

# Invasive Plant Cover and Density Following Emerald Ash Borer-induced Mortality in Southern Ontario Forests

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INVASIVE PLANT COVER AND DENSITY FOLLOWING EMERALD ASH  
BORER-INDUCED MORTALITY IN SOUTHERN ONTARIO FORESTS

By

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An undergraduate thesis submitted in partial fulfillment of the requirements for the  
degree of Honours Bachelor of Science in Forestry

Faculty of Natural Resources Management

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## ABSTRACT

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The emerald ash borer has caused widespread ash mortality in eastern North American forests, where forest managers are also facing challenges due to invasions of undesirable exotic plant species. This study aims to explore relationships between the two phenomena based on existing evidence that disturbance caused by insect pests may facilitate invasive plant colonization. The presence of invasive species was analyzed in the context of ash mortality following emerald ash borer infestation in four forests in the Region of Waterloo in Ontario. Multivariate analysis with generalized linear models was used to detect relationships between invasive plants and various environmental variables. Significant relationships with invasive plant cover and density are found for decline in ash basal area, ash mortality occurrence, change in total basal area, current basal area, canopy closure, regeneration density, and tree species composition. Potential effects of competitive exclusion and site richness on invasive plant species are discussed.

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## INTRODUCTION

Invasive plant species present a challenge in forest management where more desirable vegetation is excluded by invaders. Many invasive plants are adapted to take advantage of disturbance conditions (Webster *et al.* 2006; Eschtruth and Battles 2009; Burnham and Lee 2010), which are being created in many eastern North American forests by an invasive insect pest, the emerald ash borer (EAB) (Herms and McCullough 2014). Gap formation due to tree mortality is a normal process of forest disturbance (Oliver and Larson 1996; Muscolo *et al.* 2014). However, areas where EAB is established are experiencing the mortality of the majority of trees in an entire genus over just a few years (Herms and McCullough 2014). Widespread change in forest composition has inherent implications for merchantable tree species regeneration as well as ecological function and integrity, and so the characteristics of resulting plant communities are relevant to a wide array of forest management objectives. Given that invasive plant species have detrimental effects on both tree regeneration and ecological health (Vitousek *et al.* 1996; Mack *et al.* 2000; Pimentel *et al.* 2000; Webster *et al.* 2006), the role of such species in successional patterns following EAB disturbance is of particular interest.

## OBJECTIVE

The objective of this thesis is to investigate potential impacts of the loss of ash due to EAB on the presence of invasive species in forests in the Region of Waterloo. A wide variety of variables potentially affect the presence and abundance of invasive plant species in a given location (Eschtruth and Battles 2009), and so statistical analysis

includes a full array of forest inventory data collected in 2021 as well as data from 2002, which was before EAB was detected in the area. Using generalized linear models, relationships between the measured variables are interpreted to determine the extent to which decline in ash composition has an effect on the role of invasive species in plant communities relevant to other site characteristics. The aim of this multivariate analysis is also to capture potential interactions between the variables at play.

## HYPOTHESIS

It was hypothesized that forest stands which have experienced higher ash mortality would be occupied by higher proportions of invasive species. Specifically, it was expected that greater loss of ash basal area from 2002 to 2021 would be associated with a higher proportion of area covered by invasive plants and higher density of buckthorn species in the plots sampled. This means that the null hypothesis is that decline in ash basal area has no impact or is associated with lower invasive species cover and buckthorn density.

## LITERATURE REVIEW

### THE IMPACT OF INVASIVE PLANT SPECIES

The human-facilitated spread of non-native organisms has occurred at an unprecedented rate in recent history; Mack *et al.* (2000) describe the shifts in species as being as drastic as those precipitated by glaciation cycles but at a dramatically greater pace. The consequences of invasive species are far-ranging. Beyond directly affecting their host communities through competition, predation, and herbivory, invaders can alter entire ecological systems through impacts to disturbance regimes, nutrient cycling, productivity, hydrology, and geomorphology (Vitousek *et al.* 1996; Mack *et al.* 2000). Through these direct and indirect interactions, invasive species reduce local and overall biodiversity and drive extinctions (Woods 1993; Vitousek *et al.* 1996; Mack *et al.* 2000; Frappier *et al.* 2003a; Fagan and Peart 2004; Webster *et al.* 2006).

Across the existing body of research concerning invasive plant species, they have been found to reduce the fitness, abundance, and diversity of native plant and animal species via bottom-up impacts through trophic systems (Vilà *et al.* 2011). Many invasive plants also have serious implications for human wellbeing. Industries like agriculture must absorb huge losses in yield and costs of control measures due to weedy and pathogen-hosting exotic species (Vitousek *et al.* 1996; Mack *et al.* 2000; Webster *et al.* 2006; Francis *et al.* 2009). Human health and safety is threatened by invasive plant species in a variety of ways; increased fire incidence and severity is related to certain invaders (Mack *et al.* 2000), drought in some regions is exacerbated by invaders with high water uptake (Mack *et al.* 2000), and some invasive plants increase incidence of

human illnesses by providing habitat for disease vectors, like Japanese barberry (*Berberis thunbergii*) which hosts Lyme disease-carrying ticks in North America (Williams *et al.* 2017), and Lantana (*Lantana camara*) which hosts tsetse flies responsible for sleeping sickness in East Africa (Mack *et al.* 2000).

The success of these invaders in their non-native ranges is most widely attributed to release from natural enemies; the absence of species which have evolved to compete with, predate on, and parasitize invaders allow them to spread and reach densities not seen in their places of origin (Mack *et al.* 2000; Webster *et al.* 2006; Knight *et al.* 2007). Invasive plants also possess various combinations of traits that promote invasiveness, such as hardiness to variable conditions, dense stand formation, high fecundity, seed bank creation, and animal-dispersed seeds (Webster *et al.* 2006). In a study of 32 native and invasive plant species common in eastern North American forests, Heberling and Fridley (2013) found that in comparison with native species, invasive species exhibited superior photosynthetic abilities as well as more efficient and productive use of light and nitrogen resources. Many invaders are also aided significantly through human actions like deliberate widespread planting and creation of disturbance (Mack *et al.* 2000; Webster *et al.* 2006).

#### INVASIVE PLANT SPECIES IN THE REGION OF WATERLOO

While many invasive plants possess common characteristics, they can vary greatly in terms of the factors which contribute to their invasiveness and the consequences they impart on native ecosystems (Webster *et al.* 2006; Vilà *et al.* 2011). As such, it is necessary to examine the dynamics of invasion of each species

individually. The following species are those which are most pervasive in the Waterloo Regional Forests.

Common Buckthorn (*Rhamnus cathartica*)

Common buckthorn is a shrub native to Europe and western Asia which prefers disturbed, open, rich conditions but can tolerate wide ranges in light, moisture, and soil chemistry and is found in diverse habitats including open areas, forest understories, wetland edges, and urban areas (Knight *et al.* 2007; Kurylo *et al.* 2007; McCay and McCay 2008). It was introduced to North America for ornamental use by the early 1800s, and has since spread widely throughout the eastern and central United States and Canada (Knight *et al.* 2007; Kurylo *et al.* 2007). Its monumental success as an invader has been attributed to its ability to tolerate shade, survive flooding and drought, grow rapidly, produce copious bird-dispersed fruits with high germination rates, form large dense thickets to the exclusion of other species, leaf out earlier in the spring and retain leaves later in the fall than native species, suffer less herbivory than native competitors, and release allelopathic chemicals in the soil (Webster *et al.* 2006; Knight *et al.* 2007; Kurylo *et al.* 2007; Klionsky *et al.* 2011).

The ecological effects of common buckthorn include the displacement of native plants, lower growth and survival of tree seedlings, increased soil nitrogen, disruption of soil biota communities, reduction in leaf litter, increased invasive earthworm abundance, reduction in palatable browse for herbivores, and decreased habitat quality for birds (Webster *et al.* 2006; Knight *et al.* 2007; Klionsky *et al.* 2011). Common buckthorn also provides an alternate or overwintering host for the fungi responsible for crown rust and leaf rust of oats (*Puccinia coronata*), crown rust of barley (*Puccinia coronata* var.



*hordei*), as well as soybean aphid (*Aphis glycines*), all of which have caused massive losses in crop yields and required high expenditure on control measures by farmers (Qaderi *et al.* 2009; Ragsdale *et al.* 2011; Nazareno *et al.* 2018). Combined, these factors make common buckthorn a serious concern in conservation, forestry, and agriculture.

#### Glossy Buckthorn (*Frangula alnus*)

Glossy buckthorn is ecologically similar to common buckthorn, but prefers mesic and wetland habitats with moist, nutrient-rich soils (Frappier *et al.* 2003a; Webster *et al.* 2006; Cunard and Lee 2008). It originated in Europe, and since its introduction to North America in the late 1800s has spread through much of the northeastern United States and adjacent Canadian provinces and become one of the region's most abundant invasive shrubs (Frappier *et al.* 2003b ; Cunard and Lee 2008). Glossy buckthorn is moderately shade-tolerant, but in more open areas like canopy gaps it achieves greater heights, reproductive output, and recruitment (Frappier *et al.* 2002; Fagan and Peart 2004; Cunard and Lee 2008). This plant frequently forms a dense shrub layer in forest understories which inhibits regeneration of tree species and reduces native plant cover and diversity (Frappier *et al.* 2003a; Fagan and Peart 2004; Cunard and Lee 2008; Burnham and Lee 2009). The suppression of tree regeneration has concerning ecological and financial repercussions where canopy formation is threatened and control measures may be required (Hutchinson and Vankat 1997; Fagan and Peart 2004; Webster *et al.* 2006; Burnham and Lee 2009).

### Garlic Mustard (*Alliaria petiolata*)

Garlic mustard is a biennial forb which originated in Europe and Asia and, since its introduction in the mid-1800s, has become widespread in forests edges and understories throughout much of North America (Nuzzo 1999; Welk *et al.* 2002; Stinson *et al.* 2007). It prefers the intermediate levels of light and moisture of mesic forests, forest edges, and riparian zones (Nuzzo 1999; Meekins and McCarthy 2001; Welk *et al.* 2002). Garlic mustard more readily invades disturbed sites, but is also able to infiltrate intact forests (Stinson *et al.* 2007). It reduces the abundance and diversity of native species by outcompeting other species for light, as well as by inhibiting the germination of other species through the release of allelopathic root exudates (Meekins and McCarthy 1999; Prati and Bossdorf 2004; Stinson *et al.* 2007). Tree seedlings have been noted to be more strongly affected by increasing levels of garlic mustard invasion than other types of vegetation (Stinson *et al.* 2007).

### Other Notable Species

Other invasive species which are common or of particular concern in the Waterloo Regional Forests include Dame's rocket (*Hesperis matronalis*), bush honeysuckles (*Lonicera* spp.), wood avens (*Geum urbanum*), barberry (*Berberis thunbergii*), lily-of-the-valley (*Convallaria majalis*), invasive Phragmites (*Phragmites australis* subsp. *australis*), and Norway maple (*Acer platanoides*), among others. Dame's rocket is widespread among open forest habitats, edges, and streambanks of eastern and southern Ontario, Quebec, and the northeastern and midwestern United States, where it can crowd out native plants, reduce biodiversity, and serve as an alternative host to agricultural viruses (Francis *et al.* 2009). The invasive honeysuckle

species present in southern Ontario have many characteristics in common with both species of invasive buckthorn, including earlier and later seasonal foliation than native species, bird-dispersed seeds, few pests, shade tolerant seedlings, and rapid growth in higher light conditions (Luken and Thieret 1996; Webster *et al.* 2006). These shrubs share a tendency to form dense thickets in forest edges, openings, and understories to the exclusion of tree seedlings and understory plant cover and diversity (Woods 1993). Invasive trees species like the Norway maple, which competitively excludes even shade-tolerant native species, can be extremely disruptive where they replace native canopy cover (Webster *et al.* 2006). All of these herbaceous and woody species have troubling implications for forest management.

#### GAP DYNAMICS

The creation of canopy gaps by various forms of disturbance is a normal part of the process of forest succession (Oliver and Larson 1996), and in temperate forests is the primary determinant of regeneration development (Runkle 1982; Muscolo *et al.* 2014). Gaps differ ecologically from surrounding forest in many ways: they have higher light and temperature conditions, higher surface soil moisture, and altered soil biota, chemistry, and physical properties (Scharenbroch and Bockheim 2007; Muscolo *et al.* 2014). The loss of canopy trees reduces competitive exclusion and usually results in the release of advance regeneration, recruitment from banked or dispersed seeds, and colonization by species adapted for early stages of succession (Burnham and Lee 2009; Muscolo *et al.* 2014). The result of all of these changes within forests is increased structural complexity and diversity of habitats and species (Muscolo *et al.* 2014).

The extent of the changes in conditions and community composition is highly dependent on gap size, and shade-intolerant species require relatively large gaps (Muscolo *et al.* 2014). Halpin and Lorimer (2016) found that the structure and composition of protected northern hardwood forests in eastern North America was most likely to have been produced mainly by periodic low- to moderate-severity disturbance events. Gap openings in natural mature temperate forests occur at a rate of 0.5-2.0% of area per year, and in northeastern North America the interval of gap disturbances is generally from 50 to 200 years (Runkle 1982; Muscolo *et al.* 2014). According to Halpin and Lorimer (2016), the most common sources of large-scale disturbance in this region are windstorms and drought, but disturbances caused by fire, disease, and insect pests are also common.

#### INVASIVE PLANT COLONIZATION OF GAPS

Many invasive species are adapted to take advantage of the conditions produced by disturbance, namely high light availability and disturbed soil, and so are more abundant in canopy openings and may gain entry to forests through these openings (Woods 1993; Hutchinson and Vankat 1997; Hunter and Mattice 2002; Harper *et al.* 2005; Eschtruth and Battles 2009; Burnham and Lee 2010). Golivets *et al.* (2019) found landscape openness and temperature to be the two most important factors increasing invasive species presence and richness in forest inventory data from 14 northern US forests. Eschtruth and Battles (2009) found canopy disturbance and propagule pressure (the number of non-native individuals being introduced to the invaded area) to have the most dominant role in forest invasibility relative to other factors widely believed to be important. In a study of three invasive species in Maryland, Driscoll *et al.* (2016) found

that treefall gaps increased growth and reproduction of two species, as well as frequency, density, and establishment of one species.

The higher light availability associated with less canopy cover, lower basal area, and closer proximity to forest edges has been documented to increase invasive species occurrence in a number of studies. Exotic species richness and cover were found to be greater with less canopy cover and closer proximity to edges in an upland hardwood forest on Prince Edward Island (MacQuarrie and Lacroix 2003). Schulte *et al.* (2011) also found common buckthorn and Tartarian honeysuckle (*Lonicera tartarica*) infestation to be greater closer to edges as well as where tree basal area is lower. In another study, lower stand basal area was associated with higher abundance of invasive woody species seedlings (Hoven *et al.* 2017).

#### INVASIVE INSECT CREATION OF GAPS

While insect pests are not a new form of disturbance in North American forests, the number of exotic phytophagous insect species has exploded over the last two hundred years (Liebhold *et al.* 1995; Niemelä and Mattson 1996). Although large-scale outbreaks of native forest insect pests are a regular feature of the boreal forest, eastern deciduous forests did not experience this type of widespread disturbance prior to the introduction of invasive pests (Mattson *et al.* 1991; Gandhi and Herms 2009). The frequency and scope of these insect-induced disturbances have resulted in dramatic cascading effects altering forest composition, structure, and function by changing canopy gap dynamics, coarse woody debris abundance, and biogeochemical cycling (Gandhi and Herms 2009). The gap dynamics introduced by exotic insects are likely to differ from those created by natural tree decline and windthrow since they are usually

species-specific, and relative to storm events they progress more slowly and leave dead trees standing for longer (Krasny and DiGregorio 2001; Gandhi and Herms 2009). The increased light availability resulting from EAB outbreaks, specifically, is noted to be more gradual than that created by tree fall gaps, since infested ash tree canopies decline over time (Hoven *et al.* 2017; Baron and Rubin 2021).

Since its initial detection in North America in 2002, emerald ash borer has killed “untold millions” of native ash trees (Herms and McCullough 2014), with ash mortality exceeding 99% in forests near the invasion’s epicentre (Klooster *et al.* 2013). This pest creates a disturbance pattern of small but widespread synchronous canopy gap formation with the near-elimination of an entire genus (Gandhi and Herms 2009; Herms and McCullough 2014). The severity of disturbance caused by the loss of ash is to some extent due to the increased dominance of ash in these forests following widespread American elm (*Ulmus americana*) mortality due to Dutch elm disease, which illustrates the cascading nature of the impacts of exotic pest invasions (Gandhi and Herms 2009).

Recent research has found the ecological consequences of EAB-induced canopy gaps to include depletion of the ash seed bank (Klooster *et al.* 2013), increased coarse woody debris (Perry *et al.* 2018), decreased net primary productivity and carbon sequestration (Flower *et al.* 2013), decreased forest floor invertebrate diversity (Perry and Herms 2016), and changed plant communities (Margulies *et al.* 2017; Dolan and Kilgore 2018; Hoven *et al.* 2020). Changes to native plant communities following EAB-induced ash mortality include the increased dominance of shade-tolerant woody species; sugar maple (*Acer saccharum*) trees and seedlings have been found to experience relatively higher growth rates following EAB infestation (Hoven *et al.* 2020), and both

native and non-native shade-tolerant shrub species have been found to increase in density (Dolan and Kilgore 2018).

#### EMERALD ASH BORER FACILITATION OF INVASIVE PLANT SPECIES

Only a handful of studies have investigated the relationship between EAB-induced ash mortality and invasive plant species. One recent study in London, Ontario examined the effects of mortality due to EAB on common buckthorn, and found buckthorn abundance to be higher in EAB-induced gaps than in other canopy gaps, particularly where ecological integrity is low (Baron and Rubin 2021). They suggest that differences in gaps originating from EAB as opposed to other forms of disturbance may be their greater size, higher abundance of gaps, the synchronous formation of gaps, or the more recent creation of those gaps (Baron and Rubin 2021).

Other studies in the United States have also found evidence for increased growth of invasive plants following EAB-induced ash decline. In western Ohio, Hoven *et al.* (2017) found that where ash condition was poorer, Amur honeysuckle (*Lonicera maackii*) growth was higher, and more honeysuckle seedlings were also present where poor ash condition corresponded with greater honeysuckle basal area. They also found higher numbers of other woody invasive species seedlings in sites where ash condition was poorer and where tree basal area was lower (Hoven *et al.* 2017). In a study involving sites throughout Ohio, Hoven *et al.* (2020) found that the seedlings of non-native woody plants (along with sugar maples) experienced the highest levels of growth in EAB-induced canopy gaps relative to other seedling species, and that abundance of non-native seedlings was associated with higher ash mortality and shrub cover.

Klooster (2012) compared growth of native and non-native woody plants in canopy gaps created by EAB in Ohio and southeastern Michigan and found the rate of growth of invasive species to be up to 300% higher. Conversely, Doland and Kilgore (2018) did not detect any significant increase in non-native species relative to native ones over five years of ash decline, although both categories of shrub species were found to increase in density and some sites with pre-existing invasive shrub populations experienced increases in their density. A comparison of invasive species cover at sites where ash trees were either cut down or left to decline from EAB infestation found that the eradication treatment resulted in invasive species making up 18.7% of herbaceous cover, while that portion of cover was less than 1% at uncut sites (Hausman *et al.* 2010). Hausman *et al.* (2010) attributed this to the increased duration and intensity of light availability in the larger canopy gaps resulting from the treatment, as well as the greater soil compaction and disturbance created by machinery.

Margulies *et al.* (2017) found a negative correlation between invasive and weedy saplings and the number of ash saplings, indicating that where young ash have not yet become susceptible to EAB, this layer of remaining ash cover may suppress invasive plant growth. Saplings with diameters as small as 2.5 cm may become infested however, and since ash species do not appear to have a persistent seed bank, ash trees in this age class are expected to decline in numbers (Klooster *et al.* 2013). As the progression of the EAB invasion continues in North America, the dynamics of plant communities in northeastern hardwood forests will continue to evolve. Invasive plant species inevitably have a role to play in these changing ecosystems, and the nature of that role has yet to be fully explored.



## MATERIALS AND METHODS

### STUDY SITES

Four forests were sampled in the Region of Waterloo. This region is located in southern Ontario, and occupies a transitional area between major ecological zones (Figure 1). Most of Waterloo Region falls within the Great Lakes-St. Lawrence Forest Region and in Ecoregion 6E (Lake Simcoe-Rideau), but a relatively small portion of the Region near its southwestern border is included within the Deciduous Forest Region and Ecoregion 7E (Lake Erie-Lake Ontario) (MNDMNR 2021). This southern region is also known as the Carolinian Zone.

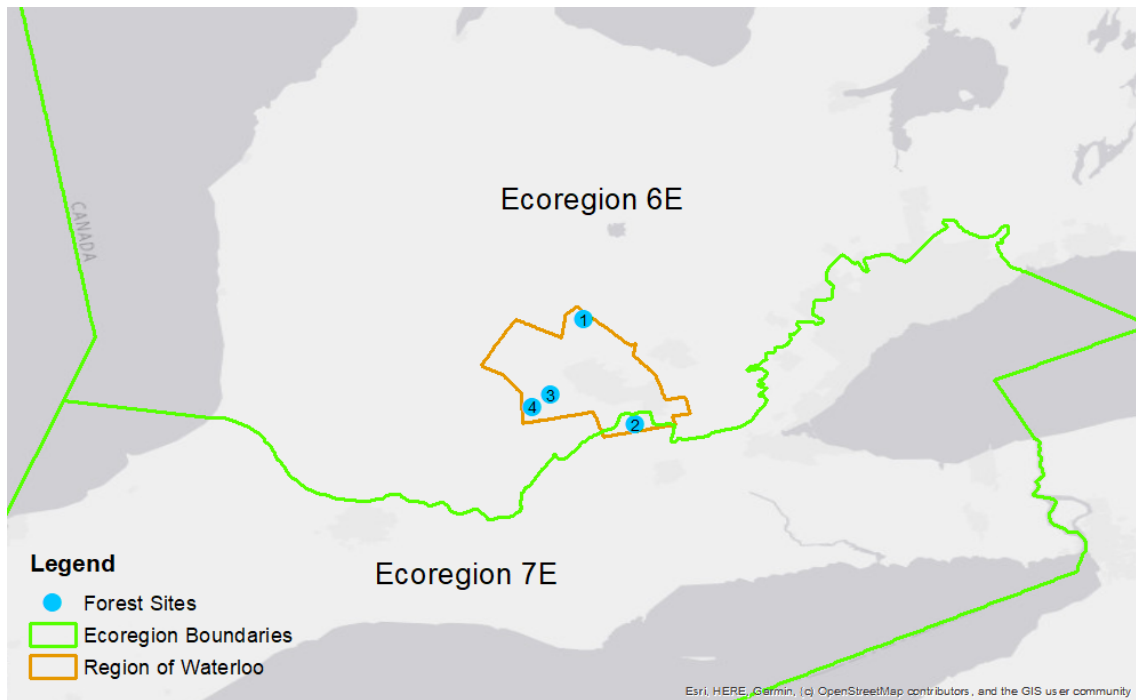


Figure 1. Map of southern Ontario's Ecoregions, the Region of Waterloo, and the four forests sampled (1: Sandy Hills, 2: Sudden, 3: Baden Hills, and 4: Walker Woods).

These delineations are related to a shift in climatic regions; the southernmost area of Waterloo Region is in the South Slopes climatic region, which has a significantly longer growing season and receives substantially less precipitation than the Huron Slopes climatic region to the north (Brown *et al.* 1980; Region of Waterloo 2006). Of the four forests sampled, only Sudden Regional Forest falls within the boundaries of the Carolinian Zone (Figure 1), but it should be noted that plant species associated with Carolinian forests are present in all of the forests sampled.

The Waterloo Regional Forests are managed with conservation as the primary objective, followed in order of priority by use for passive recreation, outdoor education and research, sustainable timber production, and other forms of recreation where permitted (Region of Waterloo 2006). These properties were formerly managed by the Ministry of Natural Resources from 1961 to 2001 under the Agreement Forest Program (Region of Waterloo 2006). During this period, timber harvesting was the central management goal, and tree planting was mainly conducted with conifer species (Region of Waterloo 2006). Prior to the Agreement Forest Program, all the properties contained at least some cleared agricultural land (Region of Waterloo 2006).

The four forests studied are all located in rural areas of the Region of Waterloo. All but Walker Woods Regional Forest contain areas of conifer plantation, and all four of the forests contained stands with an ash component at the time of the previous inventory in 2002. An overview of these forests can be found in Table 1.

Table 1. Overview of the four Regional Forests studied (Presant and Wicklund 1971; Region of Waterloo 2006).

Forest	Municipality	Area (ha)	Soil Types	General Description
Sandy Hills	Township of Woolwich	71.5	sandy loam, fine sandy loam, organic	Mainly hilly upland conifer plantation, with some young hardwood stands, underplanted red oak, and a cedar swamp
Baden Hills	Wilmot Township	8.9	sandy loam	Forested hills divided into a hardwood stand and a conifer stand, with rows of walnut in a field to the south which were planted for an abandoned agroforestry project
Walker Woods	Wilmot Township	10.6	loam	Fairly level area dominated by sugar maple and formerly managed for syrup production with lower-lying wet areas throughout
Sudden	North Dumfries	88.6	loam, sandy loam, organic	Steep hills with maple, oak and hickory, low-lying wetlands, and some former conifer plantation

EAB was first detected in North America in 2002 near Detroit, Michigan, and shortly after in Windsor, Ontario (Siegert et al. 2014), and has now eliminated nearly all mature ash in the Waterloo Regional Forests. Thus, the timing of the 2002 and 2021 inventories has resulted in snapshots of a set of forests before and after the EAB outbreak in the area.

#### SAMPLING DESIGN & DATA COLLECTION

The four forests were surveyed from May to August of 2021 using a stratified random sample, with each stand sampled at an intensity of 2%. Plot centre locations were selected randomly using ArcMap within a 15 m buffer of stand boundaries. Where features like water bodies and wide trails would make sampling impractical or biased,

plots were moved 25 m toward the centre of the stand. Fully saturated wetland areas were not sampled.

Sampling occurred within 400 m<sup>2</sup> fixed area circle plots, which were established using 11.28 m cords to measure the radius from plot centre. All trees greater than 1 cm in diameter at breast height (DBH) were tallied by species and DBH. All buckthorn stems (of both *Rhamnus cathartica* and *Frangula alnus*) with DBH above 1 cm were also tallied by DBH to quantify the density and basal area (BA) of mature buckthorn. Snags were also measured and recorded in the same manner. All DBH measurements were taken with calipers and tallied in 2 cm increments. These tallies were used to calculate stems per hectare (SPH) and BA per hectare for each category and to determine tree species composition at the plot and stand level.

Invasive species cover was quantified through a visual estimate of the percentage of ground area in the plot covered vertically by any aboveground parts of invasive plants. Plant species were considered invasive if they are listed in any of the four categories of invasiveness of the Society for Ecological Restoration's Invasive Exotic Species Ranking for Southern Ontario (UFA 2002). A list of the invasive species observed can be found in Appendix I. The invasive species cover percentage included the total cover of all invasive plants in the plot, and all invasive species present were listed for each plot.

Other data used in this study included the canopy closure, regeneration density, and percentage of conifers relative to total tree BA in each plot. Canopy closure was quantified on a scale of one to five at intervals of 0.5 via a visual estimate (Table 2). Regeneration was quantified by counting all tree seedlings or saplings less than 1 cm in DBH within a 4x4 m quadrat at plot centre, and these counts were multiplied to

extrapolate regeneration SPH. The percentage of conifer BA was quantified to the nearest 10% based on the species composition code generated for each plot.

Table 2. Scale used to quantify canopy closure.

Rating	Description
1	Completely open/no tree canopy
2	Mostly open/large canopy gaps
3	Partially closed/small canopy gaps
4	Mostly closed/dappled shade
5	Closed/dense shade

Two variables were calculated based on data from the previous forest inventory in 2002: decline in ash BA and change in total BA. While the value for change in total BA was negative in some stands and positive in others, the change in ash BA was simply quantified as a positive value of decline because nearly all the mature ash in the study areas had died. The available 2002 data includes only the basic results from a typical timber-oriented forest resource inventory, and these results were only given at the stand level. Therefore the numbers used for both ash decline and total change in BA represent the difference between current plot BA and past stand BA rather than the precise change in BA in each plot. Information about the ash component of these forests in the 2002 inventory is limited to the percentage of BA represented by ash species in each stand's species composition code, which means those values had been rounded to the nearest 10%. Thus the 2002 ash stand BA was calculated by multiplying total 2002 stand BA by that approximate percentage. A summary of the species composition and BA of each stand in the 2002 and 2021 inventories can be found in Appendix II.

Due to the challenges with precision created by the limitations of the 2002 data, a binary variable quantifying ash mortality at the plot level was also used. Plots in which

there was evidence of ash mortality occurrence were given a value of 1, and plots without such evidence were given a value of 0. Plots considered to have evidence of ash mortality included those where ash was included in the 2002 stand composition code as well as those where ash was not a major stand component but the presence of dead ash was observed during sampling in 2021.

## STATISTICAL ANALYSIS

Multivariate analysis was conducted in RStudio Version 4.0.3 using generalized linear models (GLMs). Negative binomial regression was used due to overdispersion when using Poisson regression. The combination of variables used for each model was selected for best fit based on the Akaike information criterion (AIC) value. The significance of coefficient estimates was assessed based on a 95% confidence level. Chi-squared tests were also used to assess the significance of variables at a 95% confidence level.

Models were produced to assess relationships between each of the two response variables (i.e., invasive plant cover and mature buckthorn density) and various independent variables. The main findings were produced based on models with the four combinations between these two response variables and the two independent variables related to the hypothesis (i.e., ash mortality occurrence and decline in ash BA since 2002). Other variables used to fit models included forest ID (i.e., for each of the four forests), BA, change in stand BA since 2002, canopy closure, conifer composition percentage, regeneration density, and snag BA. Models with interactions between the two ash mortality variables and each of the other independent variables were also run to explore their significance.

Regression analysis of observed data was performed by plotting relationships between the response variables and each of the independent variables using generalized additive model (GAM) smoothing with a 95% confidence interval. Outliers which exceeded three standard deviations from the mean were removed from this analysis.

## RESULTS

## ASH MORTALITY OCCURENCE

Invasive Plant Cover

In the model including ash mortality occurrence and invasive plant cover, a significant interaction was found between ash mortality and forest ID. When modeled separately for each of the four forests (Figure 2), the models showed significantly less invasive plant cover in plots with no evidence of ash mortality in Sudden Forest ( $p = 4.3e-05$ ) and Walker Woods ( $p = 0.029$ ). No significant relationship was found with ash mortality in Sandy Hills ( $p = 0.12$ ), and Baden Hills had too few plots to determine statistical significance.

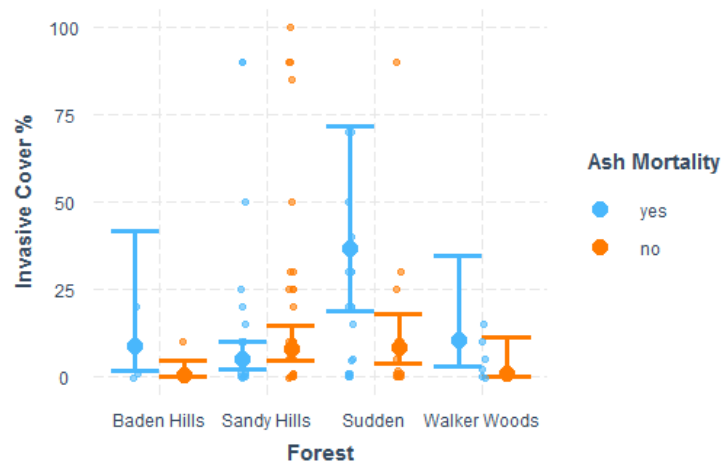


Figure 2. Invasive plant cover by ash mortality occurrence in each forest. Error bars represent 95% confidence intervals for model predictions.

Buckthorn Density

No significant relationship was found between buckthorn SPH and the occurrence of ash mortality ( $p = 0.30$ ).



## DECLINE IN ASH BASAL AREA

### Invasive Plant Cover

A significant interaction was found between forest ID and ash decline in BA. When separated by forest (Figure 3), a significant positive relationship was found between invasive plant cover and ash BA decline in Sudden Forest ( $p = 9.1e-05$ ). Baden Hills, once again, had too few plots for statistical significance to be assessed. The modeled relationships between invasive plant cover and ash BA decline in the other two forests were not significant.

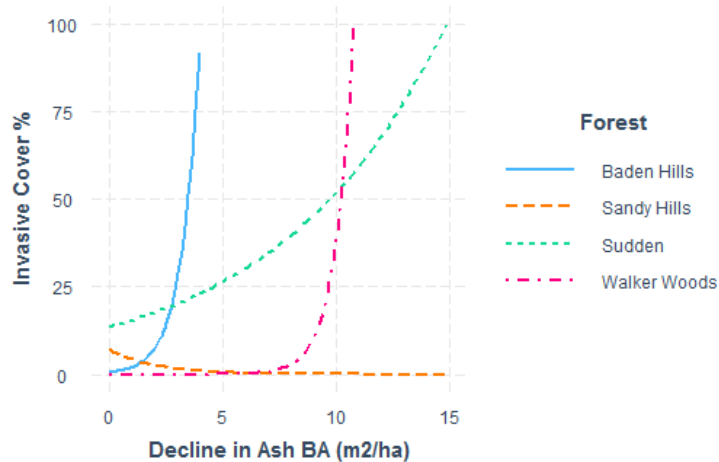


Figure 3. Model prediction curves for invasive plant cover by ash BA decline in each forest.

When modeled without the interaction between forest ID and ash BA decline, there was a significant positive relationship between ash BA decline and invasive plant cover ( $p = 0.0042$ ). In Figure 4, the relationship found between the observed values for these variables also shows an increase in invasive plant cover associated with higher ash BA decline, and additionally shows slightly higher invasive plant cover in plots where ash BA decline was lowest or absent.

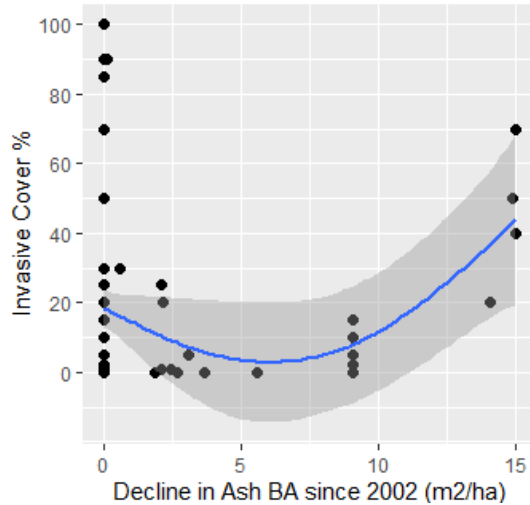


Figure 4. GAM-fitted curve with a 95% confidence interval for the relationship between invasive plant cover and ash BA decline based on observed data.

### Buckthorn Density

The interaction between forest ID and ash BA decline was not found to be significant in relation to buckthorn density. When modeled without the interaction, ash BA decline was found to have a significant positive relationship with mature buckthorn density ( $p = 0.032$ ). In Figure 5, the modeled response curve shows that buckthorn density increases when ash decline is highest, although only to  $2.6e-16$  stems per plot or  $6.5e-15$  stems per hectare. In Figure 6, the relationship found in the observed values for these variables also shows a slight increase in buckthorn density associated with higher ash BA decline. A very slight upward trend in buckthorn density is also seen where ash BA decline was lowest or absent.

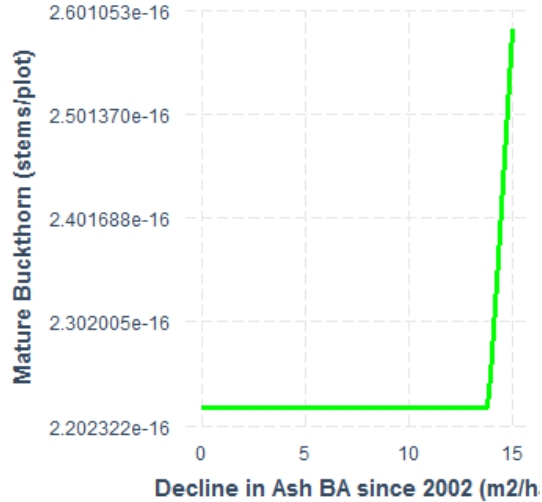


Figure 5. Model prediction curve for buckthorn density versus ash BA decline with all other variables held at their mean values.

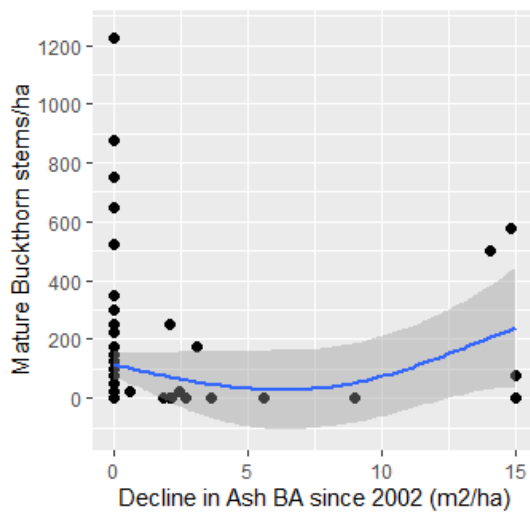


Figure 6. GAM-fitted curve with a 95% confidence interval for the relationship between buckthorn density and ash BA decline based on observed data.

## OTHER VARIABLES

Most of the other independent variables included in the models were found to have significant relationships with both invasive plant cover and buckthorn density in each of the GLMs. The exceptions were regeneration density, which was only

significant in models with buckthorn density as the response variable, and snag BA, which was not significant in any model.

### Basal Area

Higher BA was associated with lower invasive plant cover and lower buckthorn density (Figure 7). These negative relationships were significant in all models with invasive plant cover as the response variable ( $p = 3.8\text{e-}05$  to  $0.0024$ ) and all models with buckthorn density as the response variable ( $p = 0.0015$  to  $0.015$ ).

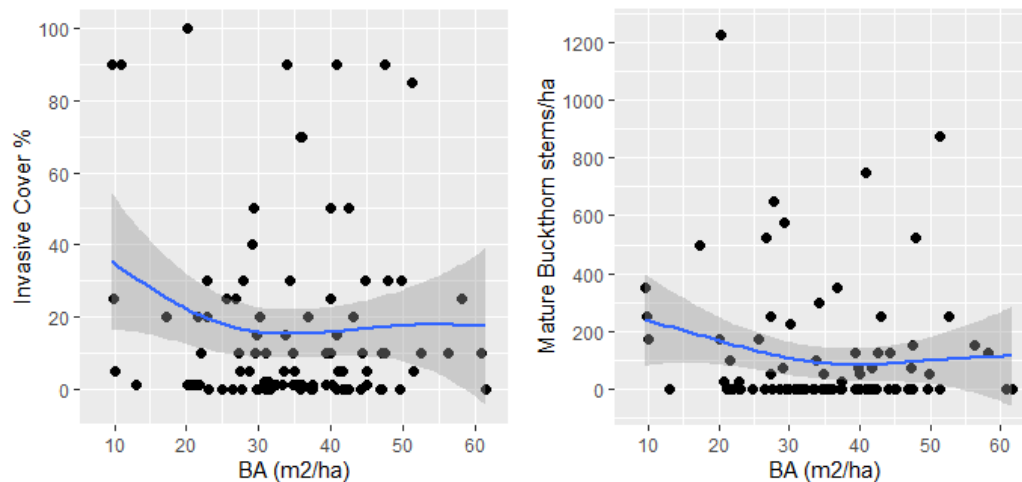


Figure 7. GAM-fitted curves with a 95% confidence interval for the relationships of invasive plant cover (left) and buckthorn density (right) with plot BA per ha based on observed data.

### Change in Basal Area

A positive correlation was found between the response variables and change in BA since 2002 in all models. The relationship with the response variables was significant in all models, with higher significance for invasive plant cover ( $p = 1.4\text{e-}05$  to  $0.00040$ ) than for buckthorn density ( $p = 0.011$  to  $0.040$ ). The trend plotted for the observed relationship with buckthorn density shows a slight negative correlation (Figure 8) contrary to the positive coefficients produced by the GLMs.

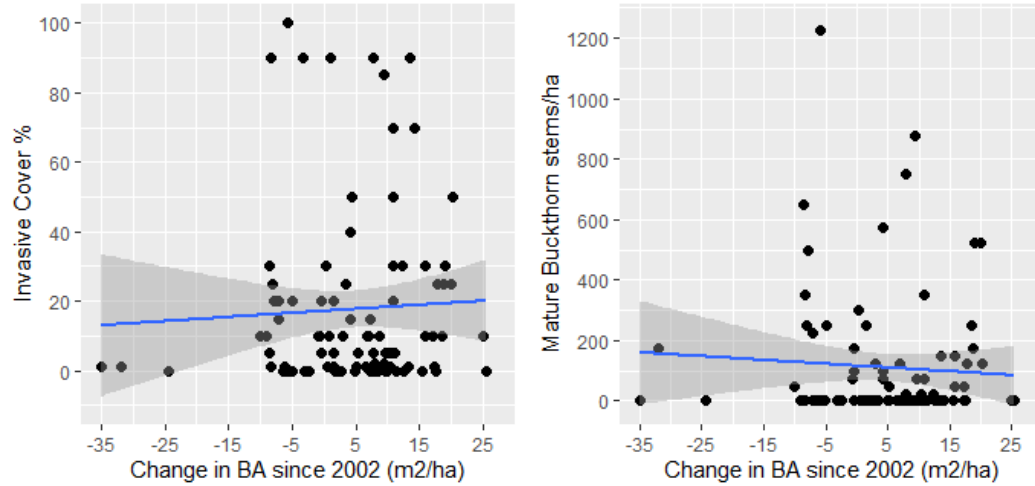


Figure 8. GAM-fitted curves with a 95% confidence interval for the relationships of invasive plant cover (left) and buckthorn density (right) with change in stand BA per ha based on observed data.

### Canopy Closure

A higher canopy closure rating was associated with lower invasive plant cover and lower buckthorn density (Figure 9). These negative relationships were significant in all models with invasive plant cover as the response variable ( $p = 1.5e-05$  to  $0.00086$ ) and all models with buckthorn density as the response variable ( $p = 0.00049$  to  $0.0025$ ).

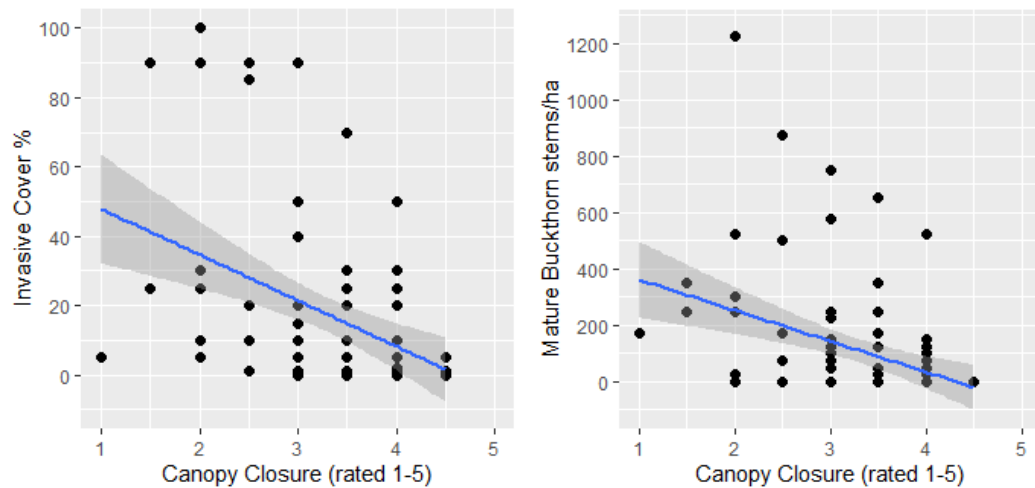


Figure 9. GAM-fitted curves with a 95% confidence interval for the relationships of invasive plant cover (left) and buckthorn density (right) with canopy closure based on observed data.

### Conifer Composition

A higher proportion of conifer BA was associated with higher invasive plant cover and higher buckthorn density (Figure 10). These positive relationships were significant in all models with invasive plant cover as the response variable ( $p = 2.2\text{e-}08$  to  $9.6\text{e-}05$ ) and all models with buckthorn density as the response variable ( $p = 0.00012$  to  $0.00076$ ).

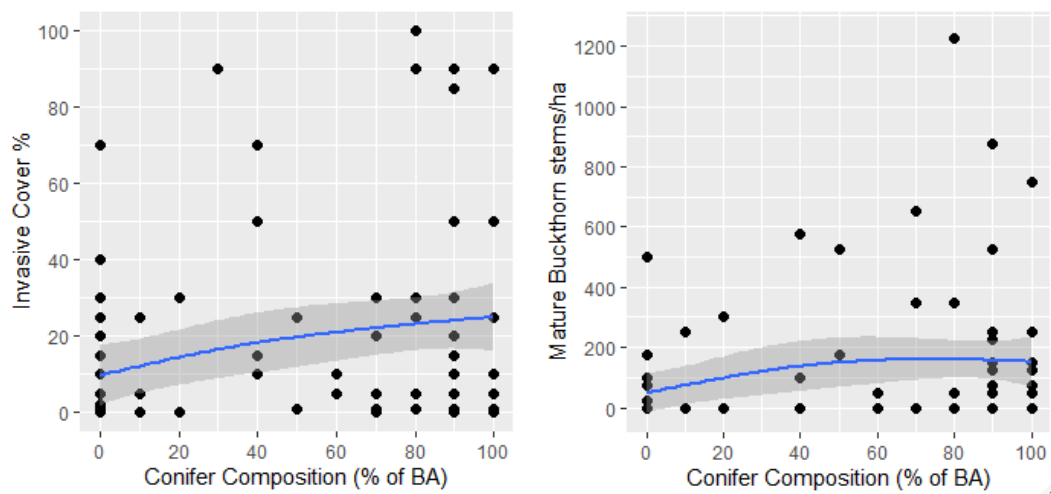


Figure 10. GAM-fitted curves with a 95% confidence interval for the relationships of invasive plant cover (left) and buckthorn density (right) with conifer composition based on observed data.

### Regeneration Density

Higher regeneration SPH was associated with lower invasive plant cover and lower buckthorn density (Figure 11). The coefficients for this variable were only significant in the models with buckthorn as the response variable ( $p = 0.0021$  to  $0.067$ ).

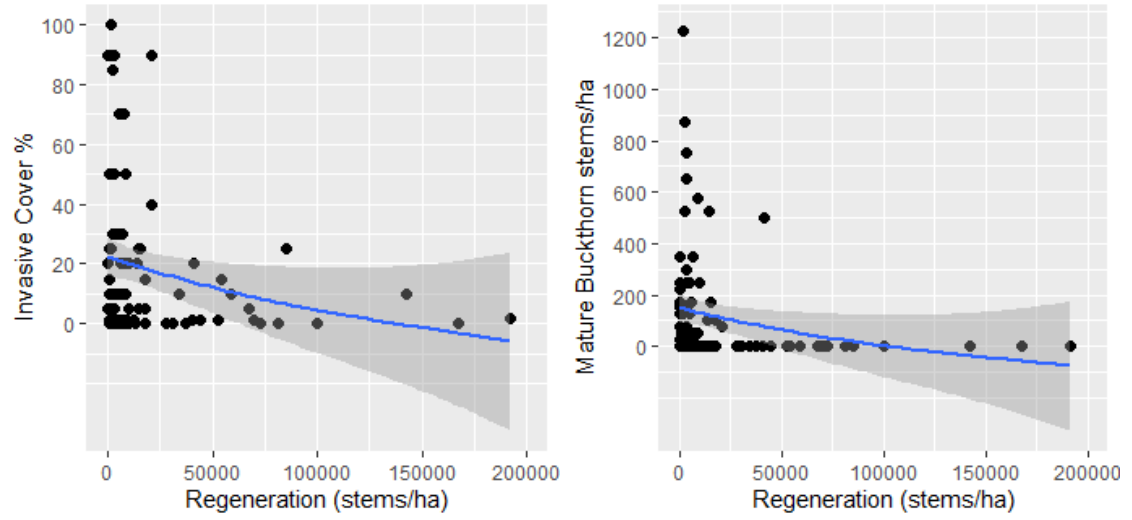


Figure 11. GAM-fitted curves with a 95% confidence interval for the relationships of invasive plant cover (left) and buckthorn density (right) with regeneration density based on observed data.

## DISCUSSION

### COMPETITIVE EXCLUSION

The results confirm findings from previous studies which have observed associations between invasive plants and the higher light environments resulting from tree mortality (Woods 1993; Hutchinson and Vankat 1997; Hunter and Mattice 2002; Harper *et al.* 2005; Eschtruth and Battles 2009; Burnham and Lee 2010). The negative relationships found with the independent variables of canopy closure, BA, and regeneration density align with the idea that greater competition for light reduces the prevalence of invasive plants. The effect may also be compounded by inhibition of tree regeneration and growth caused by invasive plants (Woods 1993; Hutchinson and Vankat 1997; Gorchoy and Trisel 2003; Hartman and McCarthy 2007; Hoven *et al.* 2017). The negative correlations with these variables may also be related to competition for other resources like soil nutrients and water (Gorchoy and Trisel 2003; Hartman and McCarthy 2007). It follows that this pattern of competitive exclusion may also explain the positive correlations found between invasive species and both ash mortality and loss of ash BA (Hausman *et al.* 2010; Hoven *et al.* 2017; Baron and Rubin 2021).

The relationships found in each model with change in stand BA since 2002, however, run counter to the competitive exclusion theory. If competitive exclusion was the only factor explaining the abundance of invasive plants, growth in tree BA would be expected to be associated with fewer invasive plants and decline in BA would be expected to be associated with more. The opposite relationship found in the models is



not explained by change in BA being unrelated to present-day total BA since these variables are positively correlated (Figure 12).

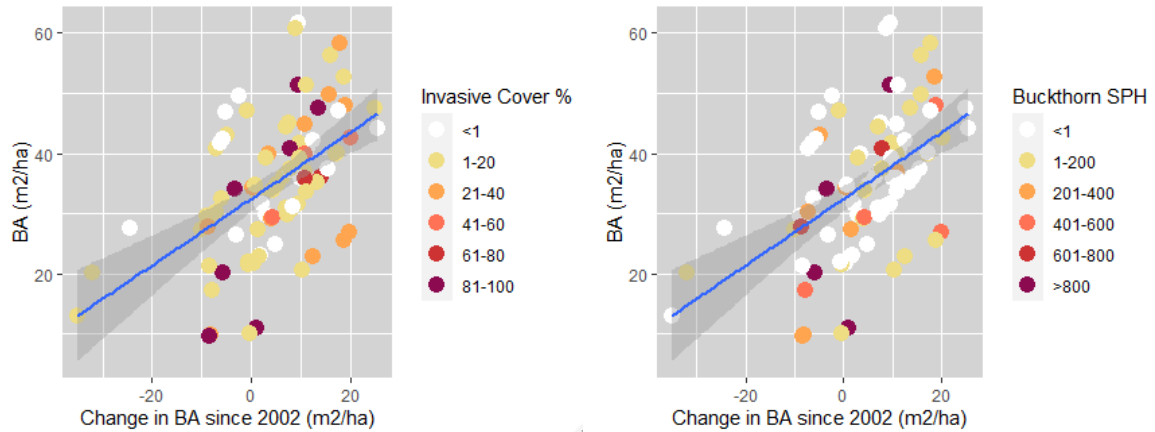


Figure 12. GAM-fitted curves with a 95% confidence interval for BA vs. change in BA with points coloured based on invasive plant cover (left) and mature buckthorn density (right).

#### INTERACTIONS WITH ASH DECLINE IN BASAL AREA

Some insight regarding the relationship between ash mortality and invasive plant species may be gleaned from modeled interactions with other independent variables. In models with buckthorn density as the response variable, interactions between ash BA decline and three of the other independent variables were found to have significant relationships with buckthorn density, albeit within a 90% confidence interval: change in total BA ( $p = 0.067$ ), canopy closure ( $p = 0.097$ ), and regeneration density ( $p = 0.096$ ).

#### Change in Basal Area

When change in BA is held constant at one standard deviation (SD) below the mean, which represents a decline in BA, greater decline in ash is associated with higher numbers of buckthorn (Figure 13). Thus where BA has decreased an equal amount, stands with larger former ash components host more buckthorn. When change in BA is

average or high, higher ash decline elicits little to no increase in buckthorn; ash decline is only associated with more buckthorn where total tree BA has decreased relative to 2002 stand levels. These findings align with the idea that invasives are limited by competitive exclusion, but also suggest that buckthorn abundance is associated with the loss of ash more than that of other tree species.

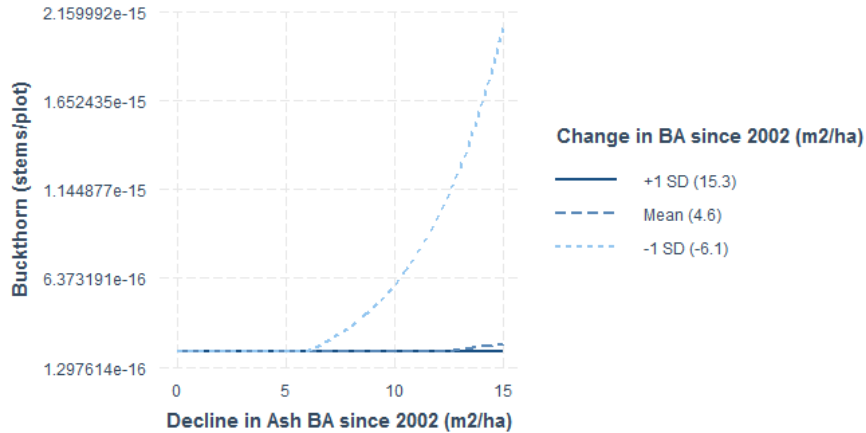


Figure 13. Relationship between buckthorn density and ash BA decline with change in BA held constant at three levels. All other variables in the model are held at their mean values.

When ash decline is high (held one SD above the mean), buckthorn numbers are unaffected by growth or moderate changes in total BA, but grow increasingly with greater decline in BA (Figure 14). When ash decline is held at the mean, decline in total BA is not associated with an increase in buckthorn. This is not consistent with the competitive exclusion theory; loss of BA is only associated with more buckthorn where more extensive loss of ash has occurred. This may indicate that buckthorn is associated with a site characteristic also formerly associated with greater numbers of ash.

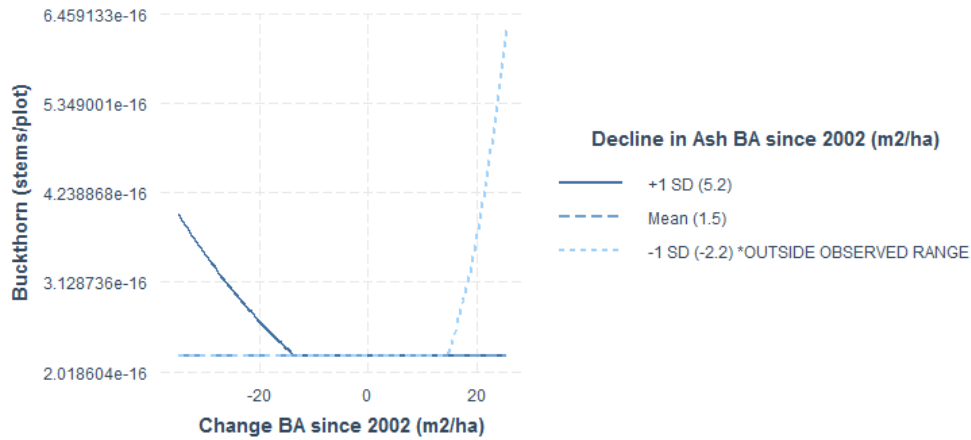


Figure 14. Relationship between buckthorn density and change in BA with ash BA decline held constant at three levels. All other variables in the model are held at their mean values.

### Canopy Closure

The interaction with canopy closure appears to confirm that light availability is important to invasive species establishment, but also indicates that some other factor related to the loss or former presence of ash is influencing buckthorn numbers. When canopy cover is high or average, the number of buckthorn does not respond to changes in ash decline, but when canopy cover is low, higher decline in ash BA is associated with higher buckthorn density (Figure 15). When ash BA decline is held constant, the increase in buckthorn associated with an increasingly open canopy is higher at higher levels of ash decline (Figure 16).

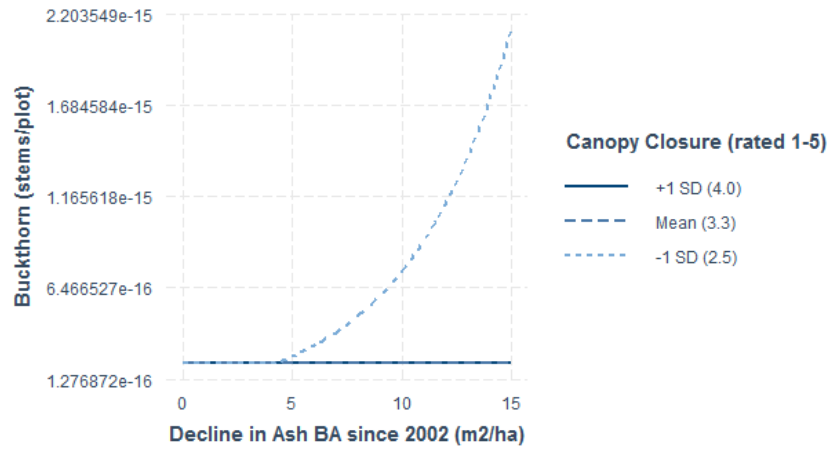


Figure 15. Relationship between buckthorn density and ash BA decline with canopy closure held constant at three levels. All other variables in the model are held at their mean values.



Figure 16. Relationship between buckthorn density and canopy closure with ash BA decline held constant at three levels. All other variables in the model are held at their mean values.

### Regeneration Density

The interaction between ash BA decline and regeneration density yields opposite responses to those that would be expected based on competitive exclusion. When regeneration is high, greater decline in ash is associated with an increase in buckthorn (Figure 17). The effect is weaker where regeneration is lower. This may indicate that sites which support high numbers of tree seedlings are also favourable to invasive

species. However, it was observed during data collection that many of plots with high regeneration were dominated by ash seedlings, so it is also possible that the trend in Figure 17 is more reflective of a positive relationship between buckthorn density and former ash abundance. Despite its significance in the models, regeneration density does not appear to be related to change in buckthorn density in the absence of interactions with other variables (Figure 18).

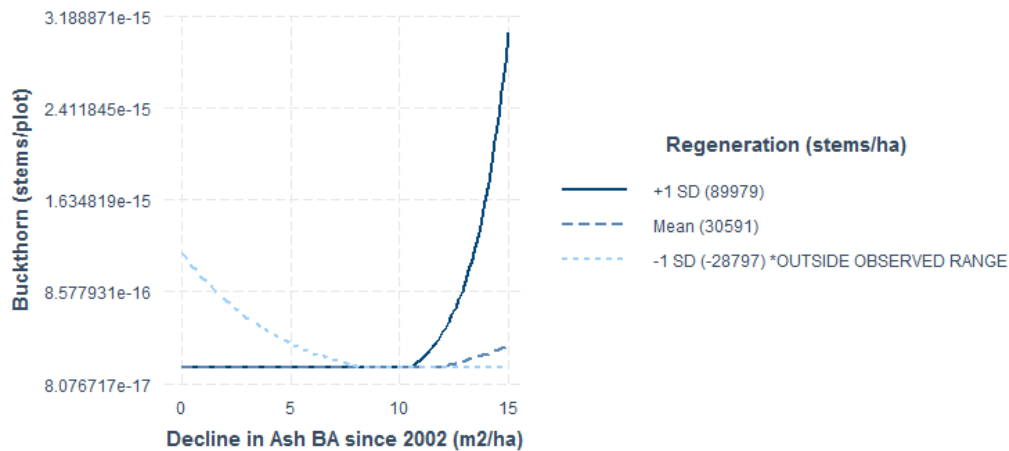


Figure 17. Relationship between buckthorn density and ash BA decline with regeneration density held constant at three levels. All other variables in the model are held at their mean values.

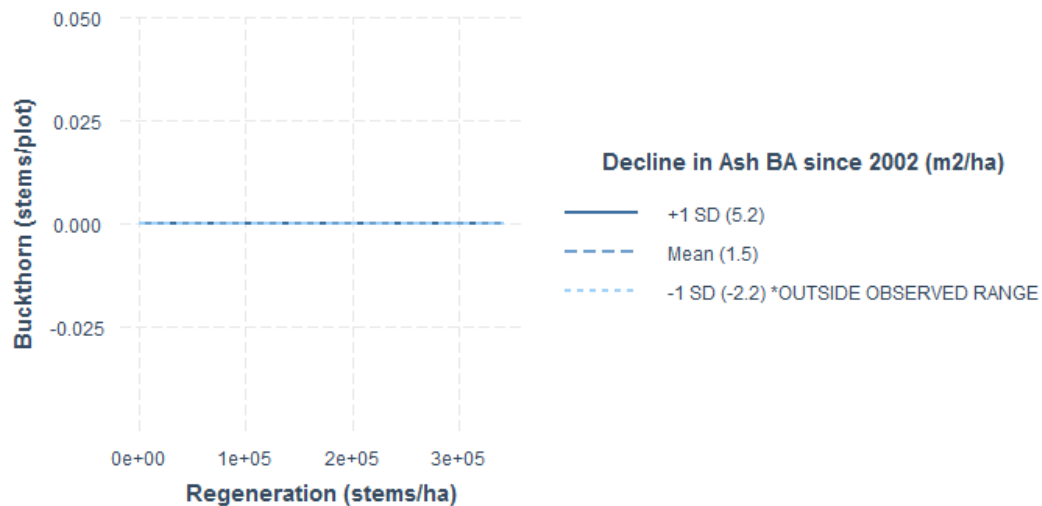


Figure 18. Relationship between buckthorn density and regeneration density with ash BA decline held constant at three levels. All other variables in the model are held at their mean values.

## OTHER SITE CHARACTERISTICS

Given that decline in total BA is associated with less invasive plant cover and buckthorn density, the increase in invasive species associated with higher ash BA decline may not be exclusively related to the increased availability of resources associated with gap formation. Additionally, since growth in total BA was found to be related to an increase in invasive plants, it is possible that site characteristics which facilitate tree growth also facilitate invasive species growth or establishment.

Since the values for ash BA decline are essentially a measure of former ash BA in each stand, it is possible that ash habitat requirements are related to invasive species prevalence. Most of the ash formerly present in the study forests were white ash (*Fraxinus americana*) or green ash (*F. pennsylvanica*), and black ash (*F. nigra*) were also present in some of the wetter stands. White ash is associated with fertile soils rich in nitrogen and calcium, has intermediate shade tolerance, and grows best on moderately well-drained soils (Burns and Honkala 1990; MNDMNRF 1998). Green ash also grows best on fertile soils, can tolerate a wide range of moisture conditions, and is intolerant to moderately shade-tolerant (Burns and Honkala 1990). Black ash is found in wetlands, riparian zones, and poorly drained soils and is shade-intolerant (Burns and Honkala 1990). All three species tolerate relatively wide ranges of soil pH (Burns and Honkala 1990). In addition to generally inhabiting more nutrient-rich sites, ash species also contribute to soil fertility since their leaves are higher in nitrogen, calcium, magnesium, and ash than many other hardwoods in this forest region (Reiners and Reiners 1970).

High soil nutrient levels are also related to greater overall forest productivity and higher tree growth rates (Li *et al.* 2020). Thus it is possible that the contradiction in the relationships of invasive plants with ash BA change and total BA change can be

explained by greater site richness where total BA change is more positive as well as where greater ash BA decline has occurred.

The findings related to ash mortality and decline are also notable in the context of the association of invasive plants with higher conifer composition. Many of the sample plots were located in former conifer plantation with little to no ash in 2002, and so a large number of plots were given an ash BA decline value of zero. All plots with recorded loss of ash were hardwood-dominated and had a conifer composition of less than 50% of BA in 2021 (Figure 19). The conifer stand plots were deliberately included in analysis to assess other variables affecting invasive species across stand types as well as to include plots where BA had declined for reasons separate from EAB, since many red pine stands in the region are experiencing dieback and some conifer stands have undergone selection harvest in recent years. It is notable that despite the large number of conifer-dominated plots with high levels of invasive species, significant positive relationships were found between ash BA decline and the two response variables.

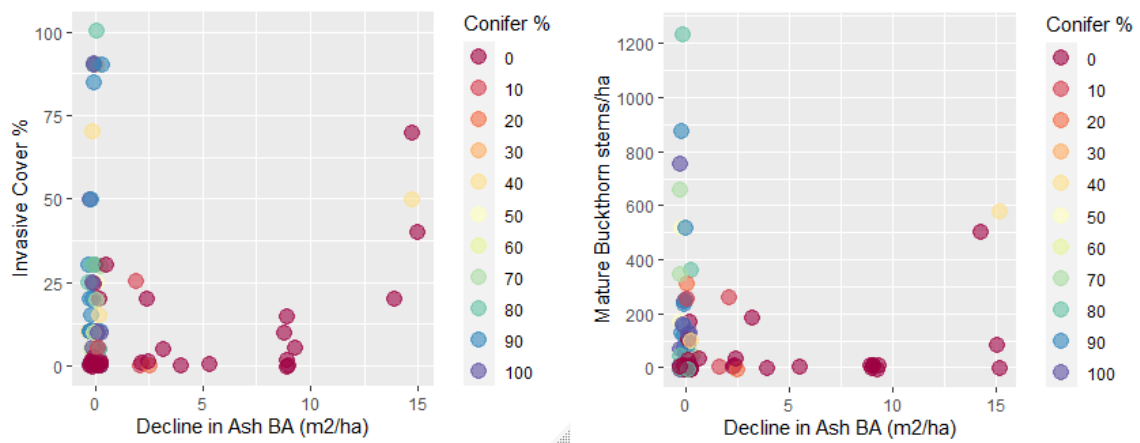


Figure 19. Scatter plots of invasive plant cover (left) and buckthorn density (right) vs. ash BA decline with points coloured based on conifer composition.

## CONCLUSION

The outcomes of the majority of the models support the hypothesis that EAB-induced ash mortality increases the cover and density of invasive plant species. Decline in ash BA since 2002 was associated with significantly higher invasive plant cover and buckthorn density. The occurrence of ash mortality was also associated with higher invasive plant cover in three of the four study forests, with significant positive relationships in the two forests with enough data for analysis. The findings also suggest that the association between loss of ash and higher invasive plant abundance is not fully explained by canopy gap opening; increases in invasive plants are not associated with loss of total BA, but are associated with greater loss of ash even when variables like canopy cover are held constant.

The relationships between invasive plant abundance and the variables found to be significant in the models suggest that competition for light and other resources is likely an important factor in invasibility of forests in this region. Higher invasive plant cover and buckthorn density were found where canopy closure, BA, and regeneration density were lower. However, competitive exclusion does not account for the positive relationship between invasive plants and total BA change, or for the relationships found in interactions between ash BA decline and other variables. It is speculated that soil fertility may be associated with the former presence of ash, BA growth, and the success of invasive species.

Additional research is required to explore these dynamics further and provide management direction where exotic plant invasion is of concern. Forest managers may



wish to limit the spread of invasive forest plants for a variety of reasons, whether to allow for tree regeneration (Woods 1993; Gorchoy and Trisel 2003; Fagan and Peart 2004; Webster *et al.* 2006; Hartman and McCarthy 2007; Stinson *et al.* 2007), improve nearby agricultural yields (Ragsdale *et al.* 2011; Nazareno *et al.* 2018), or promote and sustain ecological health and services (Vitousek *et al.* 1996; Mack *et al.* 2000; Webster *et al.* 2006; Vilà *et al.* 2011). EAB has resulted in substantial tree mortality in southeastern Canada and the northeastern US in the past two decades, and EAB will likely continue to spread where native ash populations still remain. Since ash species are very common minor components of forests in this region (MNDMNRF 1998), the ongoing canopy gap formation by EAB is widespread. Based on the results of this and other studies, canopy gaps likely increase the vulnerability of forests to invasive plants (Eschtruth and Battles 2009; Burnham and Lee 2010; Hoven *et al.* 2017; Baron and Rubin 2021). Should gaps formed by EAB-induced ash mortality be particularly susceptible to invasion, this research may be valuable to forest managers who wish to predict and mitigate the impacts of invasive plant species.

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## APPENDICES

## APPENDIX I

## INVASIVE PLANT SPECIES FOUND IN THE WATERLOO REGIONAL FORESTS

Table 3. Invasive plant species observed in the study forests.

Scientific Name	Common Name
<i>Acer platanoides</i>	Norway maple
<i>Alliaria petiolata</i>	Garlic mustard
<i>Alnus glutinosa</i>	European black alder
<i>Berberis thunbergii</i>	Japanese barberry
<i>Celastrus orbiculatus</i>	Oriental bittersweet
<i>Chelidonium majus</i>	Greater celandine
<i>Cirsium arvense</i>	Canada thistle
<i>Convallaria majalis</i>	Lily-of-the-valley
<i>Cynanchum rossicum</i>	Dog-strangling vine
<i>Frangula alnus</i>	Glossy buckthorn
<i>Epipactis helleborine</i>	Broad-leaved helleborine
<i>Geum urbanum</i>	Wood avens
<i>Glechoma hederacea</i>	Ground-ivy
<i>Hesperis matronalis</i>	Dame's rocket
<i>Hypericum perforatum</i>	Common St. John's wort
<i>Impatiens glandulifera</i>	Himalayan balsam
<i>Leonurus cardiaca</i>	Motherwort
<i>Lonicera spp.</i>	Honeysuckle
<i>Lythrum salicaria</i>	Purple loosestrife
<i>Morus alba</i>	White mulberry
<i>Myosotis sylvatica</i>	Forget-me-not
<i>Nepeta cataria</i>	Catnip
<i>Phragmites australis</i> subsp. <i>australis</i>	Phragmites
<i>Ranunculus acris</i>	Tall buttercup
<i>Rhamnus cathartica</i>	Common buckthorn

Table 3. (continued)

Scientific Name	Common Name
<i>Robinia pseudoacacia</i>	Black locust
<i>Rosa multiflora</i>	Multiflora rose
<i>Rosa rugosa</i>	Rugosa rose
<i>Silene vulgaris</i>	Bladder campion
<i>Solanum dulcamara</i>	Bittersweet nightshade
<i>Syringa vulgaris</i>	Lilac
<i>Torilis japonica</i>	Japanese hedge parsley
<i>Tussilago farfara</i>	Coltsfoot
<i>Viburnum opulus</i> var. <i>opulus</i>	European highbush cranberry

## APPENDIX II

## STAND-LEVEL DATA FROM THE 2002 AND 2021 INVENTORIES

Table 4. Species composition and BA by stand in 2002 and 2021. Stands with ash included in the species composition code (meaning that ash make up greater than roughly 5% of BA) are marked with an asterisk. (Note: Some 2002 stands were divided into multiple stands in 2021 due to either stand changes or imprecision in the 2002 stand delineation.)

Forest	2002 Inventory			2021 Inventory			Change in BA (m <sup>2</sup> /ha)	
	Stand No.	Species Composition	BA (m <sup>2</sup> / ha)	Stand No.	Species Composition	BA (m <sup>2</sup> / ha)		
Baden Hills	1*	Mh7Hib2Aw1	21.4	1	Mh4Mb2Bd1Cb 1Hb1Ohw1	22.6	3	1.2
Baden Hills	2	Pw5Sw3Pj2	38.5	2	Pw8Sw1Ohw1	31.0	2	-7.5
Sandy Hills	1	Pr8Sn1Pw1	29.6	1	Pr7Sn2Pw1	37.7	3	8.1
Sandy Hills	2	Pw7Cb1Ps1Pr1	30.7	2	Pw4Cb2Ps2Pr1 Ohw1	41.1	1	10.4
Sandy Hills	3	Le10	42.0	3	Le9Ohw1	51.3	1	9.3
Sandy Hills	4	Ps8Cb1Pw1	24.0	4	Cb4Ps4Or1Mh1	30.9	1	6.9
Sandy Hills	5	Ps5Pj3Pw1Cb1	6.9	5	Or4Cb2Pj1Pw1 Mh1Ps1	26.2	2	19.3
Sandy Hills	6*	Aw2Mh2Pj2Or2 Ps1Cb1	20.0	6	Cb7Mh3	24.9	1	4.9

Forest	2002 Inventory			2021 Inventory			No. of Sample Plots	Change in BA (m <sup>2</sup> /ha)
	Stand No.	Species Composition	BA (m <sup>2</sup> /ha)	Stand No.	Species Composition	BA (m <sup>2</sup> /ha)		
Sandy Hills	7	Pr6Pw4	32.0	7	Pr4Pw4Cb1Oc1	37.6	2	5.6
Sandy Hills	8*	Po5Aw3Ps1Cb1	9.9	8*	Ps3Aw3Pt2Cb2	11.0	1	1.1
Sandy Hills	9*	Pj6Ar4	18.0	9*	Aw5Mh3Pj1Om w1	9.8	1	-8.2
Sandy Hills	10*	Ps4Cb2Mh2Pj1 Aw1	27.0	10	Mh5Cb2Ps2Sn1	29.8	1	2.8
Sandy Hills	11	Pw5Pr2Sn2Oh1	22.8	11	Pw5Pr2Cb1Sn1 Ohw1	40.0	2	17.2
Sandy Hills	12	Sn10	34.0	12	Sn10	52.6	1	18.6
Sandy Hills	13	Pr7Sw2Ps1	37.4	13	Pr5Sw2Pw1Cb1 Oc1	36.4	7	-1.0
Sandy Hills	14	Pr10	48.0	14	Pr9Mh1	43.0	5	-5.0
Sandy Hills	14	Pr10	48.0	23	Mh10	13.0	1	-35.0
Sandy Hills	15	Sw4Pw3Pr2Le1	22.5	15	Pw5Le3Pr1Sn1	45.0	2	22.5
Sandy Hills	16	Le10	26.0	16	Le8Wb1Cb1	20.2	1	-5.8
Sandy Hills	17	Pj8Le2	18.0	17	Le6Cb3Pj1	9.6	1	-8.4

Forest	2002 Inventory			2021 Inventory			No. of Sample Plots	Change in BA (m <sup>2</sup> /ha)
	Stand No.	Species Composition	BA (m <sup>2</sup> /ha)	Stand No.	Species Composition	BA (m <sup>2</sup> /ha)		
Sandy Hills	18	Pr10	29.0	18	Pr9Ohw1	43.9	2	14.9
Sandy Hills	19	Pr5Pw4Sw1	33.0	19	Pw5Pr4Sw1	40.8	1	7.8
Sandy Hills	20	Pr6Sw2Pw2	36.4	20*	Pr5Sw2Pw1Aw 1Pj1	35.7	3	-0.7
Sandy Hills	21	Cw8Mr1Oh1	52.0	21	Cw6By1Bd1Mr 1Omw1	44.4	6	-7.6
Sudden	1	Pr6Sw2Pw1Oh1	34.0	1	Pr6Cb2Ms1Mr1	41.6	4	7.6
Sudden	1	Pr6Sw2Pw1Oh1	34.0	10	Pr6Pw2Mr2	44.9	1	10.9
Sudden	2	Mh6Mr3Oh1	22.0	2	Mh6Mr1Pw1Hs 1Ohw1	32.4	5	10.4
Sudden	3*	Ar5Oh2Ms1Ab 1Oc1	25.0	3	Mr4Bd3Or1Po1 AX1	17.2	1	-7.8
Sudden	3*	Ar5Oh2Ms1Ab 1Oc1	25.0	12	Ms6ALb3Pw1	31.5	3	6.5
Sudden	4	Or6Mh2Mr1Oh 1	29.6	4	Mh4Or3Mr1Hs 1Ow1	36.9	8	7.3
Sudden	4	Or6Mh2Mr1Oh 1	29.6	9	Or7Mr3	37.5	1	7.9
Sudden	4	Or6Mh2Mr1Oh 1	29.6	11*	Wb4Pr1AX1Pw 1Cb1Lb1Ohw1	27.5	2	-2.1

Forest	2002 Inventory			2021 Inventory			No. of Sample Plots	Change in BA (m <sup>2</sup> /ha)
	Stand No.	Species Composition	BA (m <sup>2</sup> /ha)	Stand No.	Species Composition	BA (m <sup>2</sup> /ha)		
Sudden	5	Pw9Sw1	40.4	5	Pw8Sw1Ohw1	55.3	3	14.9
Sudden	6	Pot5Mr3Ob1Oh 1	26.0	6	Pw3Mr2Po2Ob 2Ohw1	33.4	3	7.4
Sudden	7*	Ms4Ab2By2Ew 1Ar1	10.4	7	Ms6By2Mr1Oh w1	17.8	3	7.4
Sudden	8*	Mh4Aw3Be2Oh 1	18.7	8	Mh7Mr3	44.1	1	25.4
Walker Woods	1*	Mh5Aw4Oh1	22.6	1	Mh10	30.7	5	8.1
Walker Woods	1*	Mh5Aw4Oh1	22.6	2	Mb6Pm2Be1Oh w1	22.0	1	-0.6