Economic impacts of the southern pine beetle. In: Coulson, R.N., Klepzig, K.D. (Eds.), Southern Pine Beetle II. General Technical Report SRS-140. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA, pp. 213-222.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58, 501-517.

Rebain, S.A., 2010. The Fire and Fuels Extension to the Forest Vegetation Simulator: updated model documentation. In. USDA Forest Service, Forest Management Service Center, p. 403.

Reiners, W.A., 1965. Ecology of a heath-shrub synusia in the Pine Barrens of Long Island, New York. Bulletin of the Torrey Botanical Club 92, 448-464.

Reynolds, R.T., Linkhart, B.D., Jeanson, J., 1985. Characteristics of snags and trees containing cavities in a Colorado conifer forest. In. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.

Riba, M., Terridas, J., 1987. Característiques de la resposta als incendis en els ecosistemes mediterranis. Quaderns d'ecologia aplicada 10, 63-75.

Romme, W.H., Knight, D.H., Yavitt, J.B., 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? The American Naturalist 127, 484-494.

Rozman, A., Diaci, J., Krese, A., Fidej, G., Rozenbergar, D., 2015. Forest regeneration dynamics following bark beetle outbreak in Norway spruce stands: influence of meso-relief, forest edge distance and deer browsing. Forest Ecology and Management 353, 196-207.

Russell, M.B., Woodall, C.W., Potter, K.M., Walters, B.F., Domke, G.M., Oswalt, C.M., 2016. Interactions between white-tailed deer density and the composition of forest understories in the northern United States. Forest Ecology and Management 384, 26-33.

Saab, V.A., Latif, Q.S., Rowland, M.M., Johnson, T.N., Chalfoun, A.D., Buskirk, S.W., Heyward, J.E., Dresser, M.A., 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. Forest Science 60, 1-21.

Schmid, J.M., Mata, S.A., McCambridge, W.F., 1985. Natural falling of beetle-killed ponderosa pine. In. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Smith, W.B., Weist, C.A., 1982. A net volume equation for Indiana. In. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, USA.

Smolensky, D.A., Buxton, H.T., Shernoff, P.K., 1990. Hydrologic framework of Long Island, New York. In. US Geological Survey.

Stokes, M.A., Smiley, T.L., 1996. An introduction to tree-ring dating. The University of Arizona Press, Tucson, Arizona, USA.

Swain, K.M., Remion, M.C., 1981. Direct control methods for the southern pine beetle. In: USDA Forest Service, C.F.P.R.a.D.P. (Ed.), Agriculture Handbook, p. 15.

Team, R.C., 2015. R: A language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna, Austria.

Tedrow, J.C.F., 1998. Development of pine barrens soils. In: Forman, R.T.T. (Ed.), Pine barrens: Ecosystem and landscape. Rutgers University Press, New Brunswick, New Jersey, USA.

Thatcher, R.C., Searcy, J.L., Coster, J.E., Hertel, G.D.E., 1980. The southern pine beetle. Technical Bulletin 1631. Expanded Southern Pine Beetle Research and Applications Program, USDA Forest Service.

Thistle, H.W., Peterson, H., Allwine, G., Lamb, B., Strand, T., Holsten, E.H., Shea, P.J., 2004. Surrogate pheromone plumes in three forest trunk spaces: composite statistics and case studies. Forest Science 50, 610-625.

Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. In. Secretariat of the Convention on Biological Diversity, Montreal, Quebec, CA, p. 67.

Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379, 718-720.

Ton, M., Krawchuk, M.A., 2016. The effects of disturbance history on ground-layer plant community composition in British Columbia. Forests 7.

Trần , J.K., Ylioja, T., Billings, R.F., Régnière, J., Ayres, M.P., 2007. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis* (Coleoptera: Scolytinae). Ecological Applications 17, 882-899.

Trani, M.L., Brooks, R.T., Schmidt, T.L., Rudis, V.A., Gabbard, C.M., 2001. Patterns and trends of early successional forests in the eastern United States. Wildlife Society Bulletin 29, 413-424.

Troy, A., Kennedy, R.G. (Eds.), 2007. Living on the edge: Economic, institutional, and management perspectives on wildfire hazard in the urban interface. JAI Press, Amsterdam, The Netherlands, UK.

Tuininga, A.R., Dighton, J., Gray, D.M., 2002. Burning, watering, litter quality and time effects on N, P, and K uptake by pitch pine (Pinus rigida) seedlings in a greenhouse study. Soil Biology & Biochemistry 34, 865-873.

USFWS, United States Fish and Wildlife Service, 1997. Significant habitats and habitat complexes of the New York Bight watershed. In.

USCB, Unites States Census Bureau, Population Division, 2009. Cumulative estimates of resident population change for the United States, States, and Puerto Rico: April 1, 2000 to July 1, 2009. In.

Ungerer, M.T., Ayres, M.P., Lombardero, M.J., 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae). Journal of Biogeography 26, 1133-1145.

USDA, Animal and Plant Health Inspection Service, New York Wildlife Services, 2014. Long Island white-tailed deer damage management demonstration project report. In, Rensselaer, New York, USA.

USDA, United States Forest Service, Forest Health Management, 2016. Forest Health Monitoring: National status, trends, and analysis. In: Potter, K.M., Conkling, B.L. (Eds.).

Vanderwel, M.C., Malcolm, J.R., Smith, S.M., 2006. An integrated model for snag and downed woody debris decay class transitions. Forest Ecology and Management 234, 48-59.

Weed, A.S., Ayres, M.P., Hicke, J.A., 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83, 441-470.

Whelan, R.J., 1995. The ecology of fire. The Press Syndicate of the University of Cambridge, Cambridge, UK.

Zeileis, A., Hothorn, T., 2002. Diagnostic checking in regression relationships. R News 2, 7-10.