Southern Pine Beetle: Damage and Consequences in Forests of the Mid-Atlantic Region, USA

Kenneth L. Clark, Michael Gallagher, Carissa Aoki, and Matthew Ayres

Research Forester, U.S. Department of Agriculture (USDA) Forest Service, Northern Research Station (NRS), Silas Little Experimental Forest, New Lisbon, NJ; Research Ecologist, USDA Forest Service, NRS, Silas Little Experimental Forest, New Lisbon, NJ; Lecturer in Environmental Studies, Bates College, Lewiston, ME; Professor, Department of Biological Sciences, Dartmouth College, Hanover, NH.

Abstract

Coastal pitch pine (*Pinus rigida* Mill.) forests on the Mid-Atlantic Coastal Plain are threatened by the northerly migration of southern pine beetle (*Dendroctonus frontalis* Zimmerman). We quantified effects of southern pine beetle infestations and suppression treatments on composition and structure of pine-dominated forests in the Pinelands National Reserve of New Jersey. We then used a synthesis of forest census measurements, carbon (C) flux measurements, and simulations to evaluate potential effects on C sequestration. Pine tree mortality was extensive in infested areas, resulting in 94-percent reduction in basal area and 96-percent reduction in aboveground biomass, though pine seedlings and saplings were mostly unaffected in untreated infested areas. Beetle suppression treatments (cut and leave or cut and chip) further reduced pine sapling basal area whereas hardwoods were largely unaffected. Estimated leaf area recovered to 50 percent of pre-infestation levels 3 to 5 years following infestations, and estimated annual gross ecosystem production averaged 67 percent of values in uninfested areas. Estimated net ecosystem productivity, a measure of C sequestration, was lowest for cut and leave treatments and highest for cut and chip treatments where the majority of chips were hauled offsite for commercial use. Managing for pine-oak mixedwood stands can increase resistance to future outbreaks of bark beetles and other defoliators. This paper was presented at the 2019 Joint Annual Meeting of the Northeast and Southern Forest Conservation Nursery Associations (Atlantic City, NJ, July 23–25, 2019).

Introduction

Throughout the Northeast and Mid-Atlantic regions of the United States, intermediate-age forests with median tree ages of approximately 70 to 110 years have regenerated following farm abandonment, the cessation of intensive forestry practices such as clearcutting and charcoal production, and severe wildfires (Duveneck et al. 2017, Pan et al. 2011, Stambaugh et al. 2018).

On the Atlantic Coastal Plain, continued, but less extensive, wildfire activity through the 20th century, followed by active fire management with frequent prescribed burning, has limited the regeneration of oaks (*Quercus* spp.) and other hardwoods, and favored the persistence of forests dominated by pitch pine (*Pinus rigida* Mill.) and shortleaf pine (*P. echinata* Mill.) (Forman and Boerner 1981, La Puma et al. 2013, Little 1979). These globally rare pine ecosystems encompass high plant species diversity, but are threatened by land-use change and development. In addition, increasing fire suppression limits pine regeneration and recruitment and allows encroachment of oaks and other hardwoods (Gallagher 2017, La Puma et al. 2013). Preserved areas include the Pinelands National Reserve of New Jersey, the Central Pine Barrens of Long Island, NY, and small areas in coastal New England.

In addition to their unique characteristics and high biodiversity, pine-dominated forests in the Mid-Atlantic region play important roles in providing ecosystem services. These forests are as productive as other major forest types in the Mid-Atlantic region and sequester equivalent amounts of atmospheric carbon dioxide (CO_2) on an annual basis (table 1). Net primary productivity estimated for pine-dominated, oak-hickory, and mixed oak-pine stands from the U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis (FIA) data are consistent with simulations using PnET CN, a

Table 1. Productivity of pine-dominated, oak-dominated, and mixed pine-oak forests in the Mid-Atlantic region. Data are net primary production and net ecosystem production from USDA Forest Service Forest Inventory and Analysis data, simulation results using PnET CN, and carbon (C) flux measurements in the Pinelands National Reserve.

Site	Pine-dominated T C ha^{-1} yr^{-1}	Oak-dominated T C ha^{-1} yr^{-1}	Mixed pine-oak T C ha^{-1} yr^{-1}
Net primary productivity (NPP)			
FIA data[1]	4.2 ± 0.5	4.6 ± 0.5	3.8 ± 0.6
PnET CN[2]	4.3 ± 0.3	5.0 ± 0.5	3.6 ± 0.4
Net ecosystem productivity (NEP)			
FIA data[1]	1.0 to 1.6	1.7 to 2.1	1.2 to 1.7
Flux data[3]	1.8 ± 0.3	1.8 ± 0.3	1.4

T C ha^{-1} yr^{-1} = tons of carbon per hectare per year.

[1] Forest Inventory and Analysis, [2] Pan et al. 2009, 2011, [3] Clark et al. 2010, 2018.

process-based forest productivity model (Pan et al. 2006, 2009, 2011). Estimated net ecosystem production (NEP), a measure of carbon (C) sequestration, by pine-dominated, oak-dominated, and mixed pine-oak forests across the region derived from FIA data are consistent with annual NEP values calculated from eddy covariance measurements of net exchange of CO_2 (NEE) during undisturbed years in intermediate age forests of the Pinelands National Reserve of New Jersey (table 1; Clark et al. 2010, 2018).

Disturbance regimes in intermediate-age forests throughout the Northeast and Mid-Atlantic regions are now dominated by infestations of native and non-native insects, which account for a large proportion of tree damage and mortality, while windstorms, harvest activities, and managed wildland fire have become secondary (Fei et al. 2019, Kautz et al. 2017, Kosiba et al. 2018, Lovett et al. 2016, Pasquarella et al. 2018). On the Mid-Atlantic Coastal Plain, outbreaks of gypsy moth (*Lymantria dispar* L.) have resulted in oak and other hardwood mortality in oak-dominated stands, and southern pine beetle (*Dendroctonus frontalis* Zimmerman) infestations have resulted in pine (*Pinus* spp.) mortality in pine-dominated stands over the last decade. These outbreaks have been the dominant insect-driven disturbances and have far exceeded the area impacted by wildfires or windstorms (Gallagher 2017, Heuss et al. 2019, Weed et al. 2013). Pine tree mortality caused by southern pine beetle infestations can be extensive in infested stands throughout the Southeastern United States without aggressive suppression activities (Dodds et al. 2018, Guldin 2011). Without suppression activities, infestations have resulted in increased populations of oaks and other hardwoods, thereby accelerating successional changes. Although FIA data has captured the long-term impacts of other invasive insects on host species (e.g., gypsy moth and red oak decline; Morin and Leibhold 2015, Fei et al. 2019), until recently, little information existed for changes in composition and structure in pitch and shortleaf pine stands infested by southern pine beetle (Aoki et al. 2018, Clark et al. 2017, Heuss et al. 2019; reviewed in Dodds et al. 2018).

Short-term impacts of insect infestations on ecosystem functioning in Mid-Atlantic forests are well-characterized (e.g., Clark et al. 2010, 2014, 2018; Deel et al. 2012; Renninger et al. 2014), and a number of simulation models have captured the overall dynamics of C and hydrologic cycling associated with these disturbances (Kretchun et al. 2014, Medvigy et al. 2012, Xu et al. 2017). In summary, infestations of bark beetles and defoliators initially reduce leaf area of impacted stands, causing an immediate reduction in photosynthetic capacity and autotrophic respiration, which decreases NEP and reduces evapotranspiration (Amiro et al. 2010, Clark et al. 2010, 2012, 2018). Compensatory photosynthesis by the remaining foliage, which is typically exposed to higher light levels, and the rapid cycling of nutrients from nutrient-rich frass and litter facilitates resprouting of new foliage (Curtis and Gough 2018, Hornslein et al. 2019). As a result, gross ecosystem productivity (GEP), evapotranspiration (Et), and ecosystem water use efficiency (WUE_e), defined as the amount of CO_2 assimilated per unit of water transpired, often recover rapidly following insect damage (Clark et al. 2014, Guerrieri et al. 2019). Long-term consequences of insect infestations on C fluxes have been documented less frequently. These efforts have indicated that increases in standing dead and coarse woody debris following repeated defoliation or bark beetle infestations result in increased heterotrophic respiration and a long-term depression of NEP (Clark et al. 2018, Renninger et al. 2014, Xu et al. 2017).

In this research, we quantified how infestations of southern pine beetle and two frequently employed suppression treatments affected forest composition and structure of intermediate-age, pine-dominated forests, focusing on changes to leaf area and canopy nitrogen (N) content. We then evaluated how changes in forest composition and structure potentially affect ecosystem functioning, especially C sequestration, by employing a synthesis of forest census measurements, C flux measurements, and simulation models. Finally, we addressed how changes in composition of forests impacted by southern pine beetle could affect the capacity of forests to respond to future disturbances. We suggest that management for mixedwood stands, consisting of mixtures of pine and oaks, would increase associational resistance to insect infestations, reducing impacts to continuity in ecosystem services.

Methods and Materials

Site Description

Research sites were located in upland and lowland forests in Atlantic, Burlington, Cumberland, and Ocean Counties in the Pinelands National Reserve (PNR) of southern New Jersey. The PNR is 4,452 km^2 in size and is the largest continuous forested landscape on the Mid-Atlantic Coastal Plain. Approximately 4,380 km^2 of the PNR were designated as a UNESCO Biosphere Reserve in 1988 (https://nj.gov/pinelands/reserve/). Pine-dominated, mixed-composition, and oak-dominated stands comprise the upland forests, and lowland forests are dominated by pitch pine, mixed hardwoods, and Atlantic white cedar (*Chamaecyparis thyoides* (L.) B.S.P) (McCormick and Jones 1973). Most stands have regenerated naturally following the cessation of timber harvesting and charcoal production toward the end of the 19th century, and severe wildfires throughout the 20th century (Forman and Boerner 1981, La Puma et al. 2013, Little 1979). The climate is cool temperate, with mean monthly temperatures of 0.7 and 24.6 °C in January and July, respectively (1988 to 2018; State Climatologist of New Jersey). Mean annual precipitation is 1,183 ± 168 mm. Soils are derived from the Cohansey and Kirkwood formations, are sandy, coarse-grained, and have low nutrient status, cation exchange capacity, and base saturation (Tedrow 1986). The landscape is characterized by a relatively high frequency of wildfires and prescribed burns compared with other forest ecosystems in the Northeastern United States; from 2004 to 2016, over 15,000 wildfires burned 36,654 ha and prescribed fires were conducted on 84,096 ha (Gallagher 2017, La Puma et al. 2013, NIFC 2019). On average, the annual area burned in prescribed fires now exceeds that burned in wildfires by a factor of two.

Southern pine beetle infests primarily hard pines (Dodds et al. 2018, Nowak et al. 2015). In the Mid-Atlantic region, pitch pine, shortleaf pine, Virginia pine (*Pinus virginiana* Mill.), and loblolly pine (*P. taeda* L.) are vulnerable to infestations. The recent southern pine beetle outbreak in New Jersey started in approximately 2000, and by 2016, over 19,500 ha had been infested, followed by 13,520 ha of damage in Long Island, NY, by 2019 (Dodds et al. 2018, Heuss et al. 2018, NY Department of Environmental Conservation 2019). Pitch pine-dominated lowlands have been impacted to a greater extent than upland forests (Aoki et al. 2018).

Southern Pine Beetle Infestations and Forest Structure

Comparative forest census plots based on FIA protocols were installed in uninfested and infested areas in 51 stands throughout the research sites in the southern portion of the PNR in 2014 and 2015, 2 to 5 years following infestation by southern pine beetle (Clark et al. 2017). Aerial and ground-based surveys conducted by New Jersey Department of Environmental Protection (NJDEP) and Dartmouth College researchers were used to locate beetle-damaged areas on public lands (primarily State forests and wildlife-management areas). Infested areas ranged from 0.5 to 35 ha in size. All stands were dominated by pitch pine, with shortleaf and Virginia pine also present in some stands.

Sampled pine trees averaged 77 ± 24 years old (Aoki et al. 2018). Upland stands also contained mixed oaks, sassafras (*Sassafrass albidum* (Nutt.) Nees), and an occasional beech (*Fagus grandifolia* Ehrh.). Lowland stands also contained red maple (*Acer rubrum* L.), black gum (*Nyssa sylvatica* Marshall), American holly (*Ilex opaca* Aiton), and sweetgum (*Liquidambar styraciflua* L).

Both infested and uninfested areas within each of the 51sampled stands were subjected to one of three treatment strategies employed by NJDEP staff and contractors: (1) untreated, where no management occurred ($n = 12$); (2) cut and leave, where infested and buffer pine trees were felled and left in place ($n = 27$); and (3) cut and chip, where infested and buffer pine trees were felled, and either bunched and chipped and all chips scattered onsite, or chips were hauled offsite for commercial use ($n = 12$). Following FIA sampling protocols, we took measurements in four subplots (168 m^2) within each treatment strategy area although, because of size limitations, fewer subplots were sampled in some infested areas. In each subplot, species, diameter-at-breast height (dbh, 1.37 m), height, and crown condition were recorded for all live and dead trees (stems greater than 12.5 cm dbh), and all live and dead saplings (stems between 2.5 cm and 12.5 cm dbh). Additionally, each subplot was evaluated for canopy cover (visual estimate), understory height, understory species composition, cover by species (including tree seedlings, defined as stems less than 2.5 cm dbh), and the number of pine seedlings. Basal area was calculated from dbh measurements and expressed as m^2 stems ha^{-1}.

(1) $$\text{Basal area} = \pi\ (\text{dbh}/2)^2$$

Allometric equations based on destructive harvests were used to estimate total aboveground biomass, foliar biomass, and available fuel mass of pine trees and saplings in each subplot (Clark et al. 2013, 2017). Published values were used to estimate aboveground biomass and foliar biomass of oaks and other hardwoods (Chojnacky et al. 2014, Fatemi et al. 2011, Whittaker and Woodwell 1968).

Specific leaf area (SLA; m^2 g dry weight^{-1}) of the dominant canopy and understory species was measured with a leaf area meter (LI-3000a, LI-COR Inc., Lincoln, NE) and a conveyer belt (LI-3050c, LI-COR Inc.) using fresh needle fascicles and leaves sampled at six reference sites in Burlington and Ocean counties, which were then dried at 70 ºC and weighed. Canopy leaf area index (LAI; m^2 m^{-2} ground area) was estimated by multiplying leaf and needle mass calculated from allometric equations for each species by the appropriate SLA value and then summing results for all species. Projected leaf area of pine needle fascicles was multiplied by $\pi/2$ to calculate one-sided LAI. Canopy and understory foliage were sampled for N content at the time of peak leaf area during the growing season at representative stands in the PNR. Oven-dry foliar samples were ground using a Wiley mill (Thomas Scientific, Swedesboro, NJ) and analyzed for N concentration using a modified Kjeldahl method (Allen 1989). An Astoria 2 Analyzer (Astoria-Pacific International, Clackamas, OR) was used to measure the ammonium concentration of each sample, and results were converted to N concentration in foliage samples. Additional values for foliar N content were obtained from sampling conducted by Renninger et al. (2013, 2015) and Guerrieri et al. (2016, 2019). Nitrogen mass (g N m^{-2} ground area) in canopy and understory foliage was calculated for dominant species by multiplying species-specific N concentrations by corresponding estimates of foliar biomass. Literature values were used for foliar N content of the hardwood species that we did not sample.

Forest Productivity Simulations

To understand how infestations of southern pine beetle and associated suppression treatments affected C fluxes, we estimated gross ecosystem production (GEP), ecosystem respiration (R_{eco}), and NEP for uninfested, infested but untreated, and treated areas. Estimates of GEP for all areas were based on the relationship between maximum LAI during the growing season and GEP calculated from eddy covariance measurements made over 25 combined years at pine- and oak-dominated stands, documented in Clark et al. (2018).

(2) $$\text{GEP} = 232.8\ (\text{LAI}) + 388.4$$

For this relationship, $r^2 = 0.667$, $F = 49.0$, and $P < 0.01$. We assumed a baseline ecosystem respiration rate of 15.3 ± 1.2 T C m^{-2} yr^{-1} for uninfested stands, reflecting average R_{eco} for pine-dominated forests measured during undisturbed years in Clark et al. (2018). We then used relationships derived from Renninger et al. (2014) and Clark et al. (2018) to estimate C release from “excess” standing dead trees and coarse woody debris in infested but untreated and treated areas. In infested but untreated stands, we assumed that snags accounted for approximately half of the dead stem mass, and the remaining half consisted of coarse woody debris, consistent with field observations (figure 1). For the cut-and-leave treatment areas, we assumed that all of the dead pine tree and sapling stem mass was coarse woody debris. We simulated two scenarios for the cut-and-chip treatments: (1) pine trees and saplings were bunched and chipped, with all chips then broadcast scattered across the site; or (2) 70 percent of chips were hauled offsite for commercial use. We averaged decomposition rates for the 3- to 5-year period following treatments, consistent with the timing of our field census measurements. We then calculated annual R_{eco} and NEP for each treatment 3 to 5 years following infestations and suppression treatments.

Statistical Analyses

Values for basal area and aboveground biomass of trees and saplings, LAI, foliar N content, and pine seedling counts were compared using ANOVA analyses (SYSTAT 12, SYSTAT Software, Inc., San Jose, CA). Comparisons among treatments were made with Tukey´s Honestly Significant Difference (HSD) tests that adjusted significance levels for multiple comparisons. Paired sample T-tests were used to compare values for uninfested and infested areas within stands.

Results

Southern Pine Beetle Infestations and Forest Structure

Pine tree basal area and aboveground biomass averaged 21.4 ± 1.0 m^2 ha^{-1} and 74 ± 4 T ha^{-1}, respectively, in uninfested areas in the 51 stands sampled across southern New Jersey (figure 2a, table 2). Total basal area, leaf area, and foliar N in uninfested areas did not differ among treatments, with approximately equivalent distributions occurring among pines and the sum of oaks and other hardwoods. Pine trees and saplings in uninfested areas accounted for 76 percent of total basal area, 58 percent of tree and sapling leaf area, and 76 percent of tree and sapling foliar N (figure 2).

Figure 1. Extensive pine tree mortality following an infestation of southern pine beetle in Tuckahoe Wildlife Management Area, Pinelands National Reserve of Southern New Jersey. Standing pine trees are dead, and coarse woody debris has accumulated on the forest floor, while red maple (*Acer rubrum* L.) and black gum (*Nyssa sylvatica* Marshall) trees and saplings are unaffected. (Photo by Kenneth Clark 2015)

Infestations of southern pine beetle resulted in extensive mortality of pitch, shortleaf, and Virginia pine trees (figure 2). Pine tree basal area and aboveground biomass in untreated, infested areas were reduced by 94 and 96 percent compared with uninfested areas, respectively, while pine sapling basal area and aboveground biomass, and basal area of oaks and other hardwoods were nearly unaffected (figure 2a and table 2). Pine tree and sapling LAI and foliar N in untreated, infested areas averaged 14 and 15 percent of values in adjacent uninfested areas, respectively (figures 2b and 2c). Suppression treatments in infested areas reduced pine tree and sapling basal area and aboveground biomass by more than 95 percent and more than 99 percent compared to adjacent uninfested areas (figure 2a, table 2). Similarly, pine tree and sapling LAI and foliar N mass in treated areas

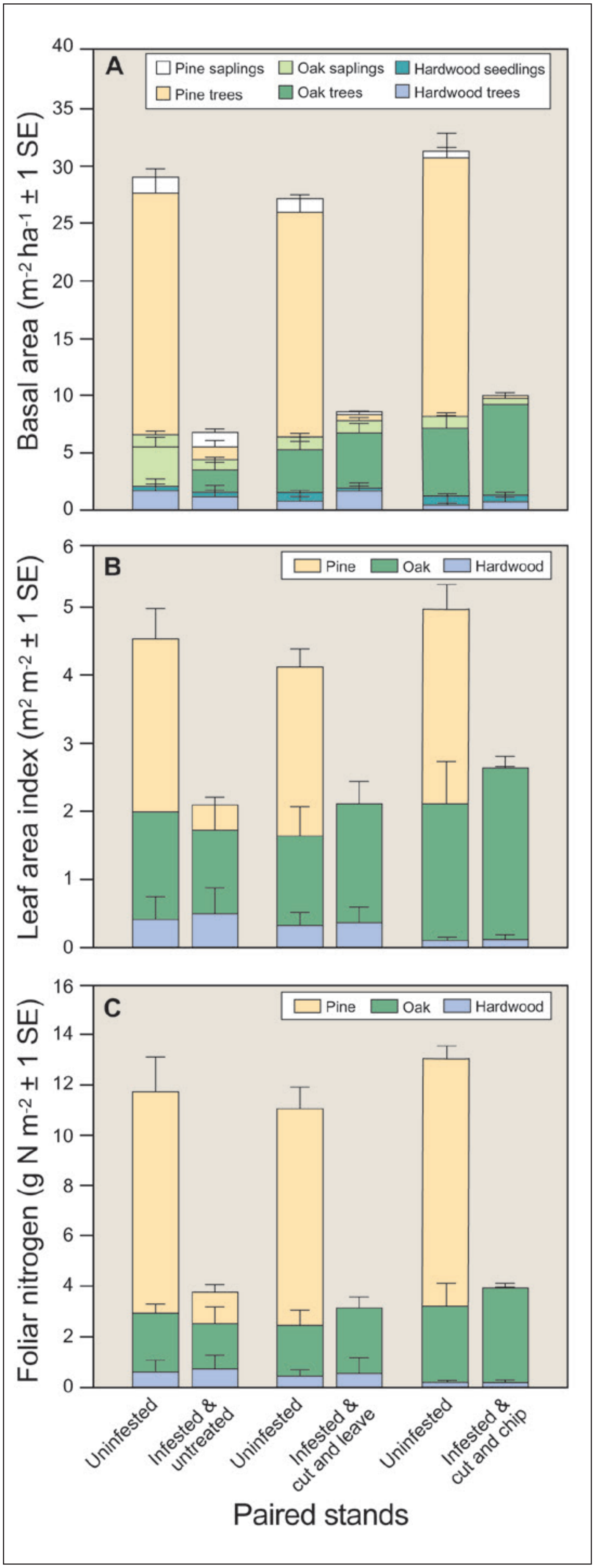

Figure 2. Effects of southern pine beetle and suppression treatments on forest composition and structure in the Pinelands National Reserve of southern New Jersey. Data are shown for (a) basal area of trees and saplings, (b) leaf area index of trees and saplings, and (c) nitrogen content in foliage of trees and saplings in uninfested areas, infested areas that were untreated, infested areas where cut-and-leave suppression treatments were conducted, and infested areas where cut-and-chip suppression treatments were conducted. Other hardwoods include red maple (*Acer rubrum* L.), black gum (*Nyssa sylvatica* Marshall), sassafras (*Sassafras albidum* [Nutt.] Nees), American holly (*Ilex opaca* Aiton), and sweet gum (*Liquidambar styraciflua* L.).

averaged only 1 and 2 percent, respectively, of the values in adjacent uninfested areas (figures 2b and 2c). Pine seedlings were most abundant in cut-and-chip treatments, where extensive disturbance of the forest floor occurred during vehicle and equipment use, exposing the bare, sandy soil (figure 3, table 2). Size-class sampling of seedlings indicated a strong decline in seedling number with height, suggesting high rates of mortality in all areas (figure 4). In contrast to pines, infestation and suppression treatments had little effect on basal area, LAI, or N mass of oak trees and saplings in upland areas or of other hardwood trees and saplings such as red maple and black gum in lowland areas (figure 2).

The distribution of snags and coarse woody debris in untreated, infested areas was highly variable, with some areas composed of nearly all standing dead trees, and other areas with a majority of beetle-killed trees already on the forest floor (figure 1). Coarse woody debris averaged 77.8 T ha^{-1} in cut-and-leave treatments, with maximum amounts of 105 ± 12 T ha^{-1} in a pitch pine lowland stand. Coarse woody debris was minimal in many of the cut-and-chip treatments, since the chips had been either scattered or removed from the site.

Forest Productivity Simulations

Estimated GEP of uninfested areas averaged 17.1 T C ha^{-1} yr^{-1}, and NEP averaged 1.8 T C ha^{-1} yr^{-1} (table 3). Estimated GEP following infestation by southern pine beetle was largely driven by oaks, other hardwoods, and understory vegetation, and averaged 11.6 T C ha^{-1} yr^{-1}, approximately 67 percent of rates in uninfested areas. Estimated R_{eco} in infested stands ranged from 16.0 to 17.9 T C ha^{-1} yr^{-1} and was a function of both the position (snags vs. coarse wood on the forest floor) and size of wood fragments following treatments. In the 3- to 5-year period simulated following infestations and treatments, reduced leaf area had a larger effect on NEP values than variation in R_{eco}. However, enhanced coarse wood mass potentially increases R_{eco} for varying lengths of time among treatments. For example, in our simulations, coarse wood in the cut-and-leave treatments took 19 years to reach 50 percent of original C mass, and 57 years to reach 10 percent of original C mass, while debris in cut-and-chip treatments took 7 years to reach 50 percent of original C mass and 22 years to reach 10 percent of original C mass. Estimated NEP was negative for all suppression treatments, reflecting a net loss of C (table 3).

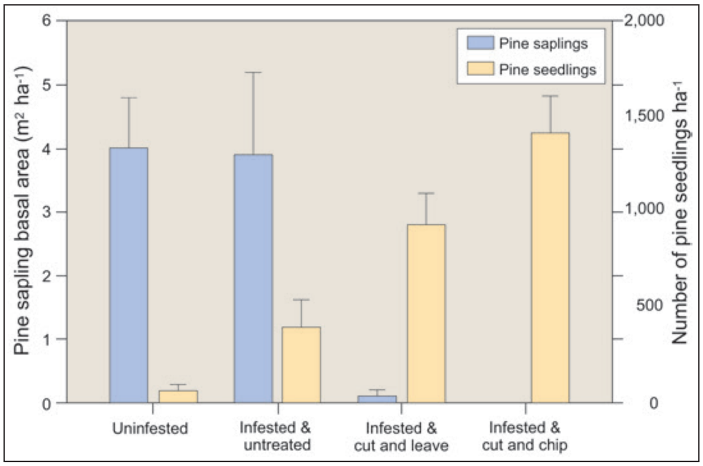

Figure 3. Basal area of pine saplings per hectare (left axis) and number of pine seedlings per hectare (right axis) in uninfested areas, infested areas that were untreated, infested areas where cut-and-leave suppression treatments were conducted, and infested areas where cut-and-chip suppression treatments were conducted.

Discussion

Stand Density and Composition

The extensive mortality of pine trees in infested stands reported here is consistent with the impacts reported for southern pine beetle in pine-dominated forests of the Southeastern United States (Guldin 2011, Nowak et al. 2015), and more recently, further north on the Atlantic Coastal Plain on Long Island, NY (Dodds et al. 2018, Heuss et al. 2019). Overall, stand density and the proportion of pine trees and saplings are critical factors in the probability of southern pine beetle aggregation and infestation leading to pine tree and sapling mortality, with basal areas greater than 28 m^2 ha^{-1} considered highly susceptible to infestations (Guldin 2011). Stand density (as reflected in basal area measurements reported here) is proportional to turbulence regimes within forest canopies, altering the dispersion of aggregation pheromone released by southern pine beetles (Thistle et al. 2004). The recent infestations in New Jersey and Long Island occurred in relatively dense pine-dominated stands with an average pine tree and sapling basal area of 21.4 ± 1.0 m^2 ha^{-1} and 23.8 ± 2.0 m^2 ha^{-1}, respectively, considerably greater than the target basal area of 18 m^2 ha^{-1} that has been effective in mitigating southern pine beetle damage in Southeastern U.S. forests (Guldin 2011, Nowak et al. 2015).

We found that oak trees and saplings in upland stands and other hardwood trees and saplings in lowland

Table 2. Structural characteristics of the canopy and understory in uninfested, infested but untreated, and infested and treated areas impacted by southern pine beetle. Values are means ± 1 SE. Significance levels were tested using ANOVAs and Tukey's HSD tests, and values indicated with different letters among treatment types are significantly different.

Variable	Uninfested (n=51)	Infested: Untreated (n=12)	Infested: Cut and leave (n=27)	Infested: Cut and chip (n=12)
Canopy				
Height (m)	15.2 ± 0.3a	10.1 ± 1.0b	10.4 ± 1.0b	12.0 ± 1.5b
Cover (%)	61.9 ± 2.4a	30.8 ± 6.0b	20.2 ± 4.8b	16.6 ± 6.1b
Aboveground pine biomass (T ha^{-1})				
Trees	74.2 ± 4.2a	2.6 ± 0.9b	0.3 ± 0.2b	0.7 ± 0.4b
Saplings	4.0 ± 0.8a	3.9 ± 1.3a	0.1 ± 0.1b	0.0 ± 0.0b
Understory				
Height (m)	0.7 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.5 ± 0.1
Cover (%)	71.6 ± 4.6	71.3 ± 8.3	72.0 ± 5.5	88.7 ± 1.0
Number of seedlings (ha^{-1})				
Count	67 ± 33a	400 ± 143b	930 ± 169c	1411 ± 201d

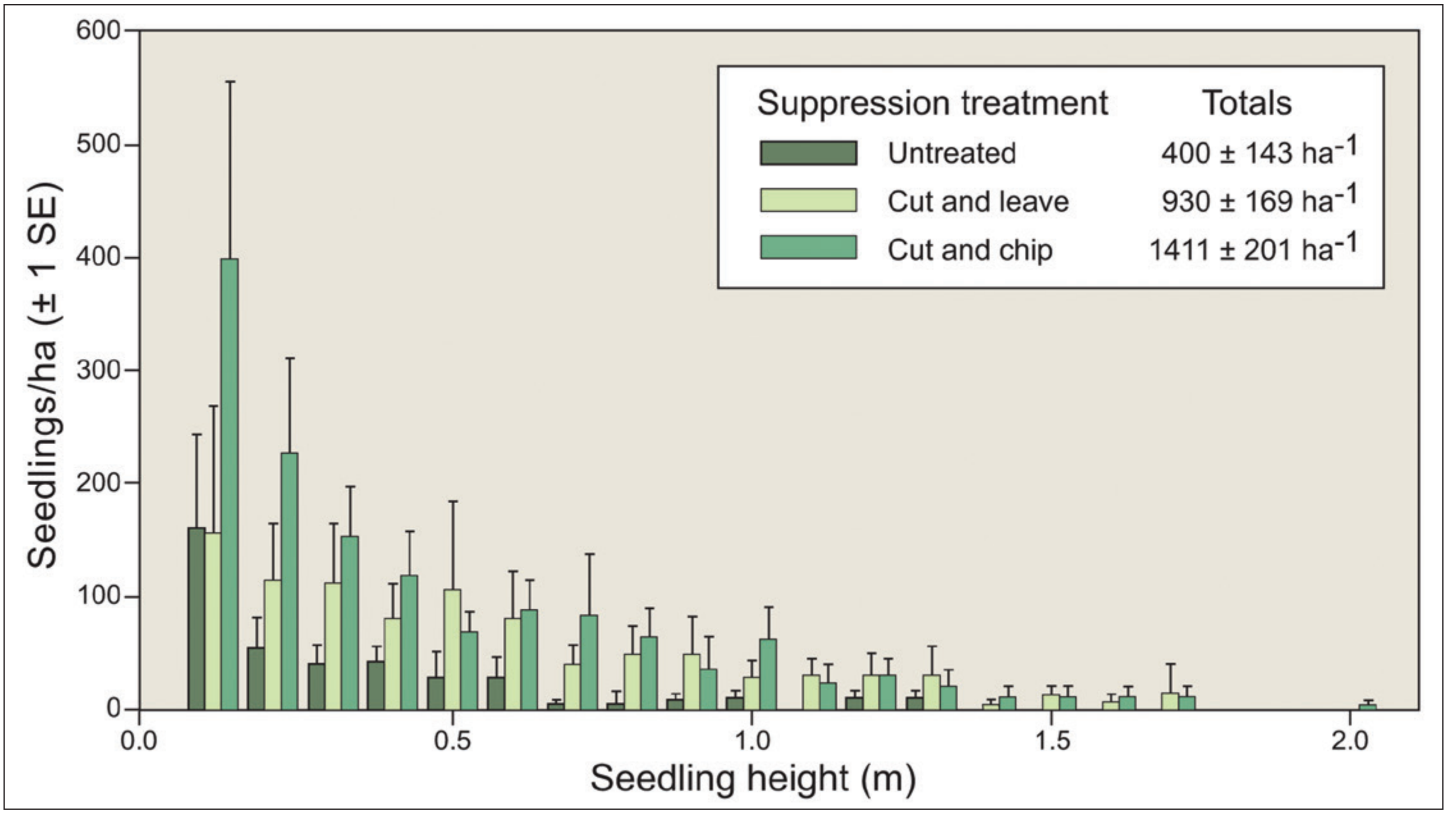

Figure 4. Number of pine seedlings by height class in 0.1-meter increments for infested but untreated areas, cut-and-leave treatments, and cut-and-chip treatments.

stands were essentially unaffected in untreated infested areas and retained to a large extent in treated areas in the Pinelands, similar to results reported by Heuss et al. (2019) for southern pine beetle infestations in Long Island, NY. In contrast to pine-dominated stands, southern pine beetle only rarely impacted pines in oak-dominated stands, and tree mortality was lower in mixed pine-oak stands in the PNR, a pattern also documented by Heuss et al. (2019) for Long Island. In their study, mortality averaged 60 percent of total basal area in pitch pine-dominated stands, and 50 percent and 35 percent in unmanaged and managed pine-oak stands, respectively.

Southern pine beetle damage accelerates succession in infested forests on the Atlantic Coastal Plain, which may ultimately result in the formation and persistence of uneven age, mixed composition stands (La Puma et al. 2013, Clark et al., in preparation). Stands consisting of mixtures of conifers and hardwoods, termed mixedwood stands, have

Table 3. Structural characteristics of the canopy and understory in uninfested, infested but untreated, and infested and treated areas impacted by southern pine beetle. Values are means ± 1 SE. Significance levels were tested using ANOVAs and Tukey's HSD tests, and values indicated with different letters among treatment types are significantly different.

Treatment	Growth Ecosystem Production (GEP) T C ha^{-1} yr^{-1}	Ecosystem Respiration (R_{eco}) T C ha^{-1} yr^{-1}	Net Ecosystem Production (NEP) T C ha^{-1} yr^{-1}
Uninfested	17.1 ± 1.1	15.3 ± 1.2	1.8 (0.7 to 2.9)
Infested, untreated	11.1 ± 2.4	16.3 ± 1.5	-5.2 (-2.8 to -7.6)
Infested, cut and leave	11.4 ± 1.5	16.6 ± 1.6	-5.2 (-3.7 to -6.7)
Infested, cut and chip[1]	12.4 ± 0.6	17.9 ± 1.9	-5.5 (-4.9 to -6.1)
Infested, cut and chip[2]	12.4 ± 0.6	16.0 ± 1.4	-3.6 (-3.0 to -4.2)

T C ha^{-1} yr^{-1} = tons of carbon per hectare per year.

[1] Assuming all chips were broadcast scattered across the area.
[2] Assuming 70 percent of chips were hauled off site for commercial use.

greater associational resistance to insect infestations and other disturbances, and tree mortality is typically reduced compared to forests dominated by a single genus or species, especially for infestations of monophagous insects (Jactel et al. 2017, Kabrick et al. 2017). In infested but untreated pine stands in the current study, the relative basal area of pine, oak, and other hardwood trees and saplings has shifted and converged on the relative basal area of trees and saplings characterizing uninfested mixed composition forests (figure 5, center bar). A similar convergence in species composition and structure towards mixedwood stands has occurred in oak-dominated stands following repeated infestations of gypsy moth and oak tree mortality in the PNR (figure 5; Clark et al. 2018). Both insect infestations are leading to the formation of pine-oak mixedwood stands that will likely persist because they may incur less damage than pine-dominated or oak-dominated stands during future insect infestations (Clark et al., in preparation). In untreated stands impacted by southern pine beetle, basal area of pine trees and saplings are well below the critical density (approximately 18 m^2 ha^{-1}) that would support future aggregations of beetles (Aoki et al. 2018, Dodds et al. 2018, Nowak et al. 2015). Similarly, oak tree and sapling density are relatively low in mixedwood stands and they experience lower mortality than oak-dominated forests, which are especially vulnerable to recurring gypsy moth infestations throughout the Mid-Atlantic region (Clark et al. 2018, Fei et al. 2019, Morin and Liebhold 2015).

Stand Productivity

Net C assimilation and stand productivity are driven by the recovery of leaf area and foliar N levels following southern pine beetle infestations and suppression treatments (Amiro et al. 2010, Clark et al. 2018, Medvigy et al. 2012). When canopy openings occur, either because of needle abscission from standing dead

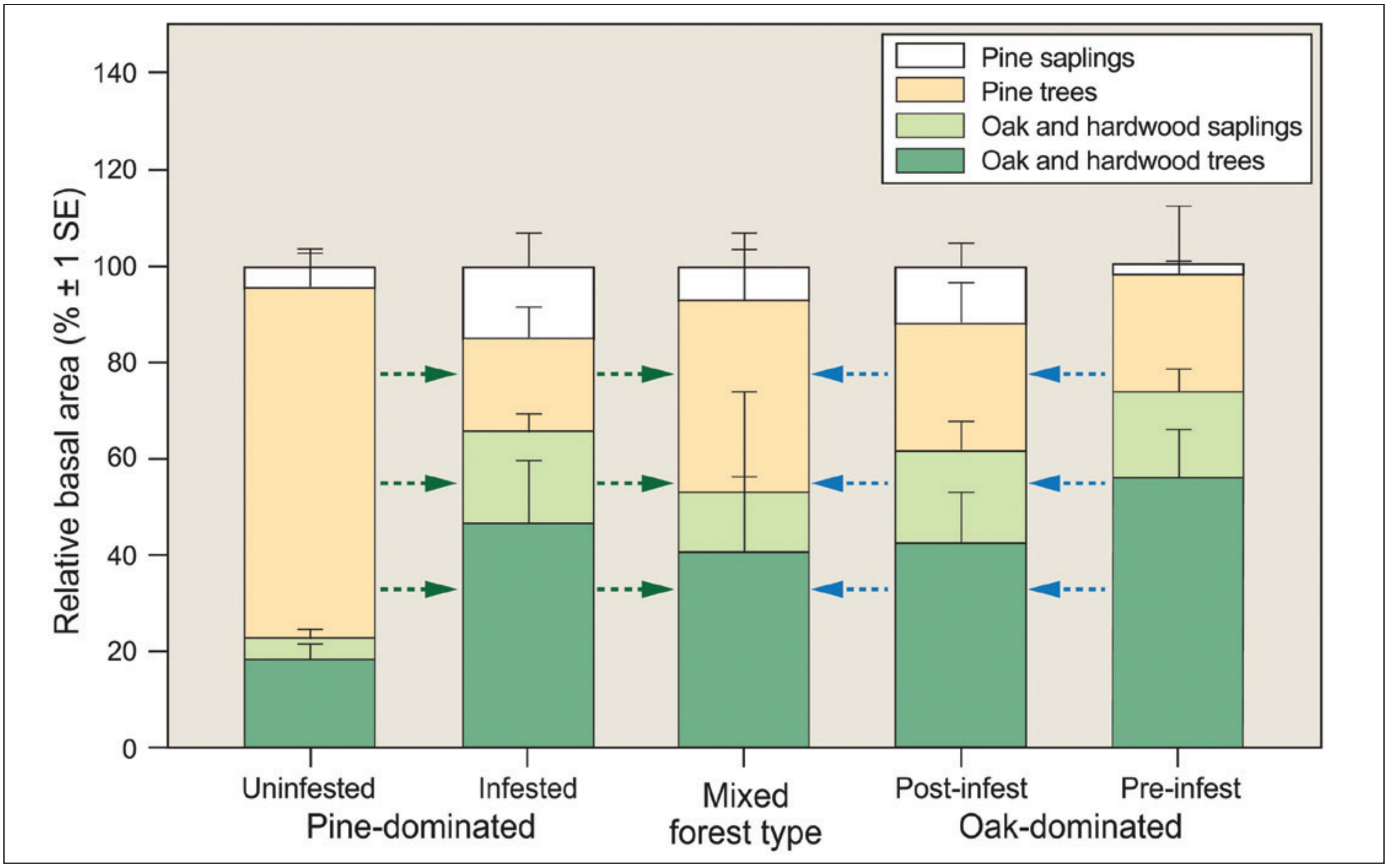

Figure 5. Relative basal area of pines and hardwood trees and saplings pre- and post-insect infestations. Data are from pine-dominated uninfested areas, untreated areas following infestation by southern pine beetle, an uninfested mixed composition stand at Fort Dix in the Pinelands National Reserve, an oak stand before gypsy moth infestation in 2005 (Pre-infest) and following tree and sapling mortality in 2018 due to gypsy moth infestations in 2007 and 2008 (Post-infest) at the Silas Little Experimental Forest in the Pinelands National Reserve (see Clark et al. 2018 for details of the field sampling). Oaks and other hardwoods have been combined as “hardwoods.” Infestation results in a convergence in species composition and structure towards mixedwood stands (indicated by arrows).

trees and saplings, treefalls following pine mortality, or damage during suppression treatments, leaf area of remaining trees, saplings, and the understory can respond rapidly (Curtis and Gough 2018). Numerous forest tree species in the Mid-Atlantic region are characterized by regeneration strategies that enhance survival following disturbance (e.g., epicormic budding in pitch and shortleaf pines, prolific resprouting in most oaks and red maple). Clark et al. (2014, 2018) showed an approximate doubling of understory and sub-canopy leaf area in the next growing season following defoliation and tree mortality during gypsy moth infestations in PNR forests, indicating a rapid recovery response to insect damage. Although gypsy moth defoliation was severe and oak tree mortality was approximately 40 percent of stand basal area, leaf area recovered rapidly and GEP and ecosystem WUE_e reached pre-defoliation levels 3 to 4 years after peak defoliation (Clark et al. 2014, 2018; Guerrieri et al. 2019). In our simulations with southern pine beetle infestations, GEP recovered to approximately 67 percent of pre-infestation levels 3 to 5 years following infestation and suppression treatments, and will likely approach pre-infestation levels within a few years.

In contrast to the rapid recovery of GEP, recovery of NEP following southern pine beetle infestations and suppression treatments will be delayed because enhanced R_{eco} following insect infestations and tree mortality is a strong function of C release from decomposing snags and coarse woody debris. We observed similar results in oak-dominated forests following gypsy moth defoliation and tree mortality; while LAI and GEP recovered rapidly, enhanced R_{eco} depressed NEP for at least a decade (Clark et al. 2018). Renninger et al. (2014) projected that NEP in oak-dominated stands where significant tree mortality occurred would be reduced for at least 2 decades as coarse wood decomposes. Although our simulations indicated that reduced GEP was more important than enhanced R_{eco} in reducing NEP, this pattern will likely reverse within a few years as leaf area and foliar N mass recover to pre-defoliation levels. NEP will then be partially a function of the fate of standing dead and coarse woody debris, and the size of the residual wood. In our study, we assumed that chips had a higher decomposition rate than whole stems, and quantification of chip decomposition through time would improve our estimates of NEP.

Management Implications

Our study (and many others) suggests a number of management practices are appropriate for reducing the impact of future southern pine beetle infestations in the Mid-Atlantic region. Reducing stand basal area by thinning to a basal area at or below 18 m^2 ha^{-1}, or at least reducing sub-canopy stem density using prescribed fire, will increase resistance to infestations (Dodds et al. 2018, Gallagher 2017, Guldin 2011, Nowak et al. 2015). Many of the unmanaged pine-dominated stands in the PNR and on Long Island are currently at or above this level, and thus will be vulnerable to future infestations (Dodds et al. 2018; Clark et al., in preparation; USDA FIA data).

Once stands have been infested, two strategies could be used to enhance ecosystem functioning and to reduce the probability of stand damage from future insect infestations. First, utilizing wood from suppression treatments following insect infestations will reduce ecosystem respiration. Our analyses indicate that when pine stems are harvested and removed from site, such as partial removal of chips in the cut-and-chip treatments, estimated R_{eco} is reduced, resulting in less negative NEP values for a shorter period of time. With that management regime, NEP, and thus C sequestration, recovers more rapidly compared to untreated or cut-and-leave treatments in infested areas. If management options for coarse, woody debris are limited, prescribed burning to reduce the risk of wildfires has two benefits: calcium, phosphorous, and other nutrients stored in coarse woody debris is released to vegetation, thereby increasing photosynthetic assimilation (Carlo et al. 2016, Renninger et al. 2013); and competition from understory vegetation is reduced to encourage pine regeneration and establishment. The second management strategy is to ensure that sufficient regeneration of pines occurs in treated areas following infestations so that future stands are composed of mixtures of pines and hardwoods. This strategy can result in uneven-age, mixedwood stands, which have greater resistance to insect infestations than either even-age and monospecific or monogeneric stands (Jactel et al. 2017). Our forest census data indicate that pine seedling and sapling densities are very low in areas where suppression treatments were conducted. Enrichment planting of pine seedlings should be considered in targeted areas where pine regeneration has failed following prescribed burn treatments to reduce competition from understory vegetation. Ensuring the regeneration of pine-oak mixedwood stands that are relatively resistant to future outbreaks of bark beetles and other defoliators will reduce economic costs associated with tree mortality and suppression treatments, as well as mitigate short-term impacts to ecosystem functioning resulting from insect damage, especially C sequestration.

Address correspondence to—

Kenneth Clark, Silas Little Experimental Forest, 501 Four Mile Road, New Lisbon, NJ 08064; email: kenneth.clark@usda.gov

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