Introduction

At present, there are around 400 species of invasive insects that have been imported to the United States from across the globe (Lovett et al., 2016). This number continues to grow by 2-3 new invasive species every year as a result of international trade (Lovett et al., 2016). Some of these insects selectively target and kill specific tree species in order to survive and persist. As a result, invasive insects have proven to be the only disturbance capable of extirpating tree species, and sometimes entire genera, from their native ranges within decades (Lovett et al., 2016). Historically, the human response to such an invasion often entails harvesting any and all trees that would otherwise be afflicted with insects, a practice called salvage logging (Smith et al., 1997).

Emerald ash borer (*Agrilus planipennis*) is an invasive insect from Asia which is currently the costliest invasive insect in North America (Lovett et al., 2016). EAB kills black (*Fraxinus nigra*), white (*F. americana*), green (*F. pennsylvanica*), and pumpkin (*F. profunda*) ash trees within a few years (Youngquist et al., 2017), with a mortality rate exceeding 99% in some areas (Klooster et al., 2018). Forested wetlands, which naturally tend to have a large proportion of ash trees, are at risk of being converted to open-canopy wet meadows, especially in occurrences of pure ash stands (Youngquist et al., 2017). This can result in changes to the hydrology of the site in some scenarios and will inevitably alter canopy cover and leaf litter deposits on the site (Youngquist et al., 2017). This could create short-term increases in species richness, but a long-term negative impact on both the site itself and the surrounding terrestrial landscape (Youngquist et al., 2017).

Hemlock woolly adelgid (*Adelges tsugae*), which also originates from Asia, primarily attacks eastern hemlock (*Tsuga canadensis*). In many of the places where eastern hemlock is found, it is a foundation species, which means that they play a significant role in defining and regulating fundamental ecosystem processes (Ellison et al., 2005). Hemlock-dominated stands provide cool, damp microclimates with acidic, nutrient deficient soils that cycle nitrogen relatively slowly (Ellison et al., 2005). Hemlock also has the ability to regulate soil moisture content, stream flow, and stream temperature variation (Ellison et al., 2005). HWA has been shown to attack and kill hemlock trees at virtually all life stages, making successful regeneration of hemlock improbable and infrequent (Orwig et al., 1998). Hemlock loss leads to the loss of hemlock-specialist ants and birds, regional homogenization of both plant and animal life, significantly altered hydrological regimes (Ellison et al., 2005), erosion, and accelerated decomposition and nutrient cycling (Orwig et al., 2008).

For many family forest owners, a pest infestation can be sufficient reason to undertake salvage logging on their property (Markowski-Lindsay et al., 2019). Although this harvesting may be done with the intent of protecting the stand, this outcome is not always achieved. In fact, many ecosystem functions are more greatly disrupted by preemptive logging than insect infestation (Foster & Orwig, 2006). Historically in the mixed forests of New England, salvage logging of a particular species has been made more economically efficient by harvesting other species that would not be affected by the incoming infestation but are much more profitable (Markowski-Lindsay et al., 2019). If most trees of high value are removed along with the host species in post-disturbance logging this practice is known as "high grading." This is not an uncommon occurrence when salvage logging is unplanned in response to forest pests. It is projected that with the management response to just EAB alone, about 12-13% of the aboveground biomass of the Connecticut River watershed will be removed, creating a disturbance twice as severe as EAB invading unchecked (MacLean et al., 2020). Salvage logging in response to HWA is projected to convert hemlock-dominated stands to red maple, while also leading to less sequestered carbon than if nothing was done at all (Krebs et al., 2016). Additionally, HWA salvage logging that has already occurred has been shown to decrease the value of those stands and alter their nitrogen cycles (Markowski-Lindsay et al., 2019).

Harvest responses to insects do not always consider the future conditions of the forest, making the incorporation of planning for future disturbances, like those projected to increase due to climate change, unlikely in a management response to insects. However, forest management, even in response to forests pests, should consider future forest health to maximize benefits from forests. Forest climate adaptation research from the Northern Institute of Applied Climate Sciences (NIACS) is field testing three alternative harvest types for managers to consider when planning future forest conditions. Their Adaptive Silviculture for Climate Change project (ASCC) involves a series of experimental forest plots on which they apply different harvests designed to manipulate forest successional trajectory in the face of disturbance and climate change (NIACS, 2018). The three treatments outlined in the ASCC project are: resistance, resilience, and transition. A resistance treatment aims to maintain current forest conditions as much as possible by harvesting single trees, meaning those that are left behind have to compete less for vital resources. A resilience treatment aims to create pockets of differing species composition and structures, so that in the event of a significant disturbance (e.g. invasive insect infestation), one or more of these pockets are resilient enough to survive and facilitate forest recovery. A transition treatment aims to help the forest transition to future climate conditions by removing trees that are not well-adapted for future climate scenarios; this is supplemented by the planting of non-endemic species that are expected to do well in future climate conditions (NIACS, 2018).

In this study, we aimed to forecast the relative impacts that both new (i.e. resistance, resilience, transition) and old (i.e. salvage logging, high grading) would have on the aboveground biomass and species composition of a simulated forest landscape when managed after insect invasion. Although there are many species of invasive insects in the Northeast, we elected to focus on two: the emerald ash borer and the hemlock woolly adelgid. To forecast the impacts of these insects and the various harvesting responses, we used a forest landscape model to apply a pest infestation and each harvest treatment to an identical starting forest. We then let the forest recover, and compared the effects of each harvest based on the differences in recovery.

Methods

This study takes place in New England, a heavily forested region where the forests are predominantly mixed. Hemlock woolly adelgid (HWA) and emerald ash borer (EAB) were both first introduced and discovered in other parts of the country first, but they eventually spread to New England in the 1980s and 2000s, respectively (UMass 2018, UMass 2020). We focused this study specifically on the Connecticut River Watershed (CTRW; Figure 1) which covers parts of New Hampshire, Vermont, Massachusetts, and Connecticut, spanning from Canada to the Long Island Sound. The forest ownership types of this part of New England is dominated by small family forest owners, each making individual decisions about the management response to invasive insects on their property (Markowski-Lindsay et al., 2019). Due to this dynamic of having a large number of individual forest owners, it is important to understand the impacts of harvest types on the long term trajectory of the forest.

To allow for multiple harvest and insect scenarios, we focused our study on six 20km x 20km sites within the CTRW; three for EAB and ash trees, and three for HWA and hemlock trees (Figure 1).

The three sites for each species were representative of a range of ash/hemlock abundances in the watershed. Representative landscapes were chosen (rather than simulating the entire CTRW) in order to reduce simulation times and simulate each management type separately. We identified the three areas for each species by selecting locations where ash or hemlock each had a comparatively high (maximum abundance of that species in the watershed for a 20 km x 20 km area), intermediate (60% of maximum), and low abundance (40% of maximum), to test the impacts at different species abundances. Note, however, that the maximum abundance for each species was different, with ash at around 9% relative abundance, and hemlock at around 15% relative abundance. The exact locations were determined using a moving window approach, restricting the sample areas to inside the CTRW. These sites were treated independently, with the ash sites only experiencing simulated mortality or harvesting due to EAB and the hemlock sites only experiencing simulated mortality or harvesting in response to HWA.

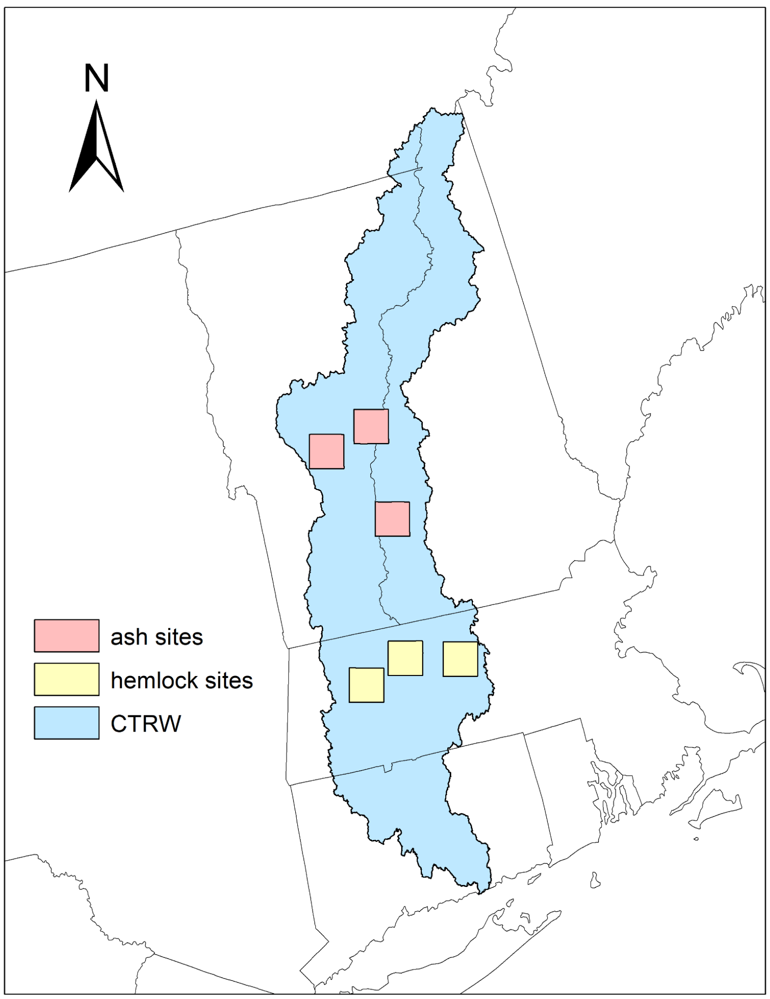

Figure 1: Map of the Connecticut River Watershed, as well as ash and hemlock sites identified within it.

Within these sites, we simulated forest growth and succession using LANDIS-II (v. 7.0), a spatially explicit, mechanistic forest landscape model that models disturbances and tracks species/age cohorts within forest raster cells. To model forest succession within LANDIS-II, we used the PnET-Succession extension (v.3.4) (de Bruijn et al. 2014) to simulate photosynthesis, respiration, and mortality based on the PnET Carbon Model (Aber et al. 1995). This usage of LANDIS-II and PnET-Succession has been used and evaluated extensively in New England (e.g., Duveneck & Thompson 2017, 2019) and beyond. We used the Base Wind extension (Mladenoff & He, 1999) for LANDIS-II to emulate low-severity wind-based mortality events. We also simulated climate change in our models using the Regional Conservation Pathway (RCP) 8.5 emission scenario (Stocker et al., 2013) as projected by the Hadley Global Environment v.2-Earth System Global Circulation Model (GCM), downscaled and obtained from the USGS Geo Data Portal (Stoner et al. 2013).

For our initial forest conditions within all sites, we used a 100 m resolution forest composition raster from Duveneck et al. (2015). This raster, which was based on an imputation of USDA Forest Inventory and Analysis (FIA) plots (Bechtold & Patterson, 2005), contained our initial forest biomass and composition that was used for 2010, the beginning date of each simulation run. Simulations were carried out for 55 years, and the total aboveground biomass of each species was recorded in five year time steps. To track aboveground biomass changes from harvesting in response to insects, we used the extension Land Use + (LU+; Thompson et al., 2016), which simulated both the mortality due to insects and the desired harvests as described below.

With LANDIS-II set up in this way, we could then feed it different scenarios of harvesting in response to insects based on the forest prescriptions we were emulating. In all, there were seven scenarios per insect (EAB or HWA); two reference scenarios: “grow only” and “insects only”; two more extreme and less planned harvest treatments: “salvage” and “high grade”; and finally, the three treatments that are being tested in the context of managing for climate adaptation: “resistance”, “resilience”, and “transition”. In the “grow only” scenario, we let the forest grow without any insect infestation or human harvesting as a comparison for all other models. In the “insects only” scenario, EAB and HWA stressed and killed their respective host species, but humans did not harvest any trees. For these scenarios we used the LU+ scenario with a new cohort stress parameter to stress and then kill the host species for each insect. The stress began after 2015 in the simulations; stress killed ash cohorts in 4-9 years (depending on other stresses on the cohort) and killed hemlock cohorts in 15-22 years.

The five harvest scenarios (i.e., salvage, high grade, resistance, resilience, and transition) all had insect stress occurring starting directly after 2015, with harvests applied to all cells only once in 2020. In order to create harvest prescriptions, we first categorized tree species into high and low value species (Table 1). We then harvested a certain percentage of tree species older than 10 years based on these categories, as shown in Table 2. In the ‘transition’ treatment, following the harvest outlined in Table 2, loblolly pine (*Pinus taeda*) and chinkapin oak (*Quercus muehlenbergii*) were planted on the landscape.

Table 1: Species categorization into high and low value, used for harvest selection.

High value	Low value
Red maple Sugar maple Yellow birch White pine Black cherry Quaking aspen White oak Scarlet oak Chestnut oak Northern red oak Black oak American basswood	Balsam fir Sweet birch Paper birch Gray birch Pignut hickory American beech Tamarack Eastern hophornbeam White spruce Black spruce Red spruce Red pine Pitch pine Balsam poplar Big-toothed aspen Northern whitecedar American elm

Table 2: Percentages of tree species removed by category in each land use scenario.

Scenario	Host	High value	Low value
Salvage	100%	0%	0%
High grade	100%	80%	20%
Resistance	50%	10%	10%
Resilience	100%	20%	40%
Transition	100%	30%	60%

We analyzed the resulting 14 simulations (7 for the hemlock sites and 7 for the ash sites) in a few different ways, primarily focusing on changes in aboveground species biomass. Analyzing outputs at 25 and 50 years after insect infestation, we grouped species outputs together based on whether they are well adapted, fairly adapted, or poorly adapted to future climate conditions in New England under emissions scenario RCP 8.5 (Table 3; NIACS, n.d.). This allowed us to see how much biomass was reserved in each category, as well as the total biomass of each simulation. We also assessed the proportions of total biomass which fell into each of these categories, so as to compare the relative proportions of biomass in each category, regardless of how much biomass it actually was. Finally, we calculated a Bray-Curtis dissimilarity index for the aboveground biomass of all tree species at 25 and 50 years after insect infestation took place. Bray-Curtis dissimilarity generates a value between 0 and 1 (where 0 is completely identical and 1 is completely dissimilar), a value it calculates using both the presence and abundance of each species in a raster cell. There is precedent for using Bray-Curtis dissimilarity in conjunction with

LANDIS-II (Duveneck & Scheller, 2015).

Table 3: Future climate adaptability of all tree species present in our simulations, based on NIACS, n.d..

Well adapted	Fairly adapted	Poorly adapted
Red maple	Yellow birch	Balsam fir
Sugar maple	Sweet birch	Paper birch
Pignut hickory	Gray birch	Black ash**
American beech	White ash**	Tamarack
Eastern hophornbeam	White spruce	Black spruce
Big-toothed aspen	Red spruce	Red pine
Quaking aspen	White pine	Pitch pine
Black cherry	Eastern hemlock**	Balsam poplar
White oak		Northern whitecedar
Scarlet oak		
Chestnut oak		
Northern red oak		
Black oak		
American basswood		
American elm		* = planted
Loblolly pine*		** = host species
Chinkapin oak*		

Results

Across all of our observations, some general patterns emerged. High grade scenarios consistently scored lowest in terms of biomass, as well as proportion of its biomass reserved as well-adapted future climate species. Transition scenarios, despite having the second-lowest total biomass, had the highest proportion of its biomass reserved as well-adapted future climate species. Additionally, all three climate smart harvests (i.e. resistance, resilience, transition) consistently had higher proportions of well-adapted future climate biomass than high grade, and similar proportions to salvage logging. We were able to observe host persistence in the insects only and resistance treatments on hemlock sites, but we did not see any significant host persistence on the ash sites.

Twenty-five years after insect infestation of EAB sites, we can see several key differences between harvests already emerging. In general, high grade is the most different from all other scenarios (Table 4; Bray-Curtis ranging from 0.132 in comparison to resistance, to 0.152 in comparison to grow only). High grade also had the lowest total biomass (Figure 2), and the lowest proportion of its biomass composed of well-adapted future climate species (Figure 3). Although it has the second-lowest biomass at this time step (Figure 2), the transition treatment has the highest proportion of its biomass as well-adapted future climate species (Figure 3). All treatments except for high grade had a higher proportion of their biomass in well-adapted future climate species than in the grow-only control (Figure 3). The two most similar scenarios at this time step are bugs only and salvage (Table 4; Bray-Curtis = 0.002).

Table 4: Bray-Curtis Dissimilarity values for ash sites at 25 years after infestation.

Bray-Curtis Dissimilarity - EAB Year 25							
	grow	bugs	salvage	high grade	resistance	resilience	transition
grow	0						
bugs	0.040	0					
salvage	0.042	0.002	0				
high grade	0.152	0.138	0.140	0			
resistance	0.031	0.018	0.020	0.132	0		
resilience	0.052	0.040	0.042	0.144	0.023	0	
transition	0.098	0.078	0.077	0.146	0.071	0.051	0

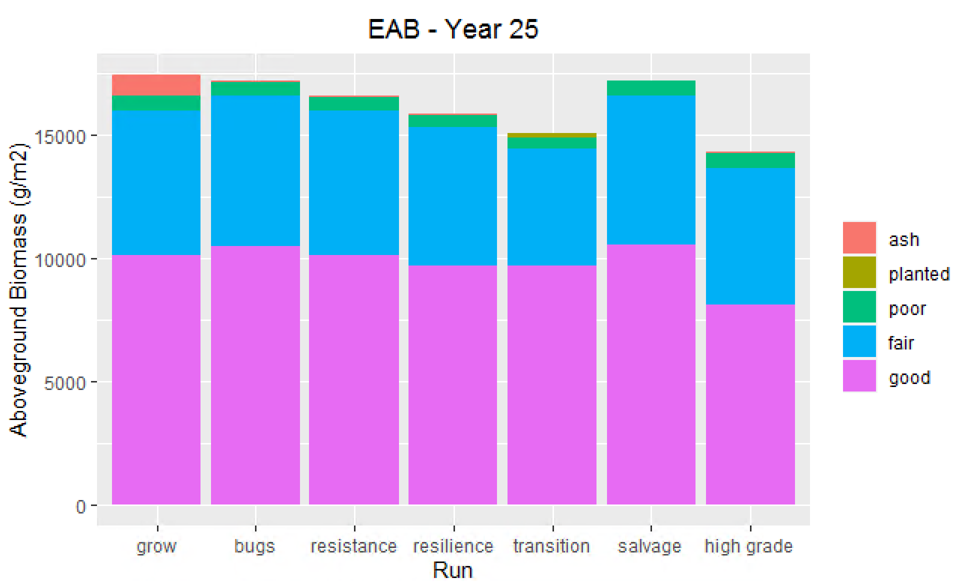

Figure 2: graph of categorized aboveground biomass on ash sites 25 years after infestation.

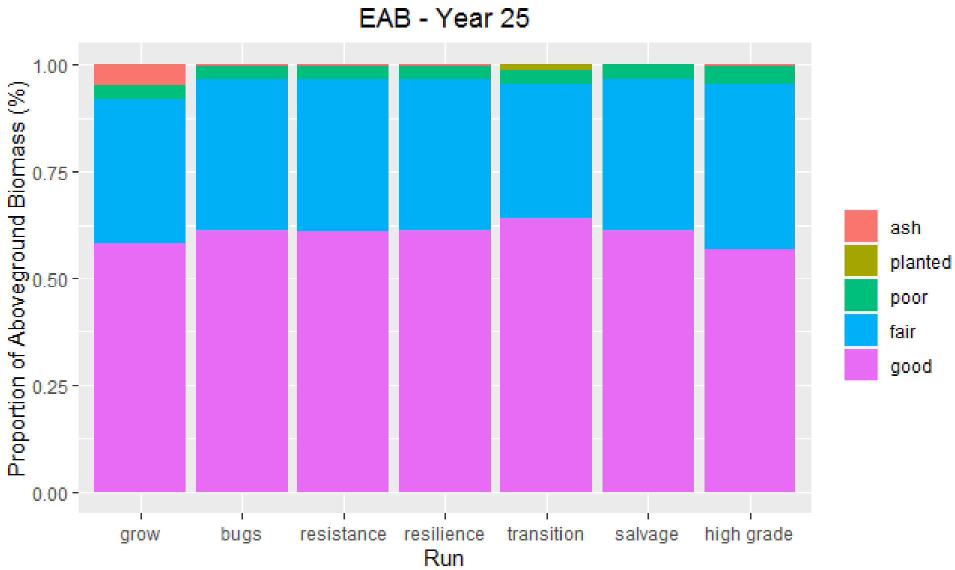

Figure 3: graph of proportions of categorized aboveground biomass on ash sites 25 years after infestation.

At 50 years after infestation, we see that Bray-Curtis values are on average lower than they were 25 years prior (Table 8; average Bray-Curtis at year 25 = 0.073, year 50 = 0.056). High grade continues to be the most different from other harvests (Table 5), and transition maintains the highest proportion of biomass reserved as well-adapted future climate species (Figure 5). By this time, we see that the forest has nearly recovered in terms of total biomass in each scenario (Figure 4). Bugs only, resistance, resilience, and salvage all maintain similar proportions of well-adapted future climate biomass (Figure 5), with only slight overall differences in biomass (Figure 4).

Table 5: Bray-Curtis Dissimilarity values for ash sites at 50 years after infestation.

Bray-Curtis Dissimilarity - EAB Year 50							
	grow	bugs	salvage	high grade	resistance	resilience	transition
grow	0						
bugs	0.045	0					
salvage	0.048	0.004	0				
high grade	0.107	0.097	0.099	0			
resistance	0.037	0.008	0.011	0.095	0		
resilience	0.049	0.019	0.021	0.106	0.017	0	
transition	0.081	0.060	0.058	0.115	0.060	0.047	0

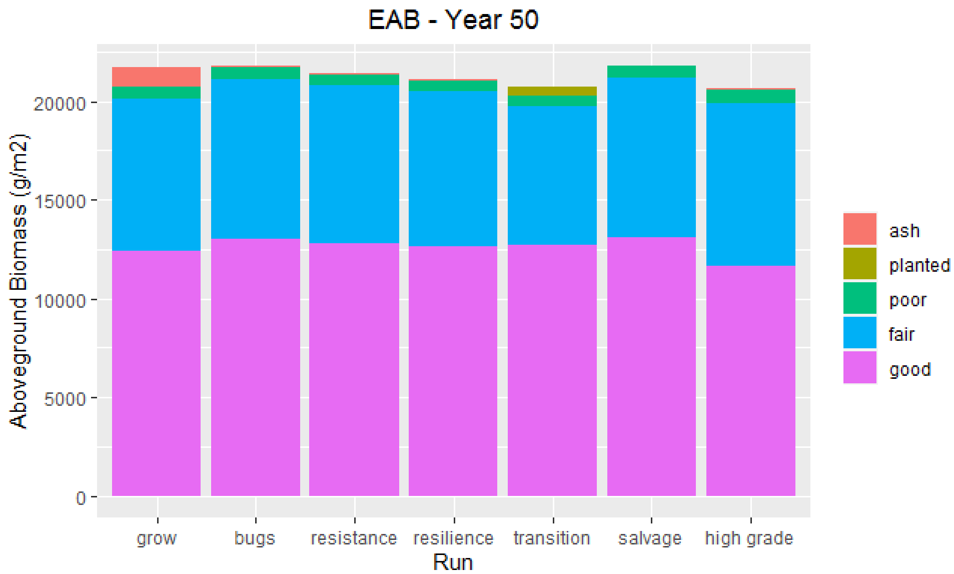

Figure 4: graph of categorized aboveground biomass on ash sites 50 years after infestation.

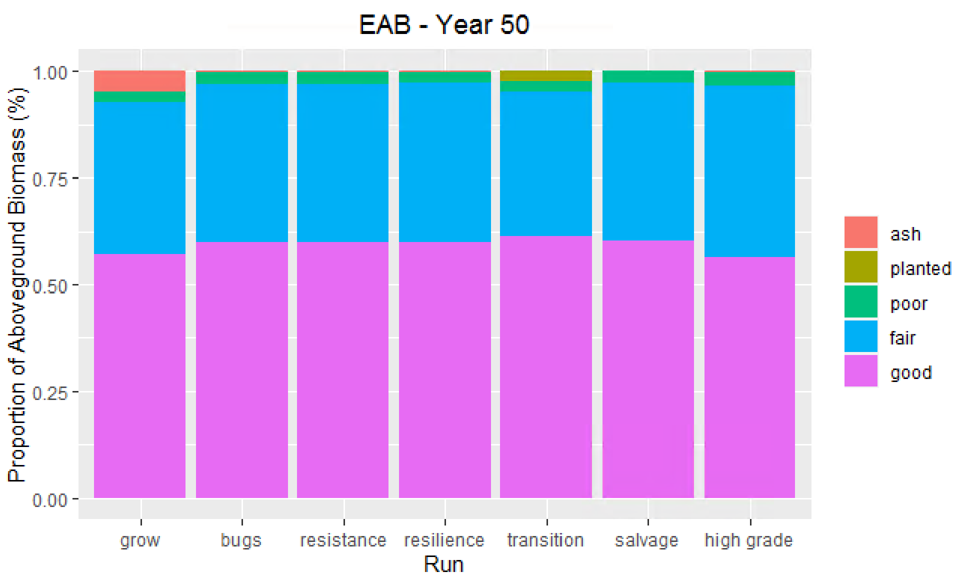

Figure 5: graph of proportions of categorized aboveground biomass on ash sites 50 years after infestation.

Twenty-five years following infestation on HWA sites, we see some similar trends as with EAB, but with slight nuances. High grade continues to be the most different from all other scenarios, but it is also more different than it was on EAB sites (Table 6; Bray-Curtis ranging from 0.124 in comparison to transition, to 0.198 in comparison to grow only). High grade has the lowest total biomass (Figure 6) and lowest proportion of well-adapted future climate biomass (Figure 7), similar to high grade scenarios on EAB sites. Transition also has the highest proportion of well-adapted future climate biomass (Figure 7) despite having the second-lowest total biomass (Figure 6), similar to EAB sites. Overall, Bray-Curtis values were higher for HWA at this point in time (average Bray-Curtis: 0.091) than they were for EAB (average Bray-Curtis: 0.073), meaning that HWA scenarios were more different from one another on average than EAB scenarios (Table 8). One thing that we see here that we did not see on EAB sites is host (hemlock) persistence, specifically in the bugs only and resistance simulations (Figure 6).

Table 6: Bray-Curtis Dissimilarity values for hemlock sites at 25 years after infestation.

Bray-Curtis Dissimilarity - HWA Year 25							
	grow	bugs	salvage	high grade	resistance	resilience	transition
grow	0						
bugs	0.079	0					
salvage	0.098	0.019	0				
high grade	0.198	0.159	0.153	0			
resistance	0.056	0.027	0.047	0.153	0		
resilience	0.084	0.043	0.040	0.143	0.033	0	
transition	0.124	0.090	0.089	0.127	0.083	0.056	0

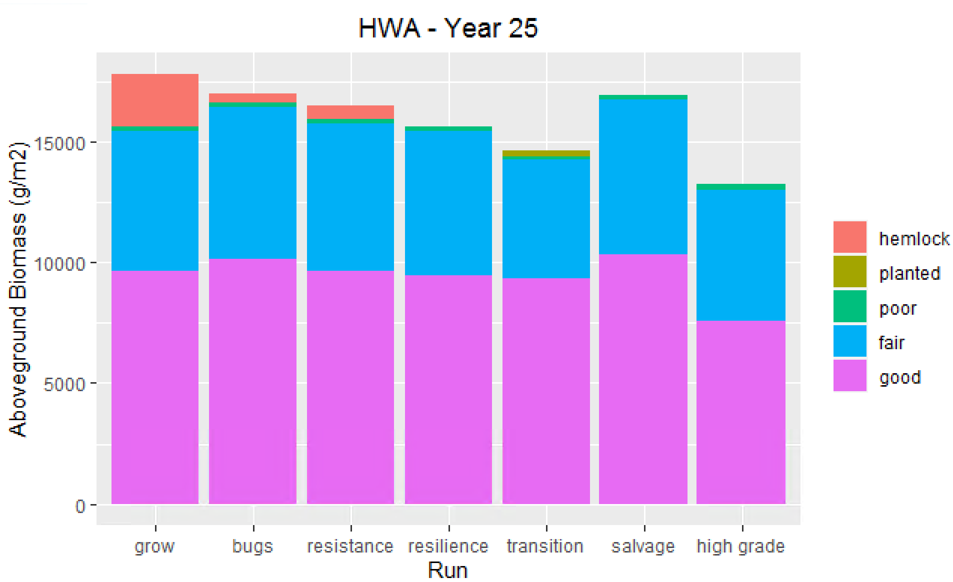

Figure 6: graph of categorized aboveground biomass on hemlock sites 25 years after infestation.

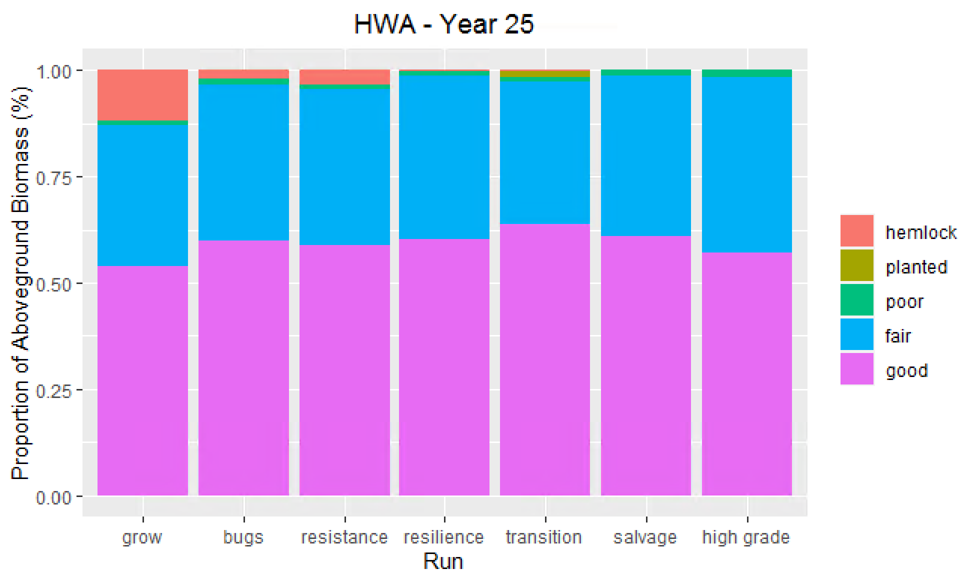

Figure 7: graph of proportions of categorized aboveground biomass on hemlock sites 25 years after infestation.

At 50 years after infestation on HWA sites, we see that Bray-Curtis values are on average lower than they were 25 years prior, similar to EAB (Table 8; average Bray-Curtis for HWA at time step 25 = 0.091, time step 50 = 0.074). High grade continues to be the most different from other harvests (Table 7), and transition maintains the highest proportion of biomass reserved as well-adapted future climate species (Figure 9), both of which emerged in EAB sites as well. Forest biomass recovery in HWA sites at this point (Figure 8) is not as complete as recovery in EAB sites by this time (Figure 4). Overall, Bray-Curtis values were higher for HWA at 50 years after infestation (average Bray-Curtis: 0.074) than they were for EAB (average Bray-Curtis: 0.056), meaning that HWA scenarios were more different from one another on average than EAB scenarios (Table 8). Hemlock continued to persist at this time step, having more biomass than it did 25 years prior (Figure 8).

Table 7: Bray-Curtis Dissimilarity values for hemlock sites at 50 years after infestation.

Bray-Curtis Dissimilarity - HWA Year 50							
	grow	bugs	salvage	high grade	resistance	resilience	transition
grow	0						
bugs	0.095	0					
salvage	0.117	0.022	0				
high grade	0.138	0.094	0.086	0			
resistance	0.073	0.024	0.046	0.095	0		
resilience	0.108	0.029	0.019	0.087	0.041	0	
transition	0.120	0.070	0.063	0.099	0.075	0.052	0

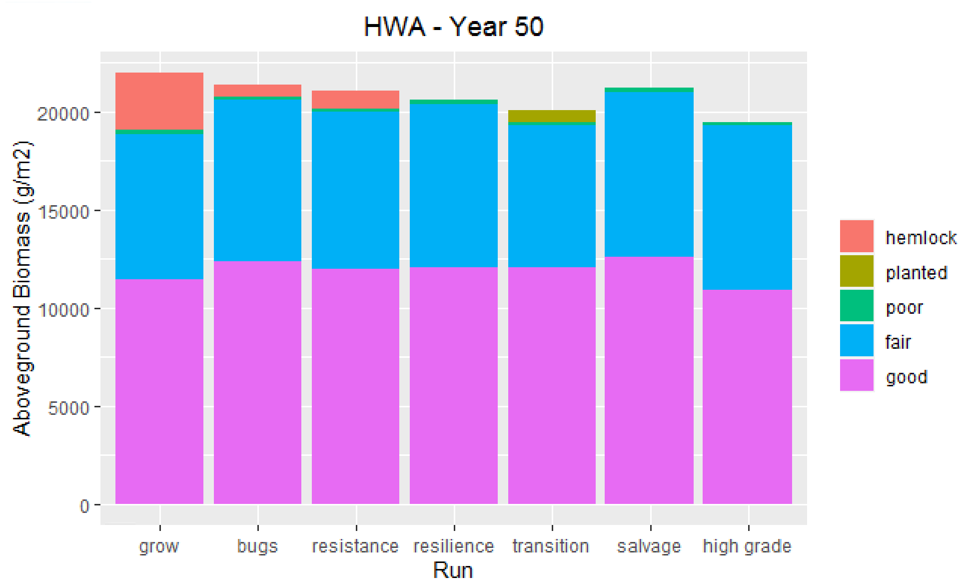

Figure 8: graph of categorized aboveground biomass on hemlock sites 50 years after infestation.

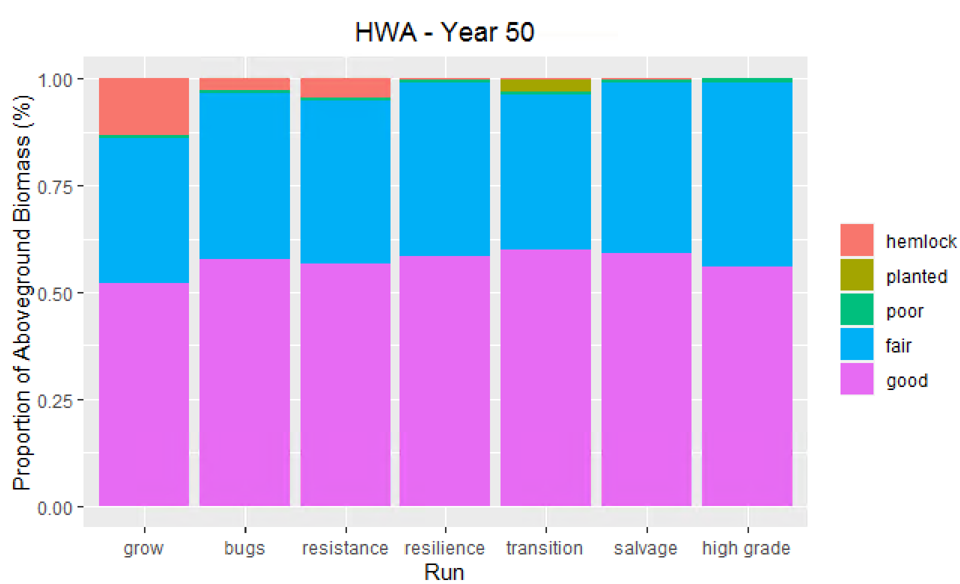

Figure 9: graph of proportions of categorized aboveground biomass on hemlock sites 50 years after infestation.

Although ash and hemlock had different study sites within the CTRW, we are still able to compare their average Bray-Curtis dissimilarity values because initial communities are similar in their species diversities. The Bray-Curtis values indicate how different the two scenarios are that are being compared, and so the average of these values at a particular site and timestep shows how generally dissimilar all scenarios are from one another. We only intend to use the average Bray-Curtis values for comparisons about the general dissimilarity of scenarios between sites and timesteps, and therefore our inferences from these averages are valid despite the differing initial conditions of the ash and hemlock sites.

Table 8: average Bray-Curtis dissimilarity values for all simulation comparisons.

	EAB	HWA
Year 25	0.073	0.091
Year 50	0.056	0.074

Discussion

Our observations revealed an overall pattern that the abundance of the host species must be factored into harvesting decisions. We observed that HWA sites had higher Bray-Curtis dissimilarity values on average at both time steps in comparison to EAB sites. This was largely driven by hemlock being naturally more abundant on the landscape than all combined ash species. When a more highly abundant species is fully removed, there is more opportunity for new trees to grow. This allows for more differences between simulations, which is what drove the Bray-Curtis dissimilarity values to be higher in HWA sites than EAB sites. Additionally, high Bray-Curtis values in harvest scenarios where well-adapted future climate species were left behind allowed for more well-adapted species filling the openings left by harvests.

As time progressed in each scenario, the Bray-Curtis dissimilarity values decreased across both ash and hemlock sites from year 25 to year 50. This represents a trend in forests to continue along their current trajectory, in this case set by the initial conditions which are the same for each scenario. This is particularly true given the way LANDIS simulates forests using a cohort model (Duveneck & Thompson, 2017). In the LANDIS-II cohort model, only partial cohorts are removed to simulate a harvest, meaning the remaining cohorts, and therefore species, are quickly able to use newly available resources such as light and water.

The high grade scenario yielded the lowest aboveground at every site for both EAB and HWA sites, at both 25 and 50 years after infestation. Additionally, we observed that high grade regularly had the highest Bray-Curtis dissimilarity values among all scenarios, and had the lowest proportion of its biomass reserved in well-adapted future climate species. These undesirable outcomes were driven by the species selection and the amount outlined by the goals of high grading. High grade harvests removed the most biomass out of all scenarios, and the species selected were chosen based on their monetary value without consideration for future forest conditions. This resulted in high grading being a very poor harvest option in terms of aiding and/or preserving forest ecology and climate adaptability.

In stark contrast, we observed the transition harvest scenario fare much better in terms of proportion of biomass in well-adapted future climate species, scoring the highest of all scenarios at all sites and at each time step. Although transition had the second-lowest biomass among all simulations at both 25 and 50 years after infestation, this heavier removal allowed for an increased rate of regeneration and growth in the remaining forest. This explains how the forest was able to recover as quickly as it did under the transition treatment. Additionally, a significant amount of the biomass that was removed in the transition scenarios was species that were poorly adapted to future climate conditions. This drove the proportion of well-adapted biomass up, and yielded a forest that was better equipped to face climate change than that of a high graded forest.

The transition treatment was not the only one to accomplish its outlined goals. The resistance treatment scored the lowest Bray-Curtis values of any simulation at any time observed in comparison to the grow only simulations. Resistance aims to maintain current forest conditions, resisting change through disturbance. The lower Bray-Curtis values indicate that the resistance treatment was more similar to grow only, the projected outcome of current forest conditions, than all other simulated treatments. Additionally, despite harvesting 50% of hemlock trees, the resistance treatment yielded more hemlock biomass than the bugs only scenario. For the resilience treatment, although it was not possible to precisely simulate the patchwork of functionally unique pockets of forest, it still maintained a higher proportion of well-adapted species biomass than the grow only simulation at all sites, but especially within the hemlock sites.

Conclusion

Overall, this study has shown that the abundance of the host species should be taken into account when making decisions about how to manage for invasive insects. The higher relative abundance of hemlock than ash on the New England landscape affected the overall impact of the different harvesting responses. Additionally, the desired outcome for the forest should be taken into account when deciding on which treatment to apply, since these treatments have different outcomes. This study also serves to support the implementation of climate smart harvesting in response to invasive insects in our forests. On our current emissions trajectory, climate change will become a significant threat within the coming decades, but this study shows that our harvesting choices in response to invasive insects can facilitate forest adaptation to changing climate conditions.

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