

Title: Tree regeneration and understory plant dynamics in the wake of emerald ash borer invasion

Location: Multiple forest sites across Connecticut (see map below)

Project leader:

Dr. Elisabeth B. Ward, Assistant Agricultural Scientist II, The Connecticut Agricultural Experiment Station

Justification:

The introduction and spread of novel pests and pathogens poses a significant threat to the structure, composition, and function of forests and the ecosystem services they provide (Liebhold *et al.*, 1995; Flower & Gonzalez-Meler, 2015; Lovett *et al.*, 2016). Over 450 non-native forest pests and pathogens have established in the conterminous United States (U.S.) since European colonization (Aukema *et al.*, 2010; Brockerhoff & Liebhold, 2017), some of which cause extensive damage to common tree species or genera. Examples include American chestnut (*Castanea dentata*) from chestnut blight (*Cryphonectria parasitica*), elms (*Ulmus* spp.) from Dutch elm disease (*Ophiostoma* spp.), oaks (*Quercus* spp.) from spongy moth (*Lymantria dispar*), eastern hemlock (*Tsuga canadensis*) from hemlock woolly adelgid (*Adelges tsugae*), American beech (*Fagus americana*) from beech bark disease (*Cryptococcus fagisuga* and *Neonectria* spp.) and beech leaf disease (*Litylenchus crenatae ssp. mccannii*), and ash (*Fraxinus* spp.) from emerald ash borer (*Agrilus planipennis*).

Within the U.S., southern New England is particularly susceptible to forest pest and pathogen invasions. The combination of high forest cover and tree species diversity along with high propagule pressure from dense human settlements and a long history of industrialization have facilitated the establishment and spread of multiple forest pests in this region (Liebhold *et al.*, 2013). Seventy-three percent of the most damaging forest pests and pathogens in the U.S. primarily affect eastern U.S. forests (Fei *et al.*, 2019). Connecticut is only paralleled by New York in terms of the high density and widespread distribution of forest pests in a U.S. state (Liebhold *et al.*, 2013), making it an important case study for understanding the future impacts of pest and pathogen invasions at a regional scale.

The cumulative effects of pest and pathogen invasions on tree mortality can be large. Altogether, they can account for up to 29% of recent losses in aboveground tree biomass in eastern U.S. forests (Anderson-Teixeira *et al.*, 2021), and they reduce live tree carbon in forests in the conterminous U.S. by an estimated 5.5 Tg per year (Fei *et al.*, 2019). Across the U.S., 8.4 million acres of forests have experienced pest- and pathogen-induced tree mortality, and an additional 5.9 million acres have had sub-lethal tree damage (Stephens *et al.*, 2022). Forty-one percent of standing tree biomass in forests in the U.S. is also susceptible to future mortality by one or more pests or pathogens (Fei *et al.*, 2019), suggesting that these impacts will continue to grow as the ranges of invasive pest and pathogen expand.

Dieback and mortality of dominant canopy tree species causes widespread shifts in forest composition (Elliott & Swank, 2008; Olson *et al.*, 2021). By increasing the availability of light and other resources in the understory, canopy gaps facilitate the growth of tree seedlings and saplings to replace overstory species. How forest composition changes in response to canopy tree mortality will, however, depend on site-specific factors. Tree species vary in shade tolerance

(Valladares & Niinemets, 2008), so the size of canopy gaps will strongly shape patterns of regeneration (Muscolo *et al.*, 2014). The abundance or basal area of susceptible host species within a stand is therefore likely to influence understory plant dynamics by affecting canopy gap sizes (Flower *et al.*, 2013). Small, single tree canopy gaps might limit tree recruitment to shade-tolerant species or fail to recruit sub-canopy species altogether as growth of adjacent trees fills the gap (Flower *et al.*, 2013; Burr & McCullough, 2014; Dolan & Kilgore, 2018; Buskey *et al.*, 2020). Larger canopy gaps, on the other hand, would be expected to recruit a higher abundance and diversity of tree species that vary in shade tolerance (Schnitzer & Carson, 2001).

In addition to directly affecting tree regeneration, canopy gap size will also influence the composition and abundance of other understory plants, which can indirectly affect patterns of regeneration. For example, elevated understory resource availability can promote secondary invasions by plants that can suppress tree regeneration and alter forest development (Royo & Carson, 2006; Baron & Rubin, 2021). Sites with higher soil nutrient availability could increase the competitive advantage of invasive plant species over regenerating trees (Davis *et al.*, 2000; Shea & Chesson, 2002; Daehler, 2003; Heberling & Fridley, 2013). Whether native, regenerating tree species replace overstory trees following their mortality could therefore depend on how understory plant communities respond to changes in light availability across environmental gradients. Silvicultural operations can directly manipulate canopy gap sizes to promote the regeneration of desired tree species assemblages (Ashton & Kelty, 2018), but this could also increase the abundance of invasive plants (Hausman *et al.*, 2010). Understanding how variation in local site conditions influences the competitive dynamics between native and non-native plants following overstory tree mortality could therefore help inform and prioritize management efforts.

Ash (*Fraxinus* spp.) mortality from the ongoing invasion of emerald ash borer (EAB) is a leading concern for forest practitioners. Since its introduction to the U.S. in 2002, EAB has killed up to 99% of mature ash trees in some forest stands (Klooster *et al.*, 2014), making it the most costly and damaging insect in the history of the U.S. (Aukema *et al.*, 2011). Ash trees are distributed in a variety of forest types throughout the northeastern U.S. but often have the highest basal area on nutrient-rich sites (MacFarlane & Meyer, 2005). The combination of high understory light and nutrient availability in sites with high ash basal area could compound the risk of secondary invasions by understory plants in ash-dominated stands (Margulies *et al.*, 2017; Hoven *et al.*, 2020). Upland sites with a more sporadic ash distribution, on the other hand, might be less susceptible to understory plant invasions, but limited understory light availability could also reduce tree regeneration.

Monitoring the fate of understory ash seedlings and saplings following EAB invasion is also critical for assessing the extent to which ash trees will persist longer-term on the landscape (Burr & McCullough, 2014; Klooster *et al.*, 2018; Engelken *et al.*, 2020). Ash seedlings less than 2 cm diameter at breast height (DBH) are not colonized by EAB and could therefore persist in the understory despite high overstory tree mortality (Kashian & Witter, 2011; Klooster *et al.*, 2014; Aubin *et al.*, 2015). In Connecticut, EAB populations are beginning to decline as a result of the loss of their host species and widespread biocontrol efforts (Rutledge & Clark, 2023). Yet whether the regenerating cohort of ash seedlings can develop into upper canopy trees following EAB decline is partially contingent on the extent to which they can compete with other understory plants, including invasive species. In addition, EAB populations could rebound as the regenerating cohort of ash seedlings advances into the midstory (Aubin *et al.*, 2015).

This project will evaluate **how understory plant composition changes over time following canopy ash tree mortality from EAB** to help inform management efforts that promote tree regeneration and native-dominated plant communities. In particular, this project will provide data to evaluate the need for management efforts that (1) expand canopy gap sizes following ash mortality to promote a greater diversity of tree regeneration, (2) control understory invasive plants, and (3) plant shade-tolerant midstory trees that can outcompete and/or suppress the growth of invasive plant species.

Previous work and present outlook:

Emerald ash borer in Connecticut

White ash (*F. americana*) is distributed across a range of upland forest types in Connecticut and, historically, was the eighth most abundant tree species based on wood volume (USDA Forest Service, 2020). Emerald ash borer was first detected in Connecticut in 2012 and has since expanded throughout the entire state (Rutledge & Clark, 2023). As such, there is wide variation in overstory ash conditions across Connecticut, ranging from the oldest sites in New Haven County where EAB was first detected in 2012 (Prospect, CT) to the most recent detections in 2021 in Windham County (Putnam, CT) (Fig. 1). This pattern of EAB invasion across Connecticut can be used to study how the effects of ash tree mortality from EAB invasion change over time using a space-for-time substitution approach (a “chronosequence”).

Impacts of ash tree mortality from emerald ash borer invasion on understory plant dynamics

Within the U.S., EAB was first detected in 2002 in Michigan. As such, research on the impacts of ash tree mortality from EAB on understory plant dynamics has largely been restricted to forests in the Midwest with less work focusing on forest types in the Northeast. Notably, however, the biocontrol program in Connecticut began at an earlier stage of the EAB invasion, suggesting that understory plant community dynamics could differ in the Northeast compared to the Midwest due to differences in the impacts of EAB on canopy ash condition. Still, research from the Midwest provides important insights into how the effects of ash tree mortality on understory plant dynamics vary under different environmental conditions.

Several studies observed positive effects of ash mortality on both native and non-native plant abundance, with the most pronounced effects in sites with a high basal area of affected ash. For instance, sites with higher ash mortality facilitated the growth of both shade-tolerant native seedlings, such as maples, as well as non-native seedlings in upland forests in Ohio (Hoven *et al.*, 2020). However, the authors found no changes in non-ash canopy tree growth, shrub cover, or invasive seedling abundance in forested wetlands in response to ash mortality, highlighting how variation in soil conditions can modulate understory responses to canopy ash mortality (Hoven *et al.*, 2020). Another study similarly showed that higher ash basal area increased the density of both native, shade-tolerant tree species and non-native species (Dolan & Kilgore, 2018). However, there was no regeneration of shade-intolerant species following ash mortality (Dolan & Kilgore, 2018).

Another study found a negative relationship between native tree seedlings and the abundance of invasive plant species as a result of differences in overstory ash condition from the biocontrol release program (Margulies *et al.*, 2017). The abundance of invasive understory plant species

could also be contingent on the health of forest stands prior to EAB invasion. For instance, one study found that ash canopy gaps facilitated the growth of an invasive shrub to a greater extent in forest stands with lower ecological integrity (Baron & Rubin, 2021). These context-dependent relationships between native and non-native understory plant growth following canopy ash mortality highlight the need to test the direction of these effects in forests in the Northeast.

One of the most consistent findings from work conducted in the Midwest on understory plant dynamics following ash tree mortality is the recruitment of shade-tolerant tree species, such as maples, and the very limited recruitment of shade-intolerant species, such as oaks (Flower *et al.*, 2013; Costilow *et al.*, 2017; Hoven *et al.*, 2020). These results highlight how understory light availability in small canopy gaps caused by ash tree mortality appears to limit the diversity of regenerating tree species. This effect is particularly pronounced in areas where compensatory growth of non-ash canopy trees excludes the recruitment of mid- and understory species by limiting understory light availability (Flower *et al.*, 2013; Burr & McCullough, 2014; Buskey *et al.*, 2020). Depending on the management goals, forest operations that increase light availability in stands with high ash mortality could enhance the recruitment of a broader diversity of tree species.

Objectives:

The goal of this project is to analyze how the composition of regenerating trees and understory plant communities changes over time following ash tree decline and mortality from EAB. Specific objectives include:

1. *Survey understory plant composition across the EAB chronosequence*

For objective 1, I will characterize changes in understory plant community composition following canopy ash tree decline and mortality across a chronosequence of time since EAB detection in Connecticut. Specifically, I will analyze changes in the relative abundance of native versus non-native plant species and the abundance and diversity of regenerating tree species with different functional traits (e.g. shade tolerant vs. intolerant). I hypothesize that the abundance of both native and non-native understory plant species will initially increase with time since EAB detection owing to greater understory light availability. Over time, as canopy gaps created by ash mortality close due to compensatory growth by surrounding trees, I expect changes in native and non-native understory plant cover to plateau or decline.

2. *Examine factors influencing understory plant composition across the EAB chronosequence*

For objective 2, I will analyze how within-site variation in environmental factors modulates the effects of time since EAB detection on understory plant communities and tree regeneration. To address this objective, I will establish multiple plots along transects within each site with the goal of capturing variation in ash tree basal area and/or soil conditions. I hypothesize that both native and non-native species will increase in abundance with higher understory light availability in sites with higher ash basal area and that invasive plant species will dominate sites with higher soil nutrient availability (i.e. higher pH and net potential nitrification rates, lower carbon availability and content).

3. *Effects of forest management practices on understory dynamics following EAB invasion*

For objective 3, I will analyze how forest management practices in ash stands affected by EAB alter successional trajectories by changing understory plant community composition.

Specifically, I will compare stands with invasive plant control treatments and salvage logging operations to untreated stands.

4. Establishment of long-term ash monitoring plots

For objective 4, I will use the baseline data from this project to establish long-term monitoring plots in a subset of the plots to track the fate of ash and other tree regeneration over a longer period of time. I will also track the recruitment, growth, and survival of ash seedlings and saplings following the EAB population crash to assess whether ash might rebound as a canopy tree on the landscape. For this project period, I will sample baseline conditions and conditions after three years. This pilot data will enable me to apply for future grants to continue monitoring efforts every 3-5 years.

Procedure:

Objective 1: Survey understory plant composition across the EAB chronosequence

Using EAB first detection and monitoring data provided by Dr. Claire Rutledge, I will work with foresters and land managers throughout Connecticut to select unmanaged ash stands from across the chronosequence (Fig. 1). In summer 2024, I will work with a master’s student from The Forest School at the Yale School of the Environment to randomly establish 10-m radius fixed-area plots within each of the sites to conduct all vegetation sampling. Specifically, we will identify and measure DBH of all overstory trees ≥ 5 cm DBH in the full plot, including snags (standing dead trees). We will also establish four nested 1-m radius subplots 5-m from plot center in each cardinal direction to measure midstory trees 1-5 cm DBH. With each of the four subplots, we will use a 1-m² PVC quadrat to survey the percent cover of all understory plant species. We will also estimate canopy transparency at the center of each of the four subplots using a densiometer.

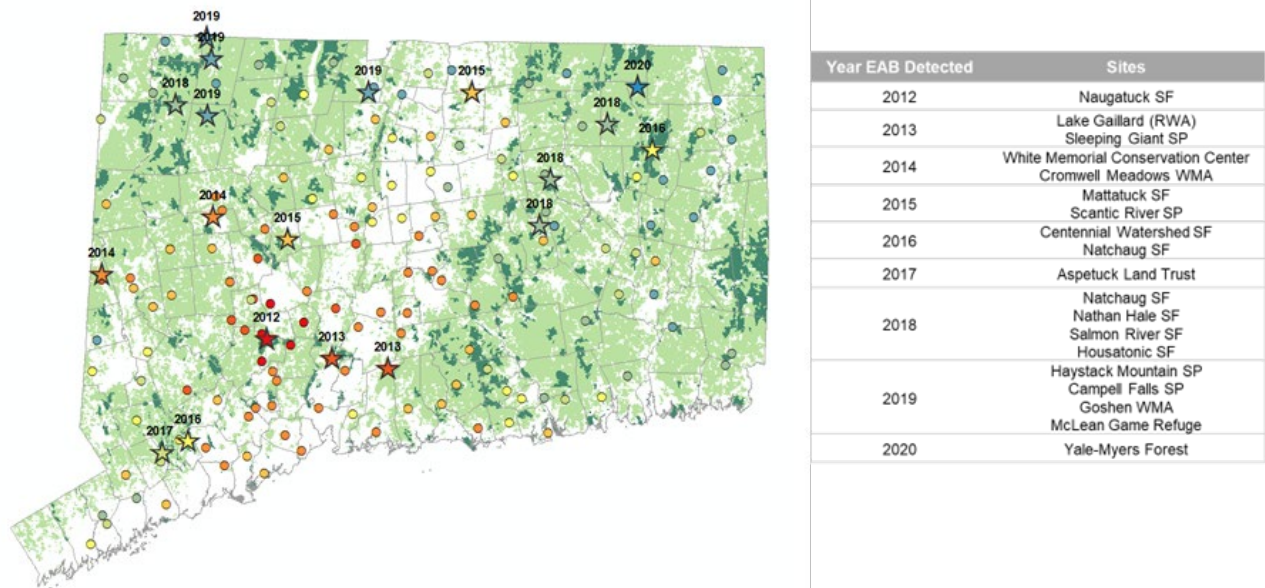


Figure 1 Study site locations across the time since EAB detection chronosequence in Connecticut. Stars indicate sites for the present study as well as the year EAB was first detected based on EAB first detection data provided by Dr. Claire Rutledge (circles). Light green areas show forested lands and dark green areas show state (CT DEEP) forest land.

Objective 2: Examine factors influencing understory plant composition across the EAB chronosequence

To analyze how variation in environmental factors modulates the effects of time since EAB detection on understory plant communities, we will establish transects within each site that capture local variation in site conditions. The transects will begin at the location of the first, randomly selected plot location and run along gradients of topography and/or ash basal area depending on the characteristics of the site. Using these transects, we will establish two additional plots 30 m apart (i.e. with plot centers 50 m apart). We will adjust the locations of the plots to include at least one ash tree ≥ 10 cm DBH while also ensuring that the 3 plots capture a range of ash basal area within each site. For these two additional plots, we will follow the same vegetation sampling protocol as objective 1.

In addition, we will collect nine 2-cm diameter, 10-cm deep soil cores within each 1-m radius subplot and pool the soil samples by plot to give us three soil samples per site. All soil analyses will be conducted by Jack Hatajik, a master's student at The Forest School at the Yale School of the Environment, as part of his thesis project. He will use laboratory facilities at Greeley Memorial Laboratory. Soil analyses will include: gravimetric water content, water holding capacity, soil organic matter content (loss on ignition), pH, net potential nitrogen mineralization, net potential nitrification, carbon mineralization, and microbial biomass (substrate-induced respiration), following standard protocols described in Ward *et al.*, (2020).

Objective 3: Effects of forest management on understory plant communities following EAB invasion

In year 2 (Summer 2025), I will sample stands with different forest management practices located in close proximity to the unmanaged chronosequence plots established in year 1. I will sample stands that include three treatments—(1) ash salvage harvest, (2) understory invasive control, and (3) salvage + invasive control—and I will compare data from these stands to the unmanaged stands. I will work with CT DEEP Forestry Division to identify sites that meet these criteria. I will follow the same vegetation sampling protocol described for objective 1.

Objective 4: Establishment of long-term ash monitoring plots

I will re-sample a subset of the plots in year 4 (Summer 2027, three years after the initial sampling) to monitor longer-term changes in the recruitment and growth of regenerating trees following ash mortality. I will follow the same vegetation sampling protocol described for objective 1.

Relevance, expected outcomes, or impacts:

This project will be one of the first studies examining understory plant dynamics and tree regeneration following ash mortality from EAB in the northeastern U.S. In addition, there is little work examining how soil conditions influence understory plant composition following EAB invasion despite a wealth of literature on the effects of soil nutrient availability on understory plant invasions. This work will therefore contribute to both scientific knowledge on how forest communities reassemble following a major canopy disturbance type as well as directly inform regional forest management efforts. Within the Northeast, EAB is affecting Connecticut's forests

earlier than most other states. In addition, the chronosequence approach will enable us to inform land management in more recently invaded areas within Connecticut based on findings from sites where EAB was detected earlier. In addition to generating 2-3 peer-reviewed papers from this project, I will also share the results through conferences, presentations, and workshops with forest practitioners and landowners through my roles at the Forest Ecosystem Monitoring Cooperative, the Northeast-Midwest State Foresters Alliance Forest Health committee, the Master Woodland Manager program, and as the state forest health lead in Connecticut.

Stakeholder engagement:

A primary goal of this project is to provide information to foresters and land managers on how forest composition is shifting in response to canopy tree mortality from EAB invasion to help inform and prioritize management efforts. As such, foresters and land managers from each of the study sites will be involved in site selection, and all results will be shared with these stakeholders to inform future management. In addition, all forest management treatments (Objective 3) will be implemented by the foresters at each site, and results from this project will be used as pilot data to apply for grants (e.g. USDA Forest Service Landscape Scale Restoration grant) to fund additional management efforts based on the needs identified through this project. Specific partners include: the Connecticut Department of Energy and Environmental Protection, White Memorial Conservation Center, Yale-Myers Forest, South Central Connecticut Regional Water Authority, Aquarion Water Company, and the Aspetuck Land Trust, among others. By establishing a network of plots across the state in forests with different land ownership, this project will facilitate communication of research findings to a broad array of stakeholders.

Integrated activities:

By conducting this research in direct collaboration with foresters and land managers at each site, this project will facilitate links between research and extension/outreach. In addition, the results from this project will be shared through presentations and workshops with the public and practitioners.

Multi-state activities:

There are no multi-state research activities associated with this project. However, the results from this project will be shared through monthly forest health update calls with NY, MA, RI, NH, VT, and ME to inform regional forest management efforts in areas where the effects of EAB have not yet peaked.

Milestones/timetable:

Objective 1 will be completed in 24 months [December 2025]

- Site selection will be completed in 5 months [January 2024 - May 2024]
- Field sampling will be completed in 5 months [June 2024 - October 2024]
- Data analysis will be completed in 7 months [November 2024 - May 2025].
- Manuscript preparation will be completed in 7 months [June 2025 - December 2025].

Objective 2 will be completed in 24 months [December 2025].

- Site selection will be completed in 5 months [January 2024 - May 2024]
- Field sampling will be completed in 5 months [June 2024 - October 2024]

- Soil laboratory analyses will be completed in 4 months [August 2024 – November 2024]
- Data analysis will be completed in 7 months [November 2024 - May 2025].
- Manuscript preparation will be completed in 7 months [June 2025 - December 2025].

Objective 3 will be completed in 48 months [December 2027].

- Site selection will be completed in 7 months [November 2024 - May 2025]
- Field sampling will be completed in 5 months [June 2025 - October 2025]
- Data analysis will be completed in 5 months [January 2026 - May 2026].
- Manuscript preparation will be completed in 12 months [June 2026 - May 2027].

Objective 4 will be completed in 48 months [December 2027].

- Establishment of plots will be completed in 5 months [January 2024 - May 2024].
- Baseline field sampling will be completed in 5 months [June 2025 - October 2025].
- Longitudinal sampling after three-years will be completed in 7 months [June 2027 - December 2027].

		2024				2025				2026				2027			
		Wint	Spr	Sum	Fall	Wint	Spr	Sum	Fall	Wint	Spr	Sum	Fall	Wint	Spr	Sum	Fall
Obj. 1	Selection of sites across the EAB chronosequence																
	Field vegetation sampling																
	Data analysis																
	Prepare manuscript																
Obj. 2	Establishment of within-site transects to capture local variation																
	Field vegetation and soil sampling																
	Soil lab work																
	Data analysis																
	Prepare manuscript																
Obj. 3	Selection of stands with different forest management treatments																
	Field vegetation sampling																
	Data analysis																
	Prepare manuscript																
Obj. 4	Establishment of longer-term monitoring plots																
	Field vegetation sampling																

Anticipated duration: Four years.

References

- Anderson-Teixeira KJ, Herrmann V, Cass WB, Williams AB, Paull SJ, Gonzalez-Akre EB, Helcoski R, Tepley AJ, Bourg NA, Cosma CT, *et al.* 2021. Long-Term Impacts of Invasive Insects and Pathogens on Composition, Biomass, and Diversity of Forests in Virginia's Blue Ridge Mountains. *Ecosystems* 24: 89–105.
- Ashton MS, Kelty MJ. 2018. *The Practice of Silviculture: Applied Forest Ecology*. John Wiley & Sons.
- Aubin I, Cardou F, Ryall K, Kreutzweiser D, Scarr T. 2015. Ash regeneration capacity after emerald ash borer (EAB) outbreaks: Some early results. *The Forestry Chronicle* 91: 291–298.
- Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, *et al.* 2011. Economic Impacts of Non-Native Forest Insects in the Continental United States. *PLOS ONE* 6: e24587.
- Aukema JE, McCullough DG, Von Holle B, Liebhold AM, Britton K, Frankel SJ. 2010. Historical Accumulation of Nonindigenous Forest Pests in the Continental United States. *BioScience* 60: 886–897.
- Baron JN, Rubin BD. 2021. Secondary invasion? Emerald ash borer (*Agrilus planipennis*) induced ash (*Fraxinus* spp.) mortality interacts with ecological integrity to facilitate European buckthorn (*Rhamnus cathartica*). *Canadian Journal of Forest Research* 51: 455–464.
- Brockhoff EG, Liebhold AM. 2017. Ecology of forest insect invasions. *Biological Invasions* 19: 3141–3159.
- Burr SJ, McCullough DG. 2014. Condition of green ash (*Fraxinus pennsylvanica*) overstory and regeneration at three stages of the emerald ash borer invasion wave. *Canadian Journal of Forest Research* 44: 768–776.
- Buskey TM, Maloney ME, Chapman JI, McEwan RW. 2020. Herb-Layer Dynamics in an Old-Growth Forest: Vegetation–Environment Relationships and Response to Invasion-Related Perturbations. *Forests* 11: 1069.
- Costilow KC, Knight KS, Flower CE. 2017. Disturbance severity and canopy position control the radial growth response of maple trees (*Acer* spp.) in forests of northwest Ohio impacted by emerald ash borer (*Agrilus planipennis*). *Annals of Forest Science* 74: 1–10.
- Daehler CC. 2003. Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. *Annual Review of Ecology, Evolution, and Systematics* 34: 183–211.
- Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.
- Dolan B, Kilgore J. 2018. Forest Regeneration Following Emerald Ash Borer (*Agrilus planipennis* Fairemaire) Enhances Mesophication in Eastern Hardwood Forests. *Forests* 9: 353.

- Elliott KJ, Swank WT. 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecology* 197: 155–172.
- Engelken PJ, Benbow ME, McCullough DG. 2020. Legacy effects of emerald ash borer on riparian forest vegetation and structure. *Forest Ecology and Management* 457: 117684.
- Fei S, Morin RS, Oswalt CM, Liebhold AM. 2019. Biomass losses resulting from insect and disease invasions in US forests. *Proceedings of the National Academy of Sciences* 116: 17371–17376.
- Flower CE, Gonzalez-Meler MA. 2015. Responses of Temperate Forest Productivity to Insect and Pathogen Disturbances. *Annual Review of Plant Biology* 66: 547–569.
- Flower CE, Knight KS, Gonzalez-Meler MA. 2013. Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. *Biological Invasions* 15: 931–944.
- Hausman CE, Jaeger JF, Rocha OJ. 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. *Biological Invasions* 12: 2013–2023.
- Heberling JM, Fridley JD. 2013. Resource-use strategies of native and invasive plants in Eastern North American forests. *New Phytologist* 200: 523–533.
- Hoven BM, Knight KS, Peters VE, Gorchov DL. 2020. Release and suppression: forest layer responses to emerald ash borer (*Agrilus planipennis*)-caused ash death. *Annals of Forest Science* 77: 1–27.
- Kashian DM, Witter JA. 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. *Forest Ecology and Management* 261: 480–488.
- Klooster WS, Gandhi KJK, Long LC, Perry KI, Rice KB, Herms DA. 2018. Ecological Impacts of Emerald Ash Borer in Forests at the Epicenter of the Invasion in North America. *Forests* 9: 250.
- Klooster WS, Herms DA, Knight KS, Herms CP, McCullough DG, Smith A, Gandhi KJK, Cardina J. 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions* 16: 859–873.
- Liebhold AM, MacDonald WL, Bergdahl D, Mastro VC. 1995. Invasion by Exotic Forest Pests: A Threat to Forest Ecosystems. *Forest Science* 41: a0001-z0001.
- Liebhold AM, McCullough DG, Blackburn LM, Frankel SJ, Holle BV, Aukema JE. 2013. A highly aggregated geographical distribution of forest pest invasions in the USA. *Diversity and Distributions* 19: 1208–1216.

- Lovett GM, Weiss M, Liebhold AM, Holmes TP, Leung B, Lambert KF, Orwig DA, Campbell FT, Rosenthal J, McCullough DG, *et al.* 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications* 26: 1437–1455.
- MacFarlane DW, Meyer SP. 2005. Characteristics and distribution of potential ash tree hosts for emerald ash borer. *Forest Ecology and Management* 213: 15–24.
- Margulies E, Bauer L, Ibáñez I. 2017. Buying Time: Preliminary Assessment of Biocontrol in the Recovery of Native Forest Vegetation in the Aftermath of the Invasive Emerald Ash Borer. *Forests* 8: 369.
- Muscolo A, Bagnato S, Sidari M, Mercurio R. 2014. A review of the roles of forest canopy gaps. *Journal of Forestry Research* 25: 725–736.
- Olson SK, Smithwick EAH, Lucash MS, Scheller RM, Nicholas RE, Ruckert KL, Caldwell CM. 2021. Landscape-Scale Forest Reorganization Following Insect Invasion and Harvest Under Future Climate Change Scenarios. *Ecosystems* 24: 1756–1774.
- Royo AA, Carson WP. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36: 1345–1362.
- Rutledge CE, Clark RE. 2023. Temporal and spatial dynamics of the emerald ash borer invasion in Connecticut as shown by the native digging wasp *Cerceris fumipennis* (Hymenoptera: Crabronidae). *Frontiers in Insect Science* 3: 1179368.
- Schnitzer SA, Carson WP. 2001. Treefall Gaps and the Maintenance of Species Diversity in a Tropical Forest. *Ecology* 82: 913–919.
- Shea K, Chesson P. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170–176.
- Stephens S, Romero S, Krist, F. 2022. Major forest insect and disease conditions in the United States: 2022. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service. 2020. Forests of Connecticut, 2019. Resource Update FS 240. Madison, WI: U.S. Department of Agriculture Forest Service, Northern Research Station. <https://doi.org/10.2737/FS-RU-240>
- Valladares F, Niinemets Ü. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology, Evolution, and Systematics* 39: 237–257.
- Ward EB, Pregitzer CC, Kuebbing SE, Bradford MA. 2020. Invasive lianas are drivers of and passengers to altered soil nutrient availability in urban forests. *Biological Invasions* 22: 935–955.